8

ECOLOGICAL HIERARCHY AND BIODIVERSITY

Christopher Lean and Kim Sterelny

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. Table 8.1 lists his estimate of the cell-level diversity of some of the better known phyla (Valentine 2004):

This table shows 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, populations comprise communities, and communities comprise ecosystems. Yet our tools for thinking about

Table 8.1 Cell diversity of metazoan clades

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	

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.

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, 2011). 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 organization to biodiversity poses no special problem to this view of biodiversity. If local groups have a particular 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. However, 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). Differences in biodiversity should make a difference; in particular to stability, productivity, and ecosystem services of various kinds.[1] If we can characterize and measure such a quantity, and if increased biodiversity would contribute positively to ecological function, 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.

Such "causal relevance" accounts of biodiversity face serious challenges. The most obvious is empirical. The evidence we have for the causal relevance of biodiversity is patchy and weakly compelling at best. Experimental studies (even in the field) of, for example, biodiversity–stability relations are constrained by problems of scale. The temporal depth and spatial extent of experimental plots do not match the spatial and temporal scales at which these effects, if they are real, will act (Tilman *et al*. 2001, Tilman and Snell-Roode 2014). The evidential value of natural experiments is eroded by the usual worries about unconstrained variables, and the less usual worry that the supposed key variable – biodiversity – can normally be measured only via proxies of doubtful reliability. A second challenge is decision-theoretic. It is hard to convincingly crunch the numbers so that prudence recommends foregoing a current benefit for a supposedly greater future benefit. For such prudence requires rational confidence in access to future benefits, and regions in which biodiversity hotspots are under threat are typically also regions of socio-political instability, and agents rationally have little confidence in institutional commitments to just futures. Moreover, prudential investment in biodiversity requires confidence that local and regional initiatives will not be swamped by the negative impact of larger scale processes; most obviously climate change and sea level shifts. Biodiversity is another commons, another tragedy.

The problems of demonstrating the causal importance and prudential value of biodiversity are important and unsolved. However, our focus in this chapter is a third challenge, the interface between species richness and ecology. The main argument of this chapter is to recognize the complexity, power, and importance of ecological interactions between populations, but to argue that ecological assemblages[2] are typically quasi-systems. They have some enduring structural properties. But they do not interact or act as wholes. Thus we resist the idea that ecological organization is an independent vector of biodiversity, one that needs to be tracked in addition to species richness (or similar species-centric measure). That problem is challenging enough. 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 8.2 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 rely just on species richness.

However, these individual organisms, and the populations they compose, seem to be components of larger, relatively stable, relatively organized ecological systems. So, for example, in urging the importance of niche construction ideas for ecology, Baker and Odling-Smee write: "organisms and their environments are in reciprocal causal relationships capable of generating feedback

Table 8.2 Common "biodiversity" measures

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

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*"[3] (Barker and Odling-Smee 2014: 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.

A paradigm of an organized 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 organization of the components, and the specific interactions scaffolded by that organization. Designed mechanisms are not ensembles of autonomous individuals, but of organized, 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, and they are not organized: 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: 147–150). Are ecological associations more like heaps of sand, or more like a village, with its division of labour, specialization, and mutual dependence?

Our example of a village is no accident: it reflects Elton's original model of a community organized through a set of complementary biological roles (Elton 1927). Elton's niche concept has been superseded, but ecologists still study the structure of these compositional systems: their food webs and other aspects of their trophic structure. Ecosystem ecologists investigate the ways material flows through these systems; for example, the ways detritivores recycle crucial nutrients back into the soil. 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 specialized 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 organization 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, Pearce 2011, Barker *et al.* 2014). History becomes even more important if, as is quite plausible, the accumulation of change is path-dependent. 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. One of us has in the

past defended this view of local communities, arguing that the stability of species associations, and of their relative abundance, is hard to explain unless they collectively organize and filter their local patch. For physical features of habitat patches vary quite significantly from year to year, yet local species lists often remain current for decades (though obviously with some changes on the margins), with common species remaining common, and rare species remaining rare (Sterelny 2006).

Phenomenologically then, these interconnected, interacting, co-located networks of populations seem to be real systems. They seem to be (in Rob Cummins's sense) functionally organized, hierarchically composed local systems. 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). Ricklefs calls this the assumption of "local determinism" in community ecology (Ricklefs 2004, 2005, 2006, 2008). If they are real, these system-level properties, with stabilized 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. The community, partially co-constructing one another's niche, stabilizes 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 stabilized associations, especially to the extent that such decisions involve trading patches of the conservation estate for land to be restored after exploitation.

A sceptical response

It is arguable, however, that this appearance of genuinely organized and structured ecological systems is an illusion. Angela Potochnik and Brian McGill have recently argued against the standard version of the view that ecological interaction is organized into real systems; a stratified conception of nested structure in ecology, with organisms comprising populations, populations comprising communities, and communities comprising ecosystems. They do not think that ecological interactions conform to the model of a system organised into discrete and well-defined levels (Potochnik and McGill 2012). They argue against the view that ecological interactions are organized 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 non-living but organized matrix, 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); its being 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.

We think that Potochnik and McGill interpret the idea of hierarchical organization 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 organization: the morphology of a metazoan, with cells organized 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 organized 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 note, the same is true of ecological interactions. Echidnas interact with termite colonies rather than individual termites. 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 conceptualize 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. The importance of these cross-species associations, both for the partners themselves and for third party interactions, is among the phenomena that make the local community perspective plausible. It is certainly no reason to reject the view that local communities are real, hierarchically organized systems. That rejection, as the comparison with morphology shows, seems to depend on saddling the classic, nested hierarchy conception of ecological organization with extraneous metaphysical and causal commitments.

The reasons for scepticism about the standard conception of ecological organization are empirical rather than metaphysical. 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. 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. If this individualist view of ecological pseudo-organization is right, then the apparently structured, compositional, and hierarchical organization 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. But the individualist perspective is at best controversial, as we shall see, even among those who reject the idea that community organization is under local control.

Ricklefs 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. We both live and work in Canberra, near a bush reserve, Black Mountain. Black Mountain has a healthy population of

brushtail 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 suburbs 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.

In one of ecology's landmark publications, in 2001 Stephen Hubbell 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; Hubbell 2001). 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: 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. 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 five 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.

In our introductory section, we suggested that a causal-relevance conception of biodiversity might have to be a two-factor model, with one factor focusing on genealogical units, reflecting the fact that species play roles (often different ones[4]) in many different ecological systems. The other derives from ecological organization, reflecting the fact – if it is a fact – that these are organized, enduring systems, with causally important properties that are not simple reflections of the properties of the genealogical units from which they are composed (Hutchinson 1965, Hull 1989, ch. 7). The Gleasonian suggestion, though, is that ecological interaction is not organized into systems at all, so the "second factor" disappears. That is not quite Ricklefs's view, as we shall see, despite his scepticism about local determinism. Rather, his positive suggestion is to increase the spatial scale of our analysis. We should think of regional systems – landscapes – as our bounded and organized ecological units. At this point, we need to introduce some conceptual machinery from Bill Wimsatt.

Flies, stones, and territories

In his "Complexity and Organisation", Bill Wimsatt compares a granite pebble and a fly to distinguish between two different forms of compositional organization. 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 organized in a way the granite cobble is not, for that cobble has a simple and privileged internal organization. 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 organization, chemical organization, 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: 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, they are not congruent.

As Wimsatt 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 explananda 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. Generalizing from the fly, Wimsatt thinks of "multiple decomposition" as a process in 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:

1) Systems can be understood given different theoretical perspectives.
2) Different theoretical perspectives give different characterizations 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.
3) 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 organization. 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 organization, even though they are not descriptively simple.

We read Ricklefs's suggestions that ecological stability depends on regional rather than local processes through the Wimsattian lens: landscapes (or territories) are real, but descriptively complex, hierarchically organized ecological systems. Landscapes 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

Figure 8.1   Kangaroo Island species distribution map. This map shows little pygmy possum (black) and western pygmy possum (grey) sightings.
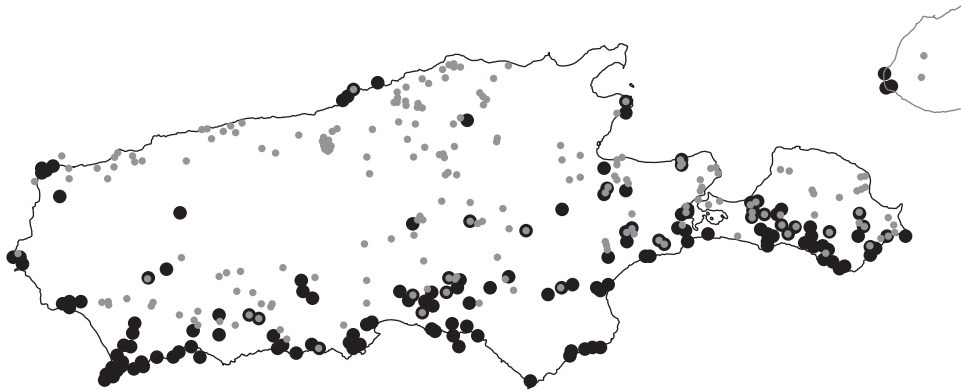

Figure 8.2   Kangaroo Island species distribution map. This map shows coast ground berry (black) and wiry ground berry (grey) sightings.

online database of species records. If one looks, say, at Kangaroo Island,[5] 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 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.[6]

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 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 censusing population distributions; for identifying and assessing ecologically relevant physical features of an environment; and for measuring the flow of materials through a system. In brief, there are multiple ecological perspectives on Kangaroo Island, and the components the different perspectives identify will often not be spatially congruent.

We also think that there is a quite persuasive case for thinking of landscapes or regions as objective features of the biological world, structuring ecological interactions. There are four considerations that favour taking landscapes 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. 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, landscapes 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 2001). Evolutionary change takes place in populations and in ensembles of populations. Local communities and the interactions therein – our Black Mountain – are too spatially localized 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 more free 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. So if we take regions or landscapes to be the most salient level of ecological organization, 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, 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.[7] 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 2005). In principle, local diversity 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. 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 (Kozak *et al.* 2008, González-Orozco *et al.* 2011).

Seeing the fresco in the ecological mosaic

In the previous sections, we developed a case for taking the apparently organized, structured character of ecological associations seriously, but on spatial scales of landscapes rather than as local communities. The broad-brush stability of local habitat patches genuinely needs explanation. But we also saw that there were powerful objections to seeing local patches as organized systems. In contrast, there is a persuasive case to be made for taking seriously regional organization. However, that case has two limitations. First, there may well be large stretches of continental plains which are not, in the relevant sense, regionalized. 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 are patchy. We simply do not know. Populations nested in Kangaroo-Island-like bounded territories may be more the exception than the rule.

Second, even if regions do have the structural and organizational 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. We see no case for thinking that territories or regions interact with other territories or regions as a single system. Nor do local communities.

So we suggest that ecological assemblages – perhaps local communities, perhaps spatially larger, bounded territories – are somewhat system-like. They are not mere aggregates, like a heap of sand. Within a territory, there are many populations, and their specific character and their spatial locations both matter to the overall ecological and evolutionary dynamics of a region. But at least in most cases, they 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. As a consequence, our best bet is that a ground-level, species richness based account of biodiversity is all we need (if indeed we can get even that).[8] Ecological organization is not machine-like enough for us to need to count machine types as well as the parts from which they are made. Moreover, conservation triage decisions almost invariably involve comparisons within landscapes or territories; not between landscapes or territories; which parts of Kangaroo Island should be in the conservation estate, not whether Kangaroo Island as a whole is more biodiverse than (say) Groote Eylandt, let alone more biodiverse in virtue of its landscape-level properties.

This chapter has explored one of the challenges to an ambitious, realist concept of biodiversity: a line of thought that suggests that such a view needs to develop ways of conceptualizing the differences between ecological systems, and ways of testing for their causal importance. We have argued that while the realist project has plenty of problems, that is not one of them. The Convention on Biological Diversity (CBD) defined biodiversity as: "Diversity between species, within species and of ecosystems." We suggest dropping the "of ecosystems". Biodiversity should be defined in terms of biological taxonomy, though we have not addressed the specifics of that project in this chapter. The specifics matter: for example, the quoll and the feral cat are both meso-predators of the Australian bushland. In our view, though not one we have defended in this chapter, the quolls's phylogenetic distinctiveness gives us *prima facie* reasons to privilege it in conservation decisions. The domestic cat has a global distribution, is closely related to many felids, and is strongly suspected of being implicated in the defence of many small Australian endemics. No similar charges are made against the quoll.

In this chapter, we have used conceptual machinery developed by Bill Wimsatt to identify the targets of conservation decisions; to zero-in on how to set conservation priorities, and to argue that while ecological aggregates have some causally important structure and organization, they are marginal rather than paradigm cases of organized system. We 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 stabilize important aspects of our biota, but if we accept Ricklefs's line of argument as we developed it in the third section, 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 seems 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 and 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.

However, this regional perspective has to connect to more localized 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. These taxon-specific and local phenomena include 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. Yet local patches and the populations they support are not inherently stable. The temporal beta-diversity in local areas often appears to be extremely high.[9] If this is indeed typical, the species composition in local communities rapidly changes. In one study of 100 biomes across Earth, 75 per cent of these systems had at least one in ten species disappear locally per decade (Dornelas *et al*. 2014). This 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 changes. 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).

Local communities are the stuff out of which landscapes or territories are composed. But if the studies we have just cited are typical of the behaviour of local communities, these highly local interactions and population fragments are often ephemeral. In many cases, there is no sense in which a stable set of population, 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 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 1 per cent of the area of Kangaroo Island.[10] But conservation biologists also have to think locally because regions are indeed ensembles of patches, and so are aggregated from patch-specific interactions. They have to act locally but think regionally.

Notes

1 Thus we think of ecosystem services as a product of biodiverse systems, and as a reason for conserving such systems. We do not think of such services as part of the diversity of a community or region. We think there is some confusion in the literature about this: see Lean and Maclaurin (forthcoming).

2 We use "ecological assemblage" as a neutral term, to capture the natural history truth that there are spatial patches where populations are found together, and interact, and that we can project from one population census to the next with some reliability, but without committing ourselves to any claim about the causal basis of these fairly stable groups of co-occurring organisms.

3 Emphasis added.

4 For example, coyotes are top predators in some regions, but not when wolves are present.

5 We choose this island as an uncontroversial example of a region; its length is about 80 km east–west; about 20 km north–south.

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

7 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.

8 Both of us support taxonomic accounts of biodiversity but one of us believes biodiversity is better understood in reference to phylogenetic structure rather than species richness.

9 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.

10 19.65 square kilometres to 4,416 square kilometres.

References

Agrawal, A. A., D. D. Ackerly, F. Adler, E. Arnold, C. Cáceres, D. Doak, E. Post, P. Hudson, J. Maron, K. Mooney, M. Power, D. Schemske, J. Stachowicz, S. Strauss, M. Turner, and E. Werner. 2007. "Filling Key Gaps in Population and Community Ecology." *Frontiers in Ecology and the Environment* 5(3): 145–152.

Barker, G., and J. Odling-Smee. 2014. "Integrating Ecology and Evolution: Niche Construction and Ecological Eengineering." In *Entangled Life: Organism and Environment in the Biological and Social Sciences*, ed. G. Barker, E. Desjardins, and T. Pearce, 187–211. Dordrecht: Springer.

Barker, G., E. Desjardins, and T. Pearce, eds. 2014. *Entangled Life: Organism and Environment in the Biological and Social Sciences*. Dordrecht: Springer.

Calcott, B. 2011. "Wimsatt and the Robustness Family." *Biology & Philosophy* 26(2): 281–293.

Colinvaux, P. 2007. *Amazon Expeditions: My Quest for the Ice-age Equator*. New Haven, CT: Yale University Press.

Cooper, G. 2003. *The Science of the Struggle for Existence*. Cambridge: Cambridge University Press.

Dornelas, M., N. J. Gotelli, B. McGill, H. Shimadzu, F. Moyes, C. Sievers, and A. E. Magurran. 2014. "Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss." *Science* 344(6181): 296–299.

Elton, C. 1927. *Animal Ecology*. New York: Macmillan.

Godfrey-Smith, P. 2009. *Darwinian Populations and Natural Selection*. Oxford: Oxford University Press.

González-Orozco, C. E., S. W. Laffan, and J. T. Miller. 2011. "Spatial Distribution of Species Richness and Endemism of the Genus *Acacia* in Australia." *Australian Journal of Botany* 59(7): 601–609.

Guttman, Burton S. 1976. "Is 'Levels of Organization' a Useful Biological Concept?" *BioScience* 26(2): 112–113.

Hacking, I. 1983. *Representing and Intervening: Introductory Topics in the Philosophy of Science*. Cambridge: Cambridge University Press.

Hubbell, S. P. 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton, NJ: Princeton University Press.

Hull, D. 1989. *The Metaphysics of Evolution*. Albany: State University of New York Press.

Hutchinson, G. E. 1965. *The Ecological Theater and the Evolutionary Play*. New Haven, CT: Yale University Press.

Jones, C., J. Lawton, and M. Shachak. 1997. "Positive and Negative Effects of Organisms as Physical Ecosystems Engineers." *Ecology* 78: 1946–1957.

Kozak, K. H., C. H. Graham, and J. J. Wiens. 2008. "Integrating GIS-based Environmental Data into Evolutionary Biology." *Trends in Ecology & Evolution* 23(3): 141–148.

Maclaurin, J., and K. Sterelny. 2008. *What is Biodiversity?* Chicago, IL: University of Chicago Press.

Pearce, T. 2011. "Ecosystem Engineering, Experiment and Evolution." *Biology & Philosophy* 26(6): 795–812.

Phillips, B. L., and R. Shine. 2004. "Adapting to an Invasive Species: Toxic Cane Toads Induce Morphological Change in Australian Snakes." *Proceedings of the National Academy of Sciences of the United States of America* 101(49): 17150–17155.

Poisot, T., D. B. Stouffer, and D. Gravel. 2015. "Beyond Species: Why Ecological Interaction Networks Vary Through Space and Time." *Oikos* 124: 243–251.

Potochnik, A., and B. McGill. 2012. "The Limitations of Hierarchical Organization." *Philosophy of Science* 79(1): 120–140.

Ricklefs, R. E. 2004. "A Comprehensive Framework for Global Patterns in Biodiversity." *Ecology Letters* 7(1): 1–15.

Ricklefs, R. E. 2005. "Historical and Ecological Dimensions of Global Patterns in Plant Diversity." *Biologiske Skrifter* 55(3): 583–603.

Ricklefs, R. E. 2006. "Evolutionary Diversification and the Origins of the Diversity–Environment Relationship." *Ecology* 57(7 Supplement): S3–S13.

Ricklefs, R. E. 2008. "Disintergration of the Ecological Community." *American Naturalist* 272(6): 741–750.

Sarkar, S. 2005. *Biodiversity and Environmental Philosophy*. Cambridge: Cambridge University Press.

Sarkar, S. 2011. *Environmental Philosophy: From Theory to Practice*. New York: John Wiley & Sons.

Sterelny, K. 2001. "Darwin's Tangled Bank." In *The Evolution of Agency and Other Essays*, 152–178. Cambridge: Cambridge University Press.

Sterelny, K. 2006. "Local Ecological Communities." *Philosophy of Science* 73(2): 215–231.

Thompson, J. N. 1994. *The Coevolutionary Process*. Chicago, IL: University of Chicago Press.

Thompson, J. N. 2005. *The Geographic Mosaic of Coevolution*. Chicago, IL: University of Chicago Press.

Thuiller, W., J. A. Slingsby, S. D. Privett, and R. M. Cowling. 2007. "Stochastic Species Turnover and Stable Coexistence in a Species-rich, Fire-prone Plant Community." *PLOS One* 2(9): e938.

Tilman, D., and E. Snell-Roode. 2014. "Ecology: Diversity Breeds Complementarity." *Nature* 515: 44–45.

Tilman, D., P. Reich, J. Knops, D. Wedin, T. Mieke, and C. Lehman. 2001. "Diversity and Productivity in a Long-term Grassland Experiment." *Science* 294(5543): 843–845.

Valentine, J. 2004. *On the Origin of Phyla*. Chicago, IL: University of Chicago Press.

Vermeij, G. 2009. *Nature: An Economic History*. Princeton, NJ: Princeton University Press.

Wilson, E. O. 1992. *The Diversity of Life*. New York: W.W. Norton.

Wimsatt, W. C. 1981. "Robustness, Reliability, and Overdetermination." In *Scientific Inquiry and the Social Sciences*, ed. M. Brewer and B. Collins, 124–163. San Francisco, CA: Jossey-Bass.

Wimsatt, W. C. 2007. "Complexity and Organisation." In *Re-Engineering Philosophy for Limited Beings: Piecewise Approximations to Reality*, ed. W. C. Wimsatt, 179–192. Cambridge, MA: Harvard University Press.

124