Nativeness as gradient: Towards a more complete value assessment of species in a rapidly changing world

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Abstract

Conservation biologists recognize a duty to maintain as much value as possible in ecosystems that are threatened by recent anthropogenic impacts. Until recently the paradigm of contemporary conservation seemed relatively straightforward: the best way to maintain the value of species and ecosystems at a given location was to maintain—or shepherd the system back towards—historical conditions. Among the most difficult theoretical tasks was the determination of "baseline" historical conditions (or trajectories) to return to, recognizing the dynamism of ecosystems over time. However, the rate, scale, and magnitude of contemporary climate change, species introductions, and land-use change make it increasingly impractical to return locations to any kind of historical state. This forces a paradigm shift which is both ongoing and difficult, and necessitates a rigorous evaluation of the scientific and ethical foundations of modern conservation along with a careful reexamination of terminology. Here, I discuss the moral relevance and waning utility of the geographically-based and dichotomous understanding of "native" (or "*in situ*") which is an important component of conservation ethics and practice. I then propose a new understanding of nativeness in which a species is native—not to a geographic location—but to a quantifiable set of biotic, climatic, geologic, and topographic conditions (i.e. its niche) that can then map to geographic space. Following this, I demonstrate the unique utility of this concept, which I will refer to as "econativeness," in thinking through conservation problems—range expansions, range contractions, species introductions, and assisted migration—where the classical understanding of nativeness has become increasingly inadequate for assessing the moral value of species.

1 Introduction

Maintaining the value of species and ecosystems (or at least mitigating the loss of it) is the moral foundation of conservation projects [Soule, 1985]. There are varied and sometimes competing approaches which emphasize different values and suggest different conservation actions. One framework emphasizes the values of 'naturalness' and suggests actions that primarily mitigate human impact. Another emphasizes the myriad values of biodiversity and favors actions that primarily increase or maintain biodiversity. Yet another emphasizes values of ecological and evolutionary situatedness and primarily encourages the protection of historical ecological structure and processes. These frameworks rely on a number of shared values (differing in emphasis) and many of these values are at least partly dependent on a species continued existence in the ecosystem to which it is adapted (i.e. its nativeness). This dependence on nativeness is part of the reason conservationists don't think of zoos as an end-goal—keeping the species alive may preserve some value, but much is lost with the loss of ecological, evolutionary, and environmental relationships. As a result, most conservation projects work towards maintaining an ecosystem's species, their relationships, and therefore the greatest amount of value in the face of anthropogenic impacts that might erode them.

This has primarily been conducted in an historically-oriented and place-based manner: at a given location, the most value is thought to be maintained if unaffected areas remain unaffected and affected areas are shepherded back toward the historical conditions of the location. This practice makes sense when the following conditions are met: (1) the species value is maximized when in the environment in which it is adapted, (2) the described 'historical conditions' or 'baseline' of a site are those that the species is best adapted to, and finally (3) a site can be managed towards the described historical conditions.

Condition 1 is commonly understood to hold true—think again of how zoos and botanical gardens fall short of central conservation goals. Condition 2, concerning the description of baseline conditions of a site, is the subject of much concern in conservation and ecology [Jachowski et al., 2015]. When this condition is violated, the conservation paradigm can fault. For example, a misunderstanding of the ecological and evolutionary forces that shaped the giant sequoia tree (*Sequoiadendron giganteum*) contributed to fire suppression which directly hindered the germination of giant sequoia seedlings for nearly a century [U.S. National Park Service, 2021]. Misunderstandings like these become less frequent as biologists learn more about the drivers of ecosystem structure and function, and Condition 2 can more often be met. Condition 3, the ability to maintain or manage a site towards historical conditions, may follow the opposite trajectory and become more difficult to satisfy as time passes. And perhaps this is the greatest threat to the traditional conservation paradigm: the rapidly diminishing likelihood that ecosystems can be returned to any kind of historical condition, due to a combination of anthropogenic drivers including climate change, land-use change, and species introductions [Camacho et al., 2010, Camacho, 2010b].

Global ecosystems may be approaching a tipping point in response to contemporary human activity [Barnosky et al., 2012]. Land cover types of human origin (e.g. agricultural land and cities) now blanket more than half of the earth's land surface [Hooke and Martín-Duque, 2012], and the rapidly increasing rate of species introductions has resulted in the establishment of more than 37,000 species outside of their historical ranges [Roy et al., 2023]. In some cases, these impacts may be reversible.

The impacts of climate change, on the other hand, will be patently irreversible in many ecosystems. Since 1850, industrial human activity has added 2,390 gigatons of CO_2 to the atmosphere, raising the atmospheric concentration of CO_2 from 280 to 410 parts per million. Consequently, global mean surface temperatures have increased by more than 1°C, arctic sea ice in September has decreased in area by 40%, and drought events have increased in severity and frequency worldwide.

These impacts are only expected to increase in both scope and severity as climate change continues, and the extent to which the impacts of climate change may be considered reversible is dependent on what we think of as being "reversed." The erosion of general ecological stability may be reversible, but the eco-evolutionary processes set in motion by global shifts in temperature, precipitation, and disturbance regimes—evidenced by evolutionary responses and shifts in the distributions of myriad species—are in many ways not. The body of work documenting observed and expected regime shifts in ecosystems is diverse, expansive, and growing [Walker et al., 2023, Scheffer et al., 2009, Reyer et al., 2015, Barnosky et al., 2012]. Altogether, the state of global environmental change and its impact on ecosystems presents a significant challenge to place-based and history-oriented conservation practices—specifically those that are motivated by the nativeness of a species.

Terms like "*in situ*," and "native habitat" have almost always been used in a geographically dependent and dichotomous way. Species are either native or non-native, and localized species databases like California's plant occurrence database Calflora are rigorous in their dichotomous classification of various plants [Calflora, 2022]. Conservationists use this native/non-native dichotomy because it has been useful in our understanding of species invasiveness and their effect on ecological stability. While this dichotomy has been useful, its utility becomes increasingly eroded due to the velocity of global environmental change. How can "native" species sometimes behave as invasive within their historical range [Nackley et al., 2017], like the explosive population growth of both the mountain pine beetle (*Dendroctonus spp.*) [Bentz et al., 2010] and Australian sandplain heath (*Allocasuarina huegeliana*) [Shackelford et al., 2013]? Are species that migrate in response to climate change non-native in their new locations and do they lose all the value that their historical range confers? And what does "native" mean for a narrow-ranged endemic species when it is unable to survive in its historical habitat due to climate change?

Recent work has highlighted the shortcomings of terms like "native" habitat for describing a species eco-evolutionary situatedness in a rapidly changing world. Some have cited the inability of "native" to properly account for species that shift their distribution in response to climate change, and suggest adding a third class to the native/non-native dichotomy, "neonative," to describe these species [Essl et al., 2019]. This contribution moves us away from a strict dichotomy, but its lack of gradient keeps it susceptible to classification problems [Wilson, 2020]. Furthermore, no attempt has been made to describe the difference in value between native, neonative, and non-native species, and it's unclear how this could be accomplished.

Others have criticized the temporal ambiguity of nativeness (e.g. the species present in the Americas and Australia before 1492 and 1770, respectively, are considered native, but the correct date for somewhere like Europe remains unclear) and spatial ambiguity (e.g. it's difficult to detect range edges and some species have inherently patchy distributions) [Hill and Hadly, 2018, Warren, 2007]. These criticisms have inspired gestures towards re-framing the "native" concept to include the niche and the dynamism of environment [Pereyra, 2020] and more rigorous efforts to classify different states of nativeness from a paleontological perspective [Crees and Turvey, 2015].

I build on this and on previous work which suggests that "native" is increasingly unhelpful while it is both dichotomous and geographically-based [Hill and Hadly, 2018, Pereyra, 2020], and argue that the eco-evolutionary situatedness of a species—and the value that is conferred thereby—is best evaluated by a niche-based, nonspatial, gradated conception of "nativeness" which can then be subsequently translated to geographic space. The novel conception of nativeness I offer below, called "econative," aims to reconcile our traditional understanding of "native" with its modern criticisms and alternatives to produce a more coherent, unified, and useful definition to describe where species belong in a rapidly changing world.

2 Introducing "Econative"

I propose that a species is *not* native to a geographic location, rather, it is native to a quantifiable set of biotic, climatic, geologic, and topographic conditions (i.e. its niche). Furthermore, a species proximity to its native niche is a gradient rather than a dichotomy. It's easy to see why "native" has come to refer to particular geographic regions: at short timescales and minimal environmental change, the environmental conditions to which a species is adapted is geographically stable. However, over longer time or during periods of rapid change the relationship between geography and a specific set of environmental conditions decouples. For example, we generally consider giant sequoias (*Sequoidendron giganteum*) native to the western slope of the Sierra Nevada mountains of California, but millions of years ago these trees were probably distributed across a much larger region in North America, perhaps as far as the modern state of Idaho [Lowe, 2014]. What then, is the native distribution of these trees? If a geographic area had to be delineated using the classical understanding of nativeness, a biogeographer would probably map the native range as the area including the current distribution and wherever else the species was recorded when Europeans arrived, whether or not the trees are found there today. Why aren't the areas in what is now called Nevada (which had these trees around 2 million years ago [Dodd and DeSilva, 2016]) included? Because the environmental conditions that the giant sequoia is adapted to are no longer present in those areas. And if the climate and fire regime changes in California over the next century such that the environmental conditions no longer support giant sequoias and the trees are entirely extirpated, will the trees still be native? An adherent to the inflexible geographically-based native/non-native dichotomy would be forced to conclude that the giant sequoias then become non-native—with repercussions for the values attributed to the species.

More nuanced and logically consistent is the understanding that giant sequoias are native to the environmental conditions to which they evolved in, and that these conditions intersect with geographic space over a continuum, where any given geographic location has some quantifiable measure of the native niche. Millions of years ago, the native niche of giant sequoias intersected with a larger portion of western North America, and today, the geographic instantiation of the native niche covers only a small, patchy area of the Sierra Nevada. However, we are not forced to conclude that future climate change will force giant sequoias into a "non-native" status—rather, increased temperatures and reduced snowpack will simply reduce the similarity of the current geographic distribution of giant sequoias to their native niche. Giant sequoias will effectively become "less native" than they are now, just like they are currently less native to Idaho or Nevada than they were millions of years ago. All species at all locations can be thought of as existing on a continuum between more native and less native, and this continuum can be imagined as the overlap between a species n-dimensional niche hypervolume and a location's n-dimensional environment hypervolume (i.e. the Hutchinsonian niche concept) [Hutchinson, 1957].

I propose that this continuum between more native and less native, "econativeness", is a more biologically informed and morally and ecologically useful term than "native" or "*in situ*" when referring to the location of species (Figure 1). Classical nativeness can be thought of as a special case of econativeness which applies only to the last few hundred years of plant and animal distributions—what we think of as "native" to a location today is simply what has been econative to a location for as long as modern science has been recording the distribution of species. Viewing ecological change through the lens of a human lifespan or during periods of little environmental change masks the distinction between econativeness and classical nativeness. However, the rate of recent change makes clear the incompetency of a dichotomous, place-based understanding of nativeness.

The econative concept depends greatly on how we understand the niche, and the details have important implications. The dominant ecological niche concept is derived from Hutchinson and is differentiated into the fundamental niche (everywhere a species *could* physiologically survive and reproduce in environmental space without biotic or dispersal limitations) and the realized niche (everywhere it *does* survive and reproduce, all factors considered) [Hutchinson, 1957]. Based solely on the Hutchinsonian niche, econativeness is the geographic expression of both the fundamental and realized environmental hypervolumes, where the realized niche clearly maps to greater econativeness because it describes more environmental axes of the species niche (e.g. competing species, predators, etc.). Importantly, this does not directly account for dispersal limitations, which are expressed in geographic rather than environmental space. So, if dispersal limitations and geography are not explicitly captured by econativeness, could a eucalyptus someday be similarly econative to its Australian geography and its introduced California range in the extremely unlikely event that all co-occurring species and environmental components are similarly present in both locations?

No, not if we consider burgeoning developments in the niche concept, which move towards more completely capturing the eco-evolutionary situatedness of a species. A key task in 'bringing the Hutchinsonian niche into the 21st century' is describing the evolutionary component of the niche [Holt, 2009]. Recent work, especially in the field of niche conservation theory, has made important contributions to this effort [Trappes, 2021], but there is considerably more work to do until these concepts are neatly integrated [Morrow, 2024]. In fear of getting cut by the bleeding edge, I will gesture towards the trajectory of these ideas and their important implications for the econative concept.

Trappes describes an "externalist evolutionary niche," popular in niche construction theory, as "the (sum of the) environmental factors that lead to fitness differences in a population" [Trappes, 2021]. She and others remark that this concept focuses on the external environmental forces that drive niche construction and largely ignores the (internal) forces of phenotypic change that can also shape the niche (as described in Aaby and Ramsey [Aaby and Ramsey, 2022]), and hints at an evolutionary niche concept that recognizes the niche-shaping potential of both species and environment. In my interpretation, this concept implies a complement akin to a "fundamental evolutionary niche" that corresponds to a hypervolume in n-dimensional environmental space to which a species *could* have have become adapted in its eco-evolutionary history. This suggests a kind of buffer zone in environmental space around the fundamental ecological niche of a species, and acknowledges the impact of geographically-adjacent environments in the development of a species ecological niche. And thus, at the frontier of niche theory, we can begin to account for geography and dispersal by considering the integration of evolution and niche construction into the ecological niche. When econativeness refers to a niche concept like this, a eucalyptus tree could only be as econative to California as Australia if all of the environmental conditions and co-occurring species are present *in addition to* all of the environmental conditions and species the eucalyptus tree *could* have become adapted to throughout its evolutionary history. In practice, this guarantees that a species cannot be more econative to a location beyond major biogeographic barriers (e.g. between continents) than they are to the geographic area they most recently evolved in.

A significant innovation provided by the econative concept is that nativeness can begin to be quantified. For decades, statistical tools have been developed and refined to characterize and quantify the ecological niche. Though imperfect, the field of ecological niche modeling (ENM) has made significant strides in modeling the fundamental and realized niches of species [Elith and Leathwick, 2009]. The most popular models are correlative statistical models which utilize known species occurrence data and corresponding environmental information to approximate the niche. These models output habitat suitability estimates along a continuous gradient, and naturally correspond to many of the abiotic dimensions of econativeness. However, the fundamental niche that most ENMs attempt to capture is incomplete, and is commonly limited to a handful of bioclimatic variables. Recent work has acknowledged the importance of—and made progress towards—including evolutionary processes [Bush et al., 2016] and biotic interactions [Wisz et al., 2013] in ENMs. As the field progresses, we will be able to more completely model a species niche, express that niche onto geographic space, and calculate a more complete econativeness score. The current capabilities of ENM provide a strong foundation—and for the practical application of econativeness we might proxy the biotic and evolutionary dimensions of the niche by both adding environmental buffer space around the modeled fundamental niche and incorporating local species composition.

The result of applying ENM to the calculation of econativeness would be an econativeness score on a gradient between 0 and 1, similar to the habitat suitability scores usually output by ENMs. Though the econativeness of a species could infinitesimally approach 0 (e.g. a great-horned owl at the bottom of the Mediterranean sea), a species would never have a score of 0 because at least *some* components of its niche are present: water, carbon, oxygen, etc. This presents an important consideration: just because a species has an econative score greater than 0 at a location does not suggest that a species "belongs" there in any way—econative is a relative metric.

The econative concept is compatible with other definitions of native, new and old. I've already elaborated the nested relationship between classical native and econative, where classical nativeness refers to a temporal snapshot of econativeness. "Neonative" can also be viewed as a special case along the econative gradient, where a species becomes much more econative to an area and establishes populations. Essl et al. recognized the underlying continuum and argued that the categorization of nonnative, native, and neonative were motivated by utility [Essl et al., 2020]. The econative concept is consistent with this and simply makes explicit the underlying continuum that is being discretized. An alternate definition proposed by Gilroy et al. states that "native" and "nonnative" hinge on human-mediated transport. While econativeness does not directly consider method of transport, the incorporation of evolutionary processes and biotic composition into the econative niche concept should ensure that human-mediated transport across major biogeographic barriers would confer significantly lower econativeness.

In the following section, I'll walk through three examples of the application of the econative concept which serve to clarify the concept, demonstrate its ethical relevance, and address some *prima facie* concerns about the implications for trans-continental translocations, species invasions, and the protection of incumbent species and ecosystems.

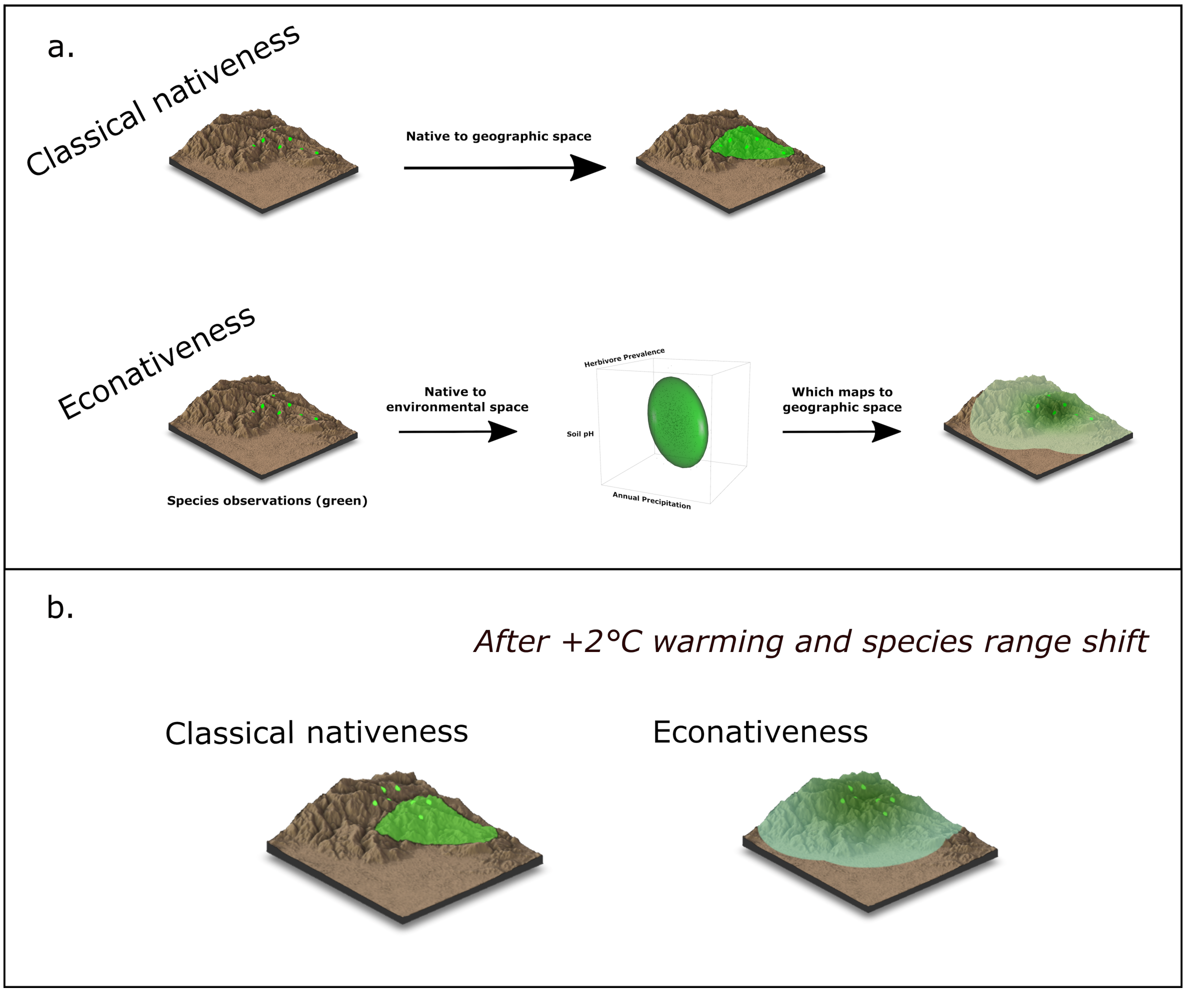

Figure 1: **Diagram comparing classical nativeness to econativeness.** a. Both accounts begin with observed species occurrences on a landscape (green dots, left), but diverge in the way that these occurrences are used to define a "native" range. In the classical understanding of nativeness, the native range is generally understood to be a contiguous geographic area which includes species presences and excludes species absences (top). Under econativeness (bottom), the species observations correspond to n-dimensional environmental space (the Hutchinsonian niche) to which the species is native. The native niche can then be mapped to geographic space, where all locations are on a continuum from less econative to more econative depending on how similar the environmental conditions are to the Hutchinsonian niche of the species. b. The different nativeness concepts yield significantly different results after a theoretical 2°C of climate warming and a resulting shift in the species distribution. The classical native concept cannot account for the individuals that migrated outside of their historical range and the significance of the lower-elevation, extirpated portion of the range is ambiguous.

3 Applying "Econative"

This reconsideration of nativeness has important implications for the attribution of value to species. A few different types of value attributed to species are at least partly dependent on nativeness, and these include instrumental values, natural historical values, and integral values (Table 1). Instrumental values are those attributed to a species when it provides a service, natural historical value is derived from an appreciation of the complex ecological relationships and evolutionary processes of a species [Katz, 1997], and integral value applies when people have a preference for a species continued existence in a way that is consistent with a person's culture or worldview [Sandler, 2012].

<table>
<tr><td colspan="4">Intrinsic Value
if valuable for its own sake</td><td colspan="2">Intrumental Value
if a means to an end that is intrinsically valuable</td></tr>
<tr><td colspan="2">Objective Intrinsic Value
if valuable for its own sake regardless of someone's opinion</td><td colspan="2">Subjective Intrinsic Value
if valuable for its own sake based on someone's opinion</td><td rowspan="2">Present Value
if currently a means to an end that is intrinsically valuable</td><td rowspan="2">Option Value
if, at some point, potentially a means to an end that is intrinsically valuable</td></tr>
<tr><td>Natural Historical Value
if a unique product of ecological relationships and evolutionary forces over long periods of time</td><td>Inherent Worth
if possesses interests of its own that ought to be valued</td><td>Existence Value
if someone has a preference for its continued existence</td><td>Integral Value
if someone has a preference for its continued existence for reasons that are consistent with their culture or worldview</td></tr>
</table>

Table 1: **Nested table of values that may be attributed to species.** A commonly adopted framework for describing the types of values that might be attributed to species nested within the two broadest categories: intrinsic and instrumental. The necessary conditions for which a species is attributed each value is briefly summarized. This is largely based on the work of Ronald Sandler [Sandler, 2012].

Can these values still be attributed in-full to a species if classical nativeness is supplanted with econative? The extremes of econativeness clearly inherit the same assortment of value from classical nativeness because they are equivalent to the native/non-native binary. A species that is entirely econative to a site possesses all of the native-dependent values that a native species would be attributed, because under these conditions native and econative mean the same thing. Conversely, a species with very little econativeness to a location has the same native-dependent value as a non-native species. The main difference, and the source of its moral utility, is that econativeness allows for some fraction of these values to be attributed to species in the increasingly frequent scenarios in which species are not fully native or non-native. Imagine a montane subalpine forest community where, due to climate change, all but a few species shift up-slope by 500m to a location where they have never historically co-occurred before. ENM would yield an econative value close to 1—the abiotic and biotic environments are very similar, but not equivalent. These shifted species are not 100% econative, and not native under the classical understanding, but certainly some measure of natural historical value and the integral values that arise from ecological and evolutionary relationships between the birds, spruces, soil microbes, etc. are maintained. Not only is econativeness morally useful in the same conditions that classical nativeness is, but also to a whole slew of scenarios that recent global change introduces. Using three examples, I will continue to explore the utility of econativeness for species value attribution and the conditions in which it outperforms the classical native concept.

The most straightforward example is one in which the environment has not changed much over the last century: the species composition has remained stable and the climate, soil, disturbance regimes, etc. are for the most part within the historical variance of the system over the last few hundred years. Imagine that the only difference is that the mean annual temperature has increased by 0.2°C. Would it make sense to introduce (or permit the introduction of) an endangered novel species to this site? A comprehensive assessment of the econativeness of all species at the recipient site and the introduced species yields an unsurprising conclusion: probably not. Although the increase in 0.2°C may be outside the temperature range that some of the local species are adapted to—resulting in a decrease in econativeness for these species—most other dimensions of econativeness are intact. And even if the increase in 0.2°C makes the introduced species slightly more econative to the recipient site, it doesn't become more econative than the incumbent species. Here, econativeness correlates with natural historical value, and other values attributed to the species that are dependent on its ecological and evolutionary situatedness. Econativeness is also correlated with the endangered species' likelihood of establishing—if the environment is very different from the conditions in which it evolved, then it is likely that it will be more difficult to survive and reproduce. The species composition component of econativeness, coupled with an analysis of the traits of the endangered species, might be useful for estimating its potential invasibility, and therefore ecological harm, in the recipient system. When isolated, the utility of the components of econativeness are obvious and have been used to estimate invasibility, habitat suitability, and value before—its strength and novelty is in its use as a unified concept. This thought experiment demonstrates that the econative concept strengthens the justification for protecting largely intact ecosystems and weakens justifications for the introduction or establishment of novel species.

Our next thought experiment concerns another extreme: an environment that is nearly unrecognizable from any historical state. An abandoned lot on the outskirts of Chicago may have few, if any, of the species that occurred there hundreds of years ago. Furthermore, the soil has contaminants from industrial activity, the winter temperature has increased by 1°C, and extreme precipitation events have increased by 40% [Illinois State Climatologist, 2021]. What species assemblage maximizes the value at this location? Econativeness alone is not sufficient for a complete value analysis because some values are largely independent from it, like many instrumental or aesthetic values. Perhaps a garden would provide the most value at this site. But an evaluation of econativeness is necessary for a complete value assessment, and a logical place to start would be to determine the econativeness of the present species, the historical species, and the historical species from nearby regions. The common "weed" species likely present at the lot, like garlic mustard (*Alliaria petiolata*) or cheatgrass (*Bromus tectorum*) have some measure of econativeness by simple virtue of being able to grow there—the climate and soil conditions must be similar to the environments in which they evolved—but the biotic components (e.g. species interactions, co-occurrences) of their econativeness is quite low. It's worth acknowledging evolution here, and the possibility that the Eurasian plants have started to form ecological and evolutionary relationships with local plants, animals, and abiotic features and that this may confer some additional measure of econativeness. Though this is probably minimal in so short a time. The historical species likely have historically co-occurring species more geographically close (perhaps somewhere else in Illinois) than the historically co-occurring partners of cheatgrass or garlic mustard (their historically co-occurring species are from Eurasia), and so have greater biotic econativeness. Consequently, those historical species that can survive in the parking lot conditions likely have more total econativeness. But due to ongoing climate change, it may be the case that the climate may be more similar to the niche of species from warmer and wetter parts of the midwestern U.S. that haven't historically occurred near Chicago. These species, like the historically occurring ones, also have members of their historical biotic assemblages closer than Eurasia. It's reasonable to think that at least some non-historical species that are newly suitable to the habitat due to climate change have greater econativeness to the abandoned lot than either the historical species or the present ("weedy") species.

This thought experiment emphasizes how econativeness can implicitly account for the relevance of geographic distance between a species' historical and introduced range. Eurasia is very distant from Illinois, both in geographic space and environmental space. Even between those areas where the climates are analogous, the species assemblages, geology, and ecological relationships might differ significantly. If the assemblage of species that cheatgrass co-occurs with in its historical range (e.g. the tens of thousands of plants, animals, and fungi around the Mediterranean sea) was translocated to central North America, then, perhaps, might cheatgrass become more econative to the Chicago lot than an Illinois species.

Our 3rd example concerns areas that are on the edge of species distributions actively shifting in response to climate change. Large swaths of conifer forests in the Sierra Nevada mountains of California are outside of the climate to which they're adapted and conifers are being replaced by oaks and chaparral at the lower-elevation and warmer edge of their distribution [Hill et al., 2023]. In these areas of active and expected transitions, which species have the greatest value conferred by ecological and evolutionary situatedness? The dichotomous understanding of nativeness is unhelpful here, and the classification of the migrating species as non-native underestimates their value. Essl et al. would call these migrating trees "neonative" [Essl et al., 2019], but it's unclear what ethical significance neonative species have, particularly in comparison to the historical species that are being actively replaced. This example especially benefits from a gradient understanding of nativeness because in many of these sites, the difference in econativeness between historical and migrating species are rapidly shrinking. As the climate continues to change and the values derived from econativeness become more equivalent between the groups of species, the other values, not dependent on ecological or evolutionary situatedness, become more relevant to the land management decisions. The species that are attributed aesthetic, instrumental, or cultural value—independent of econativeness—may be an important foundation on which to build an understanding of the species that "belong" at these locations. Because econativeness is sensitive to biotic composition, the decision to prioritize particular species affects the econativeness of others. For example, if Jeffrey Pine (*Pinus jeffreyi*) is attributed a great deal of instrumental and integral value due to the vanilla-like perfume of its furrowed bark and is decidedly worth protecting in a particular area, then a number of species that historically co-exist with Jeffrey Pine are more econative to that area by virtue of Jeffrey Pine being present even if other environmental conditions have changed. This example is relevant to all areas undergoing vegetation transitions in response to climate change—at some point the econativeness of range-expanding species may approach equivalence to that of historical species, and the decision to slow, facilitate, or passively observe will hinge on values independent of nativeness.

4 Additional considerations

One important consideration is that the econative concept is more useful to conservation efforts that have greater emphasis on native-dependent values. Some conservation projects may not consider nativeness at all. Operating at an extreme of the "biodiversity-first" framework, nativeness could be irrelevant to the goal of maximizing the species count or genetic diversity at a locality (though it's worth noting this is not a popular conservation goal). In a framework emphasizing naturalness above all else, the econative concept is only useful when considering species that are translocated without human intervention—if even then. However, conservation projects often have a diversity of goals and underlying values, and usually at least some of these values are dependent on nativeness.

Another important consideration is the proliferation of non-analog climate conditions and ecological communities expected in the coming years [Petrie et al., 2020, Williams and Jackson, 2007]. Non-analog environmental conditions introduce serious challenges for ENM, primarily because the often-used correlative modeling framework has poor performance when models are extrapolated beyond the domain of their training data [Fitzpatrick and Hargrove, 2009]. The practical application of econativeness is reduced when ENMs perform poorly. Realizing the impact of non-analog environments on ENMs did not staunch the explosion of extrapolative ENMs in the decades since, but it did introduce important considerations of the limitations. Like extrapolative ENMs, the econative concept can still be informative while acknowledging the proper limitations and uncertainties introduced by novel environmental conditions. And as is also done with ENM, econativeness can be evaluated by its component dimensions (rainfall, predator occurrence, soil type), at least some of which will remain in analogous conditions.

5 Consequences for Assisted Migration

The econative concept has important implications for the debate on Assisted Migration (AM), the conservation-motivated movement of species to areas beyond their historical range. Of the many terms used to refer to this process (e.g. assisted colonization, managed relocation, etc.), Hällfors et al. argue that assisted migration (AM) is best when referring to the practice of "safeguarding biological diversity through the translocation of representatives of a species or population harmed by climate change to an area outside the indigenous range of that unit where it would be predicted to move as climate changes, were it not for anthropogenic dispersal barriers or lack of time" [Hällfors et al., 2014]. Despite being extremely controversial since its inception in 1985 [Peters and Darling, 1985] and "ignit[ing] long-smoldering tensions in American natural resources policy" [Camacho, 2010a], AM has been recognized as a conservation tool by the International Union for Conservation of Nature [IUCN, 2013] and has been put into practice in a few isolated instances around the world (e.g. projects with *Torrey taxifolia* [Barlow, 2021] and *Pseudemydura umbrina* [Lewis, 2016]).

A number of ethical and ecological concerns have been raised in response, primarily regarding risk of ecological harm, practical efficacy, and the soundness of value-based justifications. Conservationists have good reason to be afraid of ecological harm: the movement of species outside of their historical range can lead to ecologically damaging invasions when the ecological conditions that kept a species population in control in its historical range (e.g. disease, predators, etc.) are not present in its introduced range. Populations under these conditions could increase dramatically and lead to significant damage in the recipient ecosystem [Courchamp et al., 2003]. Some argue that the risks of invasion far outweigh the potential benefit of AM [Ricciardi and Simberloff, 2009, Maier and Simberloff, 2016], and even proponents call for extensive risk assessment before implementation [Gallagher et al., 2015, Butt et al., 2021].

A number of ethical concerns compound the scientific and practical, but the primary debate centers on value: the potential benefits to target species, costs to recipient ecosystems, and underlying uncertainties [McLachlan et al., 2007, Schwartz et al., 2012]. In 2012, the Managed Relocation Working Group wrote that the first step towards developing an AM decision framework was the examination of the goals of conservation and their constituent values [Schwartz et al., 2012], and this effort is still ongoing. One important thread concerns which types of value, if any and to what extent, are maintained during the process of AM [Schwartz et al., 2012, Sandler, 2012, Maier and Simberloff, 2016, Siipi and Ahteensuu, 2016]. This is central to the debate because an effective cost-benefit analysis—weighing the benefits of AM against the cost and risks of harm in the recipient ecosystem—is entirely dependent on an accurate analysis of value for the species and ecosystems involved. Indeed, three of the four dimensions of the AM evaluation tool proposed by the Managed Relocation Working Group (focal impact, collateral impact, and acceptability) directly depend on the values attributed to the species involved [Richardson et al., 2009]. A chief concern by a number of ethicists is that many proponents of AM do not provide positive, value-based justification for its practice [Maier and Simberloff, 2016, Sandler, 2012]. For example, recent decision-making framework published by the U.S. National Park Service for the purposes of implementing AM includes a cost-benefit analysis equation where the "benefit" is exclusively a function of the reduction in the risk of extinction [Karasov-Olson et al., 2021]. Under these conditions, a zoo or conservatory might be the best choice for maximizing benefit (probability of species continuation) and minimizing the cost (ecosystem harm, resource use, etc.), but surely this is not an intended conclusion.

Proponents of AM don't typically argue on behalf of the instrumental value of species [Lavrik, 2021] (the silviculture industry is a prominent exception [Thiffault et al., 2021, Gömöry et al., 2020]), so most of the debate centers on intrinsic value either implicitly or explicitly. Objective intrinsic value (by virtue of natural historical value) and integral values are the most relevant. Some argue (even a prominent critic like Sandler) that the aesthetic, cultural, spiritual, etc. properties composing the integral value of a species (a subjective intrinsic value) might be maintained by AM [Siipi and Ahteensuu, 2016, Sandler, 2010]. Natural historical value is more contentious—even in the historical range—but is also specifically referred to in some justifications of AM [Siipi and Ahteensuu, 2016]. Because so many proponents are not explicit about the value of species, we assume that they at least indirectly rely upon the natural historical value or integral value of species when not referring to instrumental value.

Critics argue that these values are either eroded or entirely lost by translocation outside of the historical range [Sandler, 2012, Maier and Simberloff, 2016] (although some interesting exceptions might include species with integral value to indigenous peoples that were translocated outside of their historical range, like taro in Hawaii or kiore in New Zealand). Both integral and natural historical value are described as being dependent on the species being *in situ* or in their native habitat because of the ecological and evolutionary relationships therein. However, the rigid and implicit framing of these properties as dichotomous and geographically explicit is not biologically justified, and the wholesale loss of those values leads to an underestimation of the value maintained by AM in many cases.

Econativeness is helpful here, and through it we acknowledge that species can maintain at least a fraction of their eco-evolutionary situatedness and the value that it confers beyond the geographic boundaries of their historically native range. The correlation between econativeness and native-dependent value must surely be complex and nonlinear, but in general we should expect that when a species is more econative to a locality it also maintains a greater number of eco-evolutionary relationships. This helps add nuance to a number of ambiguities in AM, while simultaneously clarifying and strengthening the justifications against widely-condemned practices like transcontinental translocations.

First, the econative concept could almost never be used to justify the AM of a species across major biogeographic barriers to a locality that it has not historically occurred. For reasons described earlier, the econativeness would be quite low (even if it's still within the species fundamental niche), and the native dependent values would be minimal. When accounting for the total costs and benefits, it would be extremely unlikely that the benefits would tip the balance. This conclusion is reachable without the econative concept, but the reason why a species does not belong across major biogeographic barriers is better articulated in this framework.

In the increasingly frequent case of climate-driven ecosystem transition, as detailed in the earlier example of conifer forests in the Sierra Nevada, econative is a helpful tool in AM decision-making. As the environment changes and the econativeness of the incumbent and migrating species become commensurate, other values and conservation goals become more likely to tip the cost-benefit calculations. Under the econative concept, we don't *prima facie* reject AM on the grounds of nativeness because we can appreciate that the migrating oaks have a number of eco-evolutionary relationships in the locality. At the same time, the incumbent conifers have less and less. All other values held equal, the dramatic shift in relative econativeness between the species might eventually prompt AM, in order to maximize total value among species at the locality. This is easiest to imagine in a scenario where the incumbent conifer species are slowly dying, becoming more susceptible to catastrophic wildfire, and competitively excluding oak trees and others that may otherwise be able migrate unassisted.

The last example builds on the abandoned Chicago lot thought experiment discussed earlier. Most of the species in this lot evolved a continent away, and the sum econativeness of the ecological community is quite low. When calculating the sum econativeness before and after the potential introduction of a nearby AM target species, the low econativeness of the incumbent species would be dwarfed by the econativeness of a migrating species from further south in Missouri. According to native-dependent values, there would be strong incentive to consider AM. Dramatically altered sites like this are the most easily justified recipient locations for AM, and may be helpful for establishing populations along the climate change-induced migration trajectory of a species. However, feasibility is a significant consideration in examples like this (abandoned lots probably aren't suitable for most endangered species), and many other values are perhaps more important than those related to conservation at an urban location like this (such as those related to affordable housing).

6 Conclusion

The challenges faced by the conservation community are broad and broadening. I think that "econative" may be an important part of the lexicon of the next conservation paradigm and a useful tool for thinking through some of the difficult decisions that rapid global change brings. Conservation is motivated by the protection of the value of species and ecosystems, and a careful and comprehensive assessment of the value of each species at a site is necessary. Much of a species' value is tied to its ecological and evolutionary relationships, and the classical conception of nativeness is too inflexible to be useful for assessing a species value in a rapidly changing world. The practice of Assisted Migration has been so contentious because it forces some of the most difficult conservation questions to the fore. This proposed re-conceptualization of nativeness, 'econativeness', provides a nuanced and theoretically quantifiable framework that might help to think through these challenges. Important future directions include a coherent integration of evolution into the ecological niche concept, more complete ecological niche modeling of all the environmental components that describe a species niche, and the experimental application of the econative concept to real-world conservation decisions. Ultimately, this work calls for—and contributes to—a careful consideration of which species belong where, and our role in stewarding these impending transitions.

Supplementary information

Not applicable

Declarations

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