Ecological Kinds and the Units of Conservation

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Statement

This thesis is solely the work of this author. No part of it has been submitted for any degree, or is currently being submitted for any other degree. To the best of my knowledge, any help received in preparing this thesis, and all sources used, have been duly acknowledged.

To Eleanor and Barry Lean,

you both passed in the years of my research. I was glad to see you one last time.

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Abstract

Conservation has often been conducted with the implicit internalization of Aldo Leopold's claim: "A thing is right when it tends to preserve the integrity, stability and beauty of the biotic community." This position has been found to be problematic as ecological science has not vindicated the ecological community as an entity which can be stable or coherent. Ecological communities do not form natural kinds, and this has forced ecological scientists to explain ecology in a different manner. Individualist approaches to ecological systems have gained prominence. Individualists claim that ecological systems are better explained at the population level rather than as whole communities. My thesis looks at the implications of the current state of ecological science on conservation biology and emphasizes the importance of biodiversity as assessed at the population level. I defend the position that biodiversity should represent taxonomy and be quantified in reference to phylogenetic structure. This is a defence of biodiversity realism, which conceives of biodiversity as a natural quantity in the world which is measurable, valuable to prudent agents, and causally salient to ecological systems. To address how biodiversity at the population level relates to larger ecological systems I create a methodology designed to identify the relevant ecological system which biodiversity maintains and is maintained by biodiversity. This is done through the context dependent modelling of causal networks indexed to populations. My causal modelling methodology is then utilized to explicate ecological functions. These chapters together provide a framework for conservation science, which can then be applied to novel problems. The final section of the thesis utilises this framework to address whether de-extinction is a worthwhile conservation technique.

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Chapter 1. Introduction: Nature without balance.

It is often repeated that the "balance of nature" is a myth, long dispelled by ecologists (Kricher 2009). It has meant too many things to too many people, been re-explained and refuted, been broken into so many little pieces that it is unrecognizable, but still it remains, bubbling beneath the surface of conservation and environmental ethics. It appears most obviously at the point at which conservation interfaces with the public. Here the folk belief that all life is deeply interconnected in a predetermined balance acts as a strong rhetorical tool, allowing for the sense that there is a holistic natural system humanity is engaging with, and hopefully preserving. Human beings search for agency and are able to project it onto the world regardless of whether there is a system worthy of agency or not. In environmental ethics, the presupposition of a balance of nature is sometimes hidden in a nexus of background assumptions and sometimes is blatant. The tradition built from Aldo Leopold's *Sand County Almanac* is at times explicit in its appeal to a balance of nature to justify moral stances towards the natural world. This is born of a straightforward interpretation of the statement, *'A thing is right when it tends to preserve the integrity, stability and beauty of the biotic community.'* (Leopold 1949). Given this, holistic ecological systems deserve our moral consideration and are the focus of our moral theorising.

My conjecture is the reach of teleological thought, in which ecosystems are quasi-Aristotelian entities with a stable form and a function, is so ingrained into our thinking about preserving nature that any attempt to build upon the traditions of environmental ethics as it stands will be similarly infected. This position mischaracterises nature and ultimately cannot provide a strong foundation for conservation into the future. The Ship of Theseus must be docked and built anew. This thesis aims to do that. To build from the ground up a conception of conservation not from a notion of ecosystems but from biodiversity, real biodiversity, not some proxy for our preferences in nature. There are ways to measure and categorize the diversity of life on earth and we have an obligation to preserve this heritage and nest of possibilities for the future.

My plan is to show what can be done with these building blocks of normative worth in the natural environment; how we can build a completely scientifically respectable justification for preserving nature. This starts with biodiversity and uses causal structure to identify the causal relations that sustain biodiversity and the other features of the environment we find desirable. This causal structure is understood as dynamic, without a clear typological categorization from which the system oscillates, rather than the static systems described by “ecological fixism” (Robert et al. 2017). As such, ecological systems are evolving path dependent causal systems, built from populations. This view is both critical of and sympathetic to ecological individualism, the idea that only co-located populations exist, not communities or any other higher-level ecological composition. This forces us to reconsider how we categorise, characterise, and investigate ecological systems.

However, before going on, I introduce a few concepts that lie in the background of this project. If I aim to construct a philosophy of conservation without a balance of nature, what is a balance of nature and what role has it played in conservation thus far? This section will not laboriously tread over this well-trodden ground but will briefly familiarize the reader with these concepts. I introduce some classic formulations of the balance of nature and its influence on conservation ethics. Then I turn to introducing my thesis, which is structured in three parts. The first section sets out to characterize biodiversity, the second, ecological communities without a balance of nature, and the third applies the framework provided by the previous two sections to a novel case in conservation science, de-extinction.

1.1. The Balance of Nature and Ecological Kinds

The balance of nature involves the idea that there is an ecological type, a standard system, around which we find variation. This theory is usually thought to refer to a set of populations, which occupy a geographical region. For these populations to remain in a region their abundance must have been, in some sense, stable. It is the consistency of species identity and abundance in an ecological system that a balance of nature aims to describe. This creates a typological core around which we can explain ecological dynamics and identity.

This mode of thinking comes naturally; Ernst Mayr (1959) and Elliott Sober (1980) refer to it as typological thinking and believe that it is misplaced in post- Darwinian biology. Typological thinking contrasts with population thinking in which there is no type around which variation deviates. This thinking has often been applied to species and populations, describing a standard individual of that kind from which variation deviates. As Mayr explains; '*For the typologist the type (eidos) is real and the variation an illusion, while for the populationist, the type (average) is an abstraction and only the variation is real'* (Mayr 1959, p. 29). Biology has developed considerably by treating biological kinds, like species, as populations rather than types. In ecology, there have been attempts to describe ecological kinds around which regulated variation deviates. If we consider ecological systems as oscillating around a demographic core, then there is a neat conceptual connection between ecosystem kinds and the balance of nature.

I start from the position that we have good reason to believe there is no balance of nature that maintains ecological communities[1]. This undermines the idea that stable self-maintaining functionally integrated ecological systems exist. The balance of nature is frequently used to establish the existence of 'real' ecological systems that emerge from lower-level constituents (Rolston III 1975). Ecological systems are dissimilar to organisms, and the ethical theories that apply to organisms should not apply to them. An irrefutable argument against the existence of ecological systems or a balance of nature likely does not exist; it is still subject to the evidence of the ecological sciences, but I aim to establish that the weight of evidence is against this idea. Given the lack of justification for ecological kinds resulting from a balance of nature, these kinds cannot be assumed, as they often have been for the purposes of environmental ethics. This project is influenced by the work of Kristin Shrader-Frechette

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[1] I will disambiguate two types of balance of nature arguments below; one describes how population interactions stabilise the composition of a community, the other that describes population self-regulation.

who has similarly argued against the use of the balance of nature in environmental ethics over the last 25 years (Shrader-Frechette and McCoy 1993; Shrader-Frechette 1995; 1996).

There have been instances of treating ecological systems as if they were organisms with strongly typological reasoning. Frederick Clements (1916) is renowned for his attempt to categorise different ecological systems using a super-organismal view of ecological communities, both describing ecosystem types and their stages of development. The balance of nature, and system homeostasis, is a product of the system resembling organisms in his view. He strongly considers communities as the sort of entity we can categorise and describe in the same manner of organisms.

> *‘The developmental study of vegetation necessarily rests upon the assumption that the unit or climax formation is an organic entity. As an organism the formation arises, grows, matures, and dies. Its response to the habitat is shown in processes or functions and in structures which are the record as well as the result of these functions. Furthermore, each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development. The life history of a formation is a complex but definite process, comparable in its chief features with the life history of an individual plant.’*
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> *Clements 1916, p. 33*

While Clements’ theory was impressive in its scope and ambition it has not left much in terms of a practical legacy, few scientists could implement his taxonomy of ecological systems (see Eliot 2007 for a generous analysis of Clements work). Clements’ ecological theory assumes a strong version of a balance of nature, organismic homeostasis; viewing ecological systems as semi-closed self-maintaining units like organisms. While his strong organicism was not adopted by the next generation of ecologists, many different ecological hypotheses were developed which incorporated a balance of nature.

The balance of nature has a strong intuitive pull and a deep history of usage, being assumed as far back as antiquity (Egerton 1973). On first pass, it is easy to see why folk ecology would expect ecosystems to exist in a balance. Populations appear to persist in an area and they appear to interact.

These interactions do not seem epiphenomenal, they have tangible impacts on other populations. Wolves really look like they are influencing deer populations when they hunt and eat individual deer. One could worry that predation would always eliminate other populations if there were no checks for this action; equally one could worry that herbivores would increase in abundance indefinitely without some constraint. Therefore, people have inferred that if populations interact and persist there must be a relationship between these phenomena. This idea is clearly explained by Charles Darwin:

> *'Battle within battle must ever be recurring with varying success; and yet in the long-run the forces are so nicely balanced, that the face of nature remains uniform for long periods of time, though assuredly the merest trifle would often give the victory to one organic being over another'.*
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> *Darwin 1859, p. 73*

Balance of nature arguments come in different forms, but they all attempt to address the issue of how populations can both interact and persist. I will draw from the work of Greg Cooper (2001) to describe the main modes of defending the existence of a balance of nature. Arguments for a balance of nature are not arguments in the sense of axiomatised premises leading to a conclusion. The arguments are better thought of as constellations of mutually reinforcing ideas and research programs that search for particular patterns in nature. Cooper (2001) describes two different modes of justification for a balance of nature. The first, *Balance of Nature Argument I (BNA I)* follows:

'(1) The relative constancy of population sizes, given what the capacity for increase would allow, implies that populations are regulated.

(2) Since this order, in the face of a fluctuating abiotic world, is the product of evolution by natural selection, the forces that achieve it must themselves be under evolutionary control – i.e. they must be biotic forces.

(3) When these biotic forces are unimpeded by noise from the abiotic environment and the vagaries of history, they should issue in equilibrium populations.

(4) Effective regulatory control presupposes sensitivity to changes in population density – we should expect these biotic factors to be density dependent.

(5) Competition is the most likely mechanism for the implementation of these controls.'

(Cooper 2001, p. 483-484)

The BNA I attempts to identify how populations have evolved to regulate each other. Ecological interactions form the basis of evolutionary change and this evolutionary change will dictate the ongoing presence of species in ecosystems. This view originated in the work of Charles Darwin and lead to multiple different research programs that attempt to discover how competition (usually interspecific competition) leads to equilibrium. Darwin (1859) describes competition as leading a saturated economy of nature where only highly adapted organisms can invade an otherwise stable ecosystem as displayed in this famous quote:

> *'One might say there is a force like a hundred thousand wedges trying to force every kind of adapted structure into the gaps in the economy of Nature, or rather forming gaps by thrusting out weaker ones'*
>
> *Darwin 1859, pg. 135.*

Darwin's idea was developed by G. Evelyn Hutchinson (1957). Hutchinson directly ties the balance of nature to competition over resource use, which creates an efficient and stable economy of nature. Within his theoretical framework, the resource usage of a population is represented by a "niche". Hutchinson described niches as multidimensional hyper-volumes; the different dimensions represent the resources that a population utilizes. Each population has resources it currently uses, and resources it could possibly use: their realised and fundamental niche. If we assume the resources available in ecosystems are limited, and cannot radically increase, there will be competition between populations. When populations are added to the ecosystem, they occupy niche space by consuming the available resources. The more populations added, the more tightly packed the niche space[2]. Populations will specialize on a more constrained set of resources to outcompete other populations leading to limited realised niche space. Tight packing of niche space creates stable ecosystems, as other populations cannot invade the community due to the lack of available resources to utilise. This acts to stabilise the system, which can then be maintained at equilibrium barring some strong external perturbation (Hutchinson 1948).

A related view, developed by Charles Elton (1927) in his book *Animal Ecology,* describes a balance of nature as emerging from the functional correspondence of species interactions. Different species have their own "way of making a living" leading Elton to recommend that *'when an ecologist says "there goes a badger" he should include in his thoughts some definite idea of the animal's place in the community to which it belongs, just as if he had said "there goes the vicar".'* (1927, p. 64). By species playing diverse, functionally correspondent, roles in ecological systems they cause resources to cycle through the local community and stabilize the presence of the other populations. Functional correspondence is what creates equilibrium; cyclical networks, built of populations, distribute resources through the community's populations, which in turn maintains each population.

> *'There are, in fact, chains of animals linked together by food, and all dependent in the long run upon plants. We refer to these as "food-chains", and to all the food chains in a community as a "food-cycle."'*
>
> *Elton 1927, p. 56*

The maintenance of the community under this research tradition is due to the roles individual populations play in the overall economy of that community. Eltonian ecology still incorporates competition; there may be multiple vicars competing for the ear of the public and there can be multiple predators competing for a tasty morsel, but the Eltonian view encourages the ecologist to

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[2] Barring unique hyper-specialisation, where there is no competition due to the use of completely free resources.

attempt to record the functional correspondence of different ways of making a living into a single structure. Ecological communities then are explained by the roles individual populations play in the distribution and flow of resources through the system[3].

This style of argument for the balance of nature (BNA I) describes stability as emerging from the biotic interactions of co-located populations of different species. It focuses the scientist's attention on the larger system these populations belong to, when attempting to explain the distribution and abundance of organisms. Interspecific interactions, populations and their properties ground the existence ecological communities. I stop at Elton and Hutchinson as this is the point at which this ecological theory was adopted by early environmental ethicists, but I return to further developments in the ecology of interspecific interactions in Section 3.1.

The BNA I is, however, one way of explaining the regulation and maintenance of populations. Another prominent argument for the balance of nature plays little attention to the biotic interactions for populations. This is the *Balance of Nature Argument II (BNA II)* which Cooper (2001) describes as follows:

'(1) Persistence is an ecological fact – the populations are here.
(2) Since unregulated populations are statistically destined to random walk their way into extinction, most populations must be regulated.
(3) Since being regulated *just is* having an equilibrium, most populations are equilibrium populations.
(4) Furthermore, since regulation implies density dependence, most populations are under the influence of density dependent factors.
(5) Finally, since biotic forces are the most likely mechanisms for density dependence, we should expect biotic forces to be important determinants of population behaviour.'

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[3] It should be noted that Elton also criticised the balance of nature trope within *Animal Ecology*. He was in no means naively pushing the idea forward. His focus was on trophic interactions. Competition emerges from the shared occupation, by multiple populations, of a single trophic level. However, some of the conceptual frameworks he put in place were accepted by figures like Leopold as supporting a balance of nature.

(Cooper 2001, p. 493)

This argument can be summarised through the presentation I received of it in undergraduate ecology. My Professor stated, as I remember it: “Whenever you see a population you only need to ask two questions; why has the population not crashed to zero? And, why has the population not increased exponentially?” The key idea is if populations exist, there must be some process that acts to maintain their existence; it cannot purely be by luck. This, however, makes a balance of nature tautological; it is a logical necessity in some of the lazier statements of ecologists. This makes it either an uninteresting claim or wrong. If we introduce populations consistently to an area, and have their population fluctuate as a random walk[4], depending on their frequency of introduction or reintroduction, we will have populations persist in a region (Cooper 2001). Therefore, there is an open empirical question whether populations are regulated.

This second argument is more strongly focused on density dependency, where population growth rates are affected by the spatial density of populations. The idea is that the more organisms are present in an area the less resources available and the more competition. This then limits the population growth. Consequently, populations are thought to self-stabilize. Whereas BNA I focused on interspecific competition, with different species competing in ecosystems for resources and depending on functional relations between different populations in a community for their resources, BNA II primarily focuses on intraspecific competition[5].

While BNA II is a significant argument for the balance of nature, it is the scepticism of the BNA I argument that is most directly connected to the interests of this thesis. While I am sceptical of

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[4] A random walk is stochastic process by which a mathematical object path-dependently moves through a succession of random steps. In the ecological case, a population’s abundance fluctuates randomly in a stepwise matter.

[5] If two species are similar enough in their niches, they will compete over the same resource and be subject to density dependent dynamics. According to traditional niche theory, they will differentiate or competitively exclude each other, leading to a BNA I dynamic. However, if this does not happen, and both species can be maintained by the resource pool, we will have two species subject to BNA II style density dependence. It is again an empirical question as to which type of population dynamic appears in the wild.

the significance of BNA II arguments for density dependency, the reasons for such scepticism are not critical for reasoning about the significance of ecological communities in ecology. If populations are solely self-stabilizing, the ecological community they belong to does not need to be an important factor in maintaining species composition in an area. The ecological system then can be a collection of purely independent self-regulating populations. It is the assumed connection between a balance of nature and stable ecological communities that I interrogate throughout this thesis. Now I turn to how compositionally stable communities maintained in equilibrium have featured in foundation texts in environmental ethics.

1.2. The Balance and Ethics

There has been a long and continuous history of utilizing the apparent balance of nature to establish that ecological communities exist and possess intrinsic worth. The modern tradition goes back to Alexander Von Humboldt who wrote extensively on how exploitive agricultural practices, particularly in South America, lead to the decline of the land’s health (Von Humboldt 1877). Inspired by Humboldt, the first generation of American environmentalists like George Perkins Marsh and later John Muir argued for the separation of wilderness areas from man due to humanity’s ability to disturb these self-maintaining natural systems (Wulf 2015). However, a major influence of environmental ethics, as it currently stands, is Leopold’s “land ethic” and the major interpretations of the “land ethic”, which have directly connected ethics to stable ecosystems.

Leopold was not a professional philosopher and his work mixes philosophical conjecture with many other strands of writing; including natural history, journaling, and romantic ruminations on nature. This leaves his work open to interpretation. What I consider here is one strand of thought that has sprung from his work, heavily influencing modern environmental ethics. Recently, Roberta Millstein has committed valiantly to correcting our understanding of Leopold’s work (Millstein 2017; 2018). I am open to, and welcome, the reinterpretation of Leopold’s work to cohere better with modern conservation practice. However, I address the influential interpretation that Millstein (2017;

2018) wishes to correct. What she describes as myths, I consider influential interpretations. Even if many environmental ethicists have misinterpreted Leopold’s body of work, they have done it together and created a cannon of theorising which has dictated how environmental ethics is conducted. This thesis responds to this popular strain of environmental ethics not by correcting it but by discarding it.

The “land ethic” is an essay embedded within *The Sand County Almanac* (1949). In this essay, Leopold develops a description of ecological processes highly influenced by Elton’s *Animal Ecology* (1927). It describes ecological systems, “biotic communities” as he describes them, as functionally integrated resources cycling systems. In healthy ecological systems, large volumes of resources are cycled quickly through the system. Often this concept of health was directly connected with soil health. When resources do not cycle quickly back into the soil these are leached away and lost from that ecological community. Therefore, the health of the overall system is highly dependent on the functional correspondence of the different populations that form the biotic community. This property of functional correspondence within a community is what Leopold refers to as “interdependence”. When interdependent biota are removed from the community, the overall structure is damaged and the fertility of the land will suffer.

With Leopold’s conception of biotic communities and their health, we can explore how he extended ethical consideration to these entities. There is classical view of the moral development of society, in which there are expanding spheres of consideration. Moral progress is the result of the extension of moral consideration to more entities. The Whig history is that morality was only afforded to land holding men, then extended to men, then extended to women, and so on. Each time this expansion is due to the recognition of each group having key moral properties. The moral properties that the land has is its ability to self-maintain under a common interpretation of environmental ethics. So, when Leopold states, *‘A thing is right when it tends to preserve the integrity, stability and beauty of the biotic community. It is wrong when it tends otherwise’* (Leopold 1949, p. 224-225), he is arguing for an expansion of our moral consideration to ecological communities insofar as they possess integrity, stability and beauty.

This idea was the flint from which modern environmental ethics was lit. Richard Sylvan (formerly Routley) was one of the earliest philosophers to adopt the land ethic as a major innovation in ethical thought, claiming a new “environmental ethic” was required to supplement traditional ethics.

> *‘If Leopold is right in his criticism of prevailing conduct, what is required is a change in ethics, in attitudes, values and evaluations. For, as matters stand, . . . men do not feel morally ashamed if they interfere with a wilderness, if they maltreat the land, extract from it whatever it will yield, and then move on; and such conduct is not taken to interfere with and does not arouse the moral indignation of others. . . . Western civilization stands in need of a new ethic . . . setting out people’s relations to the natural environment.’*
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> *Sylvan 1973, p. 205*

Nevertheless, where does the normative force for this new ethic come from? The general interpretation of Leopold was that we would expand our consideration due to our evolved capacity to have “affection and sympathy” for non-relatives. With education, these sociobiological impulses could be directed towards the biotic community as well. Both Holmes Rolston III (1975) and J. Baird Callicott (1987) similarly cite Charles Darwin’s sentimentalist moral theory in *The Descent of Man* (1888) to justify the expansion of moral consideration to ecological communities. This neatly coheres with E. O. Wilson’s sociobiology, which emerged in this period of academic environmentalism. He similarly argues in *Biophilia* that humans have a sympathetic capacity that not only can be directed towards nature but also was evolved to be directed towards nature (Wilson 1984). This sentimentalist picture of expanding our consideration to communities was widely held.

Many of these authors pressed the idea that communities were “holistic” systems. They have significance as unified entities, with worth or properties that are above those given by their parts. The unified and homeostatic structure of communities allowed them to be the subject of moral consideration. This is particularly evident in the work of Callicott (1987):

> *'The land ethic not only provides moral considerability for the biotic community per se, but ethical consideration of its individual members is preempted by concern for the preservation of the integrity, stability, and beauty of the biotic community. The land ethic, thus, not only has a holistic aspect; it is holistic with a vengeance.'*
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> *Callicott 1987, p. 196*

Rolston III is even more explicit in the way he connects ecological integrity to the balance of nature. When he states, '*morality is a derivative of the holistic character of the ecosystem'* (1975, p. 98) he means that the system is holistic insofar it is a homeostatic system. He follows other environmental theorists like Thomas B. Colwell Jr. who argues:

> *'The balance of Nature provides an objective normative model which can be utilized as the ground of human value… The balance of Nature is, in other words, a kind of ultimate value. . . . It is a natural norm, not a product of human convention or supernatural authority.'*
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> *Colwell 1969, p. 50*[6]

As such, thinkers like Rolston III drove the connection between ecology, homeostasis, and ethics. This nexus of thought can be found clearly within deep ecology as well. Warwick Fox states:

> *'Deep ecology thus strives to be nonanthropocentric by viewing humans as just one constituency among others in the biotic community, just one particular strand in the web of life, just one particular kind of knot in biospherical net.'*
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> *Fox 1984, p. 194*

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[6] Quote from Rolston III (1975).

Again, the key feature of such thought is the interconnected character of the biotic community, which grounds the moral demands of nature.

This tradition has not fallen by the wayside. Modern environmental ethics includes many sub variations of the need to establish ecological systems as holistic units worthy of moral consideration. Katie McShane (2004) argues that ecosystems are real entities dependent on research interests that can be healthy or unhealthy. These research interest dependent units have structure, function, and can be typical or atypical for their type. If they are atypical, and lack the functional arrangement of their type, then that community is unhealthy. Lisa Lee (2017) argues that for bioethics to truly represent public health ethics it must incorporate the Leopoldian land ethic. A turn to the community is what is needed to reply to the overemphasis of the individual. These views represent the respectable end of modern environmental ethics within the Leopoldian lineage but there is a long tail of various types of ecological holism. This work is usually found within books published in the fringe academic press and are not addressed in this thesis.

Ecological holism, more than just being part of the environmental ethics literature, form an alluring ideology that students and the public gravitate towards. Michael Nelson (2010) provides a guide for understanding and teaching ecological holism, stating that his motivation for producing such a guide was born from the demand of his students, who he observed as immediately drifting toward ecological holism upon entering environmental ethics courses. This is something I too have observed. The land ethic represents an appealing line of thought, and while I admire how it motivates the public to contribute towards conservation, it is ultimately untenable due to the empirical literature that I briefly survey in the next section and the arguments developed through this thesis particularly in Sections 1 and 2.

1.3. Evidence for Non-equilibrium

A comprehensive survey of the empirical literature, which has developed in reply to equilibrium ecology, is not provided. Details of the incredible and surprising discoveries of the last 60 years will be scattered through this thesis but I will introduce the major scientific developments that undercut the viability of equilibrium ecology and ecological holism. These were produced within disparate schools of ecological research ranging from modelling population dynamics, experimental research, and observational findings. Two broad intellectual developments against equilibrium ecology are described below. These are the rejection of competition as the major driver of community structure and the investigation of the role of spatial dynamics of populations in community structure. This review does not exhaust the literature but provides enough background for the rest of the thesis. But before I explain the evidence against equilibrium I consider one of the most persistent problems with equilibrium, which philosophers have often engaged with, the lack of conceptual clarity.

1.3.1. Conceptual Confusion

While there is strong empirical evidence against equilibrium ecology other problems have also undermined its credibility. A major issue is the lack of a clear or consistent usage for theoretical terms like ‘equilibrium’, ‘balance’, or ‘stability’. This is true both of the semantics of these terms and their mathematical explication. This has engendered scepticism towards equilibrium ecology and has led some to reject it as a credible scientific project. Shrader-Frechette and McCoy (1993) are the exemplars of this sceptical take, arguing that theoretical terms in ecology, particularly those associated with the balance of nature, are “ambiguous, inconsistent or otherwise imprecise” in their usage (p. 12). This is used to argue that theoretical ecology has little to offer in terms of practical advice on conservation. I am not convinced conceptual confusion is a strong enough argument on its own to reject equilibrium ecology, but it does provide further reasons to avoid basing ethics on such shaky grounds.

In ecology stability is often equated with an equilibrium ecology, but there is a galaxy of different ways to define stability. Volker Grimm and Christian Wissel (1997) amass an inventory of 163 definitions of stability, which fall under 70 different stability concepts. Broadly, they note stability refers to (p. 323):

I) Constancy: the system's ability to remain unchanged.

II) Resilience: a system's ability to return, after disturbance, to some reference state or dynamic.

III) Persistence: where a system continues to exist over time.

Stuart Pimm (1984) is often taken as providing one of the foundational taxonomies defining between the following properties (see Odenbaugh 2001 p. 495):

A) Stable: a system is stable just in case all the variables return to their initial equilibrium values following a perturbation.

B) Resilience: how fast the variables return to their equilibrium following a perturbation.

C) Persistence: how long the value of a variable lasts before it changes to a new value.

D) Resistance: the degree to which a variable is changed following a perturbation.

E) Variability: the degree to which a variable varies over time.

But we can see that even these two taxonomies of the broad features of stability are inconsistent! The differences in definitions for stability mean that some definitions are not only inconsistent in their usage but also incompatible (Shrader-Frechette & McCoy 1993). This confusion is just at the conceptual level. Jack Justus (2008) has investigated the mathematical foundations of different versions of stability, noting the poor fit of a prominent class of mathematical formulations, derived from physics, for explaining ecological systems. As such, not only are the different formulations of stability "ambiguous, inconsistent or otherwise imprecise", as claimed by Shrader-

Frechette and McCoy (1993), but they are sometimes just a poor representation of ecological phenomena.

Given this state of play I think that there is no single notion of stability or equilibrium that we can definitively point to. This makes assessing hypotheses, like the diversity-stability hypothesis, impossible to assess as a hypotheses simpliciter. This hypothesis posits ecosystem stability increases as ecological diversity increases (MacArthur 1955; Elton 1958). But given there are so many ways that both terms could be defined there are a plethora of ways the hypothesis could be, and likely is, true and false. There is, consequently, no real sense in which diversity increases stability. This, however, does not mean that this hypothesis cannot be a starting point for identifying relationships between suitable explicated versions of stability or diversity (Odenbaugh 2001). These findings could ultimately be useful but there is little sense in which they vindicate the broader hypothesis.

For my purposes I am focused on a certain type of ecological equilibrium. My rejection of equilibrium ecology is only directed towards equilibrium which is born from populations interacting in ways that bring about a homeostatic ecological system. This is an ecological community which maintains its biological character, the species within the system remain broadly the same and abundances remain within a limit. This is inclusive of large class of theories about stability. I wish to remain uncommitted to the dynamics of the system, which act to maintain this character. My focus is on the type of causal structure that leads to the maintenance of ecological identity over the periods of time conservation policy is implemented, these are usually between a decade to a century. This is causal structure in which species interactions act to maintain ecological compositions. These theories of stability will result in ecological systems that are more organism-like and functionally organised. When populations self-regulate, such as in the BNA II argument, or when the aggregational properties of causally independent populations result in some type of stability, then their stability is compatible with an individualist picture of ecological communities. In such a picture, communities can still be collections of largely independent populations rather than biological individuals (See Chapter 4). There is no teleological structure in these systems and no self-maintaining systems. This type of compositional stability cannot support the type of ethical claims discussed in the previous section and as a result fall outside of the scope of my criticisms.

1.3.2. Rejecting Competition

Balance of nature arguments have often looked to competition as the major driver of stability. The equalising force of competition steadies the structure of communities, tying populations together in a holistic composition. There is long tradition of undercutting claims that populations are in any way stabilised by interspecific interaction. One of the early seminal works was by the Australian ecologists Herbert Andrewartha and Charles Birch, *The distribution and abundance of animals* (1954). They proposed that the appearance of density dependency in populations due to competition or predation is often radically epistemically underdetermined. The tradition they started has been highly developed in the many years that have followed culminating in the research discipline of non-equilibrium ecology (Caswell 1978; Weins 1984; Begon et al. 1990; Hanski et al. 1997; Tilman & Kareiva 1997; Rohde 2006).

Andrewartha and Birch proposed two mechanisms by which the illusion of equilibrium can result, one by spatial dynamics (which will be described in the next section), and by ‘relative shortage’ of resource availability. Studying *Thrips imaginis*, a rose petal consuming insect, they found population densities are near solely a function of the weather conditions that dictate the supply of rose petals. Similar studies have found many natural populations are governed not by interspecific interactions, but by the weather, including Caribou and Red Kangaroos (Caughley and Gunn 1993). This direct relationship between populations and the abiotic factors necessary for their maintenance supports a strong individualistic interpretation of ecological systems in which populations move around largely independently within their shifting abiotic range. This population individualist picture appears to apply extremely well to desert climates where population densities stay low (Weins 1984; Sullivan 1996). Stronger extrapolations have been made by ecologists like Klaus Rohde (2006) to state that in most cases natural populations do not reach densities that allow for competition or density dependent factors to become significant (p. 62). This viewpoint is exemplified by this passage in Thomas White (1993):[7]

> *'Surviving on this earth is, and always has been, especially for the very young, a struggle, a chancey business. Nor is there an "optimum" or "equilibrium" density of a population in nature - only the maximum number that can survive each generation in a population that is pressing hard against the variable but limited supply of resources in its environment. For most the "struggle for existence" is not a tooth and claw business. It is a lonely struggle to live in an inadequate world. They die young, and their passing is passive, solitary, and unnoticed.'*
>
> *White 1993, p. 5-7*

It is not only the deserts that have provided strong evidence against structured stable communities; the tropics have provided their own evidence against competition leading to equilibrium. The tropics has an incredible density of different plant species, up to 300 in a hectare (Gentry 1988). To assume that each species has a distinct niche, which dictates the competitive advantage that allows it to live where it does, seems implausible. The seeming equivalency of species in this setting empirically supports Stephen Hubbell's Neutral Theory (2001), which treats all populations in an ecosystem as being competitively equivalent and models their distribution and abundance through "ecological drift". Neutral theory appears to apply particularly well to the tropics but has been used to model ecological systems throughout the globe. Populations under this model stochastically disperse, speciate, and become extinct and this is all that is apparently required to represent the arrangement of populations in some ecosystems. Neutral models of ecological distributions have gained considerable interest in recent years and faced much scrutiny (McGill 2003; Dornelas et al. 2006; Ricklefs & Renner 2012). However, recently neutral dynamics have been accepted as applying to ecological system in some contexts with ecologists emphasising the utility of these models (Rosindell et al. 2012; Matthews & Whittaker 2014; Leibold & Chase 2017).

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[7] Quotation from Cooper (2003).

While competition played a large role in the search for ecological stability it is not the only interspecies interaction. Other forms of species interaction could be taken as building a network which maintains ecological compositions. Many ecologists believed that stability would increase with the inclusion of more interconnected populations within a community (Deangelis & Waterhouse 1987). This view was upended by the modelling work of Robert May (1973). Through modelling randomly structured ecological systems he showed that increasing the system size, through increasing the species count, and increasing the strength of species interactions surprisingly made systems more unstable. This could be taken to show local food webs might be transient, increasing in species count as new populations move in, then crashing with local species disappearances (Deangelis & Waterhouse 1987 p. 5). Such modelling, while not conclusive for real systems, severely undercut the plausibility of complexity leading to more stable ecosystems.

Ecology has developed so that it is not solely reliant on interspecific interactions to explain the distribution and abundance of species. Interspecific interactions are necessary to get a strong metaphysics of communities off the ground, as these connections hold the community together as a spatio-temporal entity and define its typological properties[8]. Other arguments against equilibrium do not focus on the nature of the interactions but on the spatial arrangement of populations.

1.3.3. Spatial Dynamics

Within the classical versions of equilibrium ecology, the ecological community goes through developmental steps, called succession, to reach an apex community. This apex community was an equilibrium system, acting to self-maintain. This stability allowed the apex assemblage to be diverse because stable compositions allow for fine-grained adaptation. Thus, tightly packed niche space allows the community to contain high species diversity. There was, as a result, a plausible connection

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[8] In this section, I have argued against interspecific competition structuring communities. This does not bar other interactions existing in communities. The role and strength of various ecological interactions in composing ecological communities is explored at length in Chapter 4.

between equilibrium and species diversity. This hypothesis has been tidily rejected by the modelling of patch dynamics and the intermediate disturbance hypothesis (see Wu and Loucks (1995) for an excellent review). These both refer to the process by which ecological systems become mosaics of different species compositions. Within the intermediate disturbance hypothesis, mosaics result from the destruction of the local biota in a 'patch'. Patch dynamics encompasses both disturbance and other mechanisms (for example niche construction) leading to species clustering.

Patch dynamics dates back to the 1940s, but it was the work of Simon Levin and Robert Paine (1974) that developed and popularised the view. They propose that disturbance is critical for environmental heterogeneity as it stops the movement of the system toward equilibrium and breaks equilibrium dynamics. But notice, as such, the early versions of patch dynamics accepted that there was equilibrium in ecosystems, even if it never got to do any causal work. The process of creating heterogeneity was the main initial focus of the literature. Heterogeneous environments provide more niche space and allowed new species to the area to utilise newly available resources. Joseph Connell (1978) pressed the role disturbance has in promoting diversity, illustrating this relationship with his "humpback graph". This graph shows species diversity increased with the frequency of disturbance, which opens the availability of otherwise limited resources, then diversity eventually decreases as the disturbances become too frequent to allow for resource exploitation. This led Connell to coin his position the "Intermediate Disturbance Hypothesis" (IDH).

What Connell (1978) suggested, which was truly innovative, was given the extent to which disturbance is ubiquitous and necessary *'we may question the usefulness of the application of equilibrium theory to much of community ecology'* (p. 1302). The movement to explain systems well away from equilibrium was similarly pressed by Caswell in that same year (1978) who stated, *'equilibrium theories are restricted to behaviour at or near an equilibrium point, while non-equilibrium theories explicitly consider the transient behaviour of a system'* (p. 127). Patch dynamics and IDH pushed research away from looking at systems as stable entities and started considering the dynamic qualities of systems; thereby changing the direction of research. The populations moving into a patch had to come from somewhere and research turned to not just the frequency of patch formation through disturbance but also the patterns of populations moving through these patches.

Once the landscape is viewed as a spatial mosaic of patches dynamically changing, scientist must explain the movement of populations between newly created patches. Patches will need to be colonised by populations adapted to exploiting opportunities before populations highly adapted for competition move into the area. As patches are created, then stabilise, the entire landscape will oscillate between colonisation and local extinction. Populations may have a core-satellite structure. The core will have a large standing population, which is unlikely to collapse. This acts as a hub from which individuals can disperse. The dispersed populations around the core are satellites. These may be less stable and rely on individuals moving from the core population hub to be maintained. A core-satellite population structure requires some relatively stable hub to maintain the populations dispersing through the landscape, however, this arrangement is not necessary. Populations can oscillate around the larger landscape without any core. These just move from patch to patch. This movement requires no local equilibria to maintain the population, just populations surviving by their continuing probability of successful dispersal[9]. Patch dynamics has been extremely successful explaining the local variation of species and their abundances, and even can predict the species-area curve (Hanski & Gyllenberg 1997; Leibold & Chase 2017).

Patch dynamics as explained above still assumes the power of competition to exclude populations from an area. The subsequent weakening of this assumption has further distanced our picture of ecological communities from being clusters of co-adapted populations within equilibria. Locally maladapted populations can be maintained through rescue effects where the source population continually maintains the locally maladapted population (Brown & Kodric-Brown 1977). Rescue effects allow populations to disperse even further. Mass effects incorporate the movement of

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[9] Metapopulation models still involve an equilibrium to maintain populations, for example dP/dt = immigration – extinction. However, the equilibrium is not local or maintained by species interaction. Further, this phenomenon only appears at the metapopulational scale. In Chapter 3, I provide reasons for considering bioregions, the scale on which metapopulational dynamics occur, as real.

populations into habitats they are poorly adapted for and too inhospitable to maintain a standing population (Pulliam 1988; Loreau & Mouquet 1999). A prominent type of mass effect is source-sink dynamics. Populations can survive in habitat patches with a negative population growth rates (population sinks) through immigration from nearby patches with positive population growth rates (population sources). This source-sink population structure can allow for populations to locally persist in marginal environments and continue to disperse due to local replacement. If dispersal across maladaptive landscapes is rapid enough, dispersing populations can displace other species (Pacala & Roughgarden 1982).

Modelling and studying current population movements around the landscape have severely undermined the plausibility of equilibrium dynamics. Historical evidence against equilibrium ecology has also accumulated. Historical biogeography has often been taken as indicating that populations move around independently (c.f. Sterelny 2001b, to which I reply in Chapter 3). If communities formed cohesive units in equilibrium, we would expect to find several populations historically moving around a landscape together. As the climate of earth changed, populations would move in unison within their community cohort. Strong evidence has emerged, particularly out of North America, for populations historically moving around the landscape independently. Delcourt and Delcourt (1988) catalogue evidence that as land became available due to receding glaciers forest species moved at different speeds. This type of evidence has been mirrored in the Amazon in the work of Paul Colinvaux (2007) who mapped the independent movement of flora through the most recent ice age. This empirical evidence indicates that the movements of populations across the landscape is largely independent of one another.

The spatial dynamics of ecological communities severely undercuts the explanatory scope of equilibrium ecology. At best for equilibrium ecology, it argues that the diverse successional stages leading to equilibrium are critical for maintaining species diversity and abundance. This is because, as identified in the Intermediate Disturbance Hypothesis, often the stages away from equilibrium act to maintain populations within an assemblage. Insofar as we wish to explain species diversity and abundance, equilibrium then is only a limited contributor. However, the stronger interpretation is that populations move around the landscape without equilibrium or strong competitive exclusion effects. This means that populations largely survive due to their ability to move from patch to patch with little attention paid to the connections between populations. Ecological individualism, or the study of individual populations, would then likely be warranted.

While the evidence is still open to discussion and there are more extensive summaries of the current state of this debate (see Kingsland 1985 or Cooper 2003), this section should have at least introduced the idea that ecological communities are not maintained in equilibrium. Given the lack of empirical evidence for equilibrium in ecological systems, we should build our environmental ethics from a stronger bedrock. My thesis creates an alternative philosophy of conservation starting with the populations that represent biodiversity and instrumentally drawing in further biotic resources into moral consideration.

1.4. Thesis Outline.

The thesis is broken into three sections. The first two feature two chapters each and the last section comprises a single extended chapter. It is within the first two sections that I develop my key conceptual innovations and an alternate environmental ethics. These sections analyse the concepts of biodiversity, ecological communities, and ecological function; each in turn. These build upon each other: I can define functions for biodiversity through describing both what constitutes biodiversity and how to causally individuate ecological systems. This provides conceptual resources for adjudicating difficult issues including whether we should control invasive species or what role de-extinction should play in conservation.

1.4.1. Section One: Biodiversity Realism

Environmental ethics should start with biodiversity. Biodiversity is a real measurable quantity in the world, for which we can have more or less of. This quantity should identify biological differences that are explanatory and causally influence ecological systems. Given the explanatory and causal power of preserving high quantities of biodiversity prudent agents should want to preserve biodiversity. Environmental ethics grounded in biodiversity does not presume to describe all the ways we value natural environments. This is just one important way we should value the natural world and acts to either: A) provide a bare minimum for what should be preserved, a scaffold which will expand or diminish given how much prudential risk we are willing to accept or B) act to fill in the gaps of our conservation aims. We should not only preserve the populations we have a current explicit interest in but also populations that possess high quantiles of biodiversity. Therefore, under this view even individuals who have no current interest in the natural environment should invest in the preservation of biodiversity.

Not all theories of biodiversity conceive of biodiversity as an objective and causally important quantity of biological systems. In a series of well-known and important publications, Sahotra Sarkar has defended a *constrained conventionalism* about the concept of biodiversity (Sarkar 2005; Sarkar 2012). In his view, we cannot count just anything as biodiversity: any conception of biodiversity has to be measurable, comparable, and have something to do with the local biota. But within those broad limits, biodiversity measures are for the concerned parties to decide, reflecting their values, interests, preferences, and compromises. The contribution of ecological organisation to biodiversity poses no special problem to this view of biodiversity. If local groups have an attachment to patchworks of burnt grassland — the result of a culturally salient and deeply valued foraging tradition — then counting patchwork structure would be part of the relevant biodiversity measure. If not, then we ought not count patchwork structure.

Following Wilson’s original plea for conservation, Maclaurin and Sterelny aimed for something more ambitious; well-designed biodiversity measures should map onto an explanatorily important quantity of local biological systems (Wilson 1992; Maclaurin and Sterelny 2008). It is in this vein that I will defend of biodiversity realism, that there is a privileged division of biological features, which allows us the hedge our bets. Differences in biological features should make a difference also at the community level; in particular to the persistence of local composition of populations and ecosystem services of various kinds. As it might, if different kinds of communities systematically differ in their potentials to deliver ecosystem services. If we can characterise and measure such a quantity, and if increased biodiversity would contribute positively to diverse features, human communities would have good prudential reasons to value higher levels of biodiversity, both to buffer their current access to critical resources, and to hedge their bets against future contingencies. These contingencies might include nature's unexpected surprises, but also changes in the values of resources that biological systems provide, for example, changes in the terms of trade between food and other commodities. Biodiversity is viewed as an explanans for these aggregational or compositional features of ecological systems.

My first chapter looks to the biological sciences for the best carving of natural difference, a quantity which make a real difference in ecological systems and is of interest to prudent agents. This is because biodiversity is a key concept in the biological sciences not just conservation biology. It has become useful across multiple biological disciplines as a means to describe biological variation. In the next chapter, I draw from the species concept debate to argue for a set of desiderata for the concept of "biodiversity" that is both principled and coheres with the concept's use. Given these desiderata, this concept should be understood as referring to difference quantified in terms of the phylogenetic structure of lineages, also known as the 'tree of life'.

This lineage-based taxonomic description of biodiversity allows for the identification of critical populations in ecosystems. It also cements a type of methodological ecological individualism, starting conservation with the populations that constitute ecological communities rather than ecological communities. In the second chapter, I defend this taxonomic focus from a possible objection that ecological communities themselves can contribute to biodiversity. I develop an argument originally found in the work of ecologist Robert Ricklefs (2008) for ecological community eliminativism. If ecological communities do not exist as unique explanatory units then there cannot be a stable measure of their diversity. With the scope of diversity suitably narrowed, I consider the positive arguments within Ricklefs (2008) are considered for the possibility of bioregions being real explanatory ecological systems; these are linked to my global conception of biodiversity. Therefore, these two chapters identify and defend a realism about biodiversity identifying the constituents of biodiversity and defending a type of methodological individualism in ecology.

1.4.2. Section Two: Ecological Communities

The lineage-based account of biodiversity does not exhaust my conservation project; it instead provides a normative scaffold for causally identifying the wider biotic structure relevant to conservation. While there are not the biotic wholes that are assumed in the land ethic or similar ecological ontologies, there are real causal connections between populations. The natural populations that constitute biodiversity are maintained by the other populations with which they causally interact. In Chapter 4, I propose representing ecological systems indexically; identifying ecological systems via the network of weak causal interactions between populations that unfurl from a starting set of populations. This conception of communities allows us to identify the causal system influenced by or critical to biodiversity. These both provide explanatory justification for biodiversity, identifying its positive effects, and identifying requirements for the preservation of biodiversity. In distinguishing the other populations or abiotic features necessary for the maintenance of the populations that constitute biodiversity, this theory draws in other ecological features into view as conservation targets. Many populations will be instrumentally required to preserve evolving lineages and as a result necessarily preserved.

Further, this precisification of ecological communities identifies how community properties remain invariant, and why they have robust characteristics. This process allows for the identification of explanatory properties in communities. In the next chapter of this section, Chapter 5, I enquire into the possibility that ecological communities possess natural functions. The presence of natural function can be used to ground normative claims. In some versions of the land ethic, the value of ecological communities is supposedly a result of ecological communities possessing natural functions. I critically review the application of different theories of natural function to ecological systems as described in the previous chapter.

I find that ecological communities can rarely if ever support natural functions. Instead, when considering ecological functions, we are better served by utilising Robert Cummins' (1975) Causal Role functions, which act to explain systems and their collective products. While these cannot provide normative guidance, for they do not ground an objective notion of system malfunction or system ill-health, we can use them to identify the populations functional for preserving biodiversity and therefore identify functions of normative worth. Throughout this chapter, I consider the possibility of using ecological function to guide policy towards invasive species and ultimately recommend using Causal Role functions for biodiversity to provide some normative guidance towards invasive species.

1.4.3. Section Three: Applications

In the previous two sections, I provide a framework for conservation. One that starts with biodiversity and through the mapping of causal structure identifies the entities functional for biodiversity. This framework dictates what we should conserve. In Chapter 6, the process of applying this philosophy of conservation to the socially contested problem case of invasive species is explored. Within Section 3, the utility of my framework thus far is explored by providing guidance in the use of de-extinction as a conservation technique. My stalking horse throughout this chapter is not just the land ethic but also older environmental traditions. They are the traditions that treat nature's value as being derived from its authenticity and autonomy from humanity. Romantic environmental ethics directly conflicts with the use of modern biotechnology in conservation and I aim to engage with this literature while displaying the virtue of my own framework for conservation.

This extended chapter (Chapter 7) critically engages with three arguments which putatively establish that the individuals produced through de-extinction ought to be the same species as the extinct population. The first is the weakest, the conceptual argument, that de-extinction will not be de-extinction if it does not recreate an extinct species. This is misguided as de-extinction technology is not unified by its aim to recreate extinct species but in its use of the remnants of extinct species as a resource. The second is the argument from authenticity; the populations produced by de-extinction technologies will be inauthentic if they are not of the extinct species, and therefore, will not be valuable. I argue authenticity is not required in conservation as the value of authenticity varies between people and cultures, and the novelty of de-extinct species will be equally desirable in many cases. The third argument is from retributive justice; we need the de-extinct population to have the same species identity, as we owe a moral debt to the extinct population. I find the case for retributive justice unconvincing and argue that acting as if we have a duty to resurrect extinct species will result in a world with less species. Ultimately, all the arguments that connect de-extinction technology to species identity fail, leaving us to consider a more complex calculus for the justification of de-extinction in conservation. With my negative thesis established, I then turn to analysing the positive arguments for de-extinction. I particularly look at the claims of scientist that de-extinction will bring back lost ecological function and that de-extinction can spur the formation of other conservation biotechnology. Ultimately, I argue that de-extinction will largely be justified not by ecological concerns but by public interest in the production of proxies for extinct species.

1.5. Conclusion

With this comprehensive new framework for conservation, this thesis aims to spur the development of a new field of philosophy, the philosophy of conservation science. This new field is warranted due to the need for ecological research to be incorporated into our ethical theorising towards the environment. I address the key concepts for philosophy of conservation science — biodiversity, ecological communities, and ecological function — providing unique and intertwined analyses of these concepts. With these concepts defined, I can critically engage with the thorny issues of conservation; including invasive species and de-extinction. Given this, the thesis does not just positively try to contribute to standing debates but provides a template for what philosophy of conservation science is and should be.

Chapter 2. Biodiversity Realism: Preserving the Tree of Life

2.1. Introduction

This thesis provides an alternative way to construct environmental ethics. One that does not argue, or assume, that ecological systems or individual organisms are the bearers of normative worth from which we establish nature's worth. I ground my environmental ethics in the concept of biodiversity. This chapter establishes a realist theory of biodiversity, which identifies the taxa most worthy of conservation. This provides a foundation for the rest of the thesis. While there are many features of the natural world we may want to preserve, the entities that constitute biodiversity are real causal actors in ecological processes. They act as a bedrock, both in causing and constituting the reality of the ecological entities and dynamics I describe in Part II of the thesis (Chapter 4 & 5) but also supporting the normative significance of these ecological entities and processes. I defend the position that lineages, usually species but not necessarily so, are the right entities to consider as constituting biodiversity. In this Chapter, I construct the positive case for this view, in the next Chapter I will outline why ecological assemblages cannot constitute an independent factor of biodiversity in addition to the populations that comprise them.

Why ground conservation in biodiversity? Biodiversity is a key concept in the biological sciences. While it has its origin in conservation biology, it has become useful across multiple biological disciplines as a means to describe biological variation. The biodiversity concept then has two related functions: one normative, motivating conservation, and another scientific, describing how diversity manifests in biology. While the use of *biodiversity* in conservation biology has become near ubiquitous, there remains little consensus on the biological features the concept refers to (Maclaurin 2016). There are currently multiple accounts of which biological features constitute biodiversity and how these are to be measured. In this chapter, I draw from the species concept debate to argue for a set of desiderata for the concept of "biodiversity" that is both principled and coheres with the concept's use. Given these desiderata, this concept should be understood as referring to difference quantified in terms of the phylogenetic structure of lineages, also known as the “tree of life”. I then consider some difficult cases, for instance, how a tree of life view of biodiversity applies to the genealogical bush of microbes.

Current philosophical attempts to explicate biodiversity have converged on what I refer to as the “taxonomic assumption”: biodiversity necessarily measures what biological taxonomy represents (Rolston III 2001; Sarkar 2005; Maclaurin & Sterelny 2008; Lean & Maclaurin 2016). This is a natural assumption because taxonomy describes the basic ingredients that compose the biological and ecological systems that conservation looks to preserve. Given the role that we want biodiversity to play, taxonomy appears to be the best deserver for anchoring an account of biodiversity. Most authors, however, put this in terms of a particular taxonomic rank: species. I shall argue instead that we should refer to the biological features that ground all biological taxonomy: namely, lineage structure. The overall lineage structure of life is discovered through phylogenetic inference. Given this, the best option for a general measure of biodiversity will be a phylogenetic measure of biodiversity.

This is a realist interpretation of biodiversity, arguing we should measure phylogenetic structure and preserve the tree of life. But to do this just like in a game of backyard cricket, we need to establish the house rules and defend them. Is there one-hand one-bounce? Automatic wicket-keeper? Is hitting the house windows instantly out? We want everyone to know the rules and why we have them. In the Section 2.2, I explain what motivates a realist theory of biodiversity and Section 2.3 what is needed for an explication of biodiversity. In Section 2.4, I describe and defend my desiderata for this explication. These sections will provide framework for deciding what biological phenomena is constitutive of the natural quantity biodiversity. In Section 2.5, I explain why I believe that we should represent biodiversity through phylogenetic structure. I then explore how phylogenetic diversity measures best satisfy the desiderata I outlined in Section 2.6. Finally, in Section 2.7, I consider how we should assess phylogeny in cases where lineages do not form species.

2.2. Biodiversity: Categorizing to prioritize

"Biodiversity" is an indispensable concept for conservation biology. Since conservation biology emerged in the 1980s, it has been often described as a "crisis discipline". Often compared to medical practice, it applies biological science to the preservation of biological systems (Soulé 1985). For conservation to be a science, a rigorous concept was needed to describe the features biologists want to preserve. This can be viewed as analogous to establishing medical concepts like "health" or "disease". Previous notions of "wilderness" and vague demarcations between the natural world and humanity could not provide clear targets for conservation. In 1986, the same year that the journal *Conservation Biology* started, a key term for the discipline emerged: *biodiversity* (Sarkar 1999)[10]. This concept, a truncation of "biological diversity", characterises the features that conservation biology aims to preserve. These include biological features whose preservation or cultivation does not provide an immediate or obvious financial benefit.

The concept of biodiversity gained prominence as a means to replace folk notions of the "natural environment" or "wilderness" as the main target of conservation (Franco 2013). Instead of considering large ecosystems, which had supposedly had little contact with humans, as the main target of conservation, biodiversity focuses conservation on the different constituents of ecosystems. This pivot in focus was in response to the realization that conservation needed to be more scientific, in both methodology and the description of its goals. Moreover, it needed to be something measurable for these ends. Biodiversity was coupled with the formation of an autonomous conservation discipline. Conservation research had been split between disciplines including ecology, population genetics, land and park management, and botany, amongst others. By creating a single discipline, it was hoped that conservation research would become more efficient. There, however, remained some problems in defining the aims of the new discipline. It was not simply aimed at creating recreational "nature reserves" or landscapes of aesthetic beauty; instead the target of conservation was the preservation of

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[10] https://conbio.org/about-scb/who-we-are/scb-history/

biological systems (Soulé 1985; Sarkar 1999). This required serious thought about how we make decisions about conservation.

When we invest in conservation we make choices about which part of the environment we act to preserve and how we act to preserve it, then using our best current research, predict the likely outcome of our interventions. Given that funds for conservation are limited we need to choose between the different expected outcomes. This necessitates the use of prioritization procedures, particularly decision theory, to decide between the different possible actions we could take. We should act in the way which provides the best expected outcomes, given our current knowledge. Or to use the language of decision theory, we should maximise expected utility.

A controversial upshot of the use of decision theory is that sometimes conservationists should engage in *triage*. Triage is a term that come from the medical profession. In medicine, when resources are limited, we need a means of determining our treatment priorities. Triage involves assessing a patient's likelihood of survival given treatment or not. If a patient would survive regardless of treatment, they do not require immediate resource investment, equally if a patient will pass regardless of treatment, we are wiser to invest resources on someone is more likely to recover. So, doctors should aim to prioritise their resources investment in ways that provide the greatest health outcomes.

Triage has widely entered the conservation lexicon since Australian conservation biologists argued for it in the early 1990s. Brian Walker (1992) proposed that we should assess species by their functional redundancy and their likelihood of survival before we attempt to save them. Later that year Sue McIntyre et al. (1992) specifically introduced the term "triage" noting that implicitly there is already the selection of some populations over others depending on their public popularity and we should use more principled ways of selecting populations to preserve. The role of the triage concept in conservation is twofold. The first and more controversial implication is that populations, which look unlikely to survive, should be abandoned. The second point is subtler, and while at the centre of early discussions of triage, is sometimes forgotten. In conservation we actively choose to invest in some populations or environments and not others. This has been at times without clear principles or an ultimate account of what our conservation end goals are. In medicine triage involves creating targets, be it patient survivability or health, and acting to maximise these targets. Conservation requires similar overall targets to compare possible actions.

The first implication of triage in conservation I am cautiously, and context dependently, committed to. There are populations which we cannot save, and we should not invest in their preservation (Bottrill et al. 2008). Leaving extremely high-risk populations to die out has caused some controversy. Some environmental activists see this as giving up on conservation and a concession to those who would wilfully destroy the environment (Parr et al. 2009). However, in conservation practice we are choosing which of several possible areas to preserve and which of many possible species or ecosystems to allocate resources. Insomuch as we are forced to make decisions concerning conserving one area instead of another we are engaging in triage. Parr et al. (2009) underestimate the task involved in identifying and allocating resources to protect the thousands of species that go extinct every year (Ceballos et al. 2015). The magnitude of the task is too great. Even in cases where we act as if we have a flat preference over every region with endangered species, we will need to decide whether we evenly allocate our resources to every region or act according principles of triage. If we want to save more species, we will need to make wise decisions with these resources.

This does not mean that any high-risk population should be abandoned. We should always be cautious in abandoning populations and err on the side of action. It is better to act on the false positive that a population can survive than on a false negative and abandon it. Given this we should weigh our assessment procedures to reflect this (Colyvan 2012). Equally we should not deter those in our community who are willing to invest themselves vigorously into conservation projects. A strong case of this is the investment in the critically endangered California Condor (Pimm 2000). The last six birds in the world were collected and put through an extensive breeding program. This was so successful that there was enough of a standing population to re-release them into the wild. This was possible because scientists and the public were deeply invested in the survival of this population. Interest and expertise are not always transferable from one population to another. A Condor expert may not be equipped to work on amphibian extinctions. These non-transferable goods need to be accounted for in conservation decision-making. Given this I support triage but with the knowledge we should be cautious invoking it to abandon threatened populations.

I am wholeheartedly committed to the second implication of triage, and more broadly, the use of decision theory in conservation (also see Colyvan 2012; Sarkar 2012). We need to create clear conservation targets to compare outcomes for possible interventions on the environment. This is necessary part of making decisions under resource constraints. Even if we could preserve all the current biological systems there would be the further question of whether we should preserve all the biological systems. As Elliott Sober notes, there are many species that live in restricted geographic ranges and by almost, if not all metrics, are unremarkable (Sober 1986)[11]. When we accept we must prioritize some features of the environment over others, we then must find a way of categorizing these features to avoid redundancies. The creation of a systematic set of priorities is a necessary part on conservation science. Descriptors such as "the natural environment" or "wilderness" are not particularly rich in discriminatory detail on how to demarcate "man and nature", and when they are, they are wrong (Ereshefsky 2007). Regardless, often the areas we wish to preserve are restored environments or areas with a long history of human intervention, so wilderness is an obvious non-starter for a general conservation goal (c.f Woods 2017).

My focus within this thesis is not on when we should abandon populations but rather how we describe our conservation targets. Categorising the features of biological systems we wish to preserve has become part of the mission of conservation. Unfortunately, for this aim, humanity is quite ignorant of what biological systems exist; much of the biological world remains undiscovered. What we do know is that with the pace of human population growth, and the limited resources available for conservation, a considerable portion of the life on Earth is threatened. We must categorize new systems as they are discovered, so that we can weight each system for its relative value. The concept

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[11] Similarly, Maclaurin and Sterelny (2008, p. 4-5) discuss the snail darter, a type of minnow, which they describe as phylogenetically uninteresting, of no economic or cultural value, and as having a small population, of limited range, whose extinction will be unlikely to have flow-on effects to other populations.

of biodiversity both categorizes and prioritizes biological systems in accord to their uniqueness and the representation of their different properties. The preservation of these features is the outcome we desire to see at the end on any conservation procedure.

Designing a metric for conservation grounds long-term conservation planning even in the face of current ignorance. Currently humanity is deeply ignorant about what biological systems exist. There are large tracts of the Earth's surface both terrestrial and aquatic that have not been systematically explored. Recently, it was estimated that there are around 8.7 million eukaryote species of which currently 1.2 million have been catalogued (Mora et al. 2011)[12]. If this estimation is right, it leaves 86% of species uncatalogued. Of the catalogued species, we lack information about their properties and how they interact in their native environment. Ultimately, we are uninformed about many of the properties of ecological systems globally. We then need to identify key features that indicate the desirability of relatively unstudied ecological systems. A biodiversity concept serves this role.

Biodiversity measures should quantify biological difference for locating valuable areas over multiple spatial scales. The landmark paper *Biodiversity Hotspots for Conservation Priorities* identified that only 1.4% of the Earth's surface held 35% of all species in four terrestrial vertebrate groups and 44% of all vascular plant species (Myers et al. 2000). This paper focuses on threatened endemic populations and was cited almost 11,000 times providing the foundation for the protection of these areas[13]. On smaller spatial scales, biodiversity measures select areas for conservation out of available land. Potential sites are broken down into sub-sections. Place prioritization algorithms, pioneered by conservation biologists and philosophers, can be used to select from these subsections the areas which best represent biodiversity (Sarkar et al. 2006; Sarkar et al. 2016)[14]. Yet the fact that

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[12] These estimates and numbers tend to vary from year to year.

[13] For example, here is the Australian government's website on the protection of biodiversity hotspots. http://www.environment.gov.au/topics/biodiversity/biodiversity-conservation/biodiversity-hotspots

[14] Sarkar et al (2006) describes and advocates for the systematic conservation planning. Sarkar et al (2016) is a case where the procedure is used to design conservation areas in West Papua, Indonesia and then implement those conservation areas.

biodiversity measures look at biological difference at both a global and local scale can cause problems for identifying the right units to measure. The units that represent biodiversity must be general enough to represent diversity across the globe, but they also need to be specific enough to pick out features on a local scale. This is problematic and necessitates a measurement that avoids contradictory results at different scales.

This is all to say, we currently do not know all the biological features that exist in the world and we lack the resources to preserve the features we do know exist. As a result, we need to have a means of categorizing biological systems at multiple scales, so we can preserve them. This is initially what a biodiversity concept should do: provide a means for categorizing biological systems. This will then provide goals or targets in conservation that directly refer to the biological features of the world. This motivates the treatment of biodiversity as a real feature of the world that we can do a better or worse job of preserving, hence the realist position. In sum, the aim of the biodiversity concept is to have something that can aid us in rational prioritization decisions, apply at multiple scales, and be used despite our current ignorance. I believe the realist theory of biodiversity outlined in this chapter is able to accomplish this.

2.3. Explicating ‘Biodiversity’

There is a tension in the concept of biodiversity. It is thought that biodiversity must be both a scientific measure of real features in the world and something of normative worth. This leads to two differing methodologies for identifying biodiversity. One starts from our normative values towards nature and works from there to identify the particular different biological features we desire. The other starts with the biology, attempting to find the best account of biological difference and connecting it to normativity through prudential reasoning. I take this second stance towards biodiversity: that of the biodiversity realist. Realists believe biodiversity is a natural quantity and that there are better and worse ways of identifying the diversity of mind-independent biological features.

These features exist regardless of human interests, but they should be valuable to prudent rational agents and, therefore, should be preserved.

But how should we measure the natural quantity biodiversity? Most biologists, in trying to measure biodiversity, start with a permissive definition. For example, during the 1992 Rio Earth Summit, the Convention on Biological Diversity (CBD) proposed that biodiversity be defined as *'diversity within species, between species, and of ecosystems'* (CBD 1992). This definition has the virtue of being easy to assent to due to its broadness. It unfortunately is synonymous with all of biology. Under this definition, any measure of biological difference represents some aspect of biodiversity. Due to its lack of discriminatory power, it does not provide any clear guidance for making actual conservation decisions.

Permissive accounts of biodiversity have yielded a flourishing literature of different mathematical metrics for biodiversity. These measures, however, presuppose a prior choice of the biological kinds being compared. Mathematical measures of biodiversity are not aimed at measuring *biodiversity* simpliciter. They aim to describe variation in *units* which are constitutive of biological diversity. For example, the assumed unit in species richness is species, the variation is described as how many unique species are in an area. Common units that are thought to be constitutive of biodiversity include genes, species, functions, phylogeny, and morphology. Differences between units are identified through measuring character sets, which are the individual biological features of these proposed units[15]. These include individual nucleotides, functions, morphology, populations, species, etc. The mathematical formula which quantifies the difference in character sets also varies. A huge range of formulae have been proposed, often borrowed from different sciences, to analyse the data sets produced by character measurement (Magurran & McGill 2011).

This means the units, character set, and measure can be different between explications of *biodiversity*. Consequently, scientists propose ever more mathematical formulas as measures of

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[15] Character set usually refers to biological trait held by organisms. I am using it to refer to features of any biological kind.

biodiversity every year. As one researcher laments, *'in the last decade more than two measures of PD (Phylogenetic Diversity) or FD (Functional Diversity) were proposed, each year!'* (Cianciaruso 2011, p. 89). Attempts at consensus, such as *Essential Biodiversity Variables* published in *Nature*, have yielded lists of hundreds of individual measures (Pereira et al. 2013). This proliferation of methods is largely a product of the lack of consensus on what a measure of biodiversity needs to do.

This uncontrolled proliferation has negative consequences for both the biological sciences and conservation (previously outlined in Lean and Maclaurin 2016). Here are a few of the problems with such a permissive stance:

Openness to Manipulation – Without any guidelines as to what makes a good account of biodiversity, there is no limit on the measures that are admissible in conservation decision procedures. If the criteria for admission has this extreme pliability, it can be easily "gamed" by individuals so that the area which promotes their interests, regardless of the contents, is selected.

Exclusion – If we cannot discriminate between targets for conservation, we have failed. Too many measures of biodiversity include too much of the natural world. This can result in biological features being massively overdetermined for inclusion. These measures then are redundant and add no further information that can aid in decision-making. Further, since the biodiversity measures are not equivalent, they can generate conflicting recommendations about what to do. This is problematic when we have no way of weighing the relative importance of these measures.

Comparative Weighting – Conservation decision-making should involve the use of decision-theory to make optimal choices (Colyvan et al. 2011; Colyvan & Steele 2011). Variables representing different portions of the environment will need to be weighed against each other in decisions about what to conserve. While the details on how to weigh biodiversity variables will require significant debate, we still must identify which variables are the bearers of normative weight. Some biological variables are desirable in their own right as natural quantities of diversity; others are desirable due to their correlation with or promotion of these natural quantities. We can, therefore, divide variables into those which we prioritize in their own right or as means to others. This is similar to the biodiversity surrogate/ biodiversity constituent distinction Sahotra Sarkar (2012) introduces; biodiversity constituents are the features we want to preserve, as they comprise biodiversity, surrogates are only preserved insofar as they represent biodiversity constituents. We can comfortably be pluralists about measures that act as surrogates for biodiversity, as long as they approximate the natural quantity biodiversity.

Informational priorities – The information needed for decision-making in conservation is hard to collect. We need to be able to prioritize the collection of information according to which features are more desirable or indispensable[16]. Further, without priorities there is always another measure that could be added to the decision procedure. By describing what information is admissible, we have a guide for when the job is finished. This can be done in part computationally through diminishing returns in complementarity; complementarity is the addition of new desirable features, or units, to a set of desirable features or units (Sarkar 2016)[17].

These considerations provide prima facie reasons to investigate whether some variables more accurately describe the features of the world which instantiate biodiversity. This project – the attempt to identify the variables that best represent biodiversity – is described as the "units-and-difference" problem by James Maclaurin and Kim Sterelny (2008). This chapter furthers the project of identifying the preferable set of features to quantify biological difference[18]. However, it does not argue for a mathematical formula. While there is much work to be done in identifying the virtues of individual

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[16] See Colyvan 2016 for more on the value of information collection in conservation.

[17] The features or units are relative to the biodiversity measures we use. For example, assume species richness is what counts as biodiversity. If we preserve a habitat with 12 species, we have 12 units contributing to biodiversity. If we preserve another habitat with the same 12 species we will have added no new units of biodiversity; there is no complementarity between the habitats. Only complementary or new species would contribute to biodiversity.

[18] Faith (2016, p. 70) introduces an important alternative to the units and difference approach to biodiversity defended in Maclaurin and Sterelny, *variety* in which a set of elements are counted up. In this chapter, I am not committed to the framework of Maclaurin and Sterelny (2008), indeed, I am not strongly committed to any one measurement procedure over another, but I lean towards difference in terms of Sarkar’s (2016, p. 46) definition. My focus is on what features of the world we should measure not how to measure them. However, I am open to future developments in the bioinformatics literature.

measures, there first remains the job of determining which of the various proposed biological features is best used to quantify biological difference. The role of the concept of biodiversity is to provide an ‘objective’ account of the biological features that constitute the diversity of living systems. Thus, we should look to the literature on scientific concepts for guidance.

A measure of biodiversity is used to identify lineages of worth but in practice, once these lineages are identified, we preserve a plot of land that contains these lineages. One might ask: ‘how do we relate lineages to the plots of land we designate as conservation areas?’ The presence of biodiverse lineages is not the sole consideration in deciding which plot of land to preserve. Other interests will influence whether an area is going to be conserved. These interests include whether it has non-biological features of aesthetic worth or the cost of the land or its cultural significance. All interests in that land must be weighed in decision-making. The biodiversity of an area is a factor in conservation but is sometimes a defeasible factor. In place prioritisation algorithms, we integrate all these interests (Sarkar et al. 2006). These methods will be common to many conservation efforts and therefore the relationship between land preserved and the measure of biodiversity is not straightforward. In Chapter 4, I outline another way to relate the lineages we identify as biodiverse to the spatial scale on which they operate, describing how to identify the land ecological communities occupy. This method creates a more direct relationship between biodiversity, in terms of the lineages we wish to preserve, and the land we should invest in. Whatever the methodology used, we must relate conservation to the scale at which ecological processes operate.

2.4. Biodiversity as Scientific Concept

While conservation practice is taken as a form of ethical or economic action, *biodiversity* itself is a scientific concept useful across multiple biological disciplines. The attempt to categorize biological difference is central to several longstanding hypotheses in biological science, and research into biodiversity has become a common component of ecological and evolutionary journals. There is a long-standing hypothesis in ecology that ecosystem stability increases with diversity of the system

(MacArthur 1955; Elton 1958; May 1973). Previously, the measure used to describe diversity in this hypothesis was some version of species diversity (Justus 2011). Since the postulation of new measures for biodiversity, including functional and phylogenetic measures, there has been an increasing amount of work looking for relationships between these various forms of biodiversity and stability (Naeem & Wright 2003; Cadotte et al. 2012). In evolutionary studies, there is research on whether biodiverse systems have more potential for evolutionary change (Forest et al. 2007).

Treating biodiversity as a scientific concept that needs to be explicated naturally leads to the question, what makes “good” explication of a scientific concept? Fortunately, there is a long history of explicated scientific concepts we can refer to. One of, if not the, most thoroughly worked through scientific concepts is the species concept. The species concept debate is directly relevant to the biodiversity concept as they both deal with biological taxonomy, broadly construed. From this debate I take some tools to answer the question of when a measure of biodiversity successfully represents biological difference.

Elliott Sober’s *Philosophy of Biology* presents a quick sketch of how to explicate species concepts, which I think can be developed and utilized. Sober argues that a species concept should be considered for its clarity, theoretical motivation, and its conservatism (Sober 2000, p. 160, also see Ereshefsky 2000). A species concept has clarity when it makes clear distinctions between populations and can be applied to newly discovered populations. A concept is theoretically motivated when it identifies features that contribute to scientific research. Species concepts should be conservative as a new species concept should somewhat capture the historical usage of the term “species”, which has been extremely useful in the sciences, regardless of inconsistencies.

This simple, intuitive framework is applicable to the biodiversity concept with some minor tweaks. As in the case above, these different aims for an explication of biodiversity will occasionally be in tension. Nevertheless, with careful reflection we can weight our interests to resolve such tensions and converge on the best theory available. Now turning to the particular desiderata, species definitions are focused on species membership and on boundaries between putative species, whereas biodiversity measures quantities, so I substitute “*tractability*” for Sober’s “clarity”. This I understand as meaning that a biodiversity measure must be able to consistently identify features across multiple biological systems. To do this, the features it measures must not be arbitrary or local to some area of life. These features must robustly appear across the different form’s life takes.

Further, while a measure may describe robust features of a biological system, those features may not be particularly interesting. We want the features that the measure identifies to be theoretically motivated. As the concept of biodiversity plays a role in several sciences, the units it describes should be firmly grounded in general biological theory. If the units measured are selected because they are easy to discover or are only useful to a hypothesis local to a biological sub-discipline, then it cannot provide the information needed for a general biodiversity concept. Biodiversity measures should refer to biological features that are relevant to both evolutionary and ecological theory, so they must be *theoretically fundamental*.

Finally, Sober claims that any attempt to give a definition of species should be conservative. It should be able to represent the phenomena that has historically been associated with the species category. Biodiversity does not have as many historical demands, as it has a relatively short history of enquiry; while people have discussed species for thousands of years, the modern literature on biodiversity is only 30 years old. But there is a certain conservatism that should be at play when we assess measures of biodiversity. As I have noted, many biological features have been proposed as the right features to measure for biodiversity and for each feature there are numerous measures. The best individual measure of biodiversity should be able to successfully incorporate, correlate, or represent the variation in units identified by other measures. That is, we need to explain why those other measures, for the most part, seem plausible and get at something real. An explication of biodiversity that ambitiously represents variation across different biological systems is desirable. This desideratum is that a measure of biodiversity should be *representative*. Representativeness differs from tractability as tractability considers the robust appearance of biological features across life while representativeness describes the ability of a diversity measure to co-vary with other desirable diversity measures.

To this list of desiderata, I add a final virtue an explication of biodiversity must fulfil. This desideratum is not admissible to the explication of species concepts, but it is important for the biodiversity concept, given its role in conservation. Preserving high quantities of biodiversity should be desirable for prudentially rational agents. This need not account for all of our normative reasoning towards nature, but preserving high quantities of biodiversity should be valuable. Any explication of biodiversity therefore should be *normatively demanding*. This is in keeping with the conservation science literature on biodiversity and the aims of conservation science (Soulé 1985).

Using this set of criteria – tractable, representative, theoretically fundamental, and normatively demanding – I argue in the next section that biodiversity measures should refer to the overall lineage structure of life[19]. When we assess biodiversity, the more of the "tree of life" we represent the more biodiversity we represent. Under this conception, any assessment of biodiversity within a region should include a baseline measure representing the lineage structure within that area. From this baseline of lineages represented any further species preserved would increase biodiversity. Capturing intra-species diversity is also desirable as lineages form within species and a wide representation of intra-species lineages further represents biodiversity. The most direct way to represent lineage structure is through phylogenetics and therefore phylogenetic measures of biodiversity are the best prospect for a general measure of biodiversity.

2.5. Introducing Phylogenetics and Biodiversity

To preserve biodiversity is to preserve lineages across the tree of life. We do this by identifying lineages which are representative of unique evolutionary histories. Lineages are real features of the world, which can be discovered through various streams of evidence, making them tractable. The evolutionary divergence of lineages involves the divergence of biological traits from a

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[19] My criteria converges with David Hull's (1997) criteria for "an ideal species concept", which is generality, applicability, and theoretically motivated.

common population[20]. These differences make each of the lineages prudentially valuable due to these different biological features, which are or may be of utility. Finally, lineages and their historical relationships are indispensable to biological science making them fundamental to biology[21].

Information about historical relationships between lineages is gained from the science of phylogenetics. Phylogenetics is the study of the evolution of lineages through comparative data, usually molecular data. Dendrograms, or the tree-like structures commonly used to represent phylogenetic relations, depict splitting events between branches and branch lengths (Fig 2.1). These branches represent the genealogical relationships of lineages and how they separate or hybridize creating new distinct lineages[22]. The nodes of the branching patterns represent speciation “events” in which populations separate, leading to variation that eventually bars the recombination of populations[23]. Branch lengths are used to represent either length of time lineages have been distinct or evolutionary change depending on the measure.

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[20] Many of the species discovered over the last 30 years have been cryptic species, which are to the human eye phenotypically indistinct. This supports a nearly neutral interpretation of speciation were a lot of speciation is due to genetic drift. If this is the case, then such species will not possess diverging traits. This represents a problem but not an insurmountable one. Species which appear phenotypically indistinct to humans often are not to the species themselves, for example cryptic bat species have distinct call frequencies (Jones and Parijs 1993). These real differences could be discovered through future research. But even in cases were cryptic species are not phenotypically distinct, it is unclear whether this is problem for phylogenetic measures of biodiversity. If cryptic species account for little unique phylogenetic distance, then they pose few problems. Speciation may occur at first through drift and then adaptive radiation follows as the lineages genetically diverge and gain new genetic resources. Phylogenetically and phenotypically indistinct species do not pose a problem for phylogenetic measures of biodiversity, unless truly cryptic species occupy deep branches of the tree of life.

[21] This I contend even in the face of sciences like physiology. Explaining the trade-offs in proximate biological mechanisms involves comprehending evolved design.

[22] Often just the branch splitting events are depicted.

[23] The ends of the tree will sometimes feature many populations which are only vaguely distinct. They are in a process of speciation but they could possibly recombine or subdivide again. For discussion of how lineages of populations, species, and phylogenies relate see: Joel Velasco (2013).

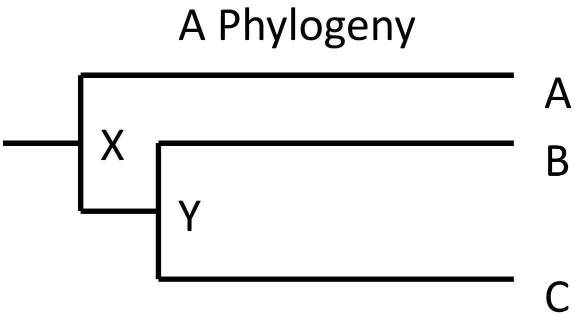

Figure 2.1. This is a basic phylogeny. This structure represents historical relationships of populations. A, B, and C are individual species. X and Y are at the nodes of the branches. Nodes display speciation events in which one lineage separates from another. Before the lineage split X A, B, and C had a common ancestor so they formed a monophyletic clade. Only B and C share a common ancestor at Y so they form another monophyletic clade. As the split between A was longer ago than the split between B and C we can expect B and C to be more similar to each other than A.

Since the 1990s, there has been a series of methods constructed to prioritize species in terms of phylogenetic distinctness. This is done in two primary ways[24]. The first proposed measure was topology based, which quantifies over the nodes of the phylogenetic tree. The node-based method was first proposed by Vane-Wright et al. (1991) and identifies the relatedness of the populations. Only speciation events are counted as relevant to a lineage's relative contribution to biodiversity under Vane-Wright et al. (1991). This is because it only counts the nodes, the points at which a lineage splits into two, not any change that occurs on a branch. As a result, sister taxa which share the same node, are evenly ranked (Fig. 2.2). The second (and more commonly used) method is based on nodes and distance (Faith 1992). Measures derived from this method quantify not just over the topological structure of the tree, like Vane-Wright et al. (1991), but also the length of the branches (Fig. 2.3). Branch lengths show the projected change of molecular characters within a lineage. This is inferred from the current species character sets and its difference from related species and a model of the rate

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[24] There are currently numerous variations on these different phylogenetic methods. They include a range of ways of providing relative weights to the branches or adding other variables, such as weighting population abundances.

of change in molecular characters[25]. Within Faith's (1992) version, within-lineage change is counted as contributing to higher biodiversity within a lineage. This is because it quantifies over branch lengths, and in doing so, incorporates evolutionary change that occurs outside of speciation events.

There is an active debate about which of the many different bio-informatic measures best represents lineage diversification. For example, I think that distance measures are preferable to node measures as they represent not only the splitting of lineages, but also the divergence of lineages once they split. And some measures tend to do better at accounting for uncertainty in tree topologies (Vellend et al. 2011). This is when a phylogenetic analysis cannot clearly determine which of several possible trees, with different genealogical relationships between lineages, is the most likely. While I describe some basic commitments on how to measure biodiversity in the next section, I will generally treat these questions as outside the scope of this paper. What measure better represents lineage structure is debatable, but fortunately, there has been considerable convergence on just a few phylogenetic measures in the conservation literature. Further, there is strong redundancy between phylogenetic diversity measures with different measures identifying similar sets of species as phylogenetically unique (Vellend et al. 2011) [26]. This will result in different measures designating the same region as biodiverse. The aim here is not to advocate for a single mathematical measure, but to advocate for a class of measures.

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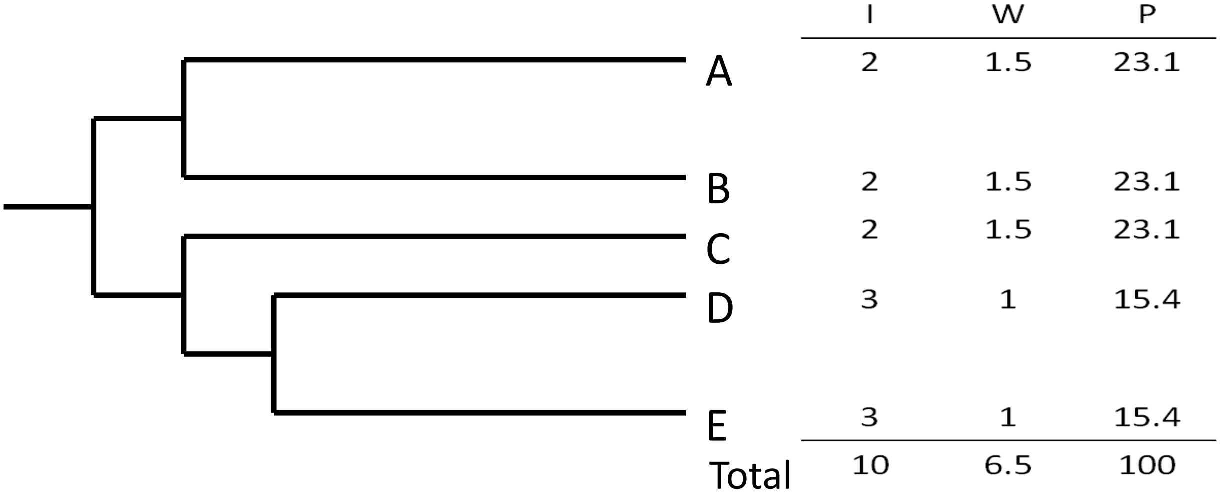
[25] The character set is usually DNA but can be done with phenotypic characters. I will focus on measures made with molecular data.

[26] Note that I will use the term Phylogenetic Diversity (PD) to refer to all measures of phylogenetic distance, the target of the chapter. The particular measure of phylogenetic diversity that Daniel Faith (1992) proposed, that many studies use, I will refer to as Faith's PD.

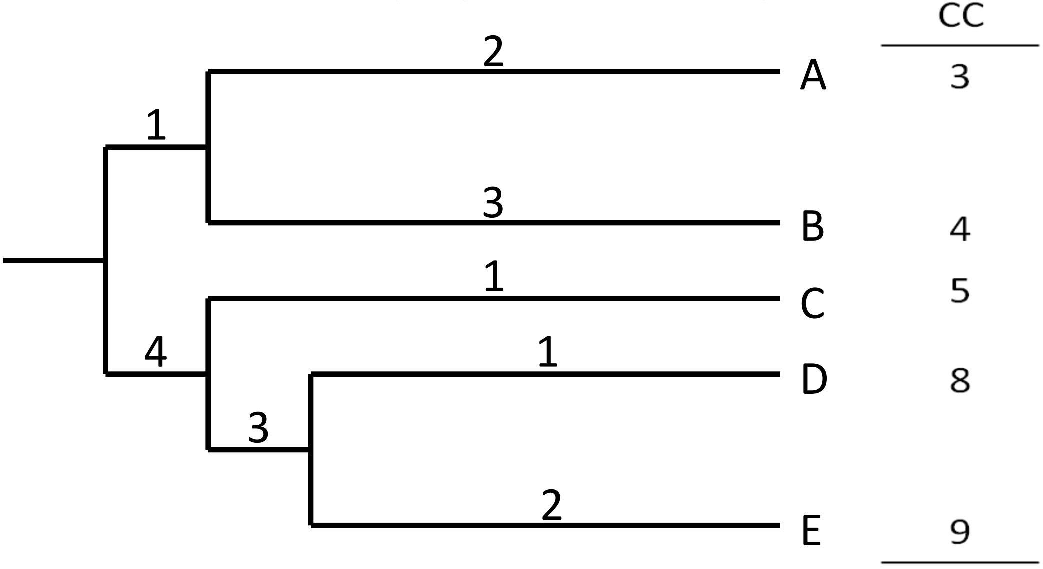
Taxonomic Distinctness



	I	W	P
A	2	1.5	23.1
B	2	1.5	23.1
C	2	1.5	23.1
D	3	1	15.4
E	3	1	15.4
Total	10	6.5	100

Fig 2.2. Taxonomic Distinctness. This is a node-based measure as it only counts splitting events. The node is base of the branch, the point at which two lineages split. Column I counts the amount of clades individual species belong to. W is the standardized weight as given by dividing each I value by the lowest I value. Column P gives the percentage contribution of taxonomic information for the total clade the individual species contributes. This method prioritizes ancient lineages.

Phylogenetic Diversity



	CC
A	3
B	4
C	5
D	8
E	9

Fig 2.3. Phylogenetic Diversity. This is a distance measure. The numbers next to the branches indicate character changes that occurred along that branch. CC is the total character change in the terminal taxa from the clades shared ancestor. If we were forced to pick just two species we would pick the two which represent the most unique character changes. In this case it would be B and E.

There are multiple different ways of weighting differences between lineages in addition to evolutionary divergence. This makes phylogenetic methods flexible and able to account for further features of conservation interest. It is not uncommon to weight phylogenetic diversity measures with features like the relative abundance of the populations. Proportional abundance is measured so that the homogeneity of the community is assessed, even if there are many phylogenetically distinct species present these may have small standing populations compared to other local species. This is done for two reasons; first, the diversity of the community could be viewed as being higher if the average organism in the community is more phylogenetically distinct, second, we may want to identify the populations that are currently having a strong impact on the ecological community. A small population may have relatively slight causal impact on the overall community structure so are not ecologically significant. Such modifications to biodiversity measures will be important for different conservation purposes but my focus in on what counts as being the same or different when assessing abundance.

The target of this chapter is the qualitative claim that the tree structure of life constitutes biodiversity. When we consider an area for conservation – assuming we are solely aiming to maximize biodiversity – we should pick the area that contains lineages that represent more evolutionary divergence. Theodosius Dobzhansky famously argued that '*Nothing in biology makes sense except in the light of evolution*' and a group of conservation biologists recently mimicked his claims arguing that '*Biodiversity only makes sense in the light of evolution'* (Dobzhansky 1973; Geeta et al. 2014). I agree with this conjecture and explain the importance of taking an evolutionary perspective on measuring biodiversity in the following section (2.5). The evolution of lineages is the driving force that creates new uniquely adapted forms of life. I argue, using the desiderata described in Section 2.3, that biodiversity is best measured through the use of phylogenetic methodologies.

2.6. Desiderata and Biodiversity

Now that I have broadly described the position I defend – that biodiversity should primarily refer to preserving the diversity of lineages and the history that they represent – I will now consider why this fulfils the desiderata described in Section 2.4. I argue that representing the difference in lineages is the best way of representing biodiversity. Maclaurin and Sterelny (2008) argue that biodiversity is species richness supplemented with other measures in some contexts, including phylogenetic measures. I believe an area's biodiversity increases when we add new species but adding more phylogenetically distinct species increases biodiversity more. The justification of this view follows.

2.6.1. Tractability

It seems evident that our measures of diversity need to be tractable, and much of the focus of current bioinformatics is on how to make the mathematics used to measure biodiversity efficient and representative of the biological features they aim to represent (see: Magurran & McGill 2011). This I take as a given; we want to be able to incorporate these measurements into scientific and conservation practice and the mathematics needs to be both efficient and descriptive of the features that they represent. There is a second sense of tractable that I wish to also raise: that the features we wish to represent are robust.

In other words, will slight variation in the initial character set represented result in radically different results in what counts as diversity? Organisms are modular; different parts evolve at different rates. Selecting different modular systems to measure the evolution of population traits will result in different diversity scores, as some systems are evolving faster than others in populations. Further, if the features we measure are not tractable, then it is impossible to compare biodiversity measurement across different biological systems or temporal time slices of the "same" biological system. We need to be able to consistently identify them across differing contexts. For example, ecological assemblages may lack distinct identity conditions and be too ephemeral to measure their diversity over time or the diversity between different ecological assemblages (Lean & Sterelny 2016).

Measurement is always based on a set of characters. For measurement to be comparable and consistent the characters need to be both general and stable features of the world. They cannot be arbitrary or idiosyncratic to a few clades. Some proposed measures of biodiversity struggle to describe biological features in a principled way. For example, morphological measures, which describe physical traits of populations, suffer from problems of arbitrariness if used as a general measure. For any set of characters described from an organism's morphology, there are always more morphological characters that can be added. For birds we can describe aspects of their morphology like their beak curvature, wingspan, and feather colour. But we can keep adding more traits, such as toe length, eye colour, or the number of feathers on its head. For any measure of characters in a population there are more characters we could add. When the difference between characters is quantified, the end result will largely be subject to which characters are included or excluded. This results in instability of the output of such a procedure. Ultimately, functional carvings of biodiversity suffer from the fact that there is no single functional description of biological features that a measurement procedure is representing.

Phylogenetic descriptions of biodiversity avoid such arbitrariness problems in two ways. First, the characters used for calculation are very clearly demarcated, as nucleotide bases are distinct. Second, what they aim to represent are robust features of the world on which multiple independent streams of evidence will converge. Phylogenies are constructed primarily using molecular data, in which differences between homologous sequences are analysed[27]. DNA is highly conserved and ubiquitous to everything we conventionally call living. The near universal nature of this data set allows for the comparison of differences between species with very few features seemingly in common. Phylogenetics utilizes a character set that allows for the comparison of all life. This set of

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[27] Phylogenies can be constructed with other data. Constructing trees from proteins is still common.

characters is resistant to gerrymandering as there is no potential for the arbitrary addition of characters.

Phylogenetic measures are usually currently applied to within clade comparisons. Conservationists are forced to compare regions which may have high phylogenetic diversity in different clades. For example, we may have to compare a region with high diversity in mammals versus areas with high diversity in passerine birds. Tania Laity et al. (2015) provide a blueprint for how to do this by comparing species within five separate phyla (acacia trees, daviesia plants, mammals, hylid frogs, myobatrachid frogs, passerine birds, and camaenid land snails) between two regions (South West Western Australia [SWWA] and South East Queensland [SEQ]). They calculate the biodiversity contributions of the different regions focusing on complementarity, the relative biodiversity gains made by preserving further areas within each region (see Section 2.3 for more on complementarity). They use these calculations to identify key areas within these regions to dedicate conservation resources towards.

In my view, the ultimate aim of using phylogenetic methodologies will be to construct a tree of all life and identify each species relative quantitative contribution to biodiversity. Recently, there have been efforts to create large scale clade tree in which multiple phylogenies are combined into a single tree. An exemplar of this methodology can be seen in recent work identifying the diversity and distribution of birds across the world (Jetz et al. 2012). Larger trees incorporating even more life will be produced allowing comparisons between species of distant clades. This will allow for comparisons of relative biodiversity across the globe.

Many living species are not known to science, as noted in Section 2.2, one may worry that this would impede the use of phylogenetic methods in conservation. This is a real problem, which faces all measurement procedures for conservation; we can only measure the biological traits we include. But phylogenetic methods have some advantages. Discovering information about a species range, abundance, and morphological traits is extremely research intensive, recording DNA is relatively simple. With the speed at which DNA sequence data is being recorded, it may be the only information we have about many species (Mace et al. 2003). A large project, the Earth BioGenome project, have been recently dedicated to recording the DNA of all eukaryotic life on earth (Lewin et al. 2018). So, there are resources actively dedicated to getting the data we need for doing this type of assessment. The information required to assess populations according to their phylogenetic diversity is relatively accessible and allows for rapid decision-making. Further, even under limited information phylogenetics analyses can be used to identify biodiversity hotspots (Sechrest et al. 2002). If remaining undiscovered biodiversity is not in radically different areas from current distribution estimates, preserving these areas will remain the best option for conservation.

To summarize, phylogenetics aims to represent the actual spatio-temporal relationships of populations; this structure is commonly referred to as the tree of life. Populations have a history of physical relationships to each other that the molecular data aims to represent (Felsenstein 1985). This includes genetic data such as nuclear or mitochondrial DNA or protein character phylogenies. Different phylogenies can be built from each set of data and can be used to support hypotheses about the historical relationships between populations. These character sets converge on the actual historical relationships between populations, displaying which populations evolved from a common ancestor. This provides a reliable and consistent procedure for describing diversity.

2.6.2. Representative

Identifying a narrow set of measures for biodiversity is preferable for the reasons described in Section 2.2. We must escape the “curse of bioinformatics”, the uncoordinated proliferation of biodiversity measures, to have a shared global measure of biodiversity (Faith and Baker 2006). But we should be conciliatory. We want a measure which correlates with the diversity of features measured in other descriptions of biodiversity. Measures of phylogenetic diversity have often been defended primarily due to their representativeness. Regions or species which are described as biodiverse under other measures tend to also appear biodiverse under phylogenetic measures. This idea is at the core of Faith’s defence of phylogenetic diversity (Faith 1992). He argues that we can use the branch lengths of phylogenies to represent the change in biological features and the functional attributes of populations. Branch length is thought to be representative of “feature diversity”, which is not a property of individual organisms, like different gene sequences, but of whole populations, like evolutionary plasticity. By finding the record of historical change in populations, we can represent the change in biological features of populations. This is the reason commonly given in the biological literature for using phylogenetic measures to represent diversity and has empirical support (Forest et al. 2007; Huang et al. 2012).

The representativeness of phylogenetic diversity is debated within the biodiversity literature. Winter et al. (2013) argue that the relationship between functional features and phylogenetic diversity is variable so we should not use phylogenetic diversity without reservations (also see Devictor et al. 2010). Other researchers have investigated the conditions that cause this relationship to diverge, such as competition driving functional differentiation in closely related species or slow trait evolution causing a population’s functional differentiation to be limited (Safi et al. 2011). The relationship between phylogenetic diversity and general trait diversity, while contested, is supported but still open to the weight of further empirical evidence.

In reply to sceptics of phylogenetic diversity’s representation of functional diversity, I believe they understate the variation in functional diversity measures, given a character set. Varying the characters included in a functional measure will result in different populations being functionally diverse. It is not possible to provide a global tractable set of characters for measuring functional diversity. This due to the radical difference in the morphology of the different clades of life. It is near impossible to have a functional measure that can assess the relative functional uniqueness of a Scribbly Gum and a Scribbly Gum Moth. Without a shared functional measure across life, we cannot anchor our judgements about the relationship of function to phylogenetics on a global scale.

Consider the diversity of function diversity methodologies. To measure functional diversity scientists must make a series of decisions as to what sort of feature in the world they want to measure and the units they want to use to measure this feature. In functional diversity, the phenomena they may aim to describe can include resource cycling, or traits that maintain populations, or morphological differences between populations. The biological phenomena these measures aim to describe will be fundamentally different, encompassing what a population does or an organism's anatomy or the behaviour of a population. We can ask about how any or all of these carvings of functional diversity relate to phylogenetics; some may co-vary more closely than others, but each will be a different question. Given this challenge, it is unsurprising that functional diversity does not always exactly track phylogenetic diversity.

Even when we reduce our scope to just consider variation in morphology or anatomy, there is no clear or principled set of traits shared across life in the way that phylogeny is (as argued in *tractability*). We cannot compare the morphology of dorsal fins with antennae. The lack of principled theoretical grounding in what biological features are measured in functional diversity is exemplified by the practice of demarcating characters to do function measures. Many biologists decide what biological features to measure through convention, diversity of functional characters in organisms is what scientists perceive as important.

It should then be expected that there are variable relationships between functional diversity and phylogenetic diversity, particularly as there will be extremely variable relationships between one measure of functional diversity and another. If we wished to force a relationship between these measures, we could systemically go through each measure and consider how the pair of functional diversity and phylogenetic diversity measures co-vary. With likely thousands of combinations some pairs of measures with co-vary strongly and some will not. This is, however, a hollow way to do research. Both measures of functional and phylogenetic diversity are independently valuable (more on the independent value of phylogeny in *theoretical fundamentality*). Phylogenetic diversity is better as a global measure of diversity due to the universality of its character set. Function diversity is valuable when it is local and goal oriented. It is best used when variation in a functional trait is known to do something in an ecosystem. This constrains what should be measured.

These measures are not completely unrelated, phylogenetic measures can aid in categorising functional and morphological character sets. Very few traits are shared throughout life. The evolution of an elephant and an ant involve very different biological mechanisms and traits. These different mechanisms and traits are, however, common to a local clade structure. The evolution of wings and chitin exoskeletons are relevant to the clade that ants (*Formicidae*) belong to but not particularly relevant to elephant evolution[28]. The relevant morphological features can be categorized through homology. These are structures, which are modified through selection on variation in developmental processes. By placing traits or mechanisms within their lineage structure, we provide a context for analysing these features in reference to their closest relatives. Phylogenetics not only correlates with other categorizations of biological difference but also provides a context that allows for their meaningful differentiation. The clade therefore provides a reference class for the description of morphological traits. This allows for what Maclaurin and Sterelny (2008) call a “local morphospace”, a limited set of morphological features which vary within a clade. These functional measures in many contexts can be used in many contexts to further supplement phylogenetic measures of diversity.

Equating biodiversity with phylogenetic structure ties biodiversity to biological relations which exist on a global scale. Global phylogenetic diversity can be used to identify key endemic taxa that represent distinct clades with long branches and few extant species. This is already being used by groups such as EDGE (Evolutionary Distinct and Globally Endangered) of Existence program operating out of the Zoological Society of London[29]. From initial global priorities we can move into finer scale, selecting between populations that equally represent clades. Considerations on the finer scale turn on choices of whether to preserve more individual lineages or preserving fewer but more representative lineages. Choices will likely be influenced by features internal to clades including biological features that are not based in phylogenies, which also contribute to biodiversity. These features could be biological, such as how plastic or morphologically diverse the clade is, or ecological like the local causal context of the population, particularly what other populations they causally influence. For example, a species with a significantly larger body size to its related sister species will be functionally unique, which gives us a reason to prefer them their nearby relatives.

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[28] Even natural selection itself may differ between these lineages if the ants are colony forming (see Godfrey-Smith 2009; Haber 2013).

[29] http://www.edgeofexistence.org/index.php

Identifying a measure which is representative over both global and local scales is critical as it has been discovered that local measures of diversity can appear to contradict global measures. Across the world, local species richness has been steadily increasing according to several meta-analyses (Vellend 2017). This finding is due to invasive species spreading across the globe, increasing the local species count. This process is coupled with species local to these regions becoming extinct, leading to global species diversity being lost. So, many habitats on earth are increasing the alpha diversity, the count of units of diversity in an area, usually counted as species. But the beta diversity, or the addition of new units of diversity added by a new region, is decreasing. Beta diversity can be equated with the complementarity of different conservation areas, which was discussed earlier in the Chapter (Section 2.3). Identifying measures of diversity that can scale relates the local diversity of these systems to the global biodiversity that is being threatened. If a measure does not translate across taxon and regions, we cannot assess the relationship between local biodiversity loss and global biodiversity loss. In Chapter 5, we will discuss the issue of invasive species further, noting how global biodiversity measures can aid in deciding whether to invest in the control of invasive species.

Representativeness is critical for my account of biodiversity as it is quite revolutionary in that it jettisons some of the historical baggage of the term. If biodiversity is constituted by phylogenetic structure then it does not refer directly to the diversity of genes, or functional features, or ecosystems. My biodiversity realism then conflicts with some of the traditions of conservation science, which want to describe diversity across all these arrangements (I argue in Chapter 3 that ecological systems cannot be described through diversity measures). However, if phylogenetic structure is representative of alternative methodologies for describing biodiversity, then it is not as radical as it may seem on first pass.

2.6.3. Normatively Demanding

The connection between norms and biological difference can found a general bet-hedging strategy in which we preserve the best range of biological features for the future. The knowledge that the loss of unique lineages is generally irreversible entails that we account for the risk of losing these options (Arrow & Fisher 1974). Diverse biological lineages, therefore, hold a certain value to agents who prudentially account for risk in the future. These should assign value to these lineages; this value is called *option value*. Option value is distinct from the various immediate instrumental values we have for the environment.

The preservation of as many distinct lineages across the tree of life is normatively demanding as these populations possess this option value. This view is shared by scientists (Faith 1992; 2013), philosophers, and economists (Nehring & Puppe 2004)[30]. Lineages, and the individuals that comprise these lineages, possess features that are relevant in evolution and ecology. Preserving lineages, therefore, preserves unique features at multiple levels of the biological hierarchy. Diverse lineages are valued as "options" as: A) the features they possess may become useful in the future; B) the features they currently have could lead to the evolution of novel features; C) they contain information about historical evolutionary change of epistemic use; D) we may value these lineages in unpredictable ways that we currently don't foresee. The distinctness and importance of lineages in biological theorising justifies confidence in their ability to represent distinct options for future use.

Some philosophers are sceptical of the normative justification of a natural quantity account of biodiversity. They argue there are "biological values" that exist as unique normative ends and that diversity indices do not model these "biological values". Therefore, biodiversity should be eliminated as a useful concept for conservation (Maier 2012; Santana 2013; 2016; 2018; Morar et al 2015). Alternatively, local stakeholders in the environment should decide what biological features count as being the relevant sort of diversity (Sarkar 2005). These authors tend to emphasise what will be left out by a measure of biodiversity. They identify features of ecological systems that people have preferences for, which biodiversity measures do not identify as of worth. They then infer that biodiversity cannot be all there is to conservation.

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[30] Nehring and Puppe have proposed their own measure of phylogenetic diversity (2004) as a development of their project formalizing diversity *simpliciter* (2002).

But this misrepresents the dialectic and reason for having the concept of biodiversity in conservation. In agreement with eliminativists and conventionalists, the realist accepts that biodiversity does not represent all the features of nature that people value. Indeed, high values of biodiversity may often clash with the parts of nature that people currently do value; that is to be expected. Many people enjoy near monotype environments, like pine forests. This is why high values of biodiversity are important: sometimes the parts of nature that are distinct are not noticed. There will of course be trade-offs between prioritising biodiversity and other ecological features that people desire but such trade-offs are part of the conservation process. So, proponents of biodiversity realism should be unfazed that people may value ecological features in addition to what is represented in biodiversity measures. There are many reasons to desire an undeveloped plot of land, biodiversity is one of them and this is realized in the conservation literature, which often refers to other values like ecosystem services.

Biodiversity is just one of many things that we are looking to preserve in conservation. Within the Intergovernmental science-policy Platform on Biodiversity and Ecosystem Services (IPBES), option value is one of eighteen different categories of nature's contribution to people (Pascual et al. 2017). Multi-criteria analyses are used to identify the particular geographical areas we should conserve (Sarkar 2016).[31] These criteria can include multiple measures of biological difference, which are significant in the local context causally or instrumentally, and "wilderness" areas of beauty or recreational use. There are many reasons to preserve an area including political, aesthetic, or economic reasons, but a general measure of biodiversity should be incorporated into any conservation decision-making procedure to identify unique overlooked features.

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[31] See Sarkar et al. (2006) for an explanation of multi-criteria analyses and systematic conservation planning. Sarkar et al. (2016) is a case where the procedure is used to design and implement conservation areas in West Papua, Indonesia.

2.6.4. Theoretically Fundamental

Biodiversity should measure and categorize a key feature of life on earth. It should be measurable across life and variations in biodiversity should be explanatory. In Section 2.5, I noted the tree of life and DNA are both shared across all life. These features ground modern taxonomy and the belief that biodiversity refers to taxonomic relations is nearly universally shared in the philosophy of biodiversity literature. Sarkar (2005; 2012) introduces it as a stipulation in his account of biodiversity. One of his four constraints for assessing any description of biodiversity is *'taxonomic spread is important'*, and this claim is further clarified in a footnote to refer to, not just diversity within a clade but across clades. Maclaurin and Sterelny (2008) centred biodiversity on species richness, supplemented along multiple different gradients. These can, but do not necessarily, include function, genes, local ecology, and phylogeny. Environmental ethicist Holmes Rolston III identifies species as the right unit for biodiversity as *'(s)pecies are a more evident, mid-range, natural kind'* (Rolston III 2001, p. 403). Phylogenetic measures take on this taxonomic assumption and base the measurement of biodiversity in the features that ground all taxonomic inferences, the lineage relations of all populations (De Queiroz 2005).

Species are elements of lineages within the larger structure, and the fact that they have these historical-causal relations is important for option value. Species richness on its own is an inadequate way to represent option value as it assumes that individual species contribute to biodiversity equally. They do not. There are many species that live in a small geographic area and are by any measure unremarkable compared to their close relatives (Sober 1986). Biodiversity is not simply a count of species but must represent the differences between species. This is necessary as the differences between species are not independent. Many features are inherited from a common ancestor. If we treat species as independent variables in a measure of biodiversity, we are committing an explanatory error, often called pseudoreplication. This is when dependent variables are treated as independent. Moving to phylogenetic measures stops biodiversity measures from suffering from the "phylogenetic pseudoreplication" that afflicts species richness (Garland 2001). Pseudoreplication is often described as a problem for experimental design, but it is apt for applying to other forms of intervention, like conservation. A measure of biodiversity should minimize pseudoreplication in which redundant features are treated as unique, like in the case of species diversity measures.

The non-independence of species is what makes phylogenetics explanatorily indispensable to the biological sciences. For example, biogeography aims to explain the distribution of species across the globe. This project requires an explanation of why similar forms, as a defeasible rule, appear near each other. Measuring species relatedness indicates species historical relations, which allows us to construct a picture of their historical distribution and migration. Otherwise a researcher could infer that local ecological conditions determine the features of organisms. Phylogeny then acts to identify real patterns in biology and the diversification of life, it grounds the scientific inferences we make[32]. This indispensability is what makes it fundamental for biological theory.

But how does theoretical fundamentality translate into conservation? If this is the best way to measure biological diversity, then phylogenetic diversity will be important to the ways in which ecological communities act. In the next two chapters I maintain that ecological communities are not the sort of entities that can feature in biodiversity measures or act like biological individuals. Nevertheless, they can have interesting aggregational properties that result in them being of explanatory interest. The diversity of the populations that aggregate in these systems can be important. Most famous is the portfolio effect where a diverse aggregation of agents, or in the case of ecology populations, results in stable system properties.

Diversity is an important property for theorising in the ecological sciences. Recently, there has been a movement to measure diversity in community ecology through phylogenetic measures, with seemingly some reasonable success. For example, the hypothesised link between diversity and stability has often been used to justify biodiversity conservation. Whereas older experiments tested the relationship using species diversity, newer experiments have used Faith's Phylogenetic Diversity.

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[32] This does not exclude there being other patterns in life and morphology. For example, convergent evolution.

These have found phylogenetic diversity promotes some measures of ecosystem stability (Cadotte et al. 2012). While I am sceptical of strong interpretations of the balance of nature, which the diversity-stability hypothesis is sometimes taken as supporting, I do think that the aggregation of diverse populations can influence community outputs over time (which I will explain further in Chapter 4). As a result, diversity can have a real effect the capacities of ecological systems and may be desirable.

More generally, the use of phylogeny in explaining ecological community structure is becoming widespread as it can explain current local population interactions and has yielded new avenues of research in community ecology (Cavender-Bares et al. 2009). Recently it was discovered that phylogenetics can predict the populations interacting within mutualistic networks; if a Banksia species forms a mutualistic relationship with a moth, a closely related Banksia species is likely to evolve a mutualistic relationship with the same moth species (Rezende et al. 2007). Due to the co-evolutionary relationships formed between phylogenetically related species there can be non-random extinction cascades within a mutualist network, which can prune large section of the tree of life. Phylogenetics aids our picture of community composition as it helps explain both the interactions of species and patterns of extinction.

Diversity can influence the output of ecological communities, the ecosystem services they provide. The biodiversity-ecosystem function hypothesis is a major justification used for biodiversity. The idea is that biological diversity yields functional diversity, which then will result in ecosystems that produce lots of immediately desirable goods for humanity. Recently, Dan Flynn et al. (2011) found that ecosystems with high phylogenetic diversity also were highly productive, more efficiently producing biomass than less phylogenetically diverse systems. Similarly, Diane Srivastava et al. (2012) found phylogenetic diversity predicts functional trait space, the properties of organisms that affect their ecosystem function. The authors tend to focus on the functional traits of plants as they are well defined, including features like root density, plant height, and nitrogen fixation. These functionally differentiated traits provide different services for human populations. There is then a plausible link between phylogenetic diversity and the ecological services that humans desire.

Finally, there are even more direct reasons for valuing taxon that represent high phylogenetic diversity. Preserving the lineage structure of life is desirable as a means of preserving heritage. Rosauer and Mooers (2013) argue that *'ED (Measures based on phylogeny) need not be a surrogate for other metrics of biodiversity because it is a fundamental measure of biodiversity'* (p. 322). Losing branches from the tree of life loses the record of the evolutionary response to Earth's changing environment. The information that can be gained from living populations exceeds what can be gained from palaeontological study. Living populations reveal information which will be lost when they become extinct.

Representing the phylogenetic structure of lineages is indispensable to the biological sciences and epistemically desirable. Referring to it grounds the concept of biodiversity in the most fundamental structure in biology. This indispensability is critical in conservation as well as research due to the effects of diversity on community structure and output, and the heritage and information phylogenetic diversity represents.

2.7. Biodiversity beyond the Species Taxa

Defending phylogenetic diversity measures as an explication of biodiversity raises questions about what I believe the role of species taxa is in conservation. Species are still central to conservation but do not exhaust our interests in biodiversity. Phylogenetic measures situate species within the larger lineage structure in which species are nested. Species are a level of lineage that is historically and genetically isolated from other lineages, in other words, where there is a distinct branching event (De Queiroz 2005). Different causal processes separate and maintain the separation of lineages. These include geographical isolation, isolation due to mate recognition, or environmental differentiation. These different processes provide species with internal cohesion and a *shared fate* that allows species to act as causal units in evolution and ecology. So, when Brent Mishler (2009) declares that *'biodiversity is the whole tree of life, not the arbitrary place at which species are named'* (p. 118), I agree that biodiversity must correspond to the overall lineage forming structure of life but disagree that species are always arbitrary and unimportant for conservation. When we have the formation of clear monophyletic groupings, usually designated as species, we have units that cohere and act in both ecosystems and biogeographic regions. As such, I believe that we are prioritising species trees, rather than gene trees or some other level of lineage formation, as these are the main actors in the ecological theatre.

There are, however, many cases in which there are not distinct branching events where lineages create new species. In some cases, this is because lineages have begun a process that could later lead to speciation. This involves the evolutionary divergence of sub-populations within a species, which is important for conservation in certain contexts. The most obvious is after we decide we should preserve a species, we need to identify the intra-species variation necessary for its long-term survival. This is to avoid inbreeding depression within that population (Frankham 1996). Intra-species variation, in that case, is preserved for the purposes of saving the species. Phylogenetic diversity within a species lineage is also in itself biodiversity and when deciding between species to allocate resources, it can act as a deciding factor. If we have two species in a clade and one of these species has more intra-specific biodiversity, we should preferentially allocate resources to it. This is because it has more biodiversity than the related species and all the associated utility of possessing higher biodiversity. These sub-species level questions of diversity cannot be addressed within a species richness framework.

Other processes can impede distinct branching events. Lateral Gene Transfer (LGT) and hybridization involve the transfer of DNA between individuals of different species. Hybridization is common within plant species and LGT is common within microbial life. Distinct branching events are difficult to identify when genes transfer between lineages. These processes mean that there is often discordance between different gene trees within a lineage. This indicates different historical relationships between related populations rather than a single distinct tree. The discordance between trees has led some to voice a strong scepticism about the existence of a single tree of life that can be identified through phylogentics (Franklin-Hall 2007; O'Malley and Koonin 2011)[33].

Trees constructed with different, or even the same, molecular data can vary but the major question is whether this variation is strong enough to lose our resolution of a single species tree. Much of the variation in phylogenetic trees is due to epistemic factors, the imprecision of our method for inferring the past, rather than whether there is a single true tree in the world. Such epistemic uncertainty should be just accepted and worked around. And while there may be reasons to be sceptical of a single species tree – for example polar bears appear to have two different phylogenetic histories (if we count them as a species) (Hailer et al. 2012) – generally, for the more complex organisms which are commonly the targets of ecology and conservation science, we can be confident that they stand in real historical relationships that molecular data can be used to infer. Gene trees may not be identical but if they robustly converge on a single historical relationship, we are vindicated in believing in a single species tree. For macrobes this is fortunate as there is a complex relationship between genomes and phenotypes. Phenotypic variation often depends on extra-genetic inheritance and development. The species tree is therefore critical to represent the phenotypic variation in these organisms with their complex scaffolded developments. As phylogenetics identifies the species tree, we capture the phenotypic variation within macrobes by following their evolutionary history.

Distinct lineages become more problematic in single-celled life, particularly prokaryotes, where LGT is common. Within a single microbe genome, we can often find clusters of genes with a different evolutionary history to other parts of the genome. These populations have had multiple evolutionary histories rather than one. In practice, scientists try to identify species lineages by limiting the genes they build phylogenies from. These genes are thought to be universal and evolutionarily stable and are referred to as "core genes" (Lan & Reeves 2001; Wertz et al 2003). The rest of the microbe genome is relegated to the descriptor of "accessory genes". Phylogenies of core genes

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[33] See the *Biology and Philosophy* Special Issue *'Biology and Philosophy of the Tree of Life'* for an in-depth debate about these issues.

unfortunately only reveal “trees of the 1%”, with the phylogenies being only representative of a small portion of the genome (Dagan & Martin 2006). These phylogenies will not be particularly representative of the evolution of the genome or the functional capacities of this population. The tight pairing of morpho-functional differentiation and evolutionary history supports the use of phylogenetic measures of biodiversity. Taking a phylogeny of such a limited set of genes will be less representative of overall morpho-functional diversity within bacteria.

The problem of core genomes not being representative of the features of a microbe can be addressed in a couple of ways, still within a phylogenetic biodiversity framework (see: Morgan 2010 and Malaterre 2013 for more on microbe biodiversity). The first is to note if LGT is high within a community these accessory genes functionally become public goods; they are shared by all or many of the local populations (see Sørensen et al. 2005 for indication of high LGT in biofilms). Preserving just a few populations within the area will preserve these genes. Microbes do not have complex relationships between genotype and phenotype; if we represented the genes in our measure of biodiversity, we have also represented the phenotypes. If LGT is ubiquitous, bacterial biodiversity should be quite easy to represent. This differs to macrobe biodiversity where extra-genetic inheritance is critical and genetic history is mostly vertical.

The shared goods model of LGT derived diversity may be assumed by some microbiologists as it is common for them to use phylogenetic measures of diversity based on “core genomes” to measure microbial evolution[34]. Scientists find these measures useful as species boundaries are vague or non-existent in microbes (Ereshefsky 2010). Instead, microbiologists categorize diversity in terms of taxonomic rank neutral phylogenetic divergence, settling on a percentage of genetic similarity to distinguish “Phylotypes”. For example, in an act of navel gazing worthy of philosophy, scientists have studied belly button microbe communities and found six phylotypes – populations of individuals with ≥ 97% genetic similarity – dominate these communities and appear in over 1/3 of the samples in 80% of humans (Hulcr et al. 2012). They also use these measures to record evolutionary responses in

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[34] There are now hundreds of papers using Faith’s PD to measure microbial diversity.

microbial populations to traditional biogeographic environmental factors like temperature and geography (Lauber et al. 2009; Chu et al. 2010). This is indicative that where scepticism about a single tree of life is strongest, the pragmatic use of phylogenetic diversity to represent populations becomes common. This is because phylogenetic differentiation is still representative of the diversity of microbes and computationally tractable despite the LGT between microbe lineages.

While phylogenetic diversity measures in their current iteration are often adequate to represent biodiversity, there are further ways these measures can be developed. Gene transfer between lineages can be represented within a phylogenetic diversity-like measure. Relaxing the bifurcating tree assumption within phylogenetic diversity measures allows for network phylogenies (Huson et al. 2010). Within a network, we can still identify the set of populations that have diverged the most. Just as in phylogenetic diversity measures of bifurcating lineages, we will preserve populations with long branches and populations that are representative of the network thicket behind them.

This allows more genes to be included within the phylogeny, but it will still not represent the majority of the accessory genes. These genes will have been passed around too many times to be able to make an alignment. If these genes are not public goods shared amongst the populations then we may need to do further work to represent them in our measures of phylogenetic diversity. Once a phylogeny is established using conserved core genes, we could modify branch lengths through a phenetic measure of accessory genes[35]. We would need to construct a presence-absence matrix of accessory genes found within different "core gene" lineages.[36] The presence of accessory genes can then act as a modifier, lengthening the branch of the 'core gene' lineage. These longer branches would be more highly valued within a phylogenetic diversity measure. It is, therefore, possible to incorporate bacterial diversity within a phylogenetic diversity framework even when there is high but non-ubiquitous lateral gene transfer between lineages.

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[35] Thanks to Rob Lanfear for this point.

[36] The description of the same gene across different bacterial lineages is subject to the problems of establishing a "gene" identity. This is easier in microbes than macrobes but is by no means unproblematic. For discussion of "genes" and identity see Griffiths and Stoltz (2013).

Microbial diversity is currently a fringe issue for conservation. There is little demand for conserving microbial diversity, as there is no clear indication that we are losing it due to human action. As we move into an era of cheap gene coding, we may discover that we are having a considerable effect on microbial diversity. But until that time, the discussion of microbial diversity and the problems it possesses for biodiversity measures will remain largely academic. While microbes and their difficult phylogenies pose a conceptual challenge for a global measure of biodiversity, it is not an insurmountable challenge.

Species often play an oversized role in thought about biodiversity. When we consider diversity above the species level and diversity below the species level, phylogenetics is consistently applicable and useful. Finally, phylogenetics also provides resources for sections of life which do not obviously form species (Ereshefsky 2010). Whereas some may view microbes as posing a problem for a phylogenetic biodiversity, I think it displays the virtues of a consistent measure that can scaffold diversity indices.

2.8. Conclusion.

This chapter has provided a means for assessing the right unit of measure for the biodiversity concept. These criteria can be used to assess the quality of any proposed measure of biodiversity. By treating biodiversity as a scientific concept, we can provide it with criteria that are receptive to new developments. As a concept still under debate, there are many competing interests to be satisfied but a measure of biodiversity needs to be both general enough to capture biological diversity on a global scale but specific enough to be empirically tractable on local scales. Describing biodiversity as referring to lineage structure can do this and, thereby, provides a firm theoretical basis for the concept. Phylogenetics is the most powerful way of representing biodiversity.

Chapter 3. Ecological Hierarchy and Biodiversity

3.1. Introduction

The conservation of biodiversity provides an alternative environmental ethics to ecological holism and the various strands of the land ethic. Instead of focusing on the welfare or integrity of the community, preserving biodiversity focuses conservation on entities of possible utility in a changing world. In the previous chapter, I have argued that this should lead us to preserve the lineages that best represent the tree of life. Nevertheless, there could be a rejoinder for those whose wish to focus conservation at the community level as well. Biology is hierarchical; there are multiple different levels of biological composition. Biological diversity could be considered at the different levels of biological composition. The ecological holist could reintroduce ecological communities as significant targets of conservation by arguing the ecological communities themselves constitute distinct contributors to biodiversity.

Ecological community individuals are stable ecological compositions above populations. Even if the lower level populations change — with populations diminishing, increasing, disappearing, and being added to local assemblages — the higher-level structure, the ecological community, could be somewhat stable in their properties. If these properties are shared across many ecological communities, we could identify ecological community kinds. Therefore, meaningful descriptors of biodiversity and possible measures of biodiversity could exist at the community level rather than just the taxonomic level. This position is implied in much of the biodiversity conservation legislation and I will argue it is ultimately unwarranted[37]. I develop an eliminativist position towards local ecological communities originally found in the work of Robert Ricklefs (Ricklefs 2004; 2005a; 2005b; 2006; 2008) to argue that ecological communities are not the right level on which to assess biodiversity.

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[37] I.e. the United Nations Convention on Biological Diversity (CBD) defined biodiversity as: “Diversity between species, within species and of ecosystems”.

Ricklefs argues that local community composition is better understood through biogeographic processes, which drive the evolution of clades in large geographic regions that encompass local ecological systems. This links local community composition to features that are captured in my description of biodiversity in the previous chapter.

I begin by outlining the prima facie case for considering communities as independently important contributors to biodiversity. Then I turn to arguments within the philosophical and scientific literature that entertain ecological community eliminativism; particularly those by Henry Gleason (1926), Angela Potochnik and Brian McGill (2012), and finally those associated with Robert Ricklefs (2008). While Potochnik and McGill’s argument is flawed, and Gleason’s position is untenable due to empirical evidence, Ricklefs eliminitivism is quite convincing. I develop Ricklefs argument with some conceptual machinery designed by Bill Wimsatt (2007, Chapter 7), this will be utilized further in the next chapter, by first describing the machinery then using this to clarify Ricklefs argument. I argue for ecological community eliminativism, there are no distinct ecological individuals. Without individual communities, there are no ecological community kinds. Ricklefs work not only eliminates ecological communities, but also argues for the reality of bioregions. I provide reasons why this is a plausible suggestion. Finally, I reintroduce the importance of understanding local ecological community interactions for practical action, for though there are no communities as cohesive wholes, populations do interact locally, supporting my overall conjecture that conservation must keep in mind global and regional biology while acting locally. In the next chapter, I develop a new positive account of ecological communities which threads a third option between treating communities as individuals and ecological individualism.

3.2. A Prima Facie Challenge

Valentine’s wonderfully rich though somewhat quirky *Origins of Phyla* includes a discussion of the cellular diversity of the various Metazoan phyla, cells after all being the essential building blocks from which organisms are constructed. Here is his estimate of the cell-level diversity of some of the better known phyla (Valentine 2004):

Phylum	Estimated basal cell diversity	Estimated Crown cell diversity (if different)
Brachiopods	34	
Arthropods	37	90
Molluscs	37	60
Chordates	60	215
Echinoderms	40	
Annelid worms	40	

Table 3.1. The estimated basal cell diversity and crown cell diversity of different phyla.

Table 3.1. suffices to show that (at least on one important conception of biodiversity) we would not measure diversity well by counting cell types; that would not, for example, capture the extraordinary exuberance of arthropod evolution. This poses no deep metaphysical mystery: different systems can be built out of a common set of basic elements; just as different sentences can be built from the same words. Development and evolution have exploited this combinatorial and structural freedom in building the incredible variety of arthropods. In general, when structured ensembles can be built from components with many degrees of freedom, and thus many different ensembles can be built from the same components, we do not track ensemble-level characteristics just by tracking characteristics of the components.

This poses a potentially very serious problem for a theory of biodiversity. Biology appears to be hierarchically organized; with higher level structures built out of lower level constituents. On one very standard formulation of this idea, organisms comprise populations of a species, populations of a species comprise communities, and communities comprise ecosystems. Yet our tools for thinking about biodiversity typically focus on the lower level components out of which biological systems are built: populations of species. If the relationship between ecological systems and the species (or, more exactly, the populations of species) from which they are built is like the relationship between morphological diversity and cell type diversity, in focusing on populations of species, we will fail to capture biologically important differences between different communities and ecosystems. Thus, when we compare the biodiversity of one region to that of another (say, in making conservation decisions), our method might be seriously flawed were we to rely on one level of analysis; as it would, if we regarded the brachiopod and arthropod clades as similarly diverse, by counting cell types.

The most systematic conceptual and theoretical work on biodiversity has been on the evolved components of biological systems: on populations and species. There is an array of sophisticated formal measures of the species richness of habitat patches; measures which combine information about the sheer number of species present with information about their abundance; information about the species profile of the focal patch, and the extent to which it contrasts with the profiles of neighbouring patches. In addition, there are measures of the phylogenetic distinctiveness of the species in the patch: ways of assessing the extent to which a focal species (say: Albert's lyrebird) has closely related species — in that patch; nearby; nowhere. Theory development has resulted in measures that combine information about the species richness of a local patch with information about their relative abundance and their phylogenetic distinctiveness.

Table 3.2 describes some of the standard measurements of "biodiversity"; they are mostly focused on species, or the attributes of species. That said, empirical data on the ecological importance of increased diversity typically relies on species. What is shared amongst these various measures is their assessment that they measure a population. They all provide different modes of assessment at the same level of biological composition. These measures, barring ecosystem function, all reduce the biodiversity of a community or ecosystem to the taxonomically described components of these systems. If these are the appropriate measures of the relative biodiversity contained in a region, then we need not count community properties as an extra vector of biodiversity.

Types of 'Biodiversity' Measurement	*Description*	*Examples of the Methodology/ Measures.*
Functional Diversity	The role that a population trait plays in maintaining an ecological system.	Convex Hull Measures. Dendrogram Measures.
Trait Diversity (Phenetic Diversity)	Morphological features.	Same as Functional Diversity but unconstrained by describing a use for the trait.
Phylogenetic Diversity	Measures the differentiation of population lineages and quantifies over the branching pattern of life.	Node Based Measures i.e. Taxonomic Distinctness. Distance Based Measures i.e. Phylogenetic Distinctness.
Genetic Diversity	The identification of alleles and their abundance in populations.	Genetic Barcoding.
Ecosystem Function	Local nutrient retention.	Onsite monitoring of nutrients and GIS studies.
Species Diversity	Combines species richness with other variables, usually relative abundance.	Shannon Evenness Indices. Simpson Evenness Indices.

Table 3.2. Standard Measures of Biodiversity

Now as many have pointed out, these individual organisms, and the populations they compose, seem to be components of larger, relatively stable, relatively organised ecological systems. So, for example, in urging the importance of niche construction ideas for ecology, Baker and Odling-Smee (2014) write: *'organisms and their environments are in reciprocal causal relationships capable of generating feedback effects; that organisms figure as agents of change rather than merely as passive objects of selection; and that* ***organisms and their local environments must be considered as***

integrated systems that evolve together[38]*'* (Barker & Odling-Smee 2014, p. 201). A crucial question is whether these ecological assemblages really are such systems, in some rich sense of "system". For if they were, that would suggest that we should incorporate their system-level properties into our measures of biodiversity, be these communities or ecosystems.

A paradigm of an organised system is a mechanism, for with a mechanism, we cannot explain the behaviour of the system as a whole just through information about its components (and their numbers). The packing slip telling you what is in the box does not double as an explanation of machine function. We need to understand the spatial organisation of the components, and the specific interactions scaffolded by that organisation. Designed mechanisms are not ensembles of autonomous individuals, but of organised, interconnected, and often quite distinct components. Typically, the behaviour of the mechanism depends on the presence and placement of all or most of these components. These systems behave predictably, for the components are reliable (given the stresses they are typically under) and so are the connections between the components. Systems built by natural selection have many of these characteristics too.

Populations are quite different from mechanisms, in that they are typically composed from a large number of individuals, but with relatively few types compared to the number of organisms, and they are not organised; what happens to the population rarely depends on the precise identity and placement of specific individuals. In deciding whether you are likely to be bogged while driving across a sand dune, the precise location and identity of any specific grain of sand is rarely salient. Population behaviour is often predictable, but only because population-level effects are aggregate outcomes of individual operations, no one of which matters. So populations are not very system-like (Godfrey-Smith 2009, p. 147-150). Are ecological associations more like heaps of sand, or more like a village, with its division of labour, specialisation, and mutual dependence?

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[38] My emphasis.

The example of a village is no accident: it reflects Elton's original model of a community organised through a set of complementary biological roles, ecological niches (Elton 1927). This same picture of community composition influenced the formation of Leopold's land ethic and other holistic conceptions of ecosystems. While Elton's niche concept has been superseded, ecologists still study the structure of these compositional systems: food webs and other aspects of their trophic structure (e.g. Jordano et al. 2003; Lewinsohn et al. 2006). Ecosystem ecologists investigate the ways material flows through these systems; for example, the ways detritivores recycle crucial nutrients back into the soil (Hunter 2016). Ecologists and natural historians track both the relative stability of the species composition of these local systems, and the predictable changes in that composition in response to major disturbance. More recently, the role of ecological engineering in these local systems has come into focus: the ways populations modify not just their own physical and biological environment but that of other organisms there too. Thus a particular stand of eucalypts, as they grow, will affect the soil chemistry, moderate the effects of storms by acting as windbreaks, and as (very leaky) umbrellas; provide numerous nesting cavities and retreats as hollows form; provide food for honeyeaters and other pollinators; more reluctantly, food for appropriately specialised herbivores as well; shelter for spiders and the like under their bark, both on and off the tree. In addition, and depending on the species, they make the site more fire-prone.

This recent turn is especially relevant to the idea that the contribution of community organisation to ecological processes does not reduce to the contribution of its member populations, for if niche construction effects are important, history is important too, for these effects accumulate and ramify over time (Jones et al. 1997; Barker & Odling-Smee 2014; Pearce 2011). History becomes even more important if, as is quite plausible, the accumulation of change is path-dependent (Desjardins 2015). It may well matter which species establishes first: tree species have different profiles as ecosystems engineers, and once a stand establishes, its members can be present for a very long time. For physical features of habitat patches vary quite significantly from year to year, yet local species lists can remain current for decades (though obviously with some changes on the margins), with common species remaining common, and rare species remaining rare (Sterelny 2006).

To both the casual and educated observer then, these interconnected, interacting, co-located networks of populations seem to be real systems. They seem to be (in Rob Cummins' sense) functionally organised, hierarchically composed local systems (more on this in Chapter 5) (Cummins 1975). There is no doubt that there has been a strong tradition within population and community ecology of treating these co-located interacting collectives as real systems (Cooper 2003), supposing that these interactions in a local patch constrain one another's abundance, impose order effects on the formation of new communities after major disturbance, and filter potential immigrants (Agrawal et al. 2007). The reality of these systems is supported by what Cooper (2001) describes as the 'Balance of Nature I" argument (See Introduction). The community structure is stabilised through competition and the tight packing of niche space.

Ricklefs calls this the assumption of "local determinism" in community ecology (Ricklefs 2004; 2005b; 2006; 2008). He argues that the legacy of Robert MacArthur (his graduate supervisor) is the conceptual separation of the region species pool and local ecological communities. MacArthur (1965) believed that processes at the larger historical and geographical scale were of little influence on local interactions as equilibrium dynamics stabilized the species composition leading to limited membership. Local scale population composition was therefore explained by processes such as local competition and ecological filtering without reference to processes at the regional level (See Ricklefs 2005b, p. 18-21 for this argument). This local determinism justifies considering ecological communities as unified entities as they display cohesion and policing mechanisms for their compositional identity.

If system-level properties are real, then the stabilised associations between local populations are plausibly relevant to the ecosystem services that supposedly make biodiversity management prudentially important. For example, if local species composition is determined by these local interactions, that will determine the extent to which, say, pollination is buffered by redundancy. If these local interactions permit a rich guild of pollinators to be present, pollination will be buffered against chance fluctuations in the number of any specific pollinator[39]. The community, partially co-constructing one another's niche, stabilises the system in the face of disturbance, excludes many potential exotic invaders; in general, it increases the robustness and predictability of the local ecological dynamics. Conservation decisions, one might suggest, should reflect the value of these stabilised associations, especially to the extent that such decisions involving trading patches of the conservation estate for land to be restored after exploitation. This would provide a good justification for a fully realised version of ecological holism in which ecological communities would feature as entities of significant value above the populations that comprise them.

3.3. Three Modes of Scepticism towards the Local Ecological Community.

I am not the first to argue that the appearance of genuinely organised and structured ecological systems is an illusion. There have been several strands of community eliminativism through the history of ecology and more recent takes within the philosophical literature. Philosopher Angela Potochnik and ecologist Brian McGill (2012) have argued against the standard version of the view that ecological interaction is organised into real systems; a stratified nested structure, with organisms comprising populations, populations comprising communities, and communities comprising ecosystems. Historically, there has been a strong population individualist program in ecological science, arguing that populations move around the landscape independently according to abiotic resources and stochastic dispersal. In contrast to these two approaches, I will describe how Ricklefs' proposed disintegration of the local ecological community provides an alternative eliminativist position toward the local ecological community and community kinds.

Potochnik and McGill (2012) do not think that ecological interactions conform to the model of a system organised into discrete and well-defined levels. They, however, construct their argument

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[39] A guild is any group of species, which exploits the same resource in an ecosystem.

based on general principles, which aim to reject nested biological composition through a largely metaphysical argument and replace these relations with scale. This argument I believe is misplaced. There is a genuine hierarchy to biology, (see Smith & Szathmary 1997; Calcott & Sterelny 2011) what differs between ecological systems and other biological structures is empirical rather than metaphysical. The compositional units, the populations, do not maintain a single higher-level system in a way that allows for the emergence of stable kind-like descriptions. Potochnik and McGill (2012) argue against the view that ecological interactions are organised into hierarchical structures on the following grounds:

Metaphysical Significance- compositional relationships are not always in the form of one level being built exclusively from elements at the next level down. A termite mound, for example, is composed from nonliving but organised matrix of termites, plant materials, fungi, bacterial colonies, and no doubt assorted fellow travellers and parasites. Likewise, properties can have a complex, multi-level structural basis. The camouflage of a nest, for example, is not only structurally complex (with the outer layer often sourced from many places); the camouflaged depends on its placement, and on the perceptual profile of the nest predators.

Explanation and Evidence- Metaphysical supervenience relations do not indicate a direction of explanation. Higher-level theories can be explanatory without direct reference to their lower level constituents. For example, the principles of island biogeography do not depend on the specific taxa on the islands.

Causal- Objects can play a causal role at more than one level; they can “cut” between “levels” (Guttman 1976). For example, waste molecules can act directly on organisms, making one organism move away from a particularly smelly deposit, serving as a signal to another, while at the same time playing a causal role in the ecosystem, moving nitrogen through the system.

Potochnik and McGill (2012) interpret the idea of hierarchical organisation in too simple and rigid a way (though it is true that ecologists sometimes write in ways that encourage this interpretation of their views). Consider an uncontroversial example of a hierarchical, nested organisation: the morphology of a metazoan, with cells organised into tissues; tissues into organs; organs into organ systems (like a mammal circulatory system). No-one supposes organs interact only with other organs. The lungs interact with gasses and particles direct from the atmosphere; with blood; with hormones and other signalling molecules; with muscles and nerves. There is plenty of cross-cutting causal interaction in a metazoan body, despite the fact that it is clearly a hierarchically organised system. Likewise, facts about that system as a whole often explain features of its components. The mass of an elephant explains the size and strength of much of its skeleton. As Potochnik and McGill (2012) note, the same is true of ecological interactions, but as the metazoan example shows, that in itself does not demonstrate that ecological systems are not hierarchically organised. Echidnas interact with termite colonies rather than individual termites, as their burrowing breaks into the colony and their feeding rarely is specific to an individual termite. Springtails and other tiny arthropods in the leaf litter interact with bacterial colonies and with biofilms, rather than individual bacteria. Likewise, in many cases, it is probably best to conceptualise phytophageous insects as interacting with a system that includes the tree and its associated symbiotic fungi, rather than with the tree alone. These causal interactions cut from organism to population and organism to community and yet are typical of what ecologists study. Getting the right grain of causal interaction rarely involves assuming interactions are between entities of the same “level”.

The importance of these cross-species associations, both for the partners themselves and for third party interactions, are amongst the phenomena that make the local community perspective plausible. It is certainly no reason to reject the view that local communities are real, hierarchically organised systems. That rejection, as the comparison with morphology shows, seems to depend on saddling the classic, nested hierarchy conception of ecological organisation with extraneous metaphysical and causal commitments. As such, when I reject the existence of communities I do so due to the empirical reasons described by ecologists like Ricklefs rather than a scepticism of biology’s hierarchical structure.

We should be sceptical about the standard conception of ecological organisation for empirical rather than metaphysical reasons. There has long been an individualist, “Gleasonian” voice in ecology that has regarded communities as no more than ephemeral associations of organisms that happen, for now, to tolerate a similar range of conditions (Gleason 1926). The distribution and abundance of organisms is essentially controlled by large-scale environmental factors: moisture, temperature, seasonality and the like. A tree cares how much it rains, perhaps how far away the next favourable patch is, but not about the specific identity of its next-door neighbour. This view of ecology regards historical evidence of the existence of very different associations revealed as the glaciers retreat and advance, as decisive evidence that so-called communities are merely unstructured multi-species associations. Colinvaux (2007) is part travelogue, part triumphalist assertion of this argument. It forcefully articulates a view that local species composition as a product of changes in abiotic factors, particularly temperature. One worry with this argument for individualism, voiced by Jay Odenbaugh (personal communication), is that just because a community can disassemble does not mean that it cannot reassemble into an integrated community. This is true, but we need strong evidence of reassembly. If the evidence of movement is continuous and the gradual movement of populations is consistent, then the same forces that appear in the historical record are at play now. These populations will not reach some reassembly end state but will continue to move as they currently are. This conjecture is dependent on the rate and consistency of the processes at play in ecological systems.

If this individualist view of ecological pseudo-organisation is right, then the apparently structured, compositional, and hierarchical organisation of ecological systems poses no special extra problem for the project of giving a realist account of biodiversity: system-level behaviour will be some form of a relatively simple statistical reflection of the properties and the numbers of the components. However, as such a position rejects the importance of population interactions, this runs against the substantive evidence that populations do interact and have an impact on each other. In the next chapter, I explore how population interactions do result in aggregational dynamics while maintaining that structured community individuals are exceedingly rare. The strong population individualist perspective is at best very controversial, even amongst those who reject the idea that community organisation is under local control.

An alternative view is eliminativist of the ecological community without eliminating the importance of inter-population interactions. Ricklefs (2004; 2005; 2006; 2008) has long rejected the view that local communities are genuine biological systems, but not from a Gleasonian perspective. He argues, first, that in the typical case, local communities are not composed from genuine biological populations. Just near the university in Canberra is a bush reserve, Black Mountain. Black Mountain has a healthy population of brush-tail possums. But the Black Mountain brushtails are not a population; they are an arbitrary and transient segment of a population, for there is a continuous population of brushtails that includes Black Mountain, the nearby O'Connor Ridge, and most of the suburban gardens of inner North Canberra. That population is real, for it has semi-permeable boundaries formed by a lake, dense urban infrastructure, and farmed open-grassland. So, the North Canberra brushtails influence one another's fate, in ways they do not influence other brushtails. A virus, for example, could spread through this group without affecting others. But this genuine demographic unit is not nested in Black Mountain; it is not a component of a Black Mountain community. Second, the demographic units are not typically spatially congruent. There are echidnas on Black Mountain too. But the North Canberra echidna population is not congruent with the brushtails. Echidnas do not mind open grassland; they are the most broadly distributed of the Australian native mammals. But they do not penetrate suburban gardens with the ease of a brushtail. This line of argument — the fact that populations are not congruent, and hence there is no local system into which they can all be nested as components — can be repeatedly recycled for other species.

The assumption here is not that we require perfect nesting of population ranges for there to be a community, but that spatial congruence is indicative and important to the formation of a real multispecies demographic unit. This community will have demographic boundaries where the populations outside that community have limited causal influence on the populations within the community. One could think that just the interaction zones of populations could comprise the community, the area comprising of the portion of multiple populations that actively interact. For this to be the community, excluding the rest of the populations that are not currently interacting with other populations, we would have to assume that interspecific interactions more strongly determine population demographics then intraspecific interactions. This I believe is unlikely, interspecific interactions will tend to be stronger determinants of a population's demographics than intraspecific interactions, but this requires empirical testing.

In one of ecology's landmark publications, Stephen Hubbell (2001) proposed a neutral model of local diversity and distribution, denying that the composition of tropical forests was structured by local competition, or by other fine-grained selective forces (the theory was general, but Hubbell's empirical research was on these forests). Ricklefs shares Hubbell's intuition that tropical forests have the wrong composition for local forest communities to be at equilibrium as the result of interspecies interactions: they have too many species, and too few exemplars of any one species (Ricklefs 2005, p. 595-597). A hectare of tropical forest sometimes supports 300 or so species of tree, but often with only one or a few individuals per species, and almost never with patches of single-species stands (Gentry 1988). So, it is extremely implausible to suppose that its diversity and richness is the effect of niche differentiation and interspecific competition, with each tree finding its way to the 5 square meters where it is competitively superior to 299 rivals for that same spot. This intuition matters. If the most rich and diverse biological assemblages on earth are not structured by local interactions, then, at the very best, the local community concept has very limited application. Ricklefs concludes that the Black Mountain community and similar ensembles are not structured out of component populations. Such communities are merely interaction zones, spaces where many distributions overlap.

If local ecological systems are just interaction zones what does this show for measured biodiversity at these levels? The biodiversity realist views biodiversity as playing a real role in the world, it is casually-relevant to ecological assemblages. In the last chapter, I outlined how the diversification of lineages allow for disparate traits that can act in unique ways in ecosystems. But the ecosystem holist may state that the ecological organisation of populations creates enduring causally important properties that are not simple aggregations of the genealogical units from which they are composed (Hutchinson 1965; Hull 1989). The Gleasonian eliminativist rejects the existence of any ecological causal organisation. This is not the Rickefian view, despite his belief that local determinism has misdirected community ecology. Rather, Ricklefs' positive suggestion is to increase the spatial and historical scale of our analysis. We should think of Bioregions — large scale landscapes containing long associated clades — are the explanatory units for the local arrangement of populations.

It is Ricklefs' eliminativism of local ecological communities that I develop and defend. With communities eliminated there is no entity on which biodiversity can be assessed. For there to be an ecological kind we require local ecosystems to be able to support robust generalisations across that grouping. Persistent communities with clustered or correlated subparts have historically been considered important for explaining the distribution and abundance of species. Ricklefs' argument is that the relevant grouping is at the larger spatio-temporal scale, which allows us to track populations in explanatory ways. There are few relevant clusterings of properties or correlations at this lower community level. To defend and develop this position I introduce the conceptual machinery outlined by Bill Wimsatt in his paper *Complexity and Organisation* (2007, Chapter 9). This I will utilise to develop this eliminativist position. In the next chapter, I develop this machinery further, applying it to local ecological communities.

3.4. Flies, Stones, and Territories.

In *Complexity and Organisation*, Bill Wimsatt (2007) compares a granite pebble and a fly to distinguish between two different forms of compositional organisation. Flies and granite pebbles are uncontroversial examples of real structures; they are discrete, bounded, can move independently of other objects; they have important collective physical properties (and in the case of the fly, biological properties too). But the fly is complexly organised in a way the granite cobble is not, for that cobble has a simple and privileged internal organisation. To a first approximation, whatever drives our scientific interest in the granite and its composition — its crystal structure, chemical composition, mass distribution, electrical and thermal conductivity — we will decompose it into parts in the same places. Its crystal organisation, chemical organisation, variance in mass, in electrical and thermal conductivity vary with one another. The boundary where one crystal gives way to another is also a boundary where tensile strength or thermal conductivity changes too. That is not true of the fly; a map of its cell types will look very different from a map of its anatomical parts, which in turn looks different from a map of the circulation of fluids or of its gas exchange with its environment (Wimsatt 2007, p. 183). Each of the maps is robust. We can (for example) investigate cell types through a number of different experimental techniques: light and electron microscopy; different staining techniques to reveal cell structures. Robustness is important: when multiple streams of evidence reveal the same structures in the same places, we can be much more confident that we have identified real features of the world (Wimsatt 1981; Hacking 1983; Calcott 2011). Though each of the maps are real depictions of the fly's organisations structure, they are not congruent.

As Wimsatt (2007) sees it, multiple decomposition reflects an objective feature of the world, and thus an inescapable feature of scientific practice. Different sub-disciplines describe their target explanada through their local theoretical perspectives, and these guide the identification of systems and their salient parts. Two different perspectives will result in different profiles of the parts of a system, and as we have seen in considering the fly, these need not be congruent. Generalising from the fly, Wimsatt thinks of "multiple decomposition" as a process is which different theoretical perspectives are overlayed onto the system under investigation. This provides information on the system's complexity and on the commensurability of differing perspectives. Wimsatt describes multiple decomposition as follows:

i) Systems can be understood given different theoretical perspectives.

ii) Different theoretical perspectives give different characterisations of the parts of the system. That is, they use different criteria, and different empirical techniques, to identify the parts of the system, and the boundaries of those parts.

iii) Once two different perspectives of the one system have been developed, we can attempt to spatially align the parts identified via one decomposition with those

> identified through other decompositions. In the case of the granite cobble they align quite well. Not so, the fly.

In Wimsatt's terminology, the granite cobble is descriptively simple, because its parts are spatially coincident over different perspectives. If not, as with the fly, the system is descriptively complex. Wimsatt's conceptual machinery helps us see the limits of the Potochnik-McGill critique of hierarchy in ecology: their tacit model is of a descriptively simple system of hierarchical organisation. This is where the higher level under multiple different perspectives decomposes into the same distinct modules. Causation is always within a level between these modules. Ecological systems are not descriptively simple; the components specified from one perspective (say: locating the different guilds in the system) do not match up with those from another (say: modelling the key factors in response to fire). But flies have genuine compositional organisation, even though they are not descriptively simple.

I read Ricklefs' suggestions that ecological stability depends on regional rather than local processes through the Wimsattian lens: bioregions are real, but descriptively complex, hierarchically organised ecological systems. They comprise of groups of lineages that have associated over evolutionary time due to shared abiotic ranges and physical barriers. The bioregions are descriptively complex, first, because as we noted above, demographically connected local populations rarely have congruent populations in a territory. So, for example, the Atlas of Living Australia maintains an online database of species records. If one looks, say, at Kangaroo Island[40], and checks the records of the Little Pygmy Possum, we see that the records are clustered heavily at the western end. By contrast, the Western Pygmy Possum is clustered at both ends (with a few records in the middle); it is reasonably congruent with the Southern Brown Bandicoot. To shift from animals to plants, the Coast

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[40] I have chosen this island as an uncontroversial example of a region; its length is about 80 kms east-west; about 20 kms north/south

Ground Berry is heavily clustered on the south coast of the island; the Wiry Ground Berry is more evenly spread, but heavily clustered towards the eastern end[41].

Figure 3.1. Kangaroo Island Species Distribution Maps. Left map shows Little Pygmy Possum (Black) and Western Pygmy Possum (Grey) sightings. Right map shows Coast Ground Berry (Black) and Wiry Ground Berry (Grey) sightings.

Community ecologists and population ecologists are often interested in explaining the distribution and abundance of specific species, especially when these are vulnerable, and those focusing on different populations will decompose Kangaroo Island into different interacting components. The Little Pygmy Possum is “near-threatened”, so a possum ecologist would need to identify the distribution of this species, and those other species with which it had important interactions (predators, host trees with hollows where it can shelter and nest; competition for those hollows; food sources). But she could probably afford to ignore the echidna distribution. The same is true when we consider the orthogonal explanatory agendas of community and ecosystem ecology. Ecosystem ecologists are primarily interested in explaining the cycling of materials through their target systems, and so the physical geography of a landscape is central to their explanatory projects; different aspects of that geography, for different materials. For example, in understanding the flow of water through the system, relief is very important, so capturing the fact that the western end is much

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[41] The examples are arbitrary, except in that I have chosen taxa where there are enough records for the recorded distribution to be some guide to where the organisms actually are.

hillier than the east is critical. In considering nutrient flows, the base geology, the ground cover, and the direction of the prevailing winds will all matter. Notice that these decompositional descriptions are all robust: there are many techniques for measuring population distributions; for identifying and assessing ecologically relevant physical features of an environment; and for measuring the flow of materials through a system (Odenbaugh 2010). In brief, there are multiple ecological perspectives on Kangaroo Island, and the components the different perspectives identify will often not be spatially congruent.

The disjunctive nature of these different perspectives at the local community scale undercut any general description of communities, which could scaffold ecological kinds. There is an incredible diversity of theories around what constitutes a natural kind (Bird and Tobin 2017). I do not place a high threshold for the existence of ecological kinds, such as essential properties or necessary and sufficient conditions. For there to be a kind in ecological science there should be a stable clustering of properties and this cluster must feature in inductive inferences and causal explanation. I take this to indicate that an ecological kind cannot be sui generis, there must be enough instances of a kind to allow for inferences and predictions to be made.

There are two distinct issues at play in making inferences about the existence of ecological kinds. Are ecological systems compositionally formed in ways that allow them to be ongoing spatio-temporally bound individuals (Hull 1976; Haber 2016)? If so, they can be individuals. Individuals can feature in science and inferences can be made of them, despite their unique nature, as they cohere in ways that allows the prediction of the causal capacities of that system. In the next Chapter, I particularly focus on whether communities are individuals. The second question is whether there are ecological types, where the type of community a specific community is predicts/explains something about that community and its interactions with others. When we encounter a new community, we can identify its type then make inferences from this type to other tokens. These questions are related. If there are no individuals then there can be no types, as there must be instances of a type. In this chapter, I argue that there are no robust generalisations about ecological kinds due to the lack of distinct individual tokens at the local community level.

In actual ecological systems, their type is massively underdetermined due descriptive complexity and disjunctive composition. There are as many different complex descriptions of a community as there are different features we would like to explain. If we wish to explain the distribution of Little Pygmy Possums, we will be given a very different community than the community that explains water cycling. Each of these decompositions features unique causal structure, making strong internal clustering unlikely. This is because ecological communities are not well-formed robust systems. This impedes the possibility of inferences from one community type to the next. Each ecosystem description is highly idiosyncratic and explanation relative to the descriptively complex decomposition. Generally, communities lack the shared properties or correlations to constitute ecological kinds. Without categorization of community kinds diversity metrics cannot develop.

3.4. Seeing the Fresco in the Ecological Mosaic.

Ecological community eliminativism is just part of Ricklefs' picture, the elimination is to another compositional structure; the biogeographic regions populations move around. There is a quite persuasive case for thinking of bioregions as objective features of the biological world, structuring ecological interactions. While I do not aim to vehemently defend the positive case for bioregions being the real ecological units in this thesis, I will explore the positive reasons here. Considering the positive reasons for bioregions constituting explanatory ecological kinds links local ecological processes to long-term evolutionary trends. This reinforces the explanatory role of evolutionary biogeography in ecology and conservation. Local conservation should consider what clades have historically been present in a region as their evolutionary interplay governs species composition at the local scale.

In ecology, we have several explanatory targets, we wish to explain demographic features of populations, primarily their distribution and abundance across the landscape, but we also want to be able to explain how these populations evolve. In both cases, the focus is on populations and their boundaries. There has been some considerable recent conceptual work on defining populations, primarily in terms of their causal cohesion across, and despite, patchy distributions (Millstein 2009; Matthewson 2015). Ricklefs (2004) claims local ecological communities are not bound in a way that allow for the proper assessment of the contained populations. When we eliminate communities, we do so to move to what are often larger scale arrangements, biogeographic regions. These encompass the area that populations move around, shifting between areas with abiotic conditions that can sustain them (their “fundamental niche” as Ricklefs describes it).

Biogeographic regions are defined by the clustering of lineages within a region and the abiotic features that explain why these species clusters have dispersed no further. Classically these factors are temperature, altitude, and precipitations or geographic barriers such as mountain ranges and water bodies. Glor and Warren (2010) provides methods to test these boundaries; Kreft and Jetz (2010) provide measurement procedures for biogeographic regions using species distributions. The relative covariation of lineages over large periods of time is indicated by the relative success of vicariance biogeography, where global population distributions are explained through phylogeny and geological change (Wiley 1988). This explanatory paradigm relies on the relative stability of sets of lineages within regions. Populations move around under the forces of geological change, which raises mountains and carves new rivers. These forces separate populations, allowing for the creation of new species through allopatric speciation. The product of these forces is the presence of many related species in a region, often with few strongly differentiated adaptations.

Vicariance biogeography has, since the time of Charles Darwin and Alfred Russell Wallace, stood in contrast to dispersalist biogeography, which emphasises the ability of populations to disperse long distances. There is good evidence for this, or example: the New World Monkeys of South America appear to be the result a lucky trip across the Atlantic Ocean by some Old World (African) monkeys (De Queiroz 2014). If dispersal is common and strongly determines the arrangement of species globally, then the same issues of non-congruence that affect local ecological communities will similarly affect bioregions. These models of population arrangement are not exclusive, it is an empirical matter to the extent one model explains the distribution of populations versus the other, but I would say the explanatory success of vicariance models of biogeography suggests the relative geographic continuity of lineages within an area. These stable continuously interacting clades within a geographical region are the best representation of the features, which Ricklefs believes are more explanatory in ecology than the local interactions of populations.

There are four considerations that favour taking bioregions seriously. First, they are bounded: the edges of landscapes or territories are defined by physical boundaries or by physical gradients, which reach thresholds (of salt levels; night temperatures (frost or snow), aridity) which influence the movement or viability of many species of organisms. Equally, mountain ranges and rivers create real boundaries to the movement of populations. When individuals breach these barriers, they often do so with such a small standing population that the genetic bottleneck facilitates speciation. Obviously, these boundaries are not absolute: some plants are salt tolerant; some animals can do without surface water. But the skin is not an absolute boundary either. Humans (like most animals) harbour huge populations of microorganisms, and some migrate in and out despite that barrier. So, these territories are the arenas in which demographically real units — demographically connected populations — interact with one another in zones of overlap, and with the abiotic environment.

Second, bioregions are the spatial scale at which ecological and evolutionary processes connect. One problem with the focus on local communities is that it makes it difficult to see how to integrate ecological and evolutionary thinking (Sterelny 2001a). Evolutionary change takes place in populations and in ensembles of populations. Local communities and the interactions therein — our Black Mountain — are too spatially localised to be of much evolutionary significance. Obviously, an important mutation might occur through a Black Mountain reproductive episode, but in the typical case the new variant cannot go to equilibrium on Black Mountain, if as Ricklefs argues, the Black Mountain animals are an arbitrary and ephemeral fragment of a population. Likewise, local communities are often too short-lived to generate significant evolutionary change; grasslands turn into forest or bake to clay; ponds dry out; silt up. The shift to landscapes takes us to the right temporal and spatial scale to link ecology and evolution. The evolutionary mechanisms that build diversity seem mostly to operate on a regional scale; the more boundaries filter movement, the freer populations are to diverge from their siblings. Ecological change, both fast and slow, takes place on all spatial scales, from the very local to the global. But disturbances — a major storm system, for example — will often have region-wide effects, and the same is true of slower environmental changes. If we take regions or landscapes to be the most salient level of ecological organisation, its scale matches the spatial and demographic scale of microevolutionary change. These evolutionary responses include responses to the other populations in the landscape, and as John Thompson has shown, these coevolutionary responses can be marked, even when the populations in question only overlap, and even when the interactions are between multiple populations. This will be the typical situation in territories, as Ricklefs repeatedly notes. Coevolution does not require congruent, tightly coupled populations (Thompson 1994; Thompson 2005).

Third: Ricklefs argues that this regional turn enables us to capture the genuine insights derived from thinking about local communities. As Ricklefs sees it, the local community paradigm is committed to making two strong predictions: (i) community richness correlates with the physical heterogeneity and productivity of the local patch; (ii) local richness is independent of regional richness: physically similar local patches embedded in different biological regions should have similar levels of diversity. While he thinks there is a reasonable case to be made for the first of these predictions, the second fails. European plant communities, for example, are impoverished (in tree species) compared to East Asian ones, and that is because the regional diversity of European trees has not recovered from glacial extinctions[42]. But he is open to the possibility that local interactions filter regional diversity. Regional diversity presents a list of potential community members to local patches, and these are filtered by habitat selection (tolerance for physical conditions, as they are originally, and as they become modified by niche construction effects); competitive interactions; mutualisms; the effects of predation and disease; and of course chance (Ricklefs 2005a). In principle, local diversity

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[42] In East Asian and North America, but not Europe, tree populations could shift south in glacial cycles, as the mountain ranges run north/south rather than east/west.

might be very strongly shaped by these local interactions, but they are interactions between population fragments whose presence and abundance is explained by events at larger spatial scales and longer temporal scales. There are echidnas on the Australian National University campus, but that might well be a consequence of source-sink dynamics; an overflow from the echidnas of Black Mountain.

Finally, it is worth mentioning that hypothesis formation and testing on regional scales is more tractable than it once was. The recent development of Geographical Information Systems (GIS) has rapidly increased the ability of scientists to test hypotheses on these larger scales (Kozak et al. 2008; González-Orozco et al. 2011). There are, however, important limits to this. While GIS provides precise detail on co-variation in population distributions, it does not directly represent the local causal interaction of the individuals that constitute these population distributions. When such causal interactions are inconsequential, this is not a problem. But, in some cases, we will want to represent these causal relations and will have to consider the local scale.

Ultimately, considering the regional scale re-orients the focus of conservation on biogeography and evolutionary history rather than local community interactions. We want to preserve the entities that form the real patterns in nature. For biology, this is the way in which lineages have evolved and fragmented across larger landscape over long periods of time. In the previous chapter, I argued that biodiversity is best measured through phylogeny: individual genealogical units constitute biodiversity. Strong correlations of lineages appear at the bioregional scale, and these explain the diversity of populations in local community patches of that region. Tying conservation to the representation of clades is prudentially wise in the long term as sampling across clades allows for different possible ecological and evolutionary interactions across the entire region as these populations move through the area in geological time.

Biogeography considers the way clades produce new lineages and the ranges these clades occupy. Given this biogeography directly speaks to my realist conception of biodiversity, which is focused of the global diversification of life. It is within biogeography that we find explanations for the ways in which lineages diverge. Speciation rates may be the result of co-evolutionary interactions between clades within a region. As phylogenetic inertia constrains the possible habitats and ecological roles that new species can fill, antagonistic or mutualistic relationships are conserved providing an engine for co-evolution (Westoby et al. 1995; Webb et al. 2002). Young clades tend to have a rapid burst of diversification (McPeek et al. 2007). This has been explained in multiple ways including adaptive release, where the new features of the clade are not subject to be exploited by other species. Geography influences the bursts of diversity in clades. Jetz et al. (2012) found that bird diversification has been immensely influenced by the opening of land in the wake of the ice age. As the glaciers disappeared, bird species rapidly evolved across the new land approaching the poles. Explanation can be neutral on the features of species in a clade; for example, the stability of regional species diversity is possibly the product of the equilibrium between the production and loss of new species in a clade (Nee 2006). These explanations provide an alternative to explain the presence of species than the local stability of ecological compositions.

The varied interplay of populations distributed over multiple community patches propels the production of diversity. This is further supplemented by allopatric speciation, driven by the gradual change of geography, to make the region the right level to consider when attempting to understand how new lineages are created. Biodiversity, as I describe it, attempts to preserve a representative sample of the taxa within a bioregion. By preserving distinct populations in clades, we preserve the means for further diversification in the future. We can act to save the long-term global diversity of life on earth by keeping in mind these bioregional patterns.

Interestingly, the stability of regional biogeographic assemblages over long periods of time solves Sterelny’s (2001b) “paleo-ecological puzzle” for ecological communities. The puzzle is the appearance in paleogeographic data of the co-ordinated stasis of co-located lineages over extremely large periods of time. This he uses to argue for the reality of local ecological assemblages. There, however, is a different way to interpret this stability. These assemblages are real but only at this larger scale of co-ordination, the correlated cohabitation of lineages over evolutionary time in large biogeographic regions. Co-located species in local patches are not stable enough to explain species diversity but lineages bound within biogeographic boundaries can be.

3.6. Bioregion Limitations

In the previous sections, I developed a case for taking the apparently organised, structured character of ecological associations seriously, but on spatial scales of bioregions rather than local communities. The broad-brush stability of local habitat patches genuinely needs explanation. However, we also saw that there were powerful objections to seeing local patches as organised systems from which we can infer ecological types. In contrast, there is a persuasive case to be made for taking seriously regional organisation. However, that case has two limitations.

First, even if regions do have the structural and organisational features we have noted, in other important respects they are not system-like. Unlike flies and rocks, they do not interact with their environment, including other flies and rocks, as a single integrated entity. Our granite cobble, swept up in a flood, bumps and bangs into other rocks, bits of wood and the like, and its global properties determines the effects of these collisions. As with local communities, there is no case for thinking that territories or regions interact with other territories or regions as a single system. But they comprise a set of lineages which can feature in scientific hypotheses.

Second, there may well be large stretches of continental plains, which are not, in the relevant sense, regionalised. It is an open empirical question whether populations are always, or typically, in bounded territories. If we consider large continental expanses without major physical barriers — for example, the western slopes and plains running west from Australia's Great Dividing Range — it is conceivable that populations reach the limits of their physical tolerances in ways that are not at all coordinated. The less heat and arid adapted populations drop off, and the more desert adapted organisms drop in, but there is no zone where the less hardy hit the wall more or less together. Phenomenologically, that does not look plausible: Australian natural historians write of red and yellow box woodlands; the Mallee belt; Mitchell grass country; saltbush-spinifex plains as if these named large stretches of country with a fairly stable and predictable character. But for most species, historical distribution data is patchy. We simply do not know. Populations nested in kangaroo-island-like bounded territories may be more the exception than the rule. So, while I am comfortable throwing my strong credence behind the negative proposal, local communities are not systemic or kind-like, the evidence is equivocal for bioregions. Possibly some bioregion may also be communities, such as small islands. The reality of bioregions will largely be decided by the extent to which populations are arranged around the globe through vicariance or dispersal. If vicariance is the main mode of biogeographic distribution, the clades that comprise a bioregion will have long-standing relationships and continuity in their geographic borders, which may warrant their assessment as biological individuals, even if not as natural kinds (Hull 1976). However, if species dispersal is commonplace then biogeographic regions may be as porous and ephemeral as the local patches that comprise them with populations moving from region to region and borders being of little consequence.

Therefore, I only tentatively support Ricklefian eliminativism. It contributes an alternative vision of hierarchical composition above the population-level. Like Gleasonian community eliminvativism it denies that ecological communities can explain population composition, distribution, and abundance. Local communities have very little structure internally that allow for explanations extending from the general, community kinds, to the particular, a particular community. Local ecological communities are far too idiosyncratic for this style of inference. However, unlike the Gleasonian perspective this is not because there are no significant local causal interaction between populations. There is real causal structure in ecological systems even if they do not allow for kind-like inferences. In conservation, we will have to relate this ephemeral, but no less real, lower level causal structure to the higher-level stability of regional areas.

3.7. Think Regional and Act Local

In this chapter, I have used conceptual machinery developed by Bill Wimsatt to argue that while ecological aggregates have some causally important structure and organisation, they are far too marginal, stable or organised systems to create measures of their biodiversity. I shall end by discussing the consequences of this view of ecological hierarchy for conservation biology, and in particular, the unresolved tension between local and regional perspectives. The project of conservation biology is to stabilise important aspects of our biota, but if we accept Ricklefs' line of argument as I developed it in Section 3.5, to the extent to which there are equilibrium processes in ecological systems, these seem mostly to be on regional rather than local scales. Conservation biologists need to think regionally, in part because stability is more regional than local. For example, since the introduction of cane toads, Australian snake species have increased in body size (making toad poison less likely to be fatal), but the head gape size has reduced (making it less likely that they will eat big poisonous toads) (Phillips & Shine 2004). There can be little doubt about the form of this interaction: it is a stable, aggregate outcome of probably quite varied and fluctuating interactions across many local patches. While the local patch does not have a systematic kind-like structure, there is stable phenomena across lineages within a region.

Local patches and the populations they support are not inherently stable. The temporal beta-diversity in local areas often appears to be extremely high[43]. If this is indeed typical, the species composition in local communities rapidly changes. In one study of 100 biomes across earth, 75% of these systems had at least one in ten species disappear locally per decade (Dornelas et al. 2014). This loss is often coupled with little change in regional diversity, which is more stable. Populations simply shift their distribution across the larger landscape (Thuiller et al. 2007). As populations change in their local abundance, so the interactions between them also change. When the populations of two different species overlap, both the strength and the type of interaction can vary over their shared range, depending on their relative abundance and the local abiotic factors (Poisot et al. 2015). This variation results in local predictions and systematic relations being very hard to project from one local area to the next (See Elliott-Graves 2016 for more on prediction). Local variation is the norm for populations

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[43] To recap, beta-diversity is $\beta = \gamma/\alpha$ where α (alpha-diversity) represents species richness in a local assemblage and γ (gamma-diversity) represents the species richness of the region comprised by all the local assemblages being analysed. Temporal beta-diversity assesses species diversity at single local assemblage over multiple time slices.

and their causal structure; stable features only emerge once this variation is washed out through larger spatio-temporal scales.

However, this regional perspective must connect to more localised and taxon specific descriptions of the causal interactions which drive change in local populations (or population fragments). For these are the typical sites of conservation interventions. I say typical with good reason. The use of wildlife corridors indicates that there is important practical action that can be taken to preserve regional mechanisms for species diversity. Taxon-specific local phenomenon includes the genetic diversity of local populations (for example, whether inbreeding depression is a threat), as well as their size, spatial distribution, age structure, gender balance. These local causal interactions will form causal networks of various kinds. We will need to re-orient our focus to the populations that comprise a local patch and mapping their weak causal relations to intervene on this scale. This is a practical necessity due to the difficulty of implementing policy and intervening on a regional scale. As action is at the local scale, we need to identify what are the causally significant factors in a local area to make effective intervention. Amongst the weak and diffuse local causal relations, there may be robust features in local communities, and when present, they must be accounted for in local conservation regimes.

So, ecological assemblages — perhaps local communities, but more likely spatially larger, bioregions — are somewhat system-like, even if not kind forming. They are not mere aggregates, like a heap of sand. Within a local patch, there are many populations, and their specific character and their spatial locations will matter to the overall ecological and evolutionary dynamics of a region. But at least in most cases, these are not tightly integrated and interdependent; despite Vermeij’s metaphor (Vermeij 2009), the communities interacting in a region are not like a modern economy, the connections are much looser. Very likely, most species on Kangaroo Island would not notice if our possums and berries were to vanish. They are quasi-systems, not contributing enough to explanation to warrant their place at the table. As a consequence, my best bet is that a lineage-based account of biodiversity is all we need. Ecological organisation is not machine-like enough, for us to need to count machine types as well as the parts from which they are made. So, while the Convention on

Biological Diversity (CBD) defined biodiversity as: '*Diversity between species, within species and of ecosystems'*, I suggest dropping the "of ecosystems". Biodiversity need only be defined in terms of biological taxonomy.

Local communities are the stuff out of which landscapes or territories are composed. But if the studies I have discussed are typical of the behaviour of local communities, these highly local interactions and population fragments are often ephemeral. There is no sense in which a stable set of populations, regulated around an equilibrium number, is their natural state. That in turn implies that there is a problem in treating local communities and their boundaries as the right area for preserving species. As a consequence of local patch dynamism, conservation of species involves not just a focus on where the population is currently found but where the population can be locally and regionally sustained. Conservation biologists have to think locally, in part for economic reasons. Very often, conservation decisions are about small patches. Sometimes quite large chunks of territory are part of the conservation estate, but active intervention tends to be on much smaller spatial scales. New Zealand's Kapiti Island is still one of the largest islands from which all rats have been removed; it is somewhat less than half of one percent of the area of Kangaroo Island[44]. But conservation biologists also have to think locally because regions are indeed ensembles of patches, and so are aggregated from patch specific interactions. They must act locally but think regionally. In the next chapter, I will explain how we can act locally despite the ephemeral nature of local ecological systems. By mapping their causal structure, we can intervene and make changes with the ultimate aim of preserving the lineages representative of biodiversity and the large-scale trends of life on earth.

3.8. Conclusion

Traditionally environmental ethics has been guided by ethical consideration towards ecosystems, as noted in the thesis introduction. My aim is to build a new ethical framework, based on

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[44] 19.65 square kilometres to 4416 square kilometres.

biodiversity. This chapter dismisses an ameliorative position, namely, that an explication of biodiversity will identify ecosystems as units of moral worth. This would align my project closely with more traditional environmental ethical positions. I have made explicit that this is not a possibility. Ecosystems cannot be counted and categorised for the means of creating biodiversity measurements. We must instead measure biodiversity at the level of taxonomic structure. But I have not accepted a solely Gleasonian position in which populations move around a landscape completely causally independent from other populations (More on this in 4.3). In the next chapter, I elucidate how we can use this causal structure to explain ecological systems without accepting the ecological communities as comprising individuals.

Chapter 4. Indexically Structured Ecological Communities

4.1. Introduction.

The gullies of Namadgi National Park seem like distinct ecological communities from the peaks of the Snowy Mountains National Park. Wild flowers are scattered across the sub-alpine landscape of the Snowy Mountains, punctuated by grizzled snow gums, and introduced brumbies; while Namadgi's dense gum forests, dominated by Red Stringy Bark and Scribble Gums, line broken granite creek-sides holding a diverse assemblage of reptiles and insects. Both of these national parks are of high conservation value and legislation is built around the need to preserve their unique identity. Yet these two communities are linked within the larger meta-community of the Australian Alps, sharing many species and being connected by forested parks. Despite this, it is assumed that their local populations interact more strongly with each other leading to the natural conclusion that the populations in the ecological community of Namadgi are strongly policed in their distribution, abundance, and persistence by the other populations of Namadgi. Likewise, for the populations in the Snowy Mountains community. Combining this causal assumption with the differing description of habitats leads to the seemingly not very radical conclusion that these habitats comprise distinct ecological communities.

Ecology studies the distribution and abundance of populations across landscapes and over time. One prominent subfield of ecology, community ecology, studies the way "local" or spatially congruent interactions result in such demographic changes. The "local ecological community" functions as the local system of interest and is the core unit of investigation for community ecology. Community ecology has long operated with the assumption of "local determinism": i.e. that ecological patterns are primarily explained by the interaction of local populations within a community (Elton 1927; Ricklefs 2005a; 2008). It is thought that these interactions operate within certain boundaries. Once we identify their boundaries we can make inferences about how they operate. The local interaction and identity of the species in Namadgi distinguish the Namadgi ecological system from the Snowy Mountains ecological system.

Ecological communities are thought to have discrete boundaries, stable composition, and predictable dynamics over time, and these characteristics allow for inferences to be made from one community to the next. But there have been many dissenting voices within the ecological research tradition who instead argue for *ecological individualism*, emphasizing that populations generally move around a landscape of their own accord driven by chance and by abiotic factors and are not heavily influenced by their local neighbours[45]. The implication being ecological communities are largely ephemeral compositions of populations. This debate drives considerations whether there are law-like regularities in community ecology (see Lawton 1999; Linquist et al. 2016). If ecological communities have shared properties, then we can make robust generalizable inference about how they act. On the other hand, if assemblages are just collections of largely independent populations then there will be little robust to say about communities.

To arbitrate this debate philosophers and biologists have provided an analysis of the conditions for an assemblage — a collection of populations in a space — to be an ecological community. Namely, assemblages should be a biological individual just like an individual organism, population, or lineage (Clarke 2013; Hull 1976; Millstein 2009). If an ecological community is a biological individual, then it is the cohesive and distinct entity that local determinism presupposes[46]. Jay Odenbaugh and Kim Sterelny independently specified the conditions under which an ecological

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[45] The scale and stochasticity of the processes that determine the distribution and abundance of populations do not necessarily co-vary. Deterministic processes include species filtering, competition, and mutualism. Stochastic processes include dispersal, speciation, and extinction. We could have stochastic or deterministic processes on both the regional or local ecological scales.

[46] A further required assumption is the group of individuals need to have features in common to support induction. Defining the boundaries of communities is the first step to determining the properties held by a community so to search for similarities in con-specific communities, and then do induction. This chapter aims to skip this step and show how explanation can occur without partitioning these units into bound individuals.

assemblage can be thought of as an objective and important unit in nature, an *ecological community* (Sterelny 2006; Odenbaugh 2007).

I shall argue that as ecological communities so rarely satisfy these conditions we need an alternative account of ecological communities. Instead, ecological systems are largely aggregations of individual populations that fail to be linked by stable, strong causal interactions. As a result, they are better described indexically, as causal networks which unfurl from a specific point of reference. This acts to fix the reference of these somewhat unsystematic systems and allows for the identification of the robust parts and robust properties of ecological systems. To infer from one community to the next we need a precise account of the identity of the units we are discussing; indexically-specified communities provides that. I am providing a third option between the two opposing pictures of ecology, one which treats communities as fictions, or takes an even stronger anti-realist position, and the other which treats them as individuals. My view does not dictate that ecological communities can never be a biological individual; there will be limiting cases. But these cases lie so far from the norm that we need a framework that better represents the degree of variation in ecological assemblages.

4.2. Communities as Biological Individuals

Ecological communities feature as distinct and countable entities in ecological science and in normative theories about the preservation of the natural environment. One way to establish that a biological entity has these features is to view it as a “biological individual”. While biological individuality has become a contested topic in philosophy of biology, with multiple attempts to precisify its description, generally biological individuals are spatio-temporally bound units that exhibit internal cohesion. This internal cohesion in ecology is expected to be largely a product of causal interactions of populations within the community regulating its overall features. Ecological communities as individuals features in major hypotheses across the related ecological sciences, particularly theories of ecological succession. And it is this causal and explanatory distinctness which undergirds the normative value of these communities. This section quickly notes the various roles that ecological communities, as distinct units, have played (or have been claimed to play) in ecology and conservation then turns to the precise description of communities as individuals that Sterelny (2006) and Odenbaugh (2007) present.

Community ecology has produced multiple research programs, which posit that there are distinct countable ecological communities. Most famous is Fredrick Clements' treatment of ecological communities as super-organisms with a developmental sequence of population's facilitating the establishment of the next population i.e. grasses releasing nutrients into the soil facilitating the establishment of larger trees. This process of succession was thought to yield a mature ecosystem, which has stable self-preserving system properties (See Eliot 2007). While Clements' superorganismal ecology has fallen by the wayside, many successors have taken up aspects of his program. Both niche theory and versions of the diversity-stability hypothesis have relied on an assumption that communities form tight-knit economies with positions that can be filled interchangeably by populations (MacArthur 1955: Milstead 1972; Herbold & Moyle 1986). When the positions in the economy are filled the economy is "stable", explaining the persistence of the assemblage and its resistance to invasion by alien populations. All these theories assume that ecological communities are the right size of object to analyze changes in a population's abundance and distribution. The local community as a result plays an explanatory role in the ecological science. This would then indicate that the number and type of ecological communities would contribute to global biodiversity (as argued against in the previous chapter).

Ecological communities have been seriously discussed as bearers of normative worth since Aldo Leopold's *Land Ethic,* which demanded the extension of ethical concern to ecological communities, not just individual populations (Leopold 1949). And while many nebulous versions of the relation between ethics and ecological holism have been posited in the following 70 years, ecological communities do play a serious role in conservation science[47]. Conservation is widely taken to have the goal of preserving biodiversity (Soulé 1985). Describing ecological communities as distinct entities also allows them to constitute biodiversity above the populations that constitute them, and many conservation programs are explicit about their aim to preserve not just the inter and intra diversity of lineages but also diversity of kinds of communities. For example, in the Australian Capital Territory 'Natural Temperate Grassland' and 'Blakely's Red Gum Grassy Woodland' are endangered ecological communities, which are afforded legal protection[48]. These form under this legislation a kind of ecological community, and within a region there may be multiple individual communities of that kind we may wish to preserve. Thus, ecological communities appear in conservation decision-making as entities that are quantifiable and distinguishable. Each individual would make a distinct kind of contribution to the ecological processes of a region given the kind of community it is.

Communities as individuals have played an important role in both the ecological sciences and conservation. But what are the criteria that an assemblage needs to fulfil to be an individual? Sterelny and Odenbaugh both present similar accounts, which I condense into a single view. While they provide a set of conditions which if fulfilled counts an ecological community as an individual, they leave it open as to whether any actual ecological community satisfies these conditions. The conditions they present follows.

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[47] For a systematic consideration of Leopold's "Biotic Communities" as real scientific entities see Millstein (forthcoming).

[48] http://www.environment.gov.au/epbc/publications/white-box-yellow-box-blakelys-red-gum-grassy-woodlands-and-derived-native-grasslands

4.2.1. Boundaries.

Individuals, as spatio-temporal entities comprised of interacting sub-parts, have boundaries. For interacting parts to make a whole there must be strong causal interactions creating internal cohesion within the system and factors that aid its isolation from external influences. The system parts in community ecology are the populations which causally interact, creating feedback loops maintaining local populations and excluding external populations from invading the local system. Sterelny identifies local niche construction as a mechanism that can allow populations to maintain an assemblage. Famously, Australian plants including Gums, Banksias, and Melaleucas are adapted to fire and facilitate the presence of each other by making their local environment more fire prone. Under this conception of boundaries ecological communities are bound by interaction strength between populations (Levins & Lewontin 1985). While this does not necessarily mean that populations in the system will be congruent, strong causal interaction is associated with spatial overlap so congruence, or at least approximate congruence, of community populations is expected.

4.2.2. Internally Structured.

The populations that belong to an ecological community should act in ways that police the composition and stability of that community, functioning as homeostatic mechanisms for self-maintenance. Interspecific interactions — such as predation, competition, and, mutualism — are thought to form a lattice of positive and negative feedback loops, regulating the community and creating stability. When you couple these interactions with stable geographic ranges of the populations, you gain a picture of a stable economy of nature in which there is persistence of local population identity due to the specific roles that these populations play. Internal structure is the product of both feedback loops that act to maintain population identity in an area and the persistence of specific populations playing particular roles in this local community.

4.2.3. System-level Properties.

If we wish to include local ecological communities in our general scientific ontology there has to be a reason to talk about communities rather than just talking about the populations that make up communities. There should be predicates that describe community level properties. System-level properties are an explanadum to be explained by the assemblage and an explanans for ecological and evolutionary hypotheses. Properties generally discussed on the community level are associated with the maintenance of multi-species interaction networks such as food webs (*community network structures*), the maintenance of composition identity or aggregative features (*emergent community properties*), or the various material outputs that the joint assemblage create (*community outputs*). Odenbaugh treats system-level properties as necessary for community existence: *'species populations form an ecological community just in case… they possess a community level property'* (p. 636). He primarily mentions interspecific interactions and feedback loops as community level properties. Sterelny describes emergent community properties, identifying several candidate emergent properties from diversity-stability hypotheses such as community population stability and community biomass production. Conservation science has a keen interest in the productivity of communities, how much biomass they produce, and the abiotic resources they cycle. Many ecologists have attempted to justify the preservation of ecological communities by appealing to "ecosystem services" - capacities commonly attributed to the community as a whole - which they provide. These system-level properties feature in ecological explanation, and they are properties *of something*; namely, a community[49].

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[49] It is convention to describe a "community" as an "ecosystem" when abiotic features are included as parts of the system.

4.3. Problems with Individuality.

According to Sterelny and Odenbaugh communities are individuals if they have three features; they should be bound causally, they should have internal regulation, and they should have system-level properties. Sterelny represents these criteria hyper-dimensionally, with each criteria occupying an axis, noting that all of them can be more or less instantiated (Figure 4.1). This is partially true, but these axes are not independent, as both authors independently note (Maclaurin & Sterelny 2008; Odenbaugh 2016). Internal regulation and boundaries are mutually dependent, spatial clustering allows regulatory interaction to be efficacious and regulation maintains community composition. This implies if an ecological assemblage does not have boundaries with internal regulation, then it is not a biological individual. Equating community identity with a stable self-regulating unit is substantial theoretical commitment; it is an open empirical question whether communities self-regulate (Cooper 2003). I am extremely skeptical of the possibility of self-regulating communities (Introduction, Chapter 3). System-level properties are usually thought to be the product of this bound and stable community. I aim to sever this relationship arguing that communities do not in general have robust boundaries and their internal structure is not as stable as individuality requires, but despite this, ecological systems can have system-level properties.

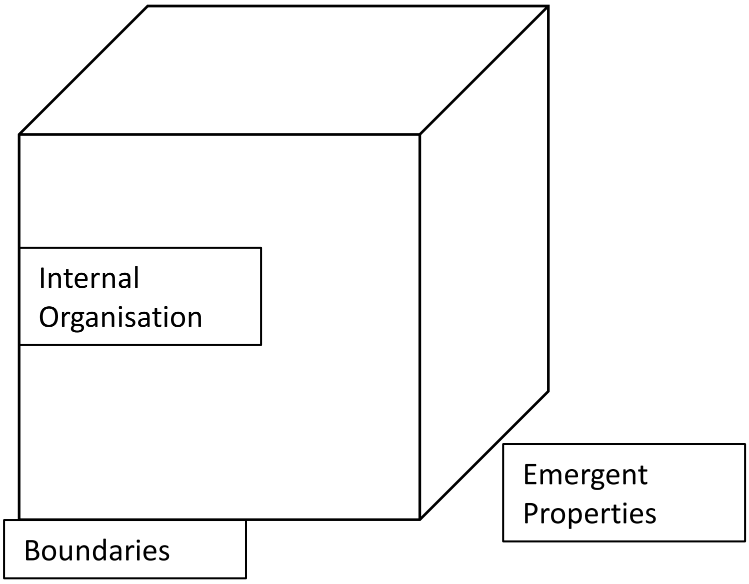

Figure 4.1. Sterelny's (2006) Multidimensional Representation of an Ecological Individual.

To establish that ecological systems lack the same boundaries and internal structure of biological individuals consider how we can identify the boundaries and composition of objects generally (Wimsatt 2007, Chapter 3). Simple objects like a granite pebble have quite neat boundaries; there is strong causal discontinuity between the pebble interior and exterior. This allows for the unit to act as a whole i.e. when thrown the pebble acts as a single unit, uniformly going in a direction. The various structural and dispositional properties are neatly congruent within the pebble. Properties like tensile strength, electrical conductivity, or crystal structure are all co-located throughout its structure. This is due to there being a fairly simple compositional structure.

Compare this with paradigmatic biological individuals. Researching these biological objects requires different theoretical perspectives, or ways of representing the system. These aid in identifying the differing sets of dispositions a system possesses. These are discovered by intervening on the system's different structures with different techniques. Think of the difference between the way a developmental biologist and physical biologist enquire into an Arabidopsis. One maps out the sequential developmental pathways that lead to the growth of cells and the other the way that, for instance, the plant surfaces reflect and capture light. These two scientists will have very different spatial maps of the distribution of properties relevant to their enquiry into that organism, and its sub-organismal components.

The fact that the two theoretical perspectives have different spatial maps of the plant's relevant properties indicates that the plant is a complex system. In the case of the Arabidopsis, despite the different perspectives used to understand the plant, all accounts roughly agree on the *overall boundaries* of the organism itself. This shows despite the various subparts of the system being non-congruent, including its differentiated cells and appendages; the plant as a whole is robust. There is a causal cohesion that holds the entire Arabidopsis structure together (the same for the granite pebble). This is what I contend is lacking in ecological communities. Different points of enquiry into the properties of ecological communities will not yield congruent structures of the overall system. Instead, they yield different networks of causal interaction between populations, which are very sensitive to our initial description of the community, and boundaries, to the extent they are sharp at all, will not be co-located.

4.3.1. Non-Robust Communities.

The lack of robust boundaries in ecological systems is revealed by the differing causal profiles of co-located populations. In the Kosciuszko National Park, the distribution and abundance of Mountain Pygmy Possums is causally determined by its predators, Foxes, and prey, Bogong Moths. While the Northern Corroboree Frog population is strongly determined by negative interactions with niche constructing hoofed animals. Despite being apparently part of the same local community, the causal profiles of what populations are relevant to them will be quite different. Each population will belong to an ecological system consisting of just those populations and physical features to which they are counterfactually sensitive.

Borrowing from Bill Wimsatt's description of complex systems I argue that an ecological community is an individual when it is *descriptively robust*; if multiple different streams of evidence describe a congruent structure (Wimsatt 2007). If we claim that a local assemblage of populations belong to the same individual then those populations should map into a single ecological system and describe the same patterns of causal relationships between populations. The discordance between descriptions of ecological systems can be seen in both the spatial discordance between population ranges and the causal discordance.

If populations have causal interaction profiles, which describe the same ecological community with congruent boundaries and the same sub-parts, then we have discovered a descriptively robust individual. The problem is that co-located populations often belong to radically different ecological systems. This is because causal relations in ecology are often asymmetrical and population distributions rarely spatially coincide. Evidence of the spatial discordance of different populations has been developed since the 1950's with Robert Whittaker's "gradient analyses" being the first step towards rejecting the idea that ecological communities are comprised of neatly congruent populations (Whittaker 1967). Whittaker graphed the abundance of different populations along abiotic gradients finding that populations occupy separate unique ranges rather than clustering into discrete communities.

Since then, Whittaker's findings have been heavily contested, with some going as far as to say that his data supports the opposite conclusion (Wilson et al. 2004). But considerably more evidence has emerged, particularly through biogeographic research, showing the lack of spatial congruence between populations. Margaret Davis' "paleoecological analysis" shows populations historically moved independently with climate change across North America (Davis 1981). Similarly, Paul Colinvaux has spent a large portion of his 50 year career showing how populations independently move across a landscape, particularly turning his eye towards the movement of populations through the Amazon rainforest after the thawing of the ice age (Colinvaux 2007). Ecologist Dan Simberloff famously declared that ecological communities were not real in the way that species are real, as populations have continuous distributions over their ranges and species boundaries do not coincide. When these conditions are violated, he claims it is due to discontinuity in the abiotic environment (Simberloff 1982). With the increasing availability of biogeographic data, the independent nature of population range is something that we can check ourselves. The maps of organism distributions given by Global Information Systems (GIS) show that populations rarely spatially coincide (as shown in the previous chapter)[50].

One could wonder "why worry about spatial relations?", thinking that causal relations are what determine whether these communities form cohesive units. But not only do causal relations determine spatial relations but also spatial relations can determine the strength and structure of causal relationships. It should come as no surprise that organisms often need to be co-present to interact! Consider the factors relevant to a population of Spotted Quolls compared to their occasional prey, Greater Gliders. Individual Quolls roam over home ranges up to 3500 hectares moving between habitat fragments via wildlife corridors, while a Glider's home range is only 2 hectares and is locked within a local habitat fragment. Unless there is a very strong counterfactual dependence between these two populations the network of populations relevant to the Quolls will be radically different to the Gliders, as Quolls interact with populations that intersect with their large home ranges. Further, due to the radically different ranges and population densities there is a strong asymmetry between these populations. Differential changes in a local Glider population are unlikely to affect the Quoll population; because the Quoll's range would include several Glider populations as well as other prey since they are generalist predators. However, differential changes that increase the Quoll population would influence the Glider population as increased predation can have large impacts on small local populations. This creates an asymmetry; intervention on Gliders has little impact on Quolls but intervention on Quolls significantly influences Gliders.

Ecological systems are not causally cohesive, as change in one population will often not influence other local populations in a consistent way. This is because populations in a community often have weak, asymmetrical, and intransitive causal relations. As a result, local ecological populations rarely form *equivalence relations* in which the populations that form a community are

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[50] See for example the Atlas of Living Australia (http://www.ala.org.au/) for spatial distributions of populations across the continent.

reflexive, symmetrical, and transitive with respect to their causal influence on each other (Godfrey-Smith 2008). Equivalence relations are used by Godfrey-Smith to establish a necessary condition for whether a population has a group fitness above its individual members. In the case of ecology, a community is a population of populations. If the network of populations possesses equivalence relations, they will causally influence each other in such a way that their ongoing survival will be dependent on each other. This is what I interpret as causal cohesion, where differences in survivability in one part of the system affects the survivability of the other parts of the system.

The populations in communities are not strongly dependent on each other for survival as they do not have reflexive, symmetrical, and transitive casual relationships. Asymmetrical causal relations in ecology are called commensalist (0,+), where one population has a positive effect on the other but the other has no effect, and amensalist (0,-), with one population having a negative effect on the other but the other having no effect. Classic cases of commensalism are clown fish and anemones, the clown fish hide in the poisonous anemones, gain protection, to no reciprocal effect on the anemone. Examples of amensalist relationships include pine tree excluding grasses through the release of chemicals, which inhibit other plant growth. Grasses are not tall enough to compete with the pine tree, so they have no reciprocal effect. These asymmetrical relations can influence food web stability (Mougi 2016). So, we know that they are significant for community structure. Intransitive relationships between populations have also been found in ecological communities (Kerr et al. 2002; Soliveres et al. 2018). These common causal relationships make ecological systems lack equivalence relations.

Causal networks that do not possess equivalence relations do not form strongly bound groups, which respond in unified ways. When there are equivalence relations, a causal factor influencing a sub-part of the network will influence other parts of the network. For it to be a strongly bound individual, a large causal influence on a sub-part of the individual will influence the entire system to some perceptible degree. In ecological systems, if we influence one population within the system, this causal influence should disperse through the system to influence other populations. If we remove a population, in an ecological individual, there will be an effect on the larger community. Alternatively, if the relationships between populations are generally weak and lack symmetrical, reflexive, and transitive dependencies, they will not affect each other. The extent to which causal influence reverberates through the system will come in degrees; this is what makes individuality of this kind such a graded notion.

Populations in an area often have weak, asymmetrical, and intransitive causal relation and non-congruent boundaries. Given there is no ecological community to identify a priori, we need to study these causal and spatial relations identify the type of causal system present. For there to be a distinct and robust ecological community a set of populations will have to act as a casually cohesive unit. In order to identify whether populations are part of the same causally cohesive unit we would intervene and see whether the other populations are also affected and vice versa. But when there are asymmetrical relations between populations and non-congruent boundaries populations do not from casually cohesive units, and so different causal communities appear given different starting points. Figure 4.2 provides a simple display of the variation in the system boundaries that can be created by tracking the causal impact of intervention in different populations. If there is no distinct causally cohesive unit, ecological boundaries are deeply dependent on the particular populations we are interested in, the populations that we causally start with. This idea that ecological boundaries are relative to populations of interest is not new, it previously been similarly defended by Steven Peck (2009) who states that we *must 'recognize that (ecological) borders are always relative to species or groups of them'* (p. 275).

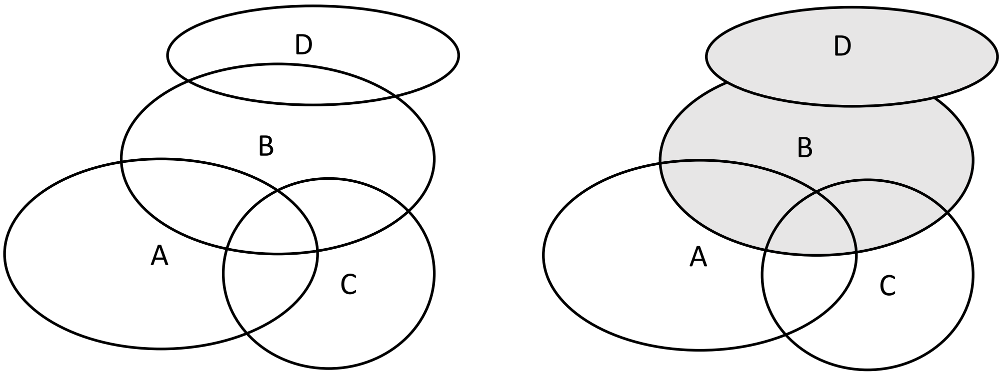

Figure 4.2. Asymmetry and Congruence. Each circle represents a population and its spatial range. These population have a causal structure of D → B → A, C→A. If we identify the relevant causal community of population A all the populations will be part of causally relevant community. If we want to find the relevant community for population B it will include just the shaded area.

So, population boundaries radically differ and the causal relations between populations are often asymmetrical and intransitive. When both these conditions are met, congruent boundaries are rare, and identifying the population network, and the space that network occupies, will be highly dependent on the initial choice of referent. Varying the starting population will yield radically different descriptions of the ecological community. There is useful theory that can be built out of the complex spatial and causal structure of populations, but this is substantively different than our theories about the actions of individuals. These have clear boundaries and their parts are cohesive and correlated over time. The individuals of ecology are lower-level entities, the organisms and populations that comprise the "community". These are the entities that instantiate biodiversity and demand our consideration in conservation (Chapter 2). This is core of my ground up ecological ethics, starting from the populations that constitute biodiversity and identifying the relevant counterfactuals for their preservation.

4.3.2. Robust Explanation in Non-Robust Systems.

The lack of ecological community boundaries could be taken to indicate that we need to adopt a Gleasonian view of ecology and reduce all ecological explanation to the components of these systems, the populations and their abiotic environment (Gleason 1926). I resist this strong reduction. There are ways in which complex systems, which do not display the cohesion of individuals, can still require higher-level, aggregation or compositional, explanation. Generally, in ecology these explanations are more aggregation then compositional as I will explain below. This is still emergent phenomena in ecology that needs to be explained in the ecological systems we commonly interact with. These local ecological communities are called phenomenological communities by Sterelny (2006) and they are the local identifiable habitat patches that humans often interact with, such as a forest or wetland.

Phenomenological communities appear to have clusters of stably interacting populations or consistent abiotic outputs that need to be explained. Such outputs are often not just the simple aggregation of component populations' actions. Diverse local species assemblages can have non-linear ecosystem outputs. Combinations of populations non-additively result in explosive combustion in forest fires or retain water in the understory (Michel et al. 2012; Van Altena et al. 2012). Further, the statistical aggregation of the actions of local populations can have system-level effects like stabilizing ecological output by statistical averaging effects, biological insurance, and sampling effects (Sterelny 2005; Bryant 2012). Community- level properties as a result appear to be ubiquitous in ecological systems even if there are no clear boundaries for these systems and the internal composition is unstable. I describe two types of explanatory robustness that can help sort through the heterogeneous structure of ecological assemblages to find the parts of these loose systems that contribute to these system-level features.

Ecological communities are particularly difficult to explain, as they are extremely heterogenous systems (Matthewson 2011). They are heterogeneous systems in that they are composed of many different populations, which strongly vary phenotypically between each other and to a lesser extent internally. Each component population of an ecological community can act differently, a brush-tail possum population acts differently than a magpie population, and these populations can vary in composition and density area to area. Heterogeneous features of the populations and varying community composition allows for many-to-many causal relations. Within any area we find populations interacting, even if often only weakly, with many other populations. For us to explain the action of such systems we need a way of sorting through this heterogeneous composition to identify the parts which contribute to an emergent property of the system or an output of the overall system.

We can explain the system-level properties of these heterogeneous systems by machine robustness and ensemble robustness. *Machine robustness* is when we explain the outputs of a system through describing a causal chain of parts in the system that sequentially cause changes in each other, bringing about this output (Levy 2014). Each of the parts that play a role in bringing about this output are stable, both in their properties and relative location, are persistent in the system, and are unlikely to be perturbed. Because of the stability and persistence of relevant system parts the outputs of the system are robust. Complex systems made of heterogeneous parts can be explained by machine robustness. Think of an Airbus A380; the parts of the plane are quite varied and the output of staying in the air is, fortunately, quite robust as by and large each individual part of the plane is persistent and stable in its effect and location (Elliott-Graves 2016)[51]. When niche construction is not strong, abiotic factors and physical features will act like this. For example, geological structures and relief will stably contribute to communities in this way

Alternatively, we can explain the output of compositionally complex systems by *ensemble robustness*. Ensemble robustness is when we have many different causal actors that can fill the same functional role in the system bringing about a certain system-level property or output. These types of explanation often feature over-determination in that if one sub-part of the system did not bring about

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[51] A reviewer notes this is not quite right as these parts can be replaced and often are. We replace fuel, pilots, and parts. This is true. Primarily I was considering how the plane acts to bring about the output of flight and maintaining flight. Generally, but not without exception, the parts of the A380 are not replaceable mid-flight so I think the example still stands.

the system-level feature then another would. Ensemble robustness occurs when the sub-parts are extremely similar; for example, steam being forced out of the top of a kettle is from the collision of many different water molecules. But ensemble robust outputs do not require the components bringing about the effect to be exactly the same. All that is required is functional similarity, the same effect can be reached by extremely heterogeneous actors. To use an ecological example, Gum trees can be pollinated by extremely taxonomically and anatomically varied populations such as pygmy possums, bees, ants, and honeyeaters (birds). The phenomena described by the stability-diversity hypothesis is best explained through ensemble robustness.

Ecology aims to explain how populations and their interactions result in system level properties like diversity, stability, or ecological services, e.g. water retention and biomass production. Local determinism supposes that stable relationships between persistent populations produce these properties, stable internal structure produces system-level properties. Explanations of this type are *machine robust*: the system-level property is a result of a particular causal sequence of interactions between persistent parts. Systems, which are organised in this manner, and display complex behaviour are required to be modular. For highly persistent and stable parts to act in multiple ways there needs to be some way of introducing structural manipulability, and modularity is the common way this is done. For example, the composition of a brick is stable and persistent, but there are not too many complex actions a brick can do. The Airbus A380 also has stable parts in persistent relationships but there are degrees of freedom introduced into the actions the plane. This is achieved using modular structures like the wing flaps, which can move up and down on their hinges. Modularity creates boundaries in systems, and if ecological communities are to be bounded, we would expect modular machine robust structures.

The assumption of persistent stable relationships in ecological communities is problematic, as populations are often highly transient. As noted in the previous chapter, populations regularly disappear from local ecosystems without radical change in regional diversity leading to the conclusion that populations simply shift their distribution across the larger landscape (Thuiller et al. 2007; Dornelas et al. 2014). These studies add further evidence for those who believe that local ecological communities are often the wrong scale for law-like generalities in ecology (Ricklefs 2008; Lean & Sterelny 2016). They claim that regional patterns better explain the local distribution and abundance of organisms than local patterns which are ephemeral and stochastic. These views explicitly reject the idea that local community identity is primarily maintained by internal composition.

Despite the highly aggregational quality of ecological systems, ecological community properties are not uniformly a product of ensemble robustness; specific populations are sometimes necessary for ecological output. Keystone species, which have disproportionate impacts on assemblage composition, function like mechanisms with particular populations playing a necessary and causally specific role in maintaining whole system features. The importance of keystone species is controversial, with some ecologists pressing that there are not such strong relationships between single populations and assemblage features (Mills et al. 1993). But there is strong evidence that in some systems particular populations do play strong roles in regulating a cluster of populations in their assemblage (Ripple et al. 2001). Classic cases of this are the strong top down effect of apex predators supressing meso-predators and herbivore populations, permitting diversity lower in the food chain. We see evidence of this in cases like the re-introduction of wolves in Yellowstone National Park and Dingoes suppressing feral cat populations in Australia. Predators may cause a local system's species diversity to be more deterministic as they can police the identity of the local composition leading to local systems with apex predators to be more similar to one another as compared to predator-less systems, whose species composition will be more subject to stochastic processes (Chase et al. 2009).

Getting the compositional structure of ecological communities right is critical for conservation science. In cases like above, where keystone species like apex predators control composition we will want to prioritise the preservation of these species. But as noted in the last chapter, local compositions are not always locally governed, and that is especially true of apex predators and other high impact species, with their large individual range sizes. We may need to priortise a network of habitats to allow for the movement of populations between parks. In these cases, instead of prioritising key local species to maintain the populations in a community we may wish to prioritise land in a region. This would preserve biodiversity regionally rather than the biodiversity held in a local ecological system. This coheres with my aim to take conservation away from focusing on the local ecological community and turning our focus towards more globally critical features of conservation particularly biodiversity.

But sometimes local features are the direct target of conservation, particularly the direct ecosystem services local communities provide people. The Biodiversity-Ecosystem Services hypothesis proposes that compositions high in biodiversity support higher-level features of ecological communities that humans find desirable (Mace et al. 2012). The route by which biodiverse assemblages produce such goods is often difficult to represent. By breaking down the different causal structures in ecological communities that bring about ecosystem outputs, I provide a way for connecting biodiversity as I have outlined in Chapter 2 with ecosystem services.

We should think of local ecological communities as highly unsystematic systems, they lack clear boundaries and persistent internal identity, but they do have robust *parts* and robust *system outputs* via the variant aggregative interactions of their constituents. Most ecological systems will sit somewhere between the extremes of machine robustness and ensemble robustness. Some will be not robust at all. Both forms of robustness come in degrees. We can ask, how much redundancy is in the system? How similar are the parts that achieve a robust effect? And how persistent are these parts?

Any account of ecological community identity needs to be able to identify explanatorily important properties and identify the components of the system that produce these properties. This is difficult as population networks will not in general be congruent over different choices of starting population as small changes in initial focal population can result in quite a different network. But ecological communities are still causal systems. Indexical communities describe communities via the network of causal interactions between populations and provide a way to represent their causal structure. This methodology aims to do the diversity of ecological causal structure credit and identify the salient features for explanation.

4.4. Indexical Communities.

On first pass of the philosophy of ecology literature, accounts of ecological communities appear to split between treating populations as largely independent of each other and describing them within an individuality framework. There are, however, other options which sit between these extremes, with Sterelny proposing “indexical communities” in contrast to ecological individuality (Sterelny 2006). My following account of ecological communities’ supplements and develops indexical communities as described by Sterelny.

4.4.1. Simple Indexical Communities.

Simple indexical communities are ecological units which aim to describe the conditions that affect the demographics of single populations. Indexically described communities are one of the most useful and utilized ecological techniques in conservation science. To preserve the critically endangered Hairy Nosed Wombat we need to know how much native grasses and tubers they eat, what is an unusual parasite load, how to separate them from wild dog populations, and competing grazers. These populations are indexed to the Wombat population as they have a causal impact on them. This framework has become commonplace, due in part, to conservation funding being directed to individual species preservation. This is due to government funding entering conservation from Endangered Species Act legislation and Non-Government Funding being raised by appealing to the public’s love of charismatic megafauna such as Blue Whales, Giant Pandas, and Bald Eagles. Conservation science as a result often aims to find the conditions that lead to the preservation of a focal population.

These simple indexical communities are not thought to be very informative for community level properties as they are constructed with limited epistemic aims, i.e. explaining the influences on a single population. Due to the limited scope of such causal units they remain silent on certain, hopefully generalizable, community level features such as the relationship between diversity and stability (Sterelny 2006). Further, it is thought information about one indexical community is difficult to apply to other assemblages due to the apparent limited nature of their scope and their heterogeneity. We can rectify these problems by building into indexical communities the means for identifying machine robustness and ensemble robustness when they are present.

This is done by intervening (sensu Woodward 2005) on communities, starting with multiple different populations of interest to identify robust community features. The aim is to find what community-level properties the populations contribute to, be these community outputs, boundaries, or causal networks. By intervening on different populations, treating them as nodes in a causal network, we can identify which relations in an assemblage are either highly central, acting as a causal hub, or have strong causal effects. Once we identify which causal relations are relevant we map where these causal actors are distributed geographically, which is the information needed to identify the spatial boundaries of the community. The innovation here is that by using multiple starting points we can build in robustness, if and when it exists, and avoid the explanatory fragility of indexical communities built around a single population. Section 4.4.2 will describe the procedure for describing an indexical community built from a starting set of populations. Section 4.4.3 provides a guide for what populations can or should be used for this starting set.

4.4.2. The Procedure for Describing Indexical Communities.

The stepwise procedure for identifying the relevant ecological community appears in Box 4.1, but here also is a description of the process. Take the starting set of populations and identify the indexical community for each individual population in the set (starting sets are discussed in 4.3). The indexical community for a population is identified by intervention, in which we systematically change the variable representing the population. These interventions can of course take many shapes including removing populations or reducing or increasing a populations spatial range or altering their accessibility to other populations but for the purposes of this paper I will use the example of interventions being used to alter population numbers. To identify the indexical community of the focal population variable, A, we intervene on populations suspected to be causally efficacious for A. An alternative population, B, is said to be part of the same community as A, as well as a cause of A, if systematic intervention on B brings about change in A. So, if we shoot some feral cats in an area it will impact the bilby population positively due to the causal relevance of the cat population to the bilby population. These causal relations will be “causal

Box.4.1. Indexical Communities can be built up from multiple indexical populations by the following procedure.

i. Define the starting set of populations and/ or a system-level property (e.g. ecosystem output) that the causal relations are to be indexed to.
    a. If system-level property then identify the set of populations that contribute to the property.
ii. Identify the populations that are causally salient for the set of populations via intervention.
iii. Overlay the different networks of counterfactual dependencies from the specific populations.
iv. If multiple interventions pick out the same connection these are the robust relationships in a community.

influence" relations as there are continuous values the exogenous population variable, the cats in the above case, can take and this allows for modulation of the response variable[52].

Once we identify that a population variable, say B, has causal influence on the focal population, A, we can ask whether intervention on populations that affect B also have "downstream" effects on A. If so, then that population is also part of the indexical community of A. For example, if population C causally influences B to the extent that the variable change it yields in B causally effects A then C is part of A's indexical community. So, if in a region dingoes supress cats, and cats supress rats, more dingoes will mean more rats. Each population node introduced between the focal population and a population of interest will necessarily reduce the counterfactual relationship between them.

This process yields a directed graphical map of the causal network indexed to population A. We repeat this procedure for all the populations in the starting set. The different causal maps built from each population in the starting set are then compared. All the populations that causally contribute to a starting population are counted as part of the community, to extent of some predetermined threshold. The scope of the boundaries of these maps can be tweaked by varying the strength of the causal effect required for inclusion (Levins & Lewontin, 1985). By setting this parameter moderately high we avoid ecological holism, where each indexical community has numerous nodes and as a result each indexical community will overlap with each other.

Actual intervention will sometimes be problematic, it is often difficult or downright dangerous to reduce or increase population size. Further, it can be difficult to get accurate records of the changes in population size. Interventionist theories of causation have long been troubled by the problem of "actual" intervention; for example, if we are not willing or able to intervene on the moon can we know it causes the tides? (Woodward 2016) In the ecological case, natural experiments can be used to infer and model casual relations, as populations repeatedly move in and out of areas as they

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[52] An exogenous variable is a variable in a causal model or system whose value is independent of the other variables in the system.

cycle a larger geographic region (see Section 3.3). Humans repeatedly intervene on communities by reducing populations or introducing invasive species in fairly systematic ways. More scientific interventions are preferable with Robert Paine providing an early archetype; he made repeat interventions to identify the "interaction strength" of populations in an intertidal rock pool (Paine 1992). As such, practical limitations make data collection difficult but not impossible.

Once we have directed causal maps, from the different populations, in the starting set we can compare their causal structure. The comparison of causal maps is made in two ways. The first is identifying whether populations, the nodes of these maps, sit within the same causal relations in strength and direction. This can identify stable causal clusters of populations, which act cohesively. Population network structures that appear in the directed graphs from multiple different indexed populations are robust in Woodward's sense. For something to be robust according to Woodward (2005), a wide range of initial conditions will identify the same event. So different causal factors and values of variables will result in the same event. In indexical communities, the event is a particular causal relationship between populations, by varying the local populations we intervene on, we vary the initial conditions of the system. Robustly connected populations are ecologically important, often acting as keystone species, and playing a role in maintaining the population network structure.

Another way of displaying the indexical community is mapping the populations that causally contribute spatially. This process allows for a visual depiction of the actual physical space that the causal processes of the community acts over; it acts as an anatomy of the ecological community. By mapping the spatial arrangement of populations that causally contribute, we can also see if the community is robust in Wimsatt's sense (Wimsatt 2007). A community is robust according to Wimsatt's view if multiple different "theoretical perspectives" identify the object that is spatially congruent. By varying the populations that we are interested in, we vary the perspective we enquire into the system with. If the different causal systems identified from different populations occupy the same space they are robust in Wimsatt's sense.

While these indexical communities are not distinct individuals or kinds in any rich sense, each can be used to explain the production of ecological features we find of explanatory and conservation interest. We rid ecology of the need to resemble organismal biology to be worthy science, while still retaining its explanatory aims. As such, I provide a way of moving forward for conservation in a way that does not connect conservation to metaphysically suspect ecological communities. Instead, I have provided a bridge directly from populations, and their causal composition, to the features ecological systems were posited to explain. This is a great step forward as populations, and the biodiversity they constitute, are bearers of normative worth that all prudential agents should desire to preserve.

4.4.3. The Starting Set.

So, what determines the starting set of populations? This is in part researcher interest defined, but there are some obvious candidates described below. Having the initial scope of systems determined by research interest better represents the practice of scientists and the differing intuitions around ecological communities. While many scientists and the public are interested in ecological communities, they clearly differ in what they are referring to. This account of communities has the flexibility to make precise the many different notions of community at play in these different discourses. Here are some different notions of ecological communities that can be described though varying the starting set. For the purposes of this thesis, the most critical of these is the communities that are identified as indexed to the populations that constitute higher quantities of biodiversity.

Biodiverse Communities: Often communities are conserved by protecting populations indexically relevant to some charismatic fauna. I have defended an alternative vision of conservation, one which focuses on sets of species which constitute high quantities of biodiversity. By identifying these populations through biodiversity measurement, we can then use this indexical community framework to identify the ecological community, which causally supports these populations. This causal structure is critical to minimize biodiversity loss from secondary extinctions (Dunne & Williams 2009). Alternatively, we can look at how this set of biodiverse species supports other populations. This could aid in the assessment of hypotheses concerning the effect of local biodiversity on ecological assemblages, such as whether higher quantities of biodiversity promote assemblage biomass production or services. We have a tool, which can both preserve and critically appraise biodiversity under the measurement procedure I propose (Chapter 2) or any other measurement procedure under consideration.

Local Ecological Communities: If we wish to determine whether a local assemblage is a unified and integrated community we would look at the indexical community built around a set of local populations. By identifying the network of populations that emanate out of co-habiting populations, we can see to what extent this local ecological community is a causally cohesive unit. This also acts to identify the ecological bounds of otherwise arbitrary units. National Parks are usually bound by geographically arbitrary borders and we may be interested in locating the causal boundaries of the ecological assemblage that inhabits this space. If we are interested in the ecological boundaries of the assemblages inhabiting a region of the Namadgi National Park, we take a census of the local populations in that region and map out the causal structure that they are related to. Often practical conservation goals are of these somewhat arbitrary entities and our theory should be able to account for them. And this might guide appropriate interventions, if we identify high value populations; or machine robustness; or potential wildlife corridors and drought refuge areas.

Community-Level Properties: Alternatively, we can look at community-level properties or outputs by starting with the set of populations that are thought to contribute to this community-level feature. Often this is a particular output of the ecological community such as water filtration around a lake. Man-made lakes produced by damming have ecological systems maintained around their border for this role. The Warragamba Dam supplies Sydney’s water and the Yerranderie State Conservation Area protects this water supply from contamination. If we wish to identify the relevant populations in the Yerranderie State Conservation Area to maintaining this “ecosystem service” we identify the populations which affect this output and the populations relevant to the maintenance of those populations. Other higher-level properties can similarly be assessed. For instance, individual populations can have disproportionate impacts on species diversity, maintaining many populations through critical services. By varying the populations in indexical communities, we can see who contributes to this higher-level feature.

Phenomenological Communities: People experience ecological communities as hikers, birders, hunters, and as participants within these systems. Environmentalists and the public often have an interest in preserving assemblages that are familiar from their experience of the wild. Phenomenological Communities are the mid-sized ecological objects that people think of when they are asked if we should preserve ecosystems. But these entities are referentially underdetermined, people struggle to describe the particular features of this system in a precise way or give an account of their extent past arbitrary boundaries. We can clarify the description of phenomenological communities though using indexical communities. Typically, phenomenological communities are described though reference to assemblages, including charismatic mammals, audible bird-life, visually stimulating angiosperms, and imposing trees. To fix the reference of such local assemblages we include in the starting set the phenomenologically prominent populations in a local area. For example, if you want to find the community of a Blue Gum forest you include Blue Gums, lyrebirds, and Waratahs, and identify the populations relevant to them. By then building in the populations that maintain the experientially salient aspects of wildlife we can identify the condition for preserving the environment the public immediately desires. This directly speaks to the practice of conserving ecological communities described by legislation. The “Blakely’s Red Gum Grassy Woodland” is a legally protected endangered community[53]. This community is identified by a list of tree species and understory plants that are “commonly associated” with the community. Indexical communities are able to represent this unique assemblage and the way that the law describes it, indexed to set of populations.

These are just some different ways we can build a starting set for an indexical community. In the picture of environmental ethics presented in this thesis all the above reasons can and should

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[53] http://www.environment.gov.au/epbc/publications/white-box-yellow-box-blakelys-red-gum-grassy-woodlands-and-derived-native-grasslands

contribute to a starting set of species. Local stakeholders will direct conservation towards the species that comprise phenomenological communities and contribute to ecosystem services. Populations which constitute biodiversity then can be added to this set to account for features of global relevance that would otherwise be unaccounted for. Once we have this starting set we can identify the populations that contribute to this community, and then preserve a community which represents both current interests in the environment and possible future interests. This will aid in the preservation of a new community, but we may want to know the causal structure of an already protected area. This is when we index the community to the populations in a local area and identify what populations in the region impact on this focal area.

There are multiple reasons for describing different starting sets for indexical communities. By allowing the starting set to be determined by the interested parties we are able to tailor the indexical community to fulfil both the epistemic and normative roles that community ecology and conservation science requires. This is a significant step forward; ecological communities as they are described by ecological sciences and the public appear to diverge but the presented conceptual system allows for us both to describe their differences and unify them in a single explanatory system. The indexical community framework is flexible but when combined with my theory of biodiversity and buttressed by my account of ecological function, described in the next chapter, to solves ecological problems like whether we should control an invasive species or whether we should de-extinct a population.

4.5. Assessing Indexical Communities.

Built into the indexical community methodology is the means of assessing an ecological community in several ways. First, for the ontological question of whether communities are real, indexical communities provides an answer. It is only when the same causal structure appears from multiple starts and has robust boundaries that we have a robust ecological community. It is, however, more likely that we will find that we have only partial overlap between the causal maps. This acts to identify the descriptively robustly sub-systems within the community. As a result, this framework provides a fine-grained way to identify the extent to which a particular local ecological community is a system that acts like an individual, like an organism, or an aggregate, like gas particles heating in a beaker. If there are no causal connections between the starting populations then this is not a unitary community. So, this approach acts not just as a descriptive tool but also as an existence test. Depending on referent choice, there can be multiple precisifications of a unitary community or none.

The robustness of the causal structure of populations allows for us to explain how system-level properties are produced. It provides a bridge between the study of single populations and the resilient generalizations in community ecology catalogued by Linquist et al. (2016). To explain how the assemblage produces a particular system-level property, be it the resilience of community composition or a community output like fire likelihood, we need to identify which counterfactual interventions affect that system-level property. Multiple interventions on the system from different indexed populations identifies the features that affect the system-level property. The primary question is whether system-level property invariance is a product of population network structure invariance or compositional invariance. Or to say it in another way, are these features machine robust or ensemble robust?

Machine robust parts of ecological networks are descriptively robust with multiple starting points identifying the causal structure between particular populations of a fixed identity. But weak aggregational interactions are extremely common in producing system-level phenomena through numerous causal relations of modest strength. The actual causal actors involved in producing these phenomena can be hard to identify, as many different parts could be contributing to a system-level property. To understand the relationship between aggregational systems and system-level properties we need to fix the identity of the system in question. Indexical communities provide a precise way to refer to such weak “systems” and in doing so provide a guide for further research into the relations between populations and system-level properties.

Some ecological assemblages may not feature any robust causal relations or outputs. In these cases, they will not be machine or ensemble robust. These systems are better explained at the level of populations, with little reference to their local neighbours. Ecological communities, when they do not have any robust features, are not vindicated as units worthy of investigation in themselves. Instead we are better off studying autoecology, the dynamics of individual populations. These cases make conservation much more population focused, we simply need to observe the populations we wish to preserve and their needs. The overall structure of the community then has little impact on our conservation goals and we can simply concentrate on the populations that are directly desirable.

Finally, the representation of ecological communities with this causal network structure has further advantages. By describing communities using a causal graph network description, we open them up to a range of formal methods of assessment. Robust networks of populations form modules or modular network structures. Strongly co-varying clusters of populations make a system more bounded and can account for particular system outputs. Formal methods familiar to the social sciences like the Girvan-Newman algorithm can quantify such structures identifying modular groupings and boundaries in complex systems (Girvan & Newman 2002). But there are also rich tools available for describing the causal structure of ecological communities within the ecological sciences, particularly from food web theory and mutualism networks. Peter Morin's (2011) introduction to food web theory (Chapter 6) provides a wealth of these formal tools with measures for a system's connectance, linkage density, and compartmentalization[54].

This is all to say indexical ecological communities open modes and opportunities for assessing communities, which are not available to biological individuals. I do not claim that no assemblages ever will be a biological individual. But I predict that these cases will be rare. The majority of communities will not be individuals, but these are still entities that play central roles in ecology and conservation. We need a way to discuss and enquire into these ecological systems in a way that does not treat individuality as the natural end point of all complex biological interactions. There is more to biology than just the study of individuals and this proposal gives an alternative framework to describe such complex biological systems. Critically, it is all we need to bridge the

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[54] Thanks to Jay Odenbaugh for this suggestion.

connection between populations and the ecosystem properties we independently desire for conservation.

Chapter 5. Invasive Species and Natural Function in Ecology

‘Your heart has great value to your body. No one would argue that point. Does a mosquito population have similar value to a marsh?’

John Kricher, The Balance of Nature: Ecology’s Enduring Myth, p .19

5.1. Introduction

There has been a persistent hope that ecological systems have natural normativity, in the same way that talk of function and malfunction has a natural and relatively uncontroversial interpretation when talking of organs and organ systems in a body. The hope is that ecological systems are structured so that their parts are functional for the whole, which can support a type of natural value. This same natural value would allow us to say; just as the heart is valuable to the body, the mosquito is valuable to the marsh. This natural normativity would facilitate objective judgements about the role of populations in an ecosystem, whether they are functional or malfunction. There is a strong analogy between these claims and the concepts of health and disease. The existence of malfunction is plausibly part of what it is to be diseased, and whether someone has a disease it is normatively relevant to how we should treat them (Griffiths & Matthewson 2016). So, the thought is, if there is an objective sense in which populations, like invasive species, cause ecosystem to act in a malfunctional or in a diseased manner it is normatively relevant to how we should respond.

The attempt to ground environmental ethics in natural normativity makes sense. Morality as a mode of thought is rarely directed towards entities other than humans. When it is not directed towards humans, it is directed towards other sentient animals. When conservation was described as a moral problem, it was natural to look for teleology in ecological systems. Teleology is a component of proto-normative properties like health, integrity, interests, or welfare. These properties all describe systems in a broadly goal directed manner. These proto-normative properties have been used through the history of environmental ethics to justify humanities ethical consideration of ecosystems (Leopold

1949; Rolston III 1975; Callicott 1984; McShane 2004; Basl 2017). The most credible way to explain teleology within a naturalistic framework is through invoking natural function (Wright 1973; Millikan 1984).

Natural function is implicit through this literature and occasionally explicit. Holmes Rolston III (1988) argues that both organisms and ecosystems are "spontaneous cybernetic system, self-maintaining with a control center, sustaining and reproducing itself on the basis of information" with "a goal" which could provide a "measure of success" (p. 98). This is taken by Rolston III to indicate these systems have their own "evaluative system" allows them to be self-valuers and hubs of self-authored value (Rolston III 1988, p. 99). J. Baird Callicott (1995) claims that ecosystems are "nested sets of linked process-functions with temporal boundaries" and, therefore, health "is an objective condition of ecosystems" (p. 345) The connection between natural function, welfare, and environmental ethics is explored in the recent work of John Basl (2019). He sceptically develops and debates the biocentrist position in environmental ethics, which argues biological systems have welfare due to their functional organisation (Taylor 1986). The connection between ecological function and ethics has been persistent throughout the history of environmental ethics.

To establish that ecological systems deserve ethical consideration due to natural normativity, rather than purely anthropocentric values, the environmental ethicist must do two things. They must establish that ecological systems in fact have natural normativity and then that natural normativity is ethically significant in ecology. Natural function is often of little ethical consequence; even in organisms, which are undoubtable highly functionally organised. We kill other organisms; whether plant, animal, or bacteria; for all sorts of reasons with little ethical squeamishness. Even when it comes to health and disease there are some who argue that there is no connection between health and natural function (Glackin 2010). This may be an insurmountable problem for environmental ethics, but it is not the problem I address in this chapter.

I focus on the prior question, of whether ecological systems are functionally organised, and argue that the search for design or functionality in ecology is misguided. This could be expected as an implication of my previous chapters in which I argue that ecological systems are not biological individuals (Chapter 4) or the sort of systems that we can assess through biodiversity measures (Chapter 3). Biological individuals are usually thought to be functionally organised. In this chapter, I systematically consider the latest theories of normative functions and argue that these only ever have limited application to ecological systems. The conceptual resources I built through my previous chapters are used to make this assessment. Throughout I consider the test case of invasive species and whether natural normativity can be used to make judgements about their role in ecological communities. This would allow for us to objectively state that invasive species harm ecosystems, contributing to the debate over whether we should control invasive species.

My aims in this chapter are then two-fold. First, I wish to provide a critical discussion of theories of ecological function. What are the most promising theories of natural function, which can be fruitfully applied to real ecological systems? This is done with an eye towards problems that have only been superficially addressed in the philosophy of ecology literature; the incredible diversity of ecological arrangements and the diversity of explananda in the ecological sciences. The second question is whether a theory of ecological function can determine whether invasive species are malfunctional for ecosystems. Invasive species form an excellent test case and providing commentary on their functional role is important regardless of the larger project of identifying function in ecological systems.

To address these issues, I will first discuss the problem case of invasive species and the reasons why natural function can help navigate the debate over whether we should eradicate or control these populations. I then commit to the foundational work of describing the main views of natural function, addressing the differences between these theories. These differences matter, as the different theories are applicable to different systems. Once the stage is set, I consider whether these theories of function can do the heavy lifting of describing the non-subjective value of populations. Ultimately, I argue for a limited pluralism towards ecological function. There are natural functions in ecology of several varieties, but these are sporadic and rare. More often than not functional relations are better understood as descriptions of causal structure. Functions in ecology are nearly always dispositional, rather than normative.

5.2. Natural Normativity and Invasion Ecology

"Invasion ecologists are xenophobes" some critics have declared. They argue there is no sound reason to control invasive species or even prefer native species over non-natives. Such preferences are just prejudice, a prejudice not always held by the layperson. For example, one critic notes that crafters in Midwest America prefer the noxious invasive Oriental Bittersweet, as it is better than native species for constructing wreaths and floral arrangements (Sagoff 2005). Locally there is an ongoing debate about presence of brumbies in the Snowy Mountains, with many viewing these invasive horses as a critical part of Australian culture and folklore. The critics of invasion biology point to the language occasionally used against invasive species (usually in the media) and its similarity to language used in anti-immigration arguments. With the implicit assumption being anti-immigration is morally wrong, they accuse invasion biology as being similarly morally suspect. This debate recently moved into the public sphere with the publication of journalist Fred Pearce's widely read *The New Wild: Why Invasive Species Will Be Nature's Salvation* (2015). Invasion ecologists and wildlife managers worldwide are feeling the pinch of increasing public scrutiny.

Why do critics of invasion biology think there is no real reason to control invasive species? Mark Sagoff (2005) puts the challenge that there is no principled distinction between native and non-native and there are no traits, which explain why non-native species could be more "harmful" than natives (p. 219). While there is a question of what unifies and individuates invasive species, I see this as secondary to the question of harm. Once we determine what harms ecological systems, we can see whether it is a good heuristic to prevent the spread and establishment of non-native species.

Concepts of harm often inform how invasive species ecologists think about the issues (Simberloff et al. 2013). The most well-known declaration of the need to rethink invasion ecology was published in the journal *Science* with Mark Davis et al. (2011) stating that *'it is time for conservationists to focus much more on the functions of species, and less on their origins'* (p. 154). Equally, invasion ecologists defend their position by the effects of invasive species on ecological function (Simberloff 2015). The invasive species debate appears to turn on determining the ecological function of these populations. Therefore, we must investigate the current theories of function to identify which theory best applies to ecological systems.

There is a common counter to the suggestion invasives cause harm to ecological function. Critics argue that invasion is not a harm, but rather the creation of new “novel ecosystems” comprising of native and non-native species in their own new functional arrangement (Hobbs et al. 2013). Pearce (2015) particularly focuses on the unique habitat of Ascension Island, a volcanic tropical island halfway between Africa and South America. The island was radically changed by sailors in the 19th century under the instruction of Joseph Hooker, with plants being introduced from all around the colonial world. The varied forest created a new, more rain intensive, microclimate allowing for the other purposively introduced plants to thrive. This is presented as an exemplary novel ecosystem worthy of praise rather than restoration to some past state. Again, functional arrangement is key to the assessment of value.

This act to redefine invaded ecosystems as novel ecosystems serves a second point, an attempt to side-step the issue of invasive species causing local extinction. The most commonly raised concern with invasive species is they cause local extinction, but defenders of invasive species argue that novel ecosystems have more species. If we think that ecosystems are justified for preservation by the fact they contain lots of different species that can provide us services, then we should prefer invaded ecosystems (or so they claim). I argue that once we understand how function can be used in ecology this argument is highly oversold and shows how invasive species can disrupt the functions biodiversity provides. Critics of invasive species science, like Pearce (2015), openly conflate local species count (alpha diversity) with global species counts (beta diversity) to defend the role of invasive species. With a theory of biodiversity, which does not rely on raw species counts, I argue for the preservation of functions that maintain global biodiversity. The effect of invasive species on global biodiversity provides shared reasons to control some invasive species.

5.3. Naturalized Function in the Sciences

There is a rich and comprehensive philosophical literature attempting to naturalize function. It takes teleological statements such as “the heart is *for* pumping blood” and redescribes them to capture the goal directed nature of such statements within a scientific worldview. The goal directed aspect of teleological statements allows for normative inferences; if a heart is not pumping blood then it is doing something wrong, in some sense. The Australian Melaleuca is invasive in the Florida everglades ecosystem as it drains the water and excludes other plants through fire. For the Melaleuca to cause the everglades to be *malfunctional* we need a notion of function that gives us objective malfunction, not just a mirror to our preferences for biological systems. Otherwise, this is simply a causal relation. Some theories of natural function dictate that we can only make statements about whether a functional effect is present or not. We may value the existence of this function or disvalue it, but the normativity involved only comes from us. So, there would be no sense in which the Melaleuca causes a malfunction, it just stopped the causal relations which previously existed in the everglades and we as agents disvalue this.

Before I place all the vying accounts of function on the table, I will dismiss one possibility; that there is a single right account of function for ecology. There has been continuous jockeying for *the* right theory of ecological function to the exclusion of all others following Maclaurin and Sterelny’s 2008 description of causal role community functions (Maclaurin & Sterelny 2008; Nunes-Neto et al. 2014; Dussault & Bouchard 2017). I believe that monistic stance towards function is misguided, in agreement with Peter Godfrey-Smith (1994) and Ron Amundson and George Lauder (1994), but functional monism is particularly misguided in the case of ecological systems[55]. All the

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[55] Often functional pluralism is interpreted as between discipline pluralism, where some accounts of function are appropriate for some research disciplines. The most common view concerning disciplinary pluralism is Selected Effects functions are appropriate for evolutionary biology and Causal Role functions as appropriate for molecular biology. In agreement with Justin Garson (2017b) I think that within discipline pluralism is viable, but I limit the application of SE functions more than he does.

theories discussed (barring one) are applicable to ecological systems due to the diversity in the composition and structure of ecological systems.

This pluralism is necessitated by the fact that our concepts of ecological function do not describe any unified phenomena. These concepts of ecological function appear in two related but separate ecological sciences, ecosystem ecology and community ecology. These sciences have their own traditions of research and focus on different explanada. Functional relations that maintain the biotic character of communities are *community functions*, and functions for the maintenance of abiotic features are *ecosystem functions*. These are not equivalent, as different species often interchangeably fill a role in maintaining a nutrient cycle. A change of species would alter the community composition without altering the ecosystem, as they have not changed the nutrient cycle. This is equally true of invasive species, we can consider the impact they have on ecosystems, the nutrient cycle, and on populations. We may find they effect standing ecological systems in different ways, "enhancing" nutrient cycles but removing local populations. This all leads to an odd situation in which some authors have argued for function monism without recognizing the different ways function has been used within the science.

I explore the major theories of natural function. This is with full knowledge that ecological systems and the explanada that ecological functions have attempted to describe are diverse. I consider three different classes of ecological function: Selected Effects Functions, Causal Roles Functions, and Organizational Functions. Each of these I will provide a brief outline and indicate the manner in which they have been applied to ecology.

5.3.1. Selected Effects Functions.

Selected Effects (SE) functions argue that the function of a trait is whatever that trait was selected for by natural selection. So, to use the canonical example; the function of the heart is to pump blood within an organism, which in turn helps it stay alive and reproduce another organism which has a functioning heart. This theory of function has several different formulations or sub-versions which have been applied to ecological systems, but the original formulations were nearly solely applied to organisms. The SE functions theory was developed concurrently by Karen Neander (1983) and Ruth Millikan (1984), under the name "Proper Function". This is a substantial modification of Larry Wright's Etiological Function (1973), which had suffered from significant counter-examples. Here is Karen Neander's formalisation of SE Function's (1991):

> *'SE Function: It is the/a proper function of an item (X) of an organism (O) to do that which items of X's type did to contribute to the inclusive fitness of O's ancestors, and which caused the genotype, of which X is the phenotypic expression, to be selected by natural selection.'*
>
> *Neander 1991, p. 174*

SE functions use the history of selection to describe functions. The paradigm cases are individuating the sub-systems and their roles in organisms. There are many different causal effects organismal sub-systems can have, the beating heart makes a phump-whump sound, but the history of selection provides a privileged and non-arbitrary means to a) identify and causally individuate these biological systems b) identify their biologically significant causal effects. This allows for the ascription of normativity to traits and the ability to discern between accidental and functional traits. "Accidental", or fortuitous new arrangements, of a trait confer an advantage but are not functional. Both fortunate accidents and malfunctions are assessed against the historically selected role of the trait. The token trait is assessed against the selected trait type, which allows for the normative dimension of functions to be identified. The functional trait must act in a historically appropriate way to be functional. Both Millikan (1984) and Neander defend SE function by showing this mode of individuating systems and their causal actions mirror the practices of biological and medical sciences; particularly medicine, homology, and neuroscience (Rosenberg & Neander 2009; Neander 2017)

Applying SE functions to ecological systems is problematic, at least under the original formulations of SE function, as the features required appear to be lacking in ecological systems. The only relevant systems that can possess functions are, at first appearance, organisms and maybe certain groups, like eusocial insect colonies (see Haber 2013 for more on insect colonies). This view has been strongly affirmed in the functions literature, with many arguing SE functions are only applicable to features that have formed due to natural selection acting on individual organisms (e.g., Sober 1984, p. 208; Neander 1991, p. 174; Walsh and Ariew 1996, p. 497; Wouters 2003, p. 649–652). This narrows the scope of the entities, which can bear functions significantly. There is good reason for this; organisms can be easily demarcated and are indisputably functionally organised. Ecological systems are not organisms or biological individuals (Chapter 4). Further, it is difficult to interpret what an ecosystem's genotype or phenotype could be. If SE functions only apply to organisms, or systems that strongly resemble organisms, they cannot be applied to ecological communities.

The narrow conception of SE function has, however, been argued against since the early 1990's following developments in the levels of selection debate. If selection could occur on multiple levels of biological organization then whatever level selection occurs at could bear SE functional traits. Godfrey-Smith (1993) describes SE functions not as traits which affect the fitness of organisms but as traits of '*biologically real systems of type X'*. This allows entities like segregation distorter genes to have SE functions for '*disrupting meiosis is something that segregation distorter genes do, that explains their survival'* (p. 347).

If ecological systems could similarly be described as "biologically real systems", of a type shaped by natural selection, then they too could have SE functions. These biologically real system would require a fitness, and as a result be able to reproduce under most standard conceptions of fitness. It is this version of SE functions that Maclaurin and Sterelny (2008) consider and dismiss as being not applicable to ecological systems (p. 114). This is because ecological communities do not appear to reproduce new ecological communities of the same type. This will be further discussed in Section 5.4.1.

Further developments of SE functions have been applied to ecological communities. Recent theories have dropped the requirement for functional systems to reproduce, removing that barrier for ecological systems to possess SE functions. Justin Garson (2017a, p. 22) suggests but does not argue for the application his Generalized Selected Effects (GSE) function to ecosystems. His theory of function introduces the idea that systems can be differentially reproduced or retained, as see below.

> *‘GSE: The function of a trait consists in that activity that historically contributed to its being differentially reproduced or differentially retained within a biological system.’*
>
> *Garson 2011, p. 555*

By including the disjunct, with “differential retention” of a trait within a biological system being treated on par with differential reproduction, his account expands the possible systems that may have functions ascribed to them. Antoine Dussault and Frederic Bouchard (2017) apply a similar theory of function to ecological systems but limit functional activity to a *‘propensity to persist’* (p. 1122), disregarding the need for reproduction and adding metaphysically fraught “propensities” to the mix.

What unites all these accounts is that the trait is assessed in terms of its role under natural selection. These system types will need to be “Darwinian individuals” (Godfrey-Smith 2009), they cannot be any mereological arrangement[56]. The overall community composition must to be able to respond to natural selection. SE functions require a system to appear consistently over time, to

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[56] There is a question as to what extent any persisting entity is a “Darwinian individual”. Garson (2011) appears to accept that natural selection occurs on Darwinian individuals while Dussault and Bouchard (2017) are not committed to Darwinian individuals in any straightforward manner. Given this, my objections to Garson (2017a) will include discussion of Darwinian individuals but my objections to Dussault and Bouchard (2017) will not.

indicate they have survived selection. This I will explain is a very suspicious assumption in ecology no matter the formulation of SE functions.

5.3.2. Causal Role Functions.

The main competitor to SE functions is the Causal Role (CR) function, devised by Robert Cummins (1975). This account of function is quite distinct, as it does not refer to the history of a trait within a system and does not distinguish accidents or malfunctions. Cummins formalism follows:

> *‘CR Function: X functions as an F in s (or: the function of X in s is to F) relative to an analytical account A of s's capacity to G just in case X is capable of F-ing in s and A appropriately and adequately accounts for s's capacity to G by, in part, appealing to the capacity of X to F in s.’*
>
> *Cummins 1975, p. 762.*[57]

A simple translation of this formalism is: the function of a trait is the actions of that trait, which causally and compositionally account for the capacities of the systems it belongs to. Therefore, the aim of this theory of function is to explain the capacities of a system given the actions of its parts. This is why describing the CR functions of a system is often referred to in the literature as “functional analysis”. This theory of function has been utilized by both Maclaurin and Sterelny (2008) and Odenbaugh (2010) for ecological functions. Maclaurin and Sterelny (2008) use it to describe community functions, and Odenbaugh (2010) uses it to describe ecosystem functions[58].

A persistent problem within CR functions is the lack of description of what counts as an “s”, or what is described as the “containing system”. “Containing systems” according to Cummins were

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[57] Variables renamed for consistency.

[58] As of this paper, Maclaurin and Sterelny (2008) are the only philosophers to write on community functions rather than ecosystem functions. This makes the objections raised against them by their critics quite odd as they aimed to describe different types of ecological systems.

intended to include the many different "systems" found throughout the sciences, not just biology. Chemical systems, sociological systems and psychological systems were all intended to have functions predicated on them under Cummins' analytic formulation of function. There appears to be at the least two features needed for a system to have functions predicated on them. First, they must be able to be differentiated so that their boundaries may be identified, and second, once differentiated they need to be able to be identified over an extended temporal period. Without these simple criteria we could not say that the part was performing a function for that system as the performance of both the trait and containing system could not be tracked. For ecological systems we will be required to provide some identity conditions to trace the effects of a trait to the larger system. This can be done using indexically structured ecological communities.

Indexically structured ecological communities fit well with Cummins functions. Cummins suggests that we identify functions through their "interestingness" i.e. their explanatory use (Cummins 1975). Interestingness tracks the features we wish to explain in the world, we may even pick a carving of nature that has little explanatory power; as long as we wish to explain it, CR functions will help. In practice, interest-dependence is a product of a researcher demarcating their system of study. Indexical communities are described through the causal relations between different interest relative features of ecological systems. The interest dependency of these systems contrasts with SE functions, which has much stronger requirements for system identity, something closer to biological individuality. This interest dependence makes CR function much more applicable to ecology, which has a diverse set of expanada and systems that are compositionally and structurally diverse, than other accounts of function.

The CR function, however, only explains these systems. It can describe the presence or absence of a function, which only means any causal effect the trait has on the overall system, but not whether the trait is malfunctional or accidental. It, therefore, has no normative component; there is no way a CR functional system "should" be acting.

5.3.3. Organizational Functions

A hybrid theory of natural functions is the Organizational (O) function. O functions do not define function in reference to the selection of a system, similar to the CR function, but represent normativity in natural systems just like SE functions. This is seen as advantageous compared to both the other major theories of function (Mossio et al. 2009). For a system to possess natural normativity, O functions require that systems be structured for self-regulation: or to use their language *a closed differentiated self-maintaining organization*. O function proponents equate normativity with self-regulation as it is for the good of the system in itself. CR functions only aim to explain how a feature of a system maintains that system's capacities, and therefore are less demanding. This theory of function has been applied up and down the biological hierarchy, describing functional composition in individual organisms and their functionally composed sub-systems. Nunes-Neto et al. (2014) aim to describe ecological compositions as O-functional but first consider how O function proponents apply this theory to less controversial cases, such as individual cells (Saborido et al. 2011). In the quote below we can see the application to such cases is straightforward.

> *'Consider, for instance, a biological cell. In a cell, different structures make distinct contributions to self-maintenance. The membrane—as a whole, integrated structure made out of many different molecules—acts as a constraint that (among other things) ensures adequate internal concentrations of metabolites. In turn, DNA (among other things) acts as a template for the synthesis of proteins, which have to be continuously renewed due to their high rate of decay. In a word, the cell possesses different* parts*, produced within and by the system, that contribute differently to the maintenance of the organization and thus, of themselves. In this way, functional attributions to each part are grounded.'*
>
> *Saborido et al. 2011 pg. 594*

Nunes-Neto et al. (2014) present an example to explain how O functions apply to ecological systems. They describe a resource cycle formed within a tropical bromeliad. The spiders that inhabit the bromeliad are functional as their consumption of small insects drops nitrogen into the pool of water formed at the bromeliad's base. The nitrogen sustains the bromeliad and the bromeliad in turn provides a habitat for both the insects and the spiders. This small ecosystem possesses O functional traits as it is "a closed differentiated self-maintaining organization".

The formalized theory of O function, which was applied to ecological systems was Mossio et al.'s (2009). They state, a trait T has a function in the organization O of a system S if and only if:

C1: T contributes to the maintenance of organization O of S

C2: T is produced and maintained under some constraints exerted by O

C3: S is organizationally differentiated (Mossio et al. 2009, p. 828).

C1 and C2 are described as combining to identify a system with *organizational closure*. This is when T maintains O and O maintains T's presence. C3 articulates *organizational differentiation*: T must be a sub-part of the overall system rather than the whole system.

In the case of the Bromeliad, all the parts of the system are organizationally differentiated with different parts doing different tasks. The spider population contributes to the maintenance of this organized system and the organized system provides a habitat and safety for the spider population. The system is differentiated as each population acts as a unique subpart, making a distinct causal contribution to maintain the overall structure. The overall composition is nicely bound in a local area. This I accept as indicative that some ecological systems may have O functions and I explore how these could guide invasive species policy.

Function	System requirements for possession of function	Historical	Self-maintenance	Normativity
Selected Effects function	Darwinian Population	Y	Y	Y
Organisational function	Organisational closure and differentiation	N	Y	Y
Causal Role function	System of explanatory interest (epistemic requirement rather than ontological)	N	N	N

Table 5.1**.** Summary of Section 5.3.

5.4. Invasion and Function

I consider each of the individual cases for ecological function; SE ecological function, O ecological function, and CR ecological functions. Their limitations and range of application will determine their ability to provide substantive guidance for invasive species policy. If the normative accounts of function, SE and O, are commonly found in ecological communities we can make non-preference based normative judgements about invasive species role in ecosystems. If most ecosystems can only be explained by CR functions, then we need to bring in other normative values to judge whether the species are a positive or negative influence on the system.

5.4.1. Selected Effects Function

SE functions are difficult to apply to ecological systems as they do not form clear lineages (Maclaurin & Sterelny 2008) and neither do they typically form Darwinian populations. SE functions require a history of selection. In ecology, this will be the parts of an ecological system; the populations, abiotic features, and the causal relationships between these entities. This is problematic, as populations are not tightly causally coupled over extended periods. An ecological lineage, of many populations with consistent causal relationships, being reproduced over multiple generations is implausible. This would require strong homeostasis with populations maintaining each other through equilibrium relations. The constant rearrangement of the relationships in ecological systems, as described in Chapter 3 and 4, obstructs the formation of the long-term relationships required for lineage formation. Further, even when populations happen to be tightly causally paired, they still lack key features of Darwinian populations. There is not a population of ecological communities, which are the product of reproduction with heritability. Without this population of communities, there cannot be competition between ecological community types, hence these lack key features of Darwinian populations (Godfrey-Smith 2009). It is hard to say what competition would look like between large scale multi-population ecological communities. This limits the number of systems that can be described as SE functional.

Given this, there is a steep hill to climb to establish there are ecological SE functions. But in a limited set of cases, there are some plausible ecological Darwinian populations. While ecological lineages are not ubiquitous, they can be found. Ecological lineages are formed through selection, they are just extremely small in scale and limited to only a few populations. The most common ecological lineages are cases of *reciprocal specialization*, in which populations co-evolve to form mutualistic relationships. A famous example of this is the Malagasy Orchid, which Charles Darwin observed with its foot-long nectary and hypothesized that there must be a moth with a foot-long proboscis. Four decades later Morgan's Sphinx Moth was discovered with a foot-long proboscis (Kritsky 1991). These two species have unique morphologies, which mean they necessarily depend on each other for survival. They, as a pair, form an ecological lineage, with two populations being recreated in the same causal relationship over time. These populations could be recreated in new habitats, forming something weakly analogous to reproduction[59]. Each of them would possess a corresponding SE function for the maintenance of this two population ecological unit. This reciprocal relationship maintains the higher-level ecological lineage, as both need to maintain their causal relationship due to their fitness dependency on the other. This strong dependency makes it plausible that they, as a unit, compete with other populations for resources. As a result, I consider reciprocal mutualistic relationships as plausibly SE functional.

I would caution that the border between CR functions and SE function is often hard to distinguish. This is why reciprocal adaptations within the species that comprise these ecosystems are

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[59] I do think this could be strongly contested. Different theories of reproduction are more or less stringent (See Griesemer 2005; Godfrey-Smith 2009).

so useful for identifying SE functions. Selection must occur at the whole community level for it to possess a function, so there must be interdependencies between the populations that comprise the community. Asymmetrical adaptation is not strong enough. The plants in an ecological community will be adapted to the provision of sunlight but the sun is not part of that community, it is an environmental condition. Equally, if a tree relies on an insect pollinator but that pollinator does not rely on it, we have an asymmetry where there is not a community fitness but only selection of populations. All natural selection is occurring at the level of the tree, not the whole community of tree and pollinator.

Most ecological networks are asymmetrical (Rezende et al. 2007; Bastolla et al. 2009). The populations within these networks will not have the reciprocal adaptations that indicate they are part of a single selectively shaped system. When the networks are symmetrical and the populations in them have a shared fate, I expect the community to be quite small. It is unlikely that you will see SE functional relationships past two or three populations. Once you expand out, the contingencies of defection or disappearance become too great. These barriers severely limit the types of ecological systems that can have ecological functions. They will only be ones with very few populations, who necessarily cohabitate, and border on, or are, symbiotic. It is evident that some ecological arrangements like holobionts and or lichens will possess SE function. There, however, are of course rarer in macroecology than other relationships between populations.

If invasive populations disrupt strongly co-evolved communities, they will be malfunctional for that community. Feral cats may be malfunctional for the Bettong and the populations that strongly depend on the niche constructing behaviour of Bettongs, were those mutualistic relationships of sufficiently selected strength. However, the negative relationships between invasives are more commonly between those species and specific native populations, or limited coevolved ecological lineages, rather than the whole community. Those who defend invasive species often claim that these species are functional for novel ecosystems. That clearly cannot be “functional” in the selected effects sense, as they have no appropriate history of coevolution to generate such effects.

Invasive species are most likely to form co-evolutionary mutualistic relationships with other invasive species. This can be because invasive species bring their mutualists with them. Invasive plants which alter fire regimes niche construct local habitats facilitating invasion by other plants adapted to fire. This can be found in the invasive grass species *Bromus tectorum* in western North America and the spread of plants from the Mediterranean basin through California (Keeley 2000; Brooks et al. 2004). Invasive ungulates often facilitate the movement of invasive weeds as in the cases of feral Goats in Australia or White-tip Deer in New Jersey overgrazing, which allows for Japanese Stilt grass to invade (Baiser et al. 2008). Invasive populations then could be functional for the novel community they build.

SE functional ecological systems cannot form immediately between invasive and native populations. With cohabitation and time there will be the opportunity for even adaptive relations to form between an invasive population and native populations. Many critics of invasion ecology strongly emphasize the formation of interdependent relationships between rare or endangered species and invasive populations. Ecologist Mathew Chew has been particularly vocal about the importance of the invasive tree Tamarisk in the ecology of the South-Western USA (Chew 2009). Introduced from Eurasia, the Tamarisk is one of the most disliked trees in the USA, but it has evolved uniquely within its new range. Three species of Tamarisk, which do not hybridize in Eurasia, have hybridized in the USA. *Tamarisk Americana* (as Chew describes it) provides a unique habitat for several endangered songbird species. This hybridized population has become the key habitat for native species viewed of high importance. With time, they may co-evolve or they may already be co-evolving. Therefore, we could have cases of a “native” and “invasive” SE functions. But this would require the evolution of strong interdependency between these populations over evolutionary time. In the vast majority of cases though, if we welcome an invasive species or wish to eradicate it, it cannot be because of the appearance of new selected effects in novel ecosystems, or the disruption of selected effects in native ones.

5.4.2. Expanding Functions through Persistence.

Garson (2011; 2017a) and Dussalt and Bouchard (2017), in response to the limitations of applying SE Function, expand what counts as selection. They defend two different theories of function through differential persistence, where the presence of a trait is thought to affect the propensity of a system to persist or its history of persistence. As these theories avoid the need for reproduction or lineage formation, they are thought to be more applicable to ecological systems. As Dussault and Bouchard (2017) describe it an ecosystem has a function if:

> *'The function of* x *in an ecosystem* E *is to* F *if, and only if,* x *is capable of doing* F *and* x*'s capacity to* F *contributes to* E*'s propensity to persist.'*
>
> *Dussault and Bouchard 2017, p. 1122*

Garson (2011) adds, in addition to differential reproduction, "differential retention" as means for selecting a trait[60]. It is thought that unlike a narrower SE function in which there are reproducing lineages, persistence functions can capture the larger scale ecological systems commonly discussed in ecology. These larger ecosystems appear to persist over time, and function could be equated with the sub-parts of these systems, which aid their continued existence. I will state upfront I cannot see how differential persistence theories of function can be fruitfully applied to ecology. This project requires a principled and objective distinction between the persistence of an ecological system and its replacement by a new system. The authors of persistence theories of function do not supply anything like this. This position stands in contrast with others who have struggled with such issues; for example, in the last chapter of Richard Dawkins' *The Extended Phenotype* he provides principled account of the conditions for the production of a new organism (Dawkins 1982). Without such due diligence these theories of function cannot be applied. Part of Garson's project I wish to affirm, that

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[60] Differential retention I find more plausible than propensity to persist, but I do not have the space to expand on why, so I will consider these accounts together.

SE function can be applied to non-paradigm Darwinian populations. But this expansion does not extrapolate to ecological systems.

Garson (2011) convincingly argues biological structures such as neural networks and immunological systems have functions as they undergo selection processes. These systems do undergo selection and, therefore possess functions, but this is not due to the expansion of function to differential retention. These systems are sub-parts of organisms and are a product of organismal development. Developmental processes form lineages, on which selection can act, and are themselves the product of natural selection. These developmental processes create Darwinian populations even if they are not paradigm Darwinian populations. This can be seen in the case of somatic cells in a body, they have many checks and balances which limit the extent to which they are subject to natural selection but retain features of Darwinian population. As these checks and balances are reduced, they tend towards becoming more paradigm Darwinian populations in the form of cancer (Lean & Plutynski 2016). These developmental Darwinian populations are extremely dissimilar to ecological communities.

This dissimilarity can be seen through comparing one of the convincing examples Garson uses, the developmental process of neural cell death, to ecological systems. Neural cell death *'involve(s) a selection process in which entire neurons (rather than synapses) 'compete' for a limited field of innervation or for a limited number of trophic resources.'* (Garson 2011, p. 554). This process does not involve the continuous reproduction of neural cells within the lifetime of an organism, but does involve the recreation of a neural cell population at each iteration of developmental process. This population competes for resources, utilized neural paths are retained while excess neurons undergo apoptosis.

Neural systems are Darwinian populations: the population of neurons are reproduced, compete for resources, and are subject to selection. The major differences between these and paradigm Darwinian populations is that the intrinsic characteristics of each neural cell has little effect on their fitness, their fitnesses are more a product of the higher-level arrangement of the system[61]. This does, however, make this aspect of the neural fitness not heritable. In the development of the neural system we have the reproduction of a neural population through a lineage. This lineage is first intergenerational, between organisms with neural systems, and then intragenerational, the neural population expands rapidly from the developmental bottleneck before undergoing selection. Now compare this to an ecological system. In ecology, there is no lineage of an ecological community. The populations move around the landscape largely independently, with no (or very few) distinct reproduction events resembling that of organisms or their constituents (see last section). There is no sense in which these communities are competing for resources, only the lower level populations compete for resources. It is the consistent recreation of a selected unit over time that SE functions require. While developmental processes can satisfy these conditions to some extent, large-scale ecological systems cannot.

The primary problem with persistence is the need to distinguish between a persisting but changing ecological system and a new one. If there is some change in the trait within the system how can we say whether the system has gained a function or been destroyed? This question of destruction versus function is central to the question of whether invasive species destroy ecological systems or create functional novel ecosystems. This is a difficult problem for those deploying persistence, as unless there is an extremely effective biocide in the area, something will persist. Reproduction and lineage formation are often used to provide a system with identity conditions in the face of change. Without this, however, we have little guidance for demarcating whether something contributed to the system's persistence or disappearance.

If ecological systems are all idiosyncratic, there is no way to compare them to identify if the trait made a difference to the system's differential persistence. For example; to identify if an increase in soil salinity allows for the differential persistence of dry sclerophyll forests, we need to look at one

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[61] See Sterelny (2011) for a sceptical take on the importance of intrinsic characteristics on selection for Darwinian populations.

dry sclerophyll forest with high salinity and compare it to another dry sclerophyll forest with low salinity (which then does not persist)[62]. For the persistence theory of function to be fruitfully applied, it is not enough for a dry sclerophyll forest to continue in roughly the same region. This forest must be individually the same forest. There is little to no way currently of determining the continued individuality of such an ecological system without any notion of growth or reproduction or internal cohesion (where internal cohesion is not defined in a way that is circular and relies on persistence). One reply that Dussault and Bouchard (2017) attempt was to have persistence indexed to ecological kinds. Utilising kinds does go against the tradition of treating ecological systems as genuinely cohesive organism-like systems, which go through multiple stages of succession. Each stage of succession could be its own kind, with stable clusters of properties. But regardless, using ecological kinds to determine identity is untenable as ecological community kinds are themselves problematic (Chapter 3). They can be described in very fine-grained and course-grained manners with no clear privileged grain of description.

For example, to identify if a dry sclerophyll forest has persisted due to an increase soil salinity over a forest in low salinity environment, we must be able to answer two questions of identity, why are these two dry sclerophyll forests the same and whether the dry sclerophyll forest that "persisted" retained its identity over time. This is a problem as dry sclerophyll forests are unique, leading to the Office of Environment and Heritage in New South Wales to distinguish between 10 different dry sclerophyll forests such as the Hunter-Macleay dry sclerophyll forest, which is dominated by spotted gum, and Upper Riverina dry sclerophyll forest, which is dominated by box gum[63]. As we go to finer and finer grains, there will be different species and proportions of species and abiotic facts and causal

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[62] We would further need to identify whether the salt makes an actual causal difference, or whether it is some other causal factor, like rainfall or the addition of a population of wedgetail eagles. This is already an extremely high epistemic barrier! Even if this theory was conceptually possible it may be impossible to implement due to these epistemic demands. Scientists may not actually be able to identify the relevant difference makers.

[63] http://www.environment.nsw.gov.au/threatenedSpeciesApp/VegFormation.aspx?formationName=Dry+sclerophyll+forests+(shrub%2Fgrass+sub-formation)

arrangements of species in each of these regions. There is, therefore, no relevant contrast class to identify whether a trait makes the relevant difference to persistence[64].

Persistence theories need to supply plausible ecosystem identity conditions over extended temporal periods. If ecological systems are deeply idiosyncratic and changing, they will not persist through internal change. Dussault and Bouchard (2017) realize that this is a problem, admitting the *'Heraclitean problem of an entity's sameness through change, is that of the ecosystem'* (p. 24). They also concede that attempts to define ecological kinds often result in large disjuncts of different ecological systems (see Jax 2006). To address this problem, they simply posit that all these different kinds exist, through John Dupré's promiscuous realism, a position which argues any mereological sum is a kind, if it is useful for agents (Dupré 1993). This seems obviously problematic for their account. Under Dupré's theory any region will have countless "real" ecological systems, some of which will persist under a given change like invasion, and others that will not. If there are multiple different functional ecological kinds within an area, Dussault and Bouchard (2017) must be able to ascribe consistent propensities for persistence to each of these kinds. These spatially co-existing propensities will need to translate across the different co-extensive ecosystems, they cannot be radically inconsistent. With so many different ecological kinds, we will be given an immense disjunction of propensities, each representing a different ecosystem present within that patch of land.

This leads them to admit:

> *'persistence may remain a non-operational concept until some identity conditions are specified: these conditions would enable one to determine, regarding a particular ecosystem change, whether the ecosystem has persisted*

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[64] One option is we could indulge in some serious metaphysics and attempt to look at the ecosystem's counterpart in the nearest possible world without that trait (Lewis 1971). I doubt the proponent of this version of naturalised function will find this desirable. Even if they do, there are issues with using such possible world semantics for identity (Mackie & Jago 2017).

> *and adapted to its new environmental conditions or whether it has collapsed and been succeeded by a new one.'*
>
> *Dussault & Bouchard 2017, p. 1139*

While they can leave this as future work to be done, without any attempt to explain how this would work, as it stands the persistence theory of function in ecosystems is non-operational. By non-operational I do not mean just that we cannot use it in the field, I mean it is conceptually non-operational as without these conceptual resources, we cannot determine what has a function. Crucially, they lack any plausible story that such resources could be produced. Any patch of an ecosystem under this view will consist of many differing overlapping ecological systems with different identity conditions. As such, it cannot be used to discern definite ecological functions. This differs from traditional SE functions which are lineages of Darwinian populations and CR functions which are explicitly defined by the system capacity an agent wants to understand. O functions, as we will see in the next section, suffer from some problems of discerning ecological identity but not to the same extent as persistence functions.

Even if there were the resources to identify persistence functions, I am unconvinced they are desirable. There needs to be some motivation for defining persisting entities as normatively functional. Both O-functions and SE functions naturalise the teleology of a system's components, the trait's actions in the larger system explain the existence of the trait. By contrast, ecosystem traits which aid the persistence of the ecosystem do not explain their own existence. For there is no feedback loop from the effect of the trait on the larger system to the continued existence of the trait. The kangaroo I ate certainly increases my propensity to persist, but it does not explain the existence of the kangaroo[65]. Equally, the microclimate which aids the persistence of an ecological community

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[65] A kangaroo steak contrasts with a beef vindaloo and a glass of red wine. My consumption of the latter two does act to explain the steer and grape vines existence.

does not necessarily explain the microclimate. It is unclear to me what we gain from this broadening of function[66].

This all leads me to the conclusion that persistence is not useful for identifying ecological function. Cases which have been used to argue for the expansion of SE function can be incorporated within the standard formulations. As it stands, it cannot be applied to ecological systems and I do not see the possibility for its future application. Even if it could be used, I do not see why we would want to.

5.4.3. Organisational Functions

For an ecological system to possess an organisational function, it should be organisationally differentiated and organisationally closed. This causal and structural profile constrains the identity of O functional systems through time. An organisationally differentiated system has modular parts with different causal profiles and organisational closure is when a trait maintains the system while the system maintains that trait. In the case of the heart, the heart is a differentiated subpart of the body, it maintains the body and the body constrains and maintains the actions of the heart. It is the co-dependency between parts and the system, in the opinion of O function proponents, which allow for natural normativity. A function is whatever is good for the existence of a system, and this allows for the identification of malfunction. When applied to ecology O functions are similar SE functions, they apply but are by no means common. Ecological systems which possess organisational differentiation and closure are rare in ecology.

To display the application of O Functions Nunes-Neto et al. (2014) describe a resource cycle formed around a tropical bromeliad. This small ecosystem processes an O function. The spiders that inhabit the bromeliad are functional as their consumption of small insects drops nitrogen into the pool

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[66] Thanks to Kim Sterelny for pressing this point.

of water formed at the bromeliad's base. The nitrogen sustains the bromeliad and the bromeliad in turn provides a habitat for the spiders. This is a nice example as the system is quite isolated and comprises few species. The system is centred on an individual plant and the way this plant provides a habitat for the species that help maintain it. This indicates that the system has organizational closure. This case also satisfies organizational differentiation as the various populations act as separate actors in the ecosystem's causal structure. Finally, the resource cycling sustains all the populations within this system meeting the self-maintenance condition. The mode for assessing whether the system continues through time appears to be whether the populations are being maintained through these actions.

While I accept the above example as a case of an ecological O function, I think such cases are the exception not the rule. Notice the ecological system in the example is physically quite small, only occupying a couple of metres cubed at the most, and is small in terms of causal actors, it only comprises the insects, spiders, and a plant. O functions become harder to apply as ecological systems scale up in their size, complexity, and openness. Invasive species are likely to disrupt O-functions when they interact with them in native ecological systems. This is largely inconsequential as O-functions are rare and exist on significantly different scales to invasive populations.

Why are O functions so rare in ecology? We must look at the conditions for O functions separately: organisational differentiation and organisational closure. Each of these are problematic. Organisational differentiation requires the entity, which possesses the functional trait, to be a sub-part of the system not the whole system. This on first pass should be easy to satisfy, as different distinguishable populations or resources can act in independent ways. These populations or resources act as causal nodes in the network of functional relationships within the ecological system. But in fact, this can be problematic as identifying and demarcating autonomous contributing sub-parts of a system can be difficult.

Abiotic units are often spatially diffused through an ecological system, exerting causal control in many ways across the entire system at once. Rain can cause plants to grow, fungi to reproduce, animals to disperse, soil to be eroded, and insects to drown; each has an impact on the composition of the ecosystem. Text-book depictions of nutrient cycles involve incredible amounts of idealization, cramming diffuse multi-factor interactions into a single node, to the extent that it is hard to see what they represent. As a result, identifying and demarcating atmospheric or mineral sub-systems into distinguishable contributors to the ecological system is difficult.

Odenbaugh suggests ecosystems, and their parts, may have some boundaries noting that watersheds form boundaries due to the topography of the land (Odenbaugh 2010, also see Post et al. 2007). Topography and geology will produce some boundaries, but distinguishing mineral and atmospheric systems as differentiated units will be challenging. It is implausible, even if we can distinguish these abiotic systems, that they will exhibit causal closure. Abiotic systems do not exhibit homeostasis or stability in the way that biotic systems do. Matter will disperse without strong redundant control mechanisms. Ecological systems do not exhibit this strong local determinism, as discussed in Chapters 3 and 4, and even less so the abiotic components of these systems. There will be very few larger ecological systems, if any, that are even approximately closed be they described biotically or abiotically.

The requirement for organizational differentiation is unlikely to apply to ecological assemblages due to the aggregational way populations contribute to ecosystem maintenance. Many of the proposed links between stability and diversity go via aggregational interactions. These include *statistical averaging effects*, where stability in community properties are maintained by the averaging of statistical fluctuations in the large set of populations; *biological insurance*, when you have many populations doing different things, it is more likely that you will have the population you need to stabilize the system; and *sampling effects*, if you are assessing the productivity of an ecological system high-diversity areas will likely have some very productive species (Sterelny 2005). The maintenance of ecological systems is often through the statistical effects of large diverse systems. Ecological system maintenance is the product of the aggregation of many different populations rather than differentiated sub-parts playing roles[67]. Given this there is not really a differentiated trait acting

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[67] Dussault and Bouchard 2017 also make this point.

to maintain the larger system. To redeploy the language of the last chapter, these systems are maintained through *ensemble robustness* while organisational functions require *machine robustness*.

While there are problems with organizational differentiation, organizational closure is the most problematic requirement for applying organizational functions to ecosystems. As discussed in the previous chapters, there is considerable evidence that ecological systems are not stable systems with consistent structural relations between their parts forming self-maintaining relationships. Ecological communities are not closed systems; they are the product of many populations moving around larger biogeographic regions (Chapter 3 & 4). This means that the causal structure of inter-population relationships is often changing over ecological time, with many systems having a large amount of species turnover. Species turnover changes not just the population playing the functional role, but more importantly changes the overall causal network structure of the system. As such, there is not a consistent identity relation of functional trait to the organization of the system over time. Populations within ecological communities are often maintained by source-sink dynamics, or similar rather than local causal interactions. Source-sink dynamics involve populations in an area declining but being maintained by the recruitment of migrants (Pulliam 1988). In these common cases, the population is not maintained or constrained by the organization of the ecosystem.

The requirement for self-maintenance is further put under pressure by the increasing evidence that ecosystems are not maintained by stabilizing dynamics between populations, as described by equilibrium ecology (Chapter 1). Equilibrium ecology starts from the assumption that populations regulate each other's abundance (Pimm 1991; Cooper 2003; Walmsley 2016). An example of equilibrium dynamics is the famous Canadian Lynx and Hare population cycle, which occurs over a 10-year period. The populations oscillate as when the Hare population increases in abundance the Lynx population increases due to having more available resources, the increase in Lynx predation causes the Hare population to drop and then the Lynx's follows. The oscillation of populations in relation to each other stabilizes the entire community and acts to efficiently utilize the available resources excluding other populations.

In contrast, non-equilibrium ecology argues communities are casually open collections of species, which are co-located due to the path-dependent historical processes of chance and random dispersal from other local communities. It is rare for a set of populations to be maintained in an area. As a result, the identity conditions for O-functions are generally too strong for ecological systems. Finding a set of populations which persist through time due to their O-functional causal structure is quite unlikely. When populations are maintained, they are maintained by the meta-community dynamics described above, not self-maintenance. Local species presence or absences are a patchwork of dispersal and local population collapse (Hubbell 2001). Likewise, models which treat population distribution and abundance as a product of drift reject equilibrium dynamics. These positions imply that there is no default state that ecological systems return to or maintain. Non-equilibrium ecological systems will not self-regulate, and we cannot make claims about what state they should be in according to their "functions".

It is an open empirical question as to which ecological systems are subject to non-equilibrium dynamics and which are in equilibrium. I suspect there are ecological systems subject to either. It appears that some tropical forests are well explained by neutral theory (Hubbell 2001). Equally, arid environments seem to be maintained by random dispersal and local population extinctions rather than networks of co-maintaining populations (Sullivan 1996). As a result, many ecological systems will not possess organizational functions.

It is likely that some O functions will occur in ecological systems. Generally, they will be small ecological systems with just a couple of populations in close physical proximity. Invasive species when they invade ecosystems can disrupt whatever O-functional systems are present. If the invaders outcompete species within these O-functional communities, they will lead to their collapse. In such cases, we can state that invasive species are malfunctional. But these cases will be rare due to the rarity of O-functional ecological arrangements.

Further, the scale at which invasive populations operate and O-functional communities exist is different. The scales on which O-functions exist will be quite small. As noted, the bromeliad O-function system is physically not a very big ecosystem. Large systems create the type of spatial and causal asymmetries that were described in Chapter 4 (i.e. the causal asymmetry between the numbat and greater glider populations due to difference in range). Invasives will causally influence populations across all their range, so narrowing our scope of concern to just the O-functional clusters of populations misses most of the causal influence invasive species have on native assemblages. To my mind, this supports looking at the causal structure of communities rather than searching for functions.

It is possible for invasives to both form O functions in novel ecosystems and destroy O functions within native ecosystems. This, however, misses most of their causal effects. As shown in the discussion of SE functions, we will find that instead of having whole functional ecosystems, in which the invasive is malfunctional, invasives affect many independent populations and the occasional small cluster of populations which form a functional unit. We are again left in the position where we need to weight our preferences between particular populations, invasive and native, and these small-scale O functional groups.

5.4.4. Causal Role Functions

It was immediately apparent to philosophers of biology that CR functions were applicable to ecological systems with Sterelny (2006), Maclaurin and Sterelny (2008), and Odenbaugh (2010) describing their application. CR functions are present in an ecological system when a part of the system makes a stable, regular contribution to the capacities of that system. This type of function is explanatory; it explains how a part contributes to a system’s capacity, whatever that capacity may be. To have a CR function an ecosystem only needs to be causally or constitutively continuous, and it needs to possess a capacity we wish to explain given its parts[68]. This capacity could be, for example;

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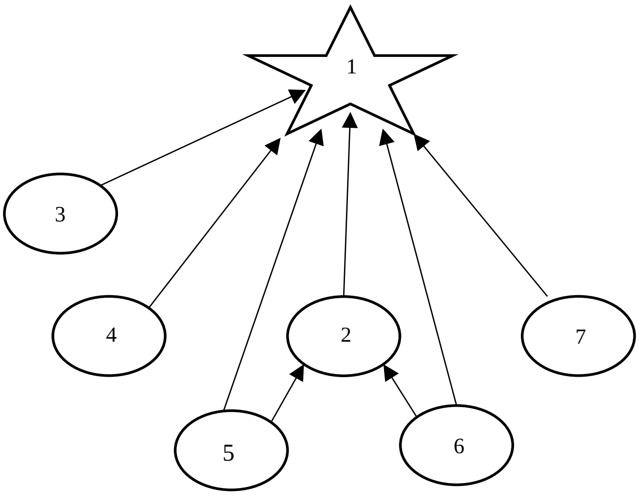
[68] A good way to do this is with my indexical ecological community framework describe in Chapter 3.

its continued existence or some abiotic output. Due to the permissiveness of CR functions, ecological systems formed without a history of selection or self-maintaining causal structure can be analysed in those terms.

A suitable example of a CR function is Robert Paine's (1966) experiment of removing the starfish *Pisaster* from intertidal rock pools. Through repeated intervention, he identified that *Pisaster* played a distinct, stable, and unique role in that system. The community described by Paine is built from the community causal relations indexed to a single population, the *Pisaster*. This food web is called a sink food web as it is indexed to a predator (the energetic sink) to which the rest of the populations are related. *Pisaster* predates on all the other populations in the community but prefers the California Mussel (*Mytilus*). When *Pisaster* is removed from the system, the Mussel population rapidly increases, spatially excluding all the other species. This causes a collapse in the species diversity within the system (Paine 1974).



5.2. The intertidal ecological community. Arrows indicate the flow of energy. The different populations are: 1) Pisaster 2) Thais 3) Chitons 4) Limpets 5) Bivalves (including Mytilus) 6) Acorn Barnacles 7) Mitella. As the apex predator, Pisaster suppresses strong competitor populations in the community increasing diversity.

The *Pisaster* population in Paine's community plays a unique role in the system. But what is the role for? We could describe the function as being for the suppression of the mussel population but that is not interesting for understanding the overall capacities of that ecological community. By suppressing the mussel population, the Pisaster maintains the community's overall species composition, the population network structure, and species richness. Counterfactually all these different features are not identical; we could have variation in one of these features and not the others. All of them are interesting, as they address scientific hypotheses, and we could aim to explain any of them using the CR function framework.

The question of system identity then arises anew in CR functions. The indexical community framework (Chapter 4) can be used to determine the identity of the system in question. As CR functions explain system capacities, they do not suffer from the problem of massively disjunctive identities that persistence functions suffer (Section 5.4.4). We get to dictate the capacities we want to understand, and then we work backwards to the relevant system. The functional parts may be time or context dependent as the relevant factor is whether these parts explain the capacity we were originally interested in. This is not true of persistence functions as there is a burden to display that there is an actual system persisting and that there are distinguishable parts which affect the propensity of that system to persist. As such, we have the tools to assess the CR functions, but not persistence functions.

This account of function can apply quite clearly to ecological systems, as long as there are constitutive and causal relations in that community. It, therefore, can describe the ways that invasive species contribute some capacity of the system. A system capacity could be very broadly construed. Possibly a little too broadly construed, at least according to CR function critics like Nunes-Neto et al. (2014) and Dussault and Bouchard (2017). They point to functional relationships in which invasive species have the function to cause the collapse or fragmentation of an ecological system. Given this, what guidance can the CR function provide for invasive species policy?

A fair bit I would say. We can use this form of functional analysis to identify the effects of invasive species, but the functional analysis in itself will not tell us whether those effects are desirable or not. The feral Goat in Australia removes Australian flora and fauna as it overgrazes Australian plants and outcompetes yellow-footed rock wallabies for rock shelters. The Goats then bring in invasive plants (weeds) into the areas by seeds carried in their dung, which can grow quickly in the soil that the Goat's hooves overturn (*Australian Government Invasive Species Fact Sheet*)[69]. They have a systemic set of causal relationships. The natural interpretation is that the Goats causally contribute to the systemic capacity of an indexical community formed around them (Chapter 4). This will be a novel ecosystem, comprising of weeds and the native plants that survive their herbivory. Goats do not contribute to the survival of the previously present ecological system; they promote their own novel ecosystem.

The conclusion that invasives, like Goats, causally support their own novel ecological system, and this does not count as a malfunction, has led some philosophers to argue that CR function cannot be applied to ecological communities (Dussault & Bouchard 2017, p. 1120). That is, invasive species act as modus tollens for the use of CR functions in ecology, as it "misdiagnoses" malfunctional relationships in ecology. This belief is a mistake derived from the often overly normative language used to describe invasive species (Chew & Laubichler 2003; Brown & Sax 2004). Functional analysis identifies invasives' effects: we have to go beyond functional analysis to assess whether those effects are desirable.

5.5. The Scope of Functions in Ecology

The debate over ecological function is usually conducted in the hope of describing functions for large ecological compositions of many species and resources. If such entities have functions, we could make conclusive statements about what is normatively functional or malfunctional. Within this chapter I have presented a quite different picture. Large scale ecological communities do not hold together in a way that allows for normative functions. They are only subject to "functional analysis",

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[69] https://www.environment.gov.au/biodiversity/invasive-species/publications/factsheet-feral-goat-capra-hircus

CR functions, as we can explain their causal relations when present. The conclusion, for which some had hoped, that invasive species are malfunctional in these systems like an infectious disease is to a body, cannot be found.

The expected alternative is that ecosystems are entirely individualistic. There is nothing but populations and their abiotic ranges with little interdependency. This is a position I have rejected in Chapter 4, these systems do have complex causal relationships. These causal relationships make CR functions particularly apt to explain how this causal structure results in various system capacities. This complex causal structure is, however, not bereft of normative functions. Such examples will just be smaller in scale and scope than has been previously believed. There are occasional examples of ecological systems which are so extensively coevolved, or tightly integrated and self-sustaining, that their component populations have organisational and/or selected effects functions. Such cases, however, are too exceptional to guide conservation biology in response to invasives or much else.

What then is the picture of communities we are left with? They feature populations with weak and inconsistent causal influences on each other. This still allows for large scale CR functions. If there are causal connections between populations and some capacity of the ecological system, then these relations are CR functional. Occasionally within these communities, there are small clusters of populations that are SE or O functional, but these are rare. These will be usually only a couple of populations, and will predominantly interact with other populations rather than other functional population clusters. It is into this system that invasive species move. When they destroy other populations, it is usually due to their direct relationship to other populations rather than functional groups. When invasive species do form functions, these are local to a small set of species, most often other invaders.

Given this picture of ecological communities what role can ecological function play in guiding our policies towards invasive species? In the next section, I will argue that explanatory function provides the best guidance for invasive species policy. Even if one were to accept that we could move from natural normativity in ecological systems to moral normativity, which is no mean feat, there is not enough natural normativity in ecology to scaffold such a move. The CR functions inform us of how a system works and this in turn will constrain what we can do but cannot on its own determine what we should do. This leaves the further problem of where we look for normative guidance, which I next address.

5.6. Causal Functions for Conservation

Function was hoped to be a means for avoiding a debate over preferences. I do not think this is an option. The teleological arrangement of ecological systems is extremely spotty. There are little blips of teleological arrangement, but these are not strong enough to support an entire ethical theory of conservation on its own. Further, I am doubtful that we should want this given that it does not include much of the phenomena conservation aims to protect, specifically, arrangements above the organism level. But there are resources available in the function literature for conservation. CR functions can identify the populations that support phenomena that we do or should want to protect. We do have some means to avoid the dull clash of idiosyncratic preferences in the public sphere.

CR functions explain the capacities of complex systems given the traits or causal actors within that system. When it comes to conservation, we wish to know the traits that causally support or maintain the features that are of moral worth or utility or preference (which is its own form of utility). Generally, features that provide utility will be those that supply ecosystem services. I see no reason to believe that ecosystem services cannot be performed by novel ecosystems (Hobbs et al. 2006; Hobbs et al. 2013). There may be cases, of course, where they don't; if an invasive species eradicates a keystone species or has a radically different effect on the native system, we can see ecosystem service deterioration. An example is the case of rabbits in Australia degrading soil quality. But ecosystem services do not appear to me to be a deciding factor in determining whether we should control invasive species.

The strongest mediators will be global biodiversity and local preferences for native species. If invasive species act to diminish the populations that represent these features, then we have reasons to wish to remove them. Local preferences obviously are contestable, but ultimately conservation must connect to the interests of local stakeholders in some fashion (Sarkar 2012). Given this, I do not at all dismiss these preferences; they are a necessary part of conservation. But I aim to focus on reasons to eradicate invasive species, which are not based on such socially contestable preferences. In contrast, global biodiversity can provide a reason, that all prudent agents should share, to preserve native species rather than invasive species. We should preserve global beta-diversity, or unique species across different ecosystems rather than just local species count (alpha-diversity). As a result, there are some reasons to eradicate invasive species.

5.6.1. Functions for Biodiversity

CR functions for biodiversity can be used to arbitrate the debate between invasive species supporters and critics. Biodiversity, as argued in Chapter 2, is valuable regardless of immediate individual preferences due to option value. If invasive species do diminish biodiversity, we have a reason to eradicate them in local habitats. By this I do not mean that there are external reasons, which dictate action regardless of agent's preferences. Option value, as I defend it, is a type of prudential reasoning; we wish to keep resources available for our use in the future. Insofar as we should act prudentially, or it is rational to act prudentially, we should preserve option value. This leaves open the question of how much we should invest in options as opposed to immediate preferences. Such questions will require decision making under risk, and agents' decisions about how much risk they wish to take. But such questions involve second order preferences, I only require that we have first order reasons to preserve biodiversity. If we have a first order preference to preserve biodiversity and invasive species reduce biodiversity, we should invest in controlling invasive species.

CR functions can identify which populations support biodiverse assemblages. In Chapter 4, I showed how indexical communities provide a means for identifying the populations that causally contribute to the maintenance of biodiversity. This is a very similar process to discerning CR functions. There are many ways to measure biodiversity apart from the species richness measure. In Chapter 2, I argue that there are better and worse ways to measure biodiversity. Pearce (2015) argues that invasive species increase biodiversity as communities with invasives have more species. This openly conflates alpha with beta diversity and is a fine example of how not to measure biodiversity. For biodiversity to represent options, it needs to predicate on biological differences worldwide rather than just a local species count. Just using local species counts will represent fewer options for use in the future.

There are better ways to measure biodiversity and I specifically argue biodiversity should measure the overall structure of the "tree of life". This, however, is not the only way of representing biodiversity and other measures will be useful in some contexts. Whatever the measure we use we will need to identify the ecological features that these biodiverse populations depend on to allow for their continued existence. A population which acts to make a distinct contribution to the continued existence of these populations can be said to perform a function for maintaining higher quantities of biodiversity[70].

Populations that function to preserve or promote biodiversity in a region play a critical role in conservation science. The Southern Cassowary is a population of 1.8m tall birds found throughout Southern Queensland. These large and dangerous birds are in themselves quite evolutionarily distinct and contribute to biodiversity as their own population's self-maintenance reflexively preserves biodiversity. Cassowaries play a further critical role in preserving more biodiversity within the rainforests they inhabit. They are mega-faunal dispersers, or large animals that stand in a mutualistic relationship with plant species (Guimarães Jr et al. 2008; Janzen & Martin 1982). Many plants have

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[70] Kim Sterelny points out that I could say all this without using the word function. We can talk about nothing but causes and effects on ecological features that are desirable including biodiversity. I agree, it is not necessary. I could happily jettison such functional language from ecology, if not for the way it connects to relevant intellectual traditions. Ecologists use functional language ubiquitously in the casual manner. This is particularly clear in Kurt Jax's (2005) taxonomy of ecological functions, which does not mention any interpretations that approximate natural normativity. Further, connecting functional language to CR functions ties this discussion to a set of resources in the philosophical literature, and a history of debate. The main advantage of using CR functional language over purely causal language to my mind is communicating my ideas to the relevant parties.

large seeds and fruit made for megafauna to consume, transport, and fertilize. With the spread of humans who excel at hunting megafauna, there has been a gigantic diminution of megafauna worldwide. Some plants, like the avocado, have avoided extinction by being appealing to humans, but many plants have become extinct through the knock-on effects of losing their dispersers.

In the Cape York Peninsula rainforest, the Cassowary acts as the only local megafaunal disperser, moving around the seeds of 78 species of plant (Stocker & Irvine 1983). These seeds are of unique and distinct lineages of plants that contribute to biodiversity. Cassowaries make a distinct and persistent contribution to the maintenance of these systems as one of the world's rare remaining avian megafaunal dispersers. To preserve the plants that comprise the rainforest we need to preserve the Cassowary population on which they all causally depend.

This mode of assessment is the core of the appeal of indexical communities (Chapter 4) as we can move from a description of the populations that contribute to biodiversity in a local system to the causal structure that relates them. From this causal structure, we can determine what acts to support this structure. The functional unit may be a single population, but it might also be a set of populations that form a robust self-sustaining feedback structure, or an aggregation of populations that weakly act in unison to form a robust functional relation. In all these cases CR functions describe how these complex systems, once specified clearly, are maintained.

The invasive species that are usually discussed by conservationists are those we have strong evidence of them negatively impacting local populations. These local populations often contribute to global biodiversity to a much greater extent than the ubiquitous invasive species. As such, I can capture a reason to eradicate invasive species in the context that we most often want. We both want the ecosystem services higher levels of biodiversity provide and we should preserve biodiversity regardless due to prudential reasons. These prudential reasons should be shared by rational agents and thereby provide a bridge for negotiating the debate over invasive species.

5.7. Conclusion

Ecological function cannot do the heavy lifting some have wanted it to do. Ecological systems do not hold together in a way which will permit large scale normative functions, which require replication or self-maintenance. Instead, we see causally connected systems with pockets of functionally arranged populations, be these of the replicating or self-maintaining type. We are, however, left with resources to sort through the causal structure and identify the features we value today as well as those which provide option value for the future. This will go part of the way to providing mediation in these disputes. However, I fear much of the work will have to be done at the level of social and political discussion. We will have to ask, what sort of nature do we want to see? Do we want the same species everywhere with a scattering of local species or unique assemblages throughout the world?

Chapter 6. Why Wake the Dead?

6.1. Introduction

De-extinction, or the recreation of extinct species, is a controversial and promising prospect for biological conservation. This set of techniques are currently being invented, refined, and implemented with promising results inching towards creating a population of previously extinct organisms. Prominent techniques include back-breeding features of extinct wild-type populations from domestic populations, genetic modification of related species, and cloning. All these techniques are currently being used: back-breeding has had success producing wild cattle populations, the DNA of extinct populations is currently being sequenced for re-introduction into related species, and an extinct Bucardo clone was born and briefly lived in 2003 (Folch 2009). This rapid progress has led to some soul searching within the conservation community. A lively debate has sparked around what justifies de-extinction.

With limited money currently committed to conservation, dedicating funds towards expensive de-extinction projects seems wasteful. This chapter considers the arguments for and against de-extinction, particularly considering how historical reference states should influence conservation. Is historical fidelity the primary goal of de-extinction or do other interests trump reverence for the past? Intuitively, if there is any conservation process that should involve close adherence to history it is de-extinction. Therefore, de-extinction makes an interesting test case for exploring the methodology, tools, and themes in this thesis thus far. By basing conservation on biodiversity preservation, I incorporate history at the level of lineages, while treating ecological communities as dynamic and largely ephemeral.

Previous conservation methodologies connected historical ecological systems strongly with the ideas of homeostatic stable systems. Historical systems were thought to involve many populations with long histories of interaction, so they have casual and co-evolutionary correspondences that allow the system to be stable. Ecological communities were described as fixed entities, which maintained a state for long periods of time. In the previous chapters, I described an alternative vision of ecology and of conservation. One built from the natural quantity biodiversity and the causal structure of the populations that support biodiversity. This framework does not consider the historical fidelity of the larger systems that populations belong to but selects populations for their representation of the historical divergence of lineages. I wish to navigate the case of de-extinction within this framework to examine the extent to which history can and should play a role in conservation and ultimately how biodiversity can adjudicate the ethical justification for radical environmental interventions for conservation.

In this chapter, I ultimately defend a weak defeasible commitment to historical fidelity in de-extinction. Other goals such as the promotion of biodiversity and ecosystem services will be better reasons for de-extinction. As such, history is only a mediating factor in conservation. This will be done in two parts. In the first section, the case for strong historical fidelity in de-extinction is considered. I reject arguments which aim to establish that de-extinction is primarily justified if we create an organism which is of the same species as the extinct population. These arguments have some minor merit, but ultimately fail. This is fortunate, as I believe that the recreation of a population with strictly the same identity as the extinct population is not possible.

In the second half of the chapter the non-historical arguments for de-extinction are explored; these are not based in strong historical fidelity. I deploy my realist theory of biodiversity (Chapter 2) to establish alternative conservation goals. Building on this, I argue that if de-extinction uniquely contributes to biodiversity through establishing causal role functions for supporting and promoting biodiversity (Chapter 5) then we have a reason to engage in de-extinction. I then return historical reference states and articulate a position in which they are a good means towards different ends based in prudence and making conservation appeal to the public. Historical accuracy is desirable and a constraint on species design but not a primary goal of de-extinction.

6.2. Should De-extinction Resurrect Species?

"The Lazarus Project" is an evocative title for a de-extinction project. A group of scientists working under the moniker of the biblical resurrectee is "resurrecting" the extinct Gastric Brooding Frog. This fascinating Australian frog species gestates its own tadpoles within its stomach, "giving birth" to small frogs from its mouth. Using a process called somatic cell nuclear transfer scientists are inserting cells, extracted for the extinct frog's frozen tissue samples, into the embryos of related frog species (Archer 2013). They hope to produce a living clone of a dead individual from that extinct species. The product of this ambitious process will undoubtedly be very similar to a Gastric Brooding Frog but is it of the same species?

This is a reasonable question to ask. De-extinction is sold as the recreation of a lost population. The act of de-extinction is thought to be deeply entwined with a question of species identity. When scientists like Beth Shapiro (2015), public policy figures like Jacob Sherkow and Hank Greely (2013), or philosophers like Helena Siipi (2014), Ronald Sandler (2014) and Douglas Campbell (2016) discuss what justifies de-extinction they consider whether we can or should recreate the lost species. There has been a long, and at times entertaining, discussion in philosophy over whether personal identity can survive splitting, fusion, temporal gaps, and teleportation (Parfit 1984). The extinction and resurrection of populations through de-extinction technologies creates material and temporal discontinuities in lineages that raise analogous questions (See Delord 2014; Siipi and Finkelman 2017). Just as we may ask whether Lazarus arisen from his tomb is the same as the Lazarus who expired, we can ask whether the first batch of barfed up frogs are truly Gastric Brooding Frogs.

But there remains a further, and more important question: does it matter? There are several arguments for why identity is important for de-extinction. Some proponents of these arguments believe that de-extinction is only really justified if it recreates an individual of the previously extinct population. This chapter will show these arguments are implausible. De-extinction does not rely on the recreation of species identity for its justification. De-extinction is a sub-class of restoration ecology. The arguments deployed to link identity and de-extinction have already been used to argue restored ecosystems must have historical fidelity. I utilize the literature against historical fidelity in restoration ecology, to support the position that de-extinction does not require identity. Just as in restoration ecology, there is a swath of reasons to de-extinct species outside the scope of identity. The arguments addressed here for the recreation of species identity are not exhaustive. The debate around de-extinction will play out in the public sphere and I aim to address the ideas that are either already circulating or are likely to appear soon.

With these caveats in mind, there are three arguments for why resurrection is required of de-extinction. The first is the weakest, the conceptual argument, that de-extinction will not be de-extinction if it does not create an extinct species. This is analogous to Eric Higgs argument that restored ecosystems must be designed with historical fidelity as historical fidelity is conceptually entailed by restoration (Higgs 2003). The second is the argument from authenticity. This is a direct application of the arguments against restoration by Eric Katz and Robert Elliot to de-extinction (Elliot 1982; Katz 1996). Helena Siipi particularly defends a weakened version of an argument from authenticity to say de-extinct populations are of diminished value compared to the original population (Siipi 2014). The final argument is that we owe a duty towards species that we have caused to become extinct. Retributive justice demands that if we have the technology to do it we owe a debt to the extinct species to recreate it. Michael Archer, leader of the Lazarus Project, and several philosophers believe that anthropogenic extinction entails a moral debt being owed to the extinct species (Archer 2013).

Ultimately, all these arguments fail leaving us to consider a much more complex calculus for whether de-extinction can play a substantive role in conservation. One which involves the calculus of how de-extinction relies on public interest and support, fuels new technological, and creates organisms that can fill vital ecological roles. These goals will both drive de-extinction and constrain the design of these new populations. But first we must dispel the myth that de-extinction should requires the recreation of species lost.

6.3. Conceptual Entailment

Often philosophers are enamoured with conceptual arguments that to the general population look extraordinarily weak. These arguments are structured as follows, the proposition x has some necessary content and this content entails that some further proposition y is true analytically. It could be argued that de-extinction is necessarily the act of bringing an extinct species back into existence: species resurrection. If the species is not recreated, then de-extinction has not occurred. The need to address this argument is indicated by scientists already attempting to articulate the *true meaning* of "de-extinction" with Helen Taylor et al. (2017) stating *'(t)here is confusion generally regarding what de-extinction means; many people do not appreciate that de-extinction actually involves creating a technically feasible proxy… rather than an impossible resurrection'* (p. 1). Similar conceptual arguments to the above argument have been forwarded in restoration ecology by Eric Higgs (2003): historical fidelity is conceptually required for ecological restoration. The responses to his argument provide a guide to defending species resurrection from the conceptual argument.

To establish that restoration does not conceptually require historical fidelity Sahotra Sarkar identifies cases in which restoration ecologists conduct restoration without historical fidelity or define restoration without reference to history (Sarkar 2011; 2012). He states that in cases such as Baclones Canyonlands; *'Historical fidelity is not adopted as a goal in some circumstances because the historical past of a locale cannot be reconstructed with the data that are available.'* (Sarkar 2011, p. 353) As strong fidelity is not possible in many restoration projects, it is not reasonable to expect it (I also believe this is the case for de-extinction but wish to focus on the normative rather than the metaphysical). Further, as Garson (2016, p. 328) notes, some restoration ecologists do not use "restoration" with historical connotations (See Hobbs & Cramer 2008). As there is no necessary connection between history and restoration Sarkar (2011) avoids the use of the term "restoration ecology" preferring "habitat management" or "habitat reconstruction".

The shape of the conceptual argument as applied to de-extinction is very accessible. "De-extinction" has the linguistic content of undoing an extinction. Extinction happens to a species. If this species is not brought back, de-extinction has not occurred. We can, however, find the same disconnect between the connotations of the term and the use of the term by the informed scientific practitioners. This is up front and centre in Beth Shapiro's *How to Clone a Mammoth* (2015). As an informed scientist using this technology to recreate the passenger pigeon she states; ***'I don't care** that (a de-extinct passenger pigeon) is not the same thing as the original'* (authors emphasis) and '*there is no compelling reason to make perfect replicas of extinct species'* (p. 205). For Shapiro the project of de-extinction is disconnected from the question of identity.

This lack of care for identity makes sense. De-extinction is not necessarily connected to creating the extinct population. De-extinction is better thought of as *a set of techniques utilizing the remnants of extinct populations to make a proxy*. Therefore, de-extinction is not directed towards the recreation of an extinct population. It is directed towards using the remnants of extinct populations as biological resources. Wherever these remnants are found, be it in the preserved remains of organisms or in closely related species. Or even as information inferred from phylogenies. What unifies these techniques is the knowledge we gain from past living (and as a result viable) organisms.

Recreating "species" is not even essential to de-extinction. Reintroducing extinct variation into populations will be a growing area of de-extinction. This appears to be more important than de-extinction as focused on species and more likely to be successful. This would allow for the reintroduction of extinct variation into endangered species; like the Tasmanian Devil. The genetic diversity of extinct Devil sub-lineages, if recovered from preserved remains, could provide the genetic diversity needed for the population to recover. Further, one could consider the Tasmanian Tiger DNA in similar way. Tasmanian Tiger DNA adds diversity to help create a new Tasmanian Devil sub-lineage. When viewed from the perspective that we are aiming to preserve biodiversity, as described in Chapter 2, we see that these de-extinct techniques are better considered as the *biodiversity enhancement* of a lineage. It helps reintroduce the variation of lost lineages and spur the creation of new lineages.

To conclude, conceptual arguments are generally viewed as weak within the sciences and their application to conservation science are a case in point. Higgs (2003) has attempted to develop one in restoration ecology but has been deftly countered by Sarkar (2005; 2011; 2012) and Garson (2014; 2016). The same argument when entertained for de-extinction purports to establish that the recreation of a species identity is needed for the science to be successful. This, however, misunderstands the aims of the scientists, the techniques involved, and the goals of conservation generally.

6.4. Authenticity and Identity

Authenticity has historically been central to environmental ethics and conservation efforts within Western society. Nature historically was thought to be a teleological and powerful force separate from humanity. Something we can test ourselves against, and within it, experience something greater than ourselves. The autonomy and power of nature ground its authenticity. Any human actions that control or subdue nature are abhorrent in the view of certain environmental ethicists. This thinking has filtered through to the present day, all be it, with new justifications. New theories of authenticity have been developed for both restoration ecology and de-extinction with Elliot (1982) and Katz (1992) providing arguments that the value of ecological systems is diminished by restoration and Siipi (2014) arguing that the products of de-extinction are replacements that lack the value of the original species.

In restoration, both Elliot and Katz argue that historical etiology is necessary to retain nature's value. This is thought to be the same for species; the unique historical process of evolution is a part of what makes a species valuable. Some, like Siipi, describe de-extinct populations as "inauthentic" and of diminished value to the original. To justify the intuition that value is derived from etiology, Elliot uses a thought experiment with art forgeries. If we found out an indiscernibly identical piece of artwork was a forgery we would value it less. This thought experiment turns on individual psychology, and it may be true case to case, but Elliot intends to indicate a deeper truth about the natural value of nature. He believes that nature's value is non-anthropogenic in origin, and therefore intrinsic.

There is nothing in Elliot's thought experiment which could indicate authenticity is a source of non-anthropogenic value or why nature's non-anthropogenic value is derived specifically from a non-human etiology. I, like many others, am sceptical of nature's intrinsic value due to i) there is the ontological problem of where value could come from without an agent valuing it ii) there is the epistemic problem of how we can know exactly how much intrinsic value there is iii) if intrinsic value is priceless or of infinite value, as some claim, then it impedes environmental decision making (Weston 1985; Justus et al. 2009; Colyvan et al. 2010). Treating authenticity as a source of non-anthropogenic value for either species or ecosystems is quite implausible without some further story about what the connection between these two things is.

Katz (1992) attempts to connect authenticity to value by arguing that restoration makes nature an artefact. An artefact is thought to be different from natural systems because we imbue it with our own design, we make it functional for our purposes whereas he states that nature "lacks intrinsic functions". By imbuing function on nature, we remake the world as anthropogenic in an act of dominion over nature. This view is not particularly credible considering modern accounts of naturalized function (Garson 2016). One charitable explanation is that, according to Katz, function necessarily requires agency. But once natural systems are designed, they begin to work under their own power. When an ecosystem is restored, or a de-extinct species released, they will have their own trajectory in nature displaying their own agency. Most critically, the Katz theory of function cannot possibly apply to actual ecological systems; to apply to these systems they must not have been altered by human use. This cannot work, as all ecosystems on earth, maybe barring Antarctica, have had human populations influencing them (Cronon 1996). These systems will then be subject to the influence of human agency and as a result express the functional characteristics they create.

While Siipi does not appear to accept Katz's metaphysics of functions, she does appear to agree to his claim that intervention creates artefacts and artefacts are of diminished value. She argues that de-extinct organisms are *substitutes* and *inauthentic*. The primary aim of this discussion is to establish that saving a population is always preferable to recreating a population. Her discussion is summarized as an investigation into these two alternatives:

> *(F)irst, not having x (for example passenger pigeon) or anything of its kind; second, having y that resembles x (y is, for example, a bird that is not a passenger pigeon but resembles them to some degree). It is not self-evident that having y should then be favoured.* ***Since it is not x, bringing it to existence cannot merely be justified by anthropogenic loss of x****. Regarding the quality meaning of authenticity, the question concerns the choice between not having x and having a* ***poor or lousy x****. This may be an easier choice, and it might be claimed that as long as the existence of x is desirable, it is prima facie better to have a lousy x than no x at all.*
>
> *Siipi 2014, p. 91 (bold for my emphasis)*

Without Katz' metaphysics of functions or an explicit appeal to psychology Siipi does not provide a clear reason for why artefacts have diminished value, it appears to be just assumed. This analysis of the issue accepts that authenticity is a unique value, but that substitutes can be justified if they serve a purpose worth pursuing. While I can agree that it would be preferable to preserve species rather than recreate them, this view is due to practical and cost reasons rather than the existence of a value autonomous from our psychology.

As far as I can see, there is no option for Elliot, Katz, or Siipi to establish a basis for etiological value in nature that is not indexed to agential value. At times, all of them lean towards such a justification, Siipi quotes a quite anthropocentric Katz stating:

> ***What people value*** *in undeveloped nature is its natural history separate from human causation and activity. In an area that has been modified by human action there is a different causal history. Thus, even a perfect ecological restoration lacks the value the original natural system it is re-creating, for the restoration was the product of human action.*
>
> *Katz 2012, p. 68–9 (bold for my emphasis)*

This statement about biological systems seems plausible. If people see ecological systems and landscapes as having value derived from being separate from humanity, then this value is real. Bob Goodin outlines this relational anthropogenic source of value in *Green Political Theory* (1992). He argues nature is considered as valuable as it provides a way for people to find meaning in their lives by viewing themselves as linked to something bigger than themselves. Participating in a natural world which we view as autonomous and awe inspiring provides us with meaning[71]. Many environmentalists support similar accounts of the way nature inspires or overawes us and this experience can transform our values (Norton 1988; Sarkar 2005; Maier 2012). The important question is whether environmental awe and experience *requires us* to believe the environment has had a particular etiology.

The etiology of ecological systems will appeal to many people. I think we should concede this to the authenticity critic. People's connection to the landscape and environment is deeply cultural. The western conception of the environment is local to people of certain backgrounds, but it is no less real because of it. This is true of other cultures as well who have their own connection to the environment. I would find it sad if Kata Tjuta was levelled and then rebuilt from scratch, even sadder for the Pitjantjatjara for whom it features prominently in their Dreamtime stories. What is important is to incorporate, in the process of habitat preservation, the stakeholders who have some connection to the environment (Sarkar 2005; Sarkar 2011).

If authenticity's value is derived from cultural custom and the psychology of individuals, then it is not a particularly robust source of value in natural systems. Firstly, not everyone will particularly desire "authenticity" in ecology systems or de-extinct organisms. Siipi states that de-extinct organisms will be of diminished value due to their inauthencity, but people may value them more for being inauthentic! The novelty of bringing back an organism, which is "the same" as an extinct species adds to the value of that organism for many in the population. This feature is sometimes described as the "argument from coolness", that people are generally in awe and excited by the prospect of de-extinction (Sherkow and Greely 2013; Turner 2014). The novelty and coolness of producing previously extinct populations is much more profound than simply seeing extant species. The sight of living breathing "Thylacine" bought back after 90 years of extinction is, for many, more thrilling than

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[71] Some environmental ethicists believe intrinsic value can be relational (Sagoff 2009).

seeing the equally amazing extant Tasmanian devil. Further, once these organisms are released they will have their own autonomous trajectory, responding to current evolutionary and environmental pressures. Their novelty will build its own authentic responses to the environment.

There is no necessary connection between authenticity as people experience it and causal etiology. It is an empirical question as to people's psychological states when they go into an environment. Research is needed to determine the effects of knowing a biological system's etiology. Restored ecosystems are sought out and enjoyed by people regardless of their status as restored systems. People could have a non-causal conception of species identity and authenticity. Doug Campbell (2016) in his plea to resurrect an "authentic huia" defends the proposition that: *'for de-extinction purposes, Pb counts as being the same species as Pa just to the degree that many of the evolutionarily adaptive traits possessed by the members of Pa have been genetically inherited by and are phenotypically expressed by members of Pb.'* (p. 757).

Notice Campbell is not providing an account of species identity or taxonomy. This relation is only described as being "for de-extinction purposes". According to Campbell the purpose of de-extinction is to bring back an organism which possess certain aesthetic qualities; ones that will result in '*feelings of wonder, awe, pleasure, and appreciation'* (p. 757). These qualities will be experienced by a *'well informed person'* who *'would be recognizing them to be the product of natural selection operating on ancestral huia in the same brush'* (p. 757). On this formulation of the authenticity is the relationship between co-adaptive features and an extant environment. This is of course contingent on that historical environment being extant, which may be questionable due to environmental change since that population has become extinct (Seddon et al. 2014; Robert et al. 2017). But we can see that for at least some, authenticity is not an etiological relationship, or one coupled with a strong taxonomy of species.

Authenticity can in certain contexts play a role in conservation, but this role is not necessarily connected with identity or etiology. Attempts to establish identity and authenticity as values, which do not depend on the cultural and psychological norms of individuals, are deeply flawed. Further, the novelty of de-extinct populations will create their own value. This indicates de-extinction projects should be diligent in their public outreach, making sure their chosen project is something that interests the public and engages them. It does not show species identity is necessary for authenticity or even that authenticity is necessary for justified de-extinction.

6.5. Duties to the Dead

Public interest in de-extinction was piqued in 2013 by the TEDX public conference, which bought together the scientists at the forefront of innovative new de-extinction technologies. Michael Archer's announcement that the Lazarus project had succeeded in creating the early stage embryos of the extinct gastric brooding frog made headlines. In addition to this grand announcement Archer made a philosophically powerful claim that may have went unnoticed by some. He states that:

> *'If it's clear that we exterminated these species, then I think we not only have a moral obligation to see what we can do about it, but I think we've got a moral imperative to try to do something, if we can.'*
>
> *Archer, June 2013*

This implies we have a duty to bring back extinct species and if we have the technology we should. The recreation of species identity is critical to the de-extinction project as it is needed to satisfy this moral debt. If we create a new population that just appears to be the extinct population, we have not fulfilled our duty to the extinct population.

This deontic moral stance has been repeated within the philosophical literature with Karim Jebari (2015) arguing that causing extinction is a *'moral transgression, entailing a residual obligation'* and *'humanity has a prima facie obligation to re-create species whose extinction mankind may have caused'* (p. 211). Similarly, Shlomo Cohen (2014) argues that we have duties to resurrect as: *'If I kill you, thereby breaching my moral duty, but then serendipitously find out I can resurrect you (say, by praying for your revival), then surely a natural correlate to my duty will be to act for that restitution.'* (p. 172). He believes due to the duty to preserve life we have a duty to resurrect life even in the species case. This deontic argument has been entertained by several other authors (Thomas 2012; Greely 2013; Cottrell et al. 2014). Both the scientist Archer and Thomas and philosophers like Jebari and Cohen converge on a similar, ultimately flawed, position.

6.5.1. Against Duties

Traditionally duties are directed towards agents who can experience a wrong. To experience being wronged, an agent needs to have interests that can be impeded or welfare that can be diminished. For an agent to have either welfare or interests, then they must be alive. It is extremely implausible to think that extinct species could be entities that experience being wronged, as they are not agents and do not currently exist. Ronald Sandler (2014) particularly has emphasized the absurdity of this position as populations, or species, lack interests and have no welfare; both key for establishing agency (cf. welfare Basl 2017). One could press the idea that some collectives have agency (List & Pettit 2011). But species are not the sort of thing which share goals or actions or work in co-ordinated ways. This makes them dis-analogous from human collective institutions like corporate bodies (Feinberg 1974). Equally, there is a possibly insurmountable worry that these deontic arguments cannot avoid the Kantian problem of “ought implies can” (Kant 1999 [1781]). If it is not possible to recreate species identity through de-extinction, which looks likely, then we cannot have a duty to do it (Shapiro 2017).

But past the problems of application, even if we were to assume that there is a duty to de-extinct populations we would severely hinder conservation as an enterprise, creating counterproductive debates about blame and siphoning resources from where they are needed. The most important reason why we should not entertain duties towards extinct species is that it will overall reduce the number of species in the world. De-extinction is resource expensive and should be used sparingly and only with positive reasons, not obligation.

6.5.2. Establishing guilt

There is an epistemic burden and political cost created by believing we have moral duties to species whose extinction we caused. To know we have a duty to a species we must establish that humanity was the causal factor that resulted in the extinction. Extinction occurs constantly through the history of life (Barnosky et al. 2011; De Vos et al. 2015). Establishing that an extinction was caused by humans, or causally influenced by humans, rather than a natural extinction requires a huge investment of resources that could be spent elsewhere.

Identifying guilt has serious political ramifications when establishing causal connections between non-western populations of humans and extinct species. Debates about whether "native" populations caused the extinction of populations have been charged. For example, the debate whether Australian Aboriginals caused the extinction of Australian Megafauna, like the Diprotodon (a wombat the size of a rhinoceros), has raged for at least 40 years. Some scientists argue that the aboriginals hunted these species to extinction, while others claim that climate change was the culprit (Miller et al. 2005; Koch & Barnosky 2006; Dortch et al. 2016). These are controversial debates as aboriginal peoples are often thought of as stewards of the environment protecting the natural landscape. Their authority as owners of land is often predicated on this stewardship; it gives them tacit authority in ownership claims on lands they have traditionally occupied. Further, urban populations of western countries often desire to see native peoples as having a strong harmony with nature due to their cultural inheritance of "noble savage" cultural archetypes and use this to defend aboriginal authority (see Raymond 2007 for analysis of the "ecological noble savage hypothesis"). As a result, any claim that native peoples caused an extinction is controversial, conflicting with long held narratives in western culture about the role and legitimacy of native claims. To require the establishment of anthropogenic causation in extinction to establish a duty to resurrect a species would court controversy throughout the world. This is not to say that skewering such narratives is not valuable, or that political controversy trumps scientific fact, but I wish to point out that these are political battles that must be fought by the proponent of duties to extinct populations.

Establishing guilt, therefore, creates epistemic burdens requiring us to establish humanity had a causal role in extinction, raises conceptual questions as to whether we must be "the cause" or a "causal factor" in extinction to be morally culpable, and finally, has political ramifications as establishing aboriginal peoples are guilty of causing an extinction is extremely controversial.

6.5.3. Entertaining Duties will result in species loss.

It is believed that in just the last hundred years approximately 500 *vertebrate species* have gone extinct (Ceballos et al. 2015). The expected background extinction rate is estimated at 10 species per hundred years. So, while it is difficult to establish that any single species is extinct due to human actions, it appears clear we are causing extinctions. Extinction attributable to humans is, of course, not limited to recent times with humans causing extinctions for tens of thousands of years. The sheer count of species that we have caused to become extinct is staggering. If there are duties to resurrect species, then there are duties to an incredible amount of entities. It is obviously untenable to invest in resurrecting all these species. We may limit this to duties to species that we both caused to become extinct and it is possible to resurrect. I believe even in cases where resurrection is possible we do not have good prima facie reason to attempt resurrection. This is because at some stage we need to assess the cost of such a duty. If this cost is too high, we may not protect fragile species that are currently endangered[72].

One of the biggest impediments to conservation is the lack of funding to preserve species. Any investment in de-extinction should be assessed against what could be gained by investing that money into extant species (See section 2.2). There are currently very few individuals who advocate

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[72] This I will fully admit involves entertaining the idea that we have to do some sort of utility calculation. But many deontologists defend threshold/ non-absolutist/ moderate forms of deontology. In all these versions of deontology, duties can be weighed in some sense (Kagan 1998, pg. 79-84).

for the public funding of the de-extinction process, but there are many who assume that the state will accept the cost of maintaining these species once they are released. This will create significant burdens on environmental agencies. Even if external funding sources took on the cost of maintaining these species, the opportunity cost of these funds need to be assessed. This money could be spent on extant species to maintain their populations or do expensive translocations to preserve extant species like the reintroduction of the Eastern Bettong into Mulligans Flat Woodland in the Australian Capital Territory.

Recently, Bennett et al. (2017) calculated the cost of resurrecting an extinct species. In their calculations they generously assumed that external funding would provide the money to produce a small population of de-extinct individuals. However, once a population is produced it would create a burden on public funding to preserve this now endangered small population. They found that for the cost of funding the 11 species proposed for de-extinction in New Zealand they could preserve 31 extant species and that if the external funding for five focal extinct species in New South Wales was invested in extant species, 42 different species could be saved. These costs do not include the further cost of discovering that we caused a species to go extinct.

It is hard to justify investing money in extinct species. This is particularly problematic if one is to consider the moral weight of our duties toward extant species versus extinct species. While extinct species are non-existent non-agents, that our actions will not effect, extant species exist, and their possible existence requires our actions. It seems clear that if there is a duty to species, existing species have a much stronger claim to our public and private investment than extinct species. This claim is apart from the consideration that for the money spent on a single extinct species we could preserve considerably more extant species. Resurrecting an extinct species is not as morally important as preserving an extant species and the cost of resurrecting an extinct species could be applied to save many extant species.

6.6. Species Identity is inconsequential to De-extinction

Interest in the identity of species created by de-extinction has increased and I suspect in the next five to ten years there will be several further philosophical papers which will discuss the metaphysics of species resurrection (Delord 2014; Siipi and Finkelman 2017). While there have been a range of arguments which aim to establish that identity is important in de-extinction, I have found them all lacking. The conceptual argument is particularly weak and based on a naïve understanding of the science of de-extinction. De-extinction science uses the remnants of extinct species as a resource rather than being about the recreation of species. Authenticity is important for many agents but for many people the novelty of these species will bring about its own value.

Finally, there is no reason to believe we have distinct duties towards extinct species. Duties to extinct species demand us to act in the interests of non-existent, modally fragile non-agents, whom our current actions cannot influence. They are extremely abnormal recipients of duties. Most importantly, if we act on these perceived duties to extinct species, we will act in ways that will result in a world with less species as our resources will be draw away from more effective projects.

6.7. If not for the species lost, then why?

I have argued that there is no reason to slavishly recreate extinct species identity in de-extinction, but I have not argued against de-extinction in its entirety. To reject the idea that species identity must be recreated is not to reject the use of de-extinction technologies to create proxies for extinct species. However, the immense cost of de-extinction provides a large barrier for justifying the use of this technology. This final section has two distinct aims; to identify factors that support the use of de-extinction technologies and to consider the extent to which de-extinct proxies should resemble historical populations. I defend the position that de-extinction is permissible, and that historical resemblance is a prudential but defeasible rule in the creation of de-extinct populations.

Before addressing these reasons, I first outline what is currently the most comprehensive guide to what a successful de-extinction would look like. Seddon et al. (2014) provide an excellent guide for the conditions a de-extinction project needs to satisfy to be successful. They focus on the conditions needed for a de-extinction project to establish and maintain the population so that it does not (again) become extinct. They present these as series of questions which follow below:

1) Can the past cause(s) of decline and extinction be identified and addressed?
2) Can potential current and future cause(s) of decline and extinction be identified and addressed?
3) Are the biotic and abiotic needs of the candidate species sufficiently well understood to determine critical dependencies and to provide a basis for release area selection?
4) Is there a sufficient area of suitable and appropriately managed habitat available now and in the future?
5) Is the proposed translocation compatible with existing policy and legislation?
6) Are the socioeconomic circumstances, community attitudes, values, motivations, expectations, and anticipated benefits and costs of the translocation likely to be acceptable for human communities in and around the release area?
7) Is there an acceptable risk of the translocated species having a negative impact on species, communities, or the ecosystem of the recipient area?
8) Is there an acceptable risk of pathogen related negative impacts to the resurrected species and the recipient system?
9) Is there an acceptable risk of direct harmful impacts on humans and livelihoods, and indirect impacts on ecosystem services?
10) Will it be possible to remove or destroy translocated individuals and/or their offspring from the release site or any wider area in the event of unacceptable ecological or socioeconomic impacts?

These questions should be addressed in any de-extinction project, they are necessary conditions for de-extinction. I aim to develop sufficiency condition for going forward with one of these de-extinction projects despite the considerable cost. The conditions I explore at length intersect with questions 6, 7, and 9. There are three reasons for engaging in de-extinction projects I explore; public interest, fuelling innovation in conservation, and functional proxies. Given these reasons for conducting de-extinction, I then weight reasons for historical fidelity in de-extinction design claiming that given these interests it is prudent to be cautious in design. These arguments will complement the framework provided by Seddon et al. (2014) and provide a clear presentation of the reasons for de-extinction being a strategy within conservation policy.

6.7.1. Public Interest and Support

The strongest reason for de-extinction is that people want to see it, treat it as recreation, and will support its funding. De-extinction opens a new avenue for ecotourism (Whittle et al. 2015). There is little doubt that de-extinct populations are a huge draw for the general population, who are primed for such a development with de-extinction being part of the popular culture since the release of *Jurassic Park* in 1993. The draw of seeing these species is so profound that even ardent critics of de-extinction admit their desire to see these populations. Palaeobiologist Tori Herridge concedes that *'for all my protests, I'd pay to see one if it was there'* (Herridge 2014). Harnessing the interest in de-extinct populations to justify de-extinction is somewhat colloquially referred to as the "Argument from Coolness" (Sherkow & Greely 2013). I address some criticisms of the argument from coolness and provide some conditional support for this argument for de-extinction.

There are clear models for how de-extinction will be sold to the public. Ecotourism for "new" populations held within a national park will the mirror "last chance" ecotourism for critically endangered species or landscapes (Lemelin et al. 2013). With the growing impact of climate change on the Great Barrier Reef, tourism to this ecosystem is more and more frequently sold in this manner (Piggott-McKellar & McNamara 2017). In both these cases, the rarity and uniqueness of these environments act as draws gaining public interest. By playing to the tragedy of the impeding or historical loss of the natural world, these tourism ventures act to draw extra funding for these endangered ecological systems, providing a reason for investing in their continuing “health”.

Ecological systems with de-extinct species will also be sold to the public through a narrative of ecological optimism. Patrice Kohl (2017) notes that many interpret de-extinction as offering a scientific optimism to conservation narratives (while claiming this optimism is misplaced). Species loss and the continual failure of humanity to preserve biodiversity can led to pessimism about the long-term future of the natural world. De-extinction provides a case for people to feel optimistic about the ability of science to arrest the continual destruction of the natural world. This should not be dismissed; strong pessimism leads to conservation de-funding as people abandon what they see as hopeless projects. The science fiction aspect of these conservation technologies further accentuates the novelty of these populations. Novelty trades off against authenticity and creates its own value for de-extinct populations.

Some extinct species have become culturally significant and their resurrection will be consequently desirable. The Thylacine has gained much cultural cache in Australia featuring in the Tasmanian state cricket team’s logo and local beer companies label design, and features in numerous documentaries viewed by the public. The film of the last Thylacines walking around Hobart Zoo is etched in many people’s minds, leaving them with the strong desire to see this animal alive again. Public love for this organism plays a role in Tasmanian local culture. This interest supports the programs attempting to bring this organism back. Similar stories drive other de-extinction programs such as the Passenger Pigeon in the USA.

Basing de-extinction on the public’s willingness to pay for these organisms has been criticised by Derek Turner (2014; 2017a; 2017b). He argues that conservation based on public opinion is faulty. Firstly, public opinion is fickle; people could decide that they have no interest in the use of biotechnology. Second, conservation will only pick out organisms that the public knows and cares about; it would not encompass the many organisms that have become extinct that could contribute to the environment. Third, cool organisms are often big organisms, and there is an expectation that big organisms will have the most welfare problems in the application of biotechnology. This third issue I will put aside as I am focused on conservation issues.

All these points are salient. However, the first two problems are both shared by all conservation. The public is fickle and is often extremely inconsistent in the care it shows for the environment. The public has and will overlook extremely ecologically important species. Think of the care the public shows odd populations, which likely have very little potential for long-term survival. Chinese pandas have dominated public interest for many years as “cute” organisms, but they lack survivability in the long-term future without continuous human support. The same fickle public interests that dominate current conservation equally apply to populations we hope to de-extinct. Similarly, the arguments for harnessing to public’s interest in these animals apply to de-extinct populations. Pandas draw in money from the public for a range of conservation goals. The preservation of Pandas allows for the purchasing and defence of natural habitats for many other species which may have immense conservation value, that public cares very little for (Li and Pimm 2015). Equally, the money that is invested from the public in Panda research may develop conservation techniques and technologies that can be reapplied to other populations later.

The utilization of these single species of public interest in conservation is known as “flagship species” conservation and is well researched and debated in the conservation literature (see: Entwistle and Dunstone (Eds) 2000; Walpole and Leader-Williams 2002). De-extinction of large charismatic mega-fauna should just be treated like the preservation of any other flagship species. The justification for preserving flagship species is the public desire to see them and the resulting positive effects on the environment this investment will have. For example, the re-introduction of Mammoths would involve placing aside a huge amount of land for these animals to live on. Even without appealing to the functional role Mammoths could play in that environment the allocation of land would provide a habitat for many other species within the Siberian tundra and supply the money to maintain such parks.

Public interest and desire to see these organisms can be treated as a good in itself rather than a means to conservation. There is an open question as to whether de-extinction is justified regardless of its contribution to conservation or even if it occasionally trades off against conservation. If the public interest is high enough, this may justify de-extinction as a form of entertainment and the parks formed around them for recreation. If we were to take such a stance, then any conservation gains would be a happy by-product of de-extinction rather than its core purpose. This is a strong possibility if de-extinction is left to be researched and developed within private businesses that must turn a profit.

Public interest in de-extinct organisms will, I believe, be the strongest factor in determining which extinct species have the necessary investment for de-extinction. The question that should emerge is how to harness public interest so de-extinction projects can have a net positive effect on the environment. This will not be straightforward, but the current use of flagship species will provide guidance for future projects.

6.7.2. Fuelling Technological Innovations

De-extinction projects will fund the development of conservation technologies. These can be refined and re-applied on extant endangered populations, likely to yield more success than extinct populations. Genetic engineering will increasingly become essential to conservation in the future. Introducing genetic variation into extant populations will become a widely used conservation technique. Many populations of large conservation value have been reduced in size drastically in recent history (Frankham 1996). While these species still exist, they exist with a significant reduction in their previous genetic variation. Their inbreeding can result in genetic diseases and susceptibility to infectious diseases. A prime example of this is the Tasmanian Devil populations whose limited variation was recently further decimated by the transmissible cancer Tasmanian Devil Facial Tumour (TDFT). Some scientists researching this problem believe that the cancer is able to survive and pass between individuals due to the limited genetic variation in the population (McCallum 2008).

Endangered small populations are extinction time bombs waiting to happen. Small populations often take a “drunken walk”, not being able to arrest their decline through the sudden occurrence of stochastic events. It could take just the death of a pregnant female or the sudden introduction of a new disease to completely wipe out the population. This has led many ecologists to believe that there is an “extinction debt” in which the current degradation of habitats and population loss will result in extant species becoming extinct in the near future without large and targeted investment (Tilman et al. 1994). Increasingly direct action will be required to preserve such populations, including genetic modification.

The type of modification will depend on the case but there are a couple of obvious candidates. Variation can be introduced through cross-breeding, for example some Tasmanian devils appear to be resistant to cancer and these individuals are being cross-breed with the remaining population which lack such resistance but have other unique genetic features (Epstein et al. 2016). But sometimes there is no alternative population still extant to supply genetic variation, and in such cases genetic variation will have to be introduced through genetic engineering. Scientists are becoming more comfortable with this option. Genetic engineering to introduce genes which protect the population from diseases is largely viewed as reasonable. A recent survey of conservation scientists found that 43% of scientist supported genetic engineering of extant species, if the alternative was extinction, to 35% against (Taylor et al. 2017).

Where should the genetic variation come from if not extant populations of that species? A good option, when possible, is from deceased individuals of the same species. By finding the preserved remains of diverse individuals within a species, we can “de-extinct” extant populations by introducing diversity that was there in recent history. Sequencing the remains of dead individuals of extant populations may find a wealth of lost genetic variation. Similarly, we may look at closely related species. Introducing genetic variation from closely related populations would introduce much needed variation. This often happens naturally. With the melting of the ice caps, polar bears are losing more and more of their habitat. As polar bears are driven from their northern habitat grizzly bears are moving north with the warming of the polar region (Kelly et al. 2010). The reducing genetic variation in polar bear populations due to death and loss of habitat is being bolstered by cross breeding with grizzly bears. Genetic engineering could fill the same role introducing genetic variation from related species to ensure their survival. These related species need not currently exist, they may be extinct.

In the case of both the de-extinction of the Mammoth and the Tasmanian tiger the surrogate species are also endangered populations, the Asian elephant and the Tasmanian devil. In both cases the introduction of genetic material may help preserve these populations. For the Tasmanian devil populations, the introduction of genetic variation may provide some variety that will allow for the new “hybrid” population to avoid cancer. The case for creating Mammoths to help save Asian elephants is even stronger. The Asian elephant’s habitat is the forests of south-east Asia. Much if not all South-East Asian countries are emerging economies and are seeing rapid growth both in their economy and population. This has led to the clearing of many of the forests that form their habitat. By introducing Mammoth DNA to Asian elephants, we create an elephant population that is adapted to the much more sparsely populated tundra. This creates a secondary population of Asian elephants and increases the chance this lineage will survive into the future. Does this mean that we don’t have to worry about preserving Asian elephants? Of course not. We should invest as much resources as we can into preserving the native population, but this provides a secondary population that would not have existed otherwise.

If de-extinction appeals to the public, or wealthy individuals enamoured with recreating extinct populations with futurist technologies, there will be a source of funding for the development of new conservation technologies. If this source of funding does not compete against other conservation funding, it will provide useful techniques for future conservation work for little immediate direct costs to conservation.

6.7.3. Functional Use

A common reason for the creation of populations resembling extinct species is making functional proxies for the extinct population (Shapiro 2015). Ecological function, as argued in the previous chapter, is best construed in term of CR functions. These functions will describe the way the de-extinct populations support the capacities of the larger ecological system they belong to. The capacities that will be particularly desired are the ability of the populations to support ecosystem services for humanity and support biodiversity. Utilising functions in support of de-extinction is not, however, as strong as an argument as some proponents of de-extinction have made it (Brand 2013; Shapiro 2015). Causal capacities can be satisfied often by other populations, or direct human intervention on an ecosystem. So, while I believe that functions can support the use of de-extinction, I am sceptical that many species will have both a unique and a strongly causal role in ecological systems to the extent that would justify the investment.

To gain a more precise understanding of what sense of function scientists mean when they say that we should engage in de-extinction to recreate lost functions we should look at the cases these scientists present. Beth Shapiro starts with cases of ecosystem restoration and presents future de-extinction cases as being continuous with ecosystem restoration. She examines the purportedly analogous idea that the American Southwest should be re-wilded, with populations of giant desert tortoises and bison being reintroduced into the area (2015, p. 160). The hope is that by reintroducing the tortoises, these animals will return to grazing bunch grasses and digging burrows, this will spread seeds and change the landscape from bunch grass monocultures to a more diverse assemblage of flowering plants. The bison similarly graze away woody plants and fertilize the area with their excrement. In reintroducing these large animals, they hope to *increase the diversity of the plant populations* in the area and in doing so *increase the diversity of fauna populations*.

A similar justification is presented by Shapiro to support the de-extinction of the Mammoth. Woolly mammoths reintroducing to the tundra would, hopefully, increase the diversity of plant life and in doing so increase the diversity of animal life. The hypothesized mechanism is that Mammoths will turn over the snow to graze on the grasses underneath exposing the ground to sunlight allowing for more grasses to grow later into the winter. This changes the tundra from being covered in snow to grasslands, which in turn would attract other grazers and the predators of these grazers. Similarly, when Stewart Brand argues for the recreation of passenger pigeons, he focuses on the pigeons' effects on tree diversity (Brand 2013). The pigeons were major pollinators and seed distributors for large trees throughout North America. The recreation of this relationship justifies the investment in their resurrection or the production of pigeon proxies.

At the forefront of both the justification of restoration and de-extinction is the idea that these organisms have functions which are desirable, as they increase the biotic diversity in an area. This is indicative that the general notion of ecological function in use is that populations are functional if they promote and maintain local biodiversity. This can neatly be precisified through the framework outlined in the previous chapters (Chapter 2, 4, 5). Scientists will attempt to make inferences about which populations the de-extinct species will promote. This provides a set of populations, the indexical community, for which the focal species is functional for. If the de-extinct population promotes biodiverse populations, populations that represent considerable phylogenetic heritage, then we have general prudential reasons to support them.

Function as promoting biodiversity or populations of stakeholder interest is, however, not the only account of function being used to justify de-extinction. Shapiro provides a second function that Mammoths provide by their foraging. When Mammoths remove the top layer of snow, they expose the soil to the cold air, which freezes the soil and preserves the permafrost. Normally snow insulates the soil allowing it to be several degrees warmer than the air temperature. Mammoth grazing creates a cooler microclimate and slows the melting of artic permafrost. This allegedly could help slow down global warming! This seems to be a fairly bold claim and I am somewhat sceptical of this strategies cost-effectiveness, but let’s assume it is a major factor justifying Mammoth de-extinction. This effect does not directly preserve biodiversity, but that would be a downstream effect as reducing the impact of global warming will reduce the loss of biodiversity. Moreover, Mammoths are desirable as their actions provide a direct service to humans. The reduction of climate change is a direct and immediate utility to humanity analogous to other climate change amelioration techniques.

The framework I have previously outlined can display how de-extinct populations can form functions for biodiversity, stakeholder determined sets of populations, and ecosystem services. De-extinct populations could perform causal role functions for biodiversity or ecosystem services or a set of populations we find desirable (Chapter 2, 4, 5). In such cases, where the indexical community formed around de-extinct species acts to promote these features, we have a reason to create such organisms. Many of the proposed organisms historically had major impacts on their environments so this idea is at least plausible, but there are further considerations that need to be first addressed in order to establish de-extinction is the best plan of action.

The de-extinction supporter will hope that the introduction of de-extinct populations will form causal role functions acting to promote these desirable features. However, I have also raised a series of issues with ecological causal networks forming stable and specific causal relationships (Chapter 4). Often causal interaction in ecological assemblages are the product of *ensemble robust* interactions, where individual population are not critical for an ecological output. The issue of non-equilibrium ecology still looms. Many populations have little impact on the other local populations that constitute a community. If the de-extinct populations are similarly causally inert or indistinct, they will have no real functional upshots. Determining the possible impact of these de-extinct populations is a large epistemic barrier.

Another issue with predicating the value of de-extinction on ecological function is the issue of replaceability or functional equivalence. Many ecological functions are wide-grain descriptions of capacities that many populations can fulfil. For example, if we are looking for an organism which can fertilize the ground, there are many populations that can fill that role. Many ecological relations are highly overdetermined by many different populations playing small causal roles to produce some output, fluctuations in a single population have very little impact of the functionality of the overall system (Chapter 4). Given the highly replaceable nature of many ecological functions, there is a good chance for any extinct species there is a currently living population that can fill the same ecological role. This is less likely with charismatic megafauna, which further justifies de-extinctions engagement with these species. This theory is at the core of many restoration ecology projects, which can involve the relocation of populations to fill a functional role that was not historically present in that habitat (Seddon 2010).

If there is an extant species that can serve the same function for these systems, then it will be cheaper and more likely successful to relocate this species than to conduct expensive research into recreating a lost population. Extant species will have more genetic variation and will be less susceptible to a secondary extinction. If the population number drops low, or genetic variation reduces, individuals from the parent population can be released to reinforce the relocated population. The relocation of populations has had some success (a bit under 50% success rate by 2012) and there are case studies to base ecosystem restoration by relocation projects from (Sheean et al. 2012). Given this, if the aim of a de-extinction project is the restoration of a local ecological function, then extant species, which can act in the same functional role, should be considered first.

Due to the problems of establishing a de-extinct population that will act in a unique and causally salient way, we may doubt the role of function in justifying de-extinction. This should be true of most species. This, however, does not bar all cases. If we look at the proposed species for de-extinction, we see that these are often populations that are large charismatic megafauna. This is often thought of as problematic as it indicates that we select organisms that we find aesthetically pleasing (Turner 2014). But big organisms which consume and contain large amounts of biomass have suitably disproportionate effects on ecosystems. This can be seen in the radical changes that ecosystems underwent after the megafaunal extinctions that coincided with human movement (Miller et al. 2005). It is much more plausible that large herbivores, like Mammoths, or apex predators, like Thylacines, will have strong causal impacts on ecological systems when compared with many other species which have become extinct. This, in turn, unfortunately makes it less likely that they will have living surrogates. Similarly, large populations of organisms that coincide can have large effects on ecological systems, such as in the case of the passenger pigeon. This, however, creates a further burden in de-extincting large populations of animals to recreate their desired functional effect.

The restoration or creation of ecological function is a plausible reason to engage in de-extinction and is an undeniably good reason to engage in such expensive methods. There are two worries, however, that must be addressed for any species. Firstly, many species have little effect on their local ecosystem, and so we must determine that the extinct species will have strong local causal effects on an ecological composition. Secondly, the function should be shown to be unique. If an extant species can perform this function, we should prioritise it. I believe that there are cases that can satisfy these conditions, usually large megafauna or other populations with strong niche constructing effects. So, despite some reservations, many of the species proposed for de-extinction may be supported for investment by their potential functional action. Functions, which I view as particularly important for long-term conservation goals, include the promotion of biodiversity and the support of unique ecosystem services. De-extinct populations may, in the future, play a unique role in conservation.

6.8. Constraint in Creation

Despite the cost of de-extinction there are important positive reasons for us to permit the de-extinction of populations. The products of this technology will never be perfect copies of the lost populations. If they are created through genetic engineering or back-breeding large sections of the genome will be derived from the extant populations that are being utilized in this process. While cloning can produce very similar individual organisms, to the ones lost, to create a viable population we will need to introduce genetic variation into the population of cloned animals. This will often be from extant populations. Whatever the technique used there will be a distinct deviation in the properties of the de-extinct population from the extinct population. Given these deviations are a necessary corollary of de-extinction, then we need to ask how large the deviations should be.

Deviation from a reference state can come in several different shades, in both restoration and de-extinction. We may be worried about the extent to which the new synthetic biological system approximates the old systems. When we introduce Thylacine DNA into a Tasmanian devil how much is needed? Do we need to replace as much of the differing code as we can? There needs to be some benchmark to know when we have succeeded. This will be determined at the start of the project. For example, our modified Asian elephants must be able to survive the arctic winters and successfully forage. But we can also have more than two biology sources for a de-extinction project, we may want to be not limited to just Tasmanian devils and Thylacines in Thylacine resurrection. Other more distantly related populations may have biological features that are desirable, such as genes for resistance to cancer in the case of modifying Tasmanian devils. This would produce chimeras with features of multiple species. De-extinction techniques may of course be used in ways not at all moored to any historical reference state. Synthetic biology can create new genes from scratch with the Venter Lab in 2010 synthesizing the genome for a single cell organism (Gibson et al. 2010). With genes being able to be created at will, we could create genes without any historical precedent or indeed whole populations without a historical basis.

The possibilities biotechnology creates for conservation are gaining some initial interest. De-extinction and synthetic biology may be one of the few ways we can actively increase biodiversity within ecological time scales. Christopher Gyngell and Julian Savulescu (2017) argue that the assumed asymmetry between conserving and promoting is not justified. If we have a duty or interest in preserving extant species, we have a duty to promote and produce new species; we must promote biodiversity. They explicitly do not limit the promotion of biodiversity to organisms that have existed but are open to the creation of new organisms to promote biodiversity. *‘(I)f species diversity is not at some optimal level and increasing diversity is either intrinsically or extrinsically good, we have reasons to create novel life forms, which increase species diversity.’* (Gyngell & Savulescu 2017, p. 424-425).

While I have provided reasons to believe there is no moral requirement for de-extinction to reproduce extinct species, I do not think it is wise to completely dispense with historical reference states. Many of the reasons for this are prudential, as there is a lot of uncertainty in what populations can do when released in the wild. This is true of species we have a long history cohabiting with, let alone species we have just created (Elliott-Graves 2016). Think of the impact invasive species have had on ecosystems. Europeans have had a long history of co-habitation with rabbits but did not predict their impact on the Australian landscape. But past these known risks of introduced species destroying the environment, there are strong reasons to be more conservative in de-extinction projects. The creation of new species or radically chimeric species without clear historical references will undercut the best reasons for reproducing these species. This is particularly true of public interest and ecological function but not so true in the case of de-extinction being used as a means for technological innovation. I, therefore, find it permissible to promote phylogenetic diversity by reinforcing extant endangered lineages, but I am significantly more sceptical of the radical creation of new lineages. Below I present two further reasons for us to be conservative in our species design.

6.8.1. Historical Fidelity and Public Interest: How the Tiger lost its Stripes.

One of the, if not the, strongest reasons to engage in de-extinction is the public support it will gain. The public support is contingent with the population appearing to be the same as the species that previously existed. This produces a strong pressure, to at the very least, recreate the physical features of that population to the best of our abilities. When scientists attempt to reproduce a population of Thylacines we may succeed in producing larger more dog-like Tasmanian devils, but if these organisms have something cosmetically different, there will still be some public disappointment. It may be extremely difficult to find the genes for the Thylacines distinctive tiger-like coat, which gave the Thylacine its common name; the Tasmanian tiger. I could imagine the organism produced by genetic engineering could have the distinct black coat with white patches of the Tasmanian devil. In this case, one of the main aesthetic draws of the Thylacine would not be recreated. This difference while cosmetic would lead to significant disappointment, as the Thylacine’s stripes are commonly depicted in the artwork that the public has seen.

When the justification for de-extinction rests on the public’s interest in seeing organisms that they, like all of us, have only seen in artwork or recreation sketches; we need to be conscientious of their expectations. The standards for these de-extinction projects should then include a strong emphasis on historical fidelity in physical appearance or behavioural attributes if these are recorded and part of our social expectation. These expectations act as a benchmark to assess the products of this technology.

6.8.2. Resemblance and Function.

Resurrecting species is valuable if the population of interest has a unique functional role in ecological systems. Given the unique nature of their functional capacities historical fidelity will need to be close to the original species. The population used as the base of a de-extinct population will not have the desired functional capacity, so alterations that result in the extinct populations' functional features should be prioritized. If we are to recreate a Mammoth, or ecological proxy for the Mammoth, we will need to prioritize the addition of tundra adapted functional traits into Asian elephants. These will be the matted fur and body heat regulation that allow for them to survive in cold climates and an increase in size that facilitates their ability to consume and move so much biomass. These features would be necessary for them to perform the causal role functions they are intended to play in the systems, be it the promotion of biodiversity or some further factor. The amount of genetic information we need to add to any extant species will depend on the trait but for more complex and unique traits, we can expect that there will be significant alterations needed.

Large deviation from the historical species can lead to either the population not filling its intended role or possibly acting in unexpected ways. Genetic engineering two species together is a forced hybridization and heterosis, or “hybrid vigour”, is a well-known phenomenon. Historically it has been exploited by humans to create more resilient higher production crops, including Durum Wheat. It is possible that once a population of de-extinct organisms is large enough to have genetic variation and survivability it may exhibit such characteristics. This is another reason to show prudence in genetic manipulation.

If the aim is to recreate the functional capacities of an extinct species, we have good reason to be conservative in the populations that we create. Radical change may not produce the features we are aiming to recreate. Given the uncertainty about the properties of the de-extinct organism will possess we will need to defer to history when recreating functions.

6.9. Conclusion: Defeasible Historical Fidelity

De-extinction will very likely be utilized in the future to create organisms that will be released into the wild. This is due to the way this technology has garnered great public interest. The hope is that these populations will not be produced simply for the novelty of it, but for real conservation reasons. Utilizing historical reference states in de-extinction is preferable as it will result in the populations being desirable to the public, more predicable in the wild, and possessing the functional features we desire for these ecosystems. Historical fidelity will act as a standard by which to assess the products of this technology, that is, a bar to assess when the population being modified is ready to be released. Despite the role of history in this technology, I think that historical fidelity is defeasible. When altering the population allows for it to be viable and healthy, we need to consider introducing other features. The chimeras’ produced by such a process will require greater scrutiny for their possible effects on the environment, but this does not preclude them from being produced. Ultimately, the gains of de-extinction will need to be weighed against the costs. Public desire to see these populations will go a long way in order to support their production. If we are wise and considerate of the possible ecological ramifications, both positive and negative, we can exploit this public desire to make real conservation gains.

Chapter 7. Conclusion: Where to Now?

The need for a new philosophy of conservation science is immediately apparent to me. Environmental ethics as an intellectual endeavour predates conservation science. Whereas environmental ethics came into existence in the 1970's, inspired in part by the work of Leopold in the 1940's, conservation science was a more recent amalgamation of researchers congealing in the 1980's. The topics, trajectory, and debate of environmental ethics pre-date conservation science. Its focus remains directed at ecosystems and species as the units of conservation. Many of the actors that started environmental ethics are still at the helm of its journals, constraining the discussion of how we should morally act towards the environment. This thesis did not assume the cannon of environmental ethics is the best starting place for the moral consideration of the natural environment. Instead, I start with conservation science and concepts that it treats as central to its project, primarily biodiversity, and build a framework for philosophy of conservation science from that point. This provides an alternative view of the core units of conservation and ties those units directly to a rigorous, scientifically informed, metaphysics of ecology.

The lynchpin of this thesis was a realist theory of biodiversity. The search for the best single measurement for biodiversity is no doubt controversial. Many would prefer biodiversity to track whatever it is in the environment that we value. I provide an alternative view, attempting to explicate biodiversity so we can measure and prioritize the unique biological entities we are losing globally. I tie biodiversity to the best current science for how life differs and aim to avoid the gerrymandering of what "should" be preserved by powerful interests[73]. Higher quantities of biodiversity are something we *should preserve* as a prudentially rational action. The hope is to provide a bedrock for conservation. Other environmental features that are tracked by current preferences and other

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[73] This is not to say that *only* the biodiversity realist may avoid gerrymandering by powerful interests.

biodiversity measures are important for our varied ends but a global measure acts as a tool for co-ordination in our conservation aims.

To argue for my biodiversity realist position, I present a series of desiderata for a measure of biodiversity. This process of presenting desiderata and explicating biodiversity is similar to the attempts to explicate “species”, and it is from the species concept literature that I derive and modify my desiderata. Utilising the species concept literature is justified, as nearly all commentators in the biodiversity literature possess what I refer to as a “taxonomic assumption”; the belief an adequate measure should represent taxonomic spread. Under the analysis in Chapter 2, any measure of biodiversity should be *tractable*, *theoretically fundamental*, *representative*, and *normatively demanding*. Given these desiderata, the natural quantity in the world, biodiversity, should be measured using phylogenetic methods. Preserving biodiversity will be best achieved by preserving the distinct evolving lineages within the tree of life, preserving and providing potential for the ongoing diversification of life on earth.

This lineage-based conception of biodiversity prioritizes the entities that are subject to ongoing evolution and possess unique features. This approach provides an alternative to the land ethic, which describes the whole ecosystem as the right entity to preserve for conservation. In the third chapter, I respond to an objection to focusing on lineages rather than ecosystems. Could not ecosystems themselves be units of biodiversity? In a word, no. I deploy and develop the arguments of Robert Ricklefs (2008) to argue for a type of ecological community eliminativism. They do not hold together in ways that allow for the easy predication of properties due to their loose causal ties, lack of boundaries, and rapid change. But critically, Ricklefs argues that the predication and explanation of ecological processes are not best done at the “local ecological community” level. If we wish to explain the distribution and abundance of organisms across a landscape, we should look to the higher-level biogeographic arrangements or down at the level of individual organisms and populations. Given that there are no clear kinds to distinguish diversity between communities, there can be no biodiversity measures of ecological communities.

This scepticism is further developed in the next chapter, where I explain why the new emerging literature on biological individuality should not be applied to ecological communities. I, however, do not dwell on the negative, developing a new framework for explaining and representing ecological communities. This is achieved by deploying the interventionist causal framework from James Woodward (2005), and the causal network literature, to represent ecological communities indexically. Ecological explanation is extremely explanandum dependent; the weak causal network that unfurls from the features of interest needs to be mapped for useful explanation to follow. The explanatory dependence is critical, as a community is not a kind, it only emerges from populations and processes of interest. Given this flexibility in what indexical communities are, I can describe the relevant causal communities for multiple different ecological phenomena. Of particular interest, for this thesis is that we can identify the ecological communities that support higher quantities of biodiversity or the ecological features conservation stakeholders' desire.

Deploying a framework in which a community is identified from multiple causal networks, emerging from different points of interest, allows for the identification of robust causal structures in the system. My ontology of ecological communities is tied to the robustness of ecological causal structure. I distinguish between two types of robustness; Wimsatt robustness, when the same spatial arrangement of descriptive features emerges from different "theoretical perspectives", and, Woodward robustness, when different initial conditions result in the same causal event. The more causally and descriptively robust an ecological community is the more "real" it is.

This exploration of the ontology of ecological system continues in the next chapter, where I consider whether ecological systems can possess natural functions. A major consideration in multiple debates in ecology is whether ecological systems can possess functions with "natural normativity". Natural normativity is when a trait within a system has a functional role, which supports that system in such a way that the trait should act in certain way. If the trait does not play its functional role, it is malfunctional. This normative dimension to system composition has often been used to buttress ethical decision-making towards natural systems. Naturalising disease involves describing the natural functions of a body and the processes or factors that impede these functions. If ecological systems had a similar functionally organised structure, then many contested debates could be adjudicated by simply asking the question of whether something helps or hinders natural functions.

I analyse the possibility of natural functions in light of my graded view of communities, in which they can have more or less robust structures. Communities rarely have natural functions. When they do, these functions are localized to a small set of populations, which have usually evolved together to create mutual dependencies. A consequence of the limited presence of natural function in ecological systems is that they provide little guidance in the various debates where they have been deployed. However, while natural functions are lacking from ecological systems, explanatory functional language is generously applicable. We can explain the causal capacities of ecological systems through the causal and constitutive contributions of the lower-level parts of these systems.

Explanatory function cannot tell us what we should do but gives us a guide to the causal possibilities in a system. We can then explain what maintains features of ecological systems we desire to conserve or features we should preserve, like biodiversity. Functions for maintaining biodiversity provide a reason for the preservation of many ecological systems and is a resource for adjudicating many debates. I use explanatory functions for biodiversity to provide reasons for controlling invasive species that are not solely dependent on personal preferences. This framework is again redeployed in the next chapter to provide reasons to resurrect extinct species. If these species provide ecological functions, which promote biodiversity, we have a reason in favour of using biotechnology to bring these species back.

This final chapter, considering de-extinction, represents an engagement with both the application of the framework built in the previous chapters but also an opportunity to reply to several arguments born from the romantic environmental ethics tradition. Romantic environmental ethics strongly emphasises the separation of humans and nature, this position is naturally sceptical of the use of biotechnology for conservation. Considering de-extinction provides an opportunity to enquire into the importance of historical reference states in conservation. I argue for a limited role for historical reference states, that we have prudential reasons for deriving biological design from the past but these reasons may be overruled. Ultimately, I am convinced that public interest in these species will be the main driver of de-extinction projects.

This thesis has addressed a series of issues within philosophy of biology and environmental ethics with the aim of supporting a new sub-field, philosophy of conservation science. I analyse and interpret key concepts like biodiversity, ecological communities, and ecological function, providing a comprehensive framework for how each can help mutually define each other. This framework is then applied to questions like "when do we control invasive species?" and "should we resurrect extinct species?" This project has the potential to be developed and expanded on in multiple ways and I look forward to doing so and sincerely hope that others will find the value and potential in it to do likewise.

7.1. Future Directions, Things Unsaid.

Despite the length of this thesis, what has been provided is but a cursory glance at the possible areas to consider. There is much work to be done to develop the ideas outlined. As such, what may appear as future directions blurs into things I wish I could have said but did not have the means to say. Much of what I wish I could have further developed is the ethical and political dimensions of my work. Throughout the thesis, I have purposely avoided the ethical and political; this is with good reason. There is a lot that could be said within the ethical and political domain and my aims were to describe a comprehensive conservation ethics built from our best scientific conception of the world. In doing so I have tended to avoid describing how public interest in conservation governs environmental practice, barring the last chapter. The link between the public interest in conservation and the scientific and economically rational reasons for conservation crucially needs to be developed. There is also further potential to develop and apply the conceptual machinery in this thesis and I provide some suggestions for future direction there too.

7.1.1. To Preserve or Promote Biodiversity?

A question that could appear in Chapter 2, but appears in Chapter 6, is whether we should promote biodiversity, using technology like CRISPR to alter extant populations. De-extinction is really a special case of biodiversity enhancement, as we use extinct varietals to increase the genetic diversity of current populations. Gyngell and Savulescu (2017) directly raise the old utilitarian point that if the good is worth preserving then it is worth promoting. In the case of conservation if it is worth preserving biodiversity then it is worth promoting biodiversity. While this may seem far-fetched on first pass, upon discussion with a conservation scientist (I will not mention their name) I have come to the belief that this is a position to address seriously. We are currently living within a world with high extinction debt. The density of wild populations has reduced drastically. Many populations lack genetic diversity and live in isolated small habitat patches, which cannot support an ongoing lineage. This species loss will be further exacerbated by climate change; these populations are stuck in increasingly foreign environments without the ability to move or the extant variety to adapt. These populations are then walking dead, just waiting to finally disappear. Biodiversity promotion could involve the enhancement of populations through the introduction of variation into wild populations, which previously did not have such variation. For example, introducing genes coding for proteins that help with temperature control. This could blur into the wholesale creation of new species adapted to earth's new environments. An extended analysis of this possibility in the mould of Chapter 6 is required, first addressing whether there is an asymmetry between preservation and promotion then turning to the specifics of when promotion is acceptable.

7.1.2. Why Lineages?

In my chapter on biodiversity I defend the position that biodiversity is best preserved through the conservation of phylogenetically diverse lineages. I take for granted in my discussion that these lineages are populations that are currently “in the wild”, in some sense, they are actively interacting with other populations and subject to natural selection. But the phylogenetic diversity of lineages could be possibly represented through inert samples of lineages. This is particularly true with plants, fungi, and microbes. Immensely important projects like the Millennium Seed Bank Partnership in Kew preserve the historical diversity of many species through taking static snapshots of their populations, storing samples and seeds in laboratory conditions. This is of course harder with animals but with improvements in de-extinction technology this could be possible. In the G.R.R Martin sci-fi novel *The Plague Star* he describes an abandoned spaceship once possessed Federal Empire’s Ecological Engineering Corps. This “seedship” contains genetic material from the entire galaxy and the technology to recreate any organism stored within. This ship is used to colonize worlds and conquer adversaries with some well-deployed T-Rex’s or flesh-eating bacteria. Such a ship could be taken as representing the apex of my theory of conserving biodiversity, an encompassing static snapshot of diversity catalogued so that we may utilize it for our varied needs. But instead, I believe that we should preserve population that are extant, and in the world, both currently evolving and subject to natural selection. This is a difficult position to defend but I believe that the possibilities represented by evolvable dynamic populations, better supply us with tools for the future and would wish to defend this point.

7.1.3. Extending the Indexical Communities Framework

In Chapter 4, I provide a way to address the description and ontology of ecological communities. I argue ecological communities are best understood through indexing causal structure to points of explanatory interest. This account aims to be both explanatory and descriptive of diffuse, open, non-cohesive causal systems. There is then naturally the possibility that it can be used to describe other similar causal systems. Within the social sciences, many systems have similar diffuse causal structure and there is abundant opportunity to reapply this framework. The ontology of economics is a particularly promising area to reapply this framework. “Markets” have similar semi-modular diffuse structures and the indexical framework could be fruitfully applied to distinguish their causal structure.

The indexical community’s framework does not exclude some ecological systems bordering or achieving biological individuality. It aims to describe systems that may evolve or progress between diffuse weak causal structure and strong cohesion. This makes it a useful tool to determine the extent to which a causal system resembles an aggregation or tends toward biological individuality. An area in which this discussion is much needed is the microbiome. The microbiome is the combination of a multicellular host, like the reader of this thesis and myself, and the array of bacteria, protists, viruses, and other beasties that make their home in and on multicellular organisms. Recently, Derek Skillings (2016), in reply to the recent push to describe the microbiome as an evolutionary individual, argues that they are better conceived as an ecological community. This appears to be the right suggestion but there remains work to determine the extent to which the microbiome differs from macroscopic ecological system. The indexical community framework should provide resources for determining this.

Finally, I describe how this framework could be used to create an “anatomy” of a system. This is through using Wimsattian robustness to identify the spatial arrangement of descriptive properties. I would like to acquire some ecological community data and construct an anatomy of an ecological community. Through the implementation of this framework, I hope more precision and possibilities can be discovered.

7.1.4. What of Public Opinion?

The interaction of conservation with public opinion is something that Sahotra Sarkar (2012) takes as central to conservation; this is to the extent that he even defines biodiversity through convention. The public, according to his view, should be consulted at all stages in conservation projects and are the ultimate determinants of what features constitute biodiversity. This is how Sarkar aims to avoid powerful actors gerrymandering conservation goals to avoid incurring any costs. Biodiversity realism mitigates the impact of the public and political power by looking to provide a global and scientific interpretation of biodiversity. This interpretation of biodiversity is more limited then conventionalism as it is a baseline for conservation or a gap filler; a prudentially rational conservationism does not rely on individual interests in nature to ground conservation or any deep ethical theory. However, this only gets so far, individuals may only want to invest fleeting amounts into the mitigation of risk. Further, people really do like the environment, often for drastically different reasons.

In this thesis, I have explored the extent to which a scientific notion of biodiversity, and the causal structure that supports the populations that constitute biodiversity, can help unravel tricky problems in conservation science. If it could, we would have clear guidance in addressing difficult problems like whether we should eradicate invasive species or resurrect extinct species, objective non-politically contestable answers to fraught questions. However, as we have seen in my answers to these questions, the appeal to biodiversity can do some work, but ultimately public opinion will also be critical. As a result, public opinion is necessary for conservation decision making, but I have not developed how my framework can interact with public opinion. If this thesis was to be converted to a book, I believe that this area would require substantial development.

This would be part of a larger project to describing the relationship of my philosophy of conservation science to environmental ethics as conceived by others. I see this thesis as being mildly revisionary but mostly supplementary to environmental philosophy as described by Sarkar, but also supported by figures like Justin Garson and Mark Colyvan (Colyvan 2012; Garson 2016). Conservation involves systematic planning involving the co-ordination of stakeholders and use of decision theory to create priorities. I add a caveat that biodiversity must be represented using the best measure possible, and that causal structure of the ecological community must be accounted for.

The relationship of this work to traditional environmental ethics is less straightforward. Philosophy of conservation science is designed to supersede what I see to be the major school of environmental ethics (Leopold 1949; Rolston III 1975; Callicott 1987). But environmental ethics is a varied and continually developing field. Recently, Roberta Millstein (2017; 2018) has worked to reinterpret Aldo Leopold's work so that it does not rely on any balance of nature, and I am much more amenable to this view than other interpretations of Leopold's land ethic. The extent to which my biodiversity realism will conflict with any position in environmental ethics will depend on how much that school of environmental ethics relies on ideas like a balance of nature, intrinsic value, or holistic ecological communities; and ultimately whether they can accommodate biodiversity as a unique conservation goal. There is a long way to go to negotiate the relationship between my view on conservation and others in and outside the academe.

7.2. Meta-conclusion

This thesis has provided an original framework for the philosophy of conservation science. Methodologically I have utilised a mix of conceptual analysis, scientifically informed metaphysics, and scientific research to weave together a comprehensive picture of the relationship between key conservation concepts including biodiversity, ecological communities, and ecological function. With my analyses in hand, I have dictated what I believe to be the best formal methodologies for identifying these features in the world. The thorough description of ecological kinds helps me determine what entities we should conserve. This project will require further interaction with scientists, and I hope that I may one day be able to implement the ideas unveiled within this work. This is not supposed to be an idle act of philosophy. Earth's biodiversity is rapidly diminishing and these losses impact all of humanity. Everyone has a reason to preserve the heritage contained in life. The tree of life will suffer a horrible die back but if we direct our resources wisely, we may protect much of the opportunities and knowledge contained within it.

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