Indexically Structured Ecological Communities

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Ecological communities are seldom, if ever, biological individuals. They lack causal boundaries as the populations that constitute communities are not congruent and rarely have persistent functional roles regulating the communities' higher-level properties. Instead we should represent ecological communities indexically, by identifying ecological communities via the network of weak causal interactions between populations that unfurl from a starting set of populations. This precisification of ecological communities helps identify how community properties remain invariant, and why they have robust characteristics. This respects the diversity and aggregational nature of these complex systems while still vindicating them as units worthy of investigation.

1. Introduction. The gullies of Namadgi National Park seem like distinct ecological communities from the peaks of the Snowy Mountains National Park. Wildflowers are scattered across the subalpine landscape of the Snowy Mountains, punctuated by grizzled snow gums, and introduced brumbies; while Namadgi's dense gum forests, dominated by red stringybark and scribble gums, line broken granite creek sides holding a diverse assemblage of reptiles and insects. Both of these national parks are of high conservation value, and legislation is built around the need to preserve their unique identities. Yet these two communities are linked within the larger metacommunity of the Australian Alps, sharing many species and being connected by forested parks. Despite this, it is assumed that their local populations interact more strongly with each other, leading to the natural conclusion that the populations in Namadgi are strongly policed in their distribution, abundance,

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and persistence by the other populations of Namadgi; likewise for the populations in the Snowy Mountains. Combining this causal assumption with the differing description of habitats leads to the seemingly not very radical conclusion that these habitats comprise distinct ecological communities.

Ecology studies the distribution and abundance of populations across landscapes and over time. Community ecology often studies the way "local" or spatially congruent interactions within an assemblage result in demographic changes (Leibold et al. 2004). Local ecological communities act as a core unit of investigation for community ecology. Community ecology has long operated with the implicit assumption of "local determinism": that is, that ecological patterns are primarily explained by the rule-governed interaction of local populations within a community (Drake 1990; Ricklefs 2008).[1] It is thought that these interactions operate within certain boundaries (Roughgarden 1989). Once we identify these boundaries, we can make inferences about how the local community polices species' identity and abundance. Therefore, the local interactions and identity of the species in Namadgi distinguish the Namadgi ecological system from the Snowy Mountains ecological system.

Ecological communities are thought to have discrete boundaries, stable composition, and predictable dynamics over time, and these characteristics allow for inferences to be made from one community to the next. But there have been many dissenting voices within the ecological research tradition who instead argue for *ecological individualism*, emphasizing that populations generally move around a landscape of their own accord driven by chance and by abiotic factors without being heavily influenced by their local neighbors.[2] The implication is that ecological communities are largely ephemeral compositions of populations. This debate drives considerations whether there are law-like regularities in community ecology (see Lawton 1999; Linquist et al. 2016). If ecological communities have shared properties, then we can make robust generalizable inferences about how they act. On the other hand, if assemblages are just collections of largely independent populations, then there will be little robust to say about communities.

1. My description of "local determinism" and "local ecological communities" is derived from the arguments by Robert Ricklefs (2005, 18–21). He argues that Robert MacArthur's legacy is the conceptual separation of the region species pool and local ecological communities. Local scale population composition was thought to be explained at this local level by processes such as competition and ecological filtering without reference to the regional level.

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

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To arbitrate this debate philosophers and biologists have provided an analysis of the conditions for an assemblage—a collection of populations in a space—to be an ecological community. Namely, assemblages should be a biological individual just like an individual organism, population, or lineage (Hull 1976; Millstein 2009; Clarke 2013). If an ecological community is a biological individual, then it is the cohesive and distinct entity that local determinism presupposes.[3] Kim Sterelny (2006) and Jay Odenbaugh (2007) independently specified the conditions under which an ecological assemblage is a natural entity, an *ecological community*.

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

2. Communities as Biological Individuals. Ecological communities feature as distinct and countable entities in ecological science and in normative theories about the preservation of the natural environment. One way to establish that a biological entity has these features is to view it as a 'biological individual'. While biological individuality has become a contested topic in philosophy of biology, with multiple attempts to precisify its description, generally biological individuals are spatiotemporally bound units that exhibit internal cohesion (Hull 1976). This internal cohesion in ecology is expected to be a product of the causal interactions of populations within the community regulating its overall features. Ecological communities as individuals feature in major hypotheses across the related ecological sciences. And it is this causal and explanatory distinctness that undergirds the normative value of

3. A further required assumption is that the group of individuals must have features in common to support induction. Defining boundaries is the first step to determine the properties possessed by a community. Similarities can then be identified in conspecific communities for inductive reasoning.

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these communities. This section notes the roles that ecological communities have played in ecology and conservation and then turns to the communities as individuals thesis that Sterelny and Odenbaugh present.

Community ecology has produced multiple research programs that posit that there are distinct countable ecological communities. Most famous is Fredrick Clements's (1916) treatment of ecological communities as superorganisms with a developmental sequence of populations facilitating the establishment of the next population (e.g., grasses releasing nutrients into the soil facilitating larger trees). This process of succession was thought to yield a mature ecosystem that has stable self-preserving system properties (Eliot 2007). While Clements's superorganismal ecology has fallen by the wayside, many successors have taken up aspects of his program. Both niche theory and the diversity-stability hypothesis have relied on an assumption that communities form tight-knit economies with positions that can be filled interchangeably by populations (MacArthur 1955; Herbold and Moyle 1986). When the positions in the economy are filled the economy is 'stable', explaining the persistence of the assemblage and its resistance to invasion by alien populations. All these theories assume that ecological communities are the right size of object to analyze changes in a population's abundance and distribution. The local community as a result plays an explanatory role in the ecological science.

Ecological communities have been seriously discussed as bearers of normative worth since Aldo Leopold's (1949) "Land Ethic," which demanded the extension of ethical concern to ecological communities, not just individual populations. And while many nebulous versions of the relation between ethics and ecological holism have been posited in the following 70 years, ecological communities do play a serious role in conservation science.[4] Conservation is widely taken to have the goal of preserving biodiversity (Soulé 1985). Describing ecological communities as distinct entities also allows them to be individual bearers of biodiversity, and many conservation programs are explicit about their aim to preserve not just the inter- and intradiversity of lineages but also diversity of kinds of communities. For example, in the Australian Capital Territory, Blakely's Red Gum Grassy Woodland is an endangered ecological community that is afforded legal protection. Thus ecological communities appear in conservation decision making as entities that are quantifiable and distinguishable.

Communities as individuals have played an important role in both the ecological sciences and conservation. But what are the criteria that an assemblage needs to fulfill to be an individual? Sterelny (2006) and Odenbaugh (2007) present similar accounts, which I condense into a single view. While

4. Millstein (forthcoming) systematically defends Leopold's "Land Communities" as real scientific entities.

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they provide a set of conditions that if fulfilled counts an ecological community as an individual, they leave it open as to whether any actual ecological community satisfies these conditions. The conditions they present follow.

2.1. Boundaries. Individuals, as spatiotemporal entities composed of interacting subparts, have boundaries. For interacting parts to make a whole there must be strong causal interactions creating internal cohesion within the system and factors that aid its isolation from external influences. The system parts in community ecology are the populations that causally interact, creating feedback loops maintaining local populations and excluding external populations from invading the local system. Sterelny particularly notes that local niche construction is one way populations can maintain an assemblage (2006, 226). Famously, Australian plants including gums, banksias, and melaleucas are adapted to fire and facilitate the presence of each other by making their local environment more fire-prone. Under this conception of boundaries, ecological communities are bound by interaction strength between populations (Levins and Lewontin 1985). While this does not necessarily mean that populations in the system will be congruent, strong causal interaction is associated with spatial overlap, so congruence, or at least approximate congruence, of community populations is expected.

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

2.3. System-Level Properties. If we wish to include local ecological communities in our general scientific ontology, there has to be a reason to talk about communities rather than just talk about the populations that make up communities. There should be predicates and properties that are needed for describing phenomena at the community level. System-level properties are an explanandum to be explained by the assemblage and an explanans for ecological and evolutionary hypotheses. Properties generally discussed on the community level are associated with the maintenance of multispecies interaction networks such as food webs (*community network structures*), the

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maintenance of composition identity or aggregative features (*emergent community properties*), or the various material outputs that the joint assemblage creates (*community outputs*). Odenbaugh treats system-level properties as necessary for community existence: "species populations form an ecological community just in case . . . they possess a community level property" (2007, 636). He primarily mentions interspecific interactions and feedback loops they create as community-level properties. Sterelny (2006, 221) describes emergent community properties, identifying several candidate emergent properties from the diversity-stability hypothesis such as community population stability and community biomass production. The productivity and abiotic features ecological communities produce have become an area of keen interest for conservation science. Many ecologists have attempted to justify the preservation of ecological communities by appealing to the 'ecosystem services'—capacities commonly attributed to the community as a whole. These system-level properties feature in ecological explanation, and they are properties of something, namely, a community.

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

To establish that ecological systems lack the same boundaries and internal structure of biological individuals, consider how we can identify the boundaries and composition of objects generally (Wimsatt 2007, chap. 9). Simple objects like a granite pebble have quite neat boundaries; there is strong causal discontinuity between the pebble's interior and exterior. This allows for the unit to act as a whole; that is, when thrown the pebble acts as a single unit, uniformly going in a direction. The various structural and dispositional prop-

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erties are neatly congruent within the pebble. Properties such as tensile strength, electrical conductivity, or crystal structure are all colocated throughout its structure. This is due to there being a fairly simple compositional structure.

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

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

3.1. Nonrobust Communities. The lack of robust boundaries in ecological systems is revealed by the differing causal profiles of colocated populations. In the Kosciuszko National Park the distribution and abundance of mountain pygmy possums is causally determined by its predators, foxes, and prey, bogong moths, while the northern corroboree frog population is strongly determined by negative interactions with niche-constructing hoofed animals. Despite being apparently part of the same local community, the causal profiles of what populations are relevant to them will be quite different. Each population will belong to an ecological system consisting of just those populations to which they are counterfactually sensitive.

Borrowing from Bill Wimsatt's (2007, chap. 9) description of complex systems, I argue an ecological community is an individual when it is descriptively robust: if multiple different streams of evidence describe a congruent structure. If we claim that a local assemblage of populations belong to the

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same individual, then those populations should map into a single ecological system and describe the same patterns of causal relationships between populations. The discordance between descriptions of ecological systems can be seen in both the spatial discordance between population ranges and the causal discordance.

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

Since then Whittaker's findings have been heavily contested, with some going as far as to say that his data support the opposite conclusion (Wilson, Agnew, and Sykes 2004). But considerably more evidence has emerged, particularly through biogeographic research, showing the lack of spatial congruence between populations. Paul Colinvaux's (2007) research displays that populations within the Amazon have historically moved independently in response to climate change. With the increasing availability of biogeographic data, the independent nature of population ranges is something that we can check ourselves.[5] Indeed, Dan Simberloff (1982) famously declared that ecological communities were not real in the way species are real, as populations have continuous distributions over their ranges and species boundaries do not coincide. When these conditions are violated, he claims, it is due to discontinuity in the abiotic environment. The explanatory importance of community boundaries is debated. Historically they were very important to the projects outlined by G. E. Hutchinson (Odenbaugh 2007). But they appear to be not as central to modern community ecology, playing a more modest role (see Yarrow and Marín 2007).

Ecological systems are also not causally cohesive as change in one population will often not influence other local populations in a consistent way. The reason is that populations in a community often have asymmetrical and intransitive causal relations. Asymmetrical causal relations are called commensalist (0, +) and amensalist (0, −), and their impact on food web stability is an ongoing area of research (e.g., Mougi 2016). Intransitivity is equally well studied with populations existing in rock-paper-scissors relations (e.g.,

5. See the Atlas of Living Australia (http://www.ala.org.au/).

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Kerr et al. 2002). As a result local ecological populations rarely form equivalence relations in which the populations that form a community are reflexive, symmetrical, and transitive with respect to each other (Godfrey-Smith 2008). Causal networks that lack equivalence relations do not form strongly bound groups that respond in unified ways.

Populations, therefore, often have asymmetrical causal relations and noncongruent boundaries. As there is no ecological community we can immediately identify a priori, we need to study populations to identify an ecological community. For there to be a distinct and robust ecological community, a set of populations will have to act as a causally cohesive unit. To identify whether populations are part of the same causally cohesive unit, we would intervene on them and see whether the other populations are also affected and vice versa. But when there are asymmetrical relations between populations and noncongruent boundaries, populations do not form causally cohesive units. Different causal communities appear given different starting points. As a result, ecological boundaries are deeply dependent on the particular populations we are interested in, the populations that we causally start with. This idea that ecological boundaries are relative to populations of interest is not new; it has previously been defended by Steven Peck, who states that we must "recognize that [ecological] borders are always relative to species or groups of them" (2009, 275).

Causal relations determine spatial relation, and spatial relations can determine the strength and structure of causal relationships. Consider the factors relevant to a population of spotted quolls compared to their occasional prey, greater gliders. Individual quolls roam over home ranges up to 3,500 hectares moving between habitat fragments via wildlife corridors, while a glider's home range is only 2 hectares and is locked within a local habitat fragment. Unless there is a very strong counterfactual dependence between these two populations, the network of populations relevant to the quolls will be radically different from that of the gliders, as quolls interact with populations that intersect with their large home ranges. Further, due to the radically different ranges and population densities, there is a strong asymmetry between these populations. Differential changes in a local glider population are unlikely to affect the quoll population because the quoll's range would include several glider populations as well as other prey since they are generalist predators. However, differential changes that increase the quoll population would affect the glider population as increased predation can have large impacts on small local populations. This creates an asymmetry: intervention on gliders has little impact on quolls but intervention on quolls significantly affects gliders.

Consequently, population boundaries radically differ, and the causal relations between populations are often asymmetrical and intransitive. When both these conditions are met, congruent boundaries are rare, and identifying

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the population network, and the space that network occupies, will be highly dependent on the initial choice of referent. Varying the starting population will yield radically different descriptions of the ecological community.

3.2. Robust Explanation in Nonrobust Systems. The lack of ecological community boundaries could be taken to indicate that we need to adopt a Gleasonian view of ecology and reduce all ecological explanation to the components of these systems, the populations, and their abiotic environment (Gleason 1926). I resist this conclusion by providing some ways in which complex systems, which do not display the cohesion of individuals, can still require higher-level, or compositional, explanation.

Local communities appear to have clusters of stably interacting populations or consistent abiotic outputs that need to be explained. Such outputs are often not just the simple aggregation of component populations' actions. Diverse local species assemblages can have nonlinear ecosystem outputs. Combinations of populations nonadditively result in explosive combustion in forest fires or retain water in the understory (Michel et al. 2012; Van Altena et al. 2012). Further, the statistical aggregation of the actions of local populations can have system-level effects such as stabilizing ecological output by statistical averaging effects, biological insurance, and sampling effects (Bryant 2010). Community-level properties as a result appear to be ubiquitous in ecological systems even if there are no clear boundaries for these systems and the internal composition is unstable. I describe two types of explanatory robustness that can help sort through the heterogeneous structure of ecological assemblages to find the parts of these loose systems that contribute to these system-level features.

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

We can explain the system-level properties of these heterogeneous systems by machine robustness and ensemble robustness. *Machine robustness* occurs when we explain the outputs of a system through describing a causal chain of parts in the system that sequentially cause changes in each other

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bringing about this output (Levy 2014). The parts that produce this output are each stable, in both their properties and relative location, and are persistent in the system and unlikely to be perturbed. As a result of the stability and persistence of relevant system parts, the outputs of the system are robust. Complex systems made of heterogeneous parts can be explained by machine robustness. Think of an Airbus A380: the parts of the plane are quite varied, and the output of staying in the air is fortunately quite robust as by and large each individual part of the plane is persistent and stable in its effect and location (Elliot-Graves 2016).

Alternatively, we can explain the output of compositionally complex systems by *ensemble robustness*. Ensemble robustness occurs when we have many different causal actors that can fill the same functional role in the system bringing about system-level properties or outputs. These types of explanation often feature overdetermination; if one subpart of the system did not bring about the system-level feature, then another would. Ensemble robustness occurs when the subparts are similar. For example, steam being forced out of the top of a kettle is a product of the collision of many different water molecules. But ensemble robust outputs do not require the components bringing about the effect to be exactly the same. All that is required is functional similarity; the same effect can be reached by extremely heterogeneous actors. To use an ecological example, gum trees can be pollinated by extremely taxonomically and anatomically varied populations such as pygmy possums, bees, ants, and honeyeaters (birds).[6]

Ecology aims to explain how populations and their interactions result in system-level properties such as diversity, stability, or ecological services, for example, water retention and biomass production. Local determinism supposes that stable relationships between persistent populations produce these properties; stable internal structure produces system-level properties. Explanations of this type are *machine robust*: the system-level property is a result of a particular causal sequence of interactions between persistent parts. These can be serial interactions or, alternatively, allow for feedback. Systems that are organized in this manner and display complex behavior are required to be modular. For highly persistent and stable parts to act in multiple ways, there needs to be some way of introducing structural manipulability, and modularity is the common way this is done. For example, the composition of a brick is stable and persistent, but there are not too many complex actions a brick can do. The Airbus A380 also has stable parts in persistent relationships, but there are degrees of freedom introduced into the actions of the plane, for example, by having modular structures like wing flaps, which are able to move up and down on their hinges. Modularity creates boundaries

6. Functional similarity comes in degrees.

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in systems, and if ecological communities are to be bound, we would expect modular machine robust structures.

The assumption of persistent stable relationships in ecological communities is problematic as populations are often highly transient. In one study of 100 biomes across earth, 75% of these systems had at least one in 10 species disappear locally per decade (Dornelas et al. 2014). This is often coupled with little change in regional diversity as populations simply shift their distribution across the larger landscape (Thuiller et al. 2007). This is further evidence for those who believe that local ecological communities are the wrong scale for law-like generalities in ecology (Ricklefs 2008; Lean and Sterelny 2016). They claim that regional patterns better explain the local distribution and abundance of organisms than local patterns that are ephemeral and stochastic. These views explicitly reject the idea that local community identity is primarily maintained by internal composition.

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

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

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

4. Indexical Communities. On a first pass of the philosophy of ecology literature, accounts of ecological communities appear to split between treating populations as largely independent of each other and describing them within an individuality framework. There are, however, other options that sit between these extremes. I consider and expand Sterelny's (2006) 'indexical communities' as a contrasting framework to ecological individuality. My account of ecological communities supplements and develops indexical communities as described by Sterelny by providing the conceptual apparatus to identify robustness and utilizing the Woodwardian interventionist framework to fix the reference of the causal system involved (Woodward 2005).

4.1. Simple Indexical Communities. Simple indexical communities are ecological units that aim to describe the conditions that affect the demographics of single populations. Indexically described communities are one of the most useful and utilized ecological techniques in conservation science. To preserve the critically endangered hairy nosed wombats, we need to know how much native grass and how many tubers they eat, what is an unusual parasite load, and how to separate them from wild dog populations and competing grazers. These populations are indexed to the wombat population as they have a causal impact on them. This framework has become commonplace due in part to conservation funding being directed to individual species preservation. This is due to government funding entering conservation from Endangered Species Act legislation and nongovernment funding being raised by appealing to the public's love of charismatic megafauna such as blue whales, giant pandas, and bald eagles. Conservation science as a result often aims to find the conditions that lead to the preservation of a focal population.

These simple indexical communities are not thought to be very informative for community-level properties as they are constructed with limited epistemic aims, that is, explaining the influences on a single population. Due to the limited scope of such causal units, they remain silent on certain, hopefully generalizable, community-level features such as the relationship between di-

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versity and stability (Sterelny 2006, 227). Further, it is thought that information about one indexical community is difficult to apply to other assemblages due to the apparent limited nature of their scope and their heterogeneity. We can rectify these problems by building into indexical communities the means for identifying machine robustness and ensemble robustness when they are present.

This is done by intervening on communities, starting from multiple different populations of interest to identify robust community features. The aim is to find what community-level properties the populations contribute to, be they community outputs, boundaries, or causal networks. By intervening on different populations, treating them as nodes in a causal network, we can identify which relations in an assemblage either are highly central, acting as a causal hub, or have strong causal effects. Once we identify which causal relations are relevant, we map where these causal actors are distributed geographically, which is the information needed to identify the spatial boundaries of the community. The innovation here is that by using multiple starting points, we can build in robustness and avoid the explanatory fragility of indexical communities built around a single population. Section 4.2 will describe the procedure for describing an indexical community built from a starting set of populations. Section 4.3 provides a guide for what populations can or should be used for this starting set.

4.2. Identifying Indexical Communities. The stepwise procedure for identifying the relevant ecological community appears below (summary 1), but I will elaborate through this section. Take the starting set of populations and identify the indexical community for each individual population in the set (starting sets are discussed in sec. 4.3). The indexical community for a population is identified by intervention, in which we systematically change the variable representing the population. These interventions can of course take many shapes including removing populations or reducing or increasing a population's spatial range or altering their accessibility to other populations; but for the purposes of this article, I will use the example of interventions being used to alter population numbers. To identify the indexical community of the focal population variable, A, we intervene on populations suspected to be causally efficacious for A. An alternative population variable, B, is said to be part of the same community as A, as well as a cause of A, if systematic intervention on B brings about change in A. So if we shoot some feral cats in an area, it will have a positive impact on the population of bilbies due to the causal relevance of the cat population to the bilby population. These causal relations will be 'causal influence' relations as there are continuous values the exogenous population variable can take, and this allows for modulation of the response variable.

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

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

Actual intervention will sometimes be problematic; it is often difficult or downright dangerous to reduce or increase population sizes. Further, it can be difficult to get accurate records of the changes in population size. Interventionist theories of causation have long been troubled by the problem of 'actual' intervention; for example, if we are not willing or able to intervene on the moon, can we know it causes the tides (Woodward 2016)? In the ecological case, natural experiments can be used to infer and model casual relations as populations repeatedly move in and out of areas as they cycle a larger geographic region (see sec. 3.2). Humans repeatedly intervene on communities by reducing populations or introducing invasive species in fairly systematic ways. More scientific interventions are preferable, with Robert Paine (1992) providing an early archetype; he made repeat interventions to identify the 'interaction strength' of populations in an intertidal rock pool. As such, practical limitations make data collection difficult but not impossible.

Once we have directed causal maps from the different populations in the starting set, we can compare their causal structure. The comparison of causal maps is done in two ways. The first is identifying whether populations, the nodes of these maps, sit within the same set of causal relations in strength and direction. This can identify stable causal clusters of populations, which act cohesively. Population network structures that appear in the directed graphs from multiple different indexed populations are robust in Woodward's sense (2005, chap. 6): something to be robust according to Woodward

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if a wide range of initial conditions identify the same event. Here the event is a particular causal relationship between populations. By varying the local populations we intervene on, we vary the initial conditions of the system. Robustly connected populations are ecologically important, often acting as keystone species, and playing a role in maintaining the population network structure.

Another way of displaying the indexical community is mapping the populations that causally contribute spatially. This allows for a visual depiction of the actual physical space that the causal processes of the community act over; it acts as an anatomy of the ecological community. By mapping the spatial arrangement of populations that causally contribute, we can also see if the community is 'descriptively robust' in Wimsatt's sense (Wimsatt 2007, chap. 9). A community is robust according to Wimsatt's view if multiple different 'theoretical perspectives' identify objects that are spatially congruent. By varying the populations that we are interested in, we vary the perspective we inquire into the system with. If the different causal systems identified from different populations occupy the same space, they are robust in Wimsatt's sense.

Summary 1. Procedure for identifying indexical communities:

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

4.3. The Starting Set. So what determines the starting set of populations? This is in part researcher or local community stakeholder interest defined, but there are some obvious candidates described below. Having the initial scope of systems determined by research interest better represents the practice of scientists and the differing intuitions around ecological communities. While many scientists and the public are interested in ecological communities, they clearly differ in what they are referring to. This account of communities has the flexibility to make precise the many different notions

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of community at play in these different discourses. Here are some different notions of ecological communities that can be described through varying the starting set.

Local Ecological Communities. If we wish to determine whether a local assemblage is a unified and integrated community, we would look at the indexical community built around a set of local populations. By identifying the network of populations that emanate out of cohabiting populations, we can see to what extent this local ecological community is a causally cohesive unit. This also acts to identify the ecological bounds of otherwise arbitrary units. National parks are usually bound by geographically arbitrary borders, and we may be interested in locating the causal boundaries of the ecological assemblage that inhabits this space. If we are interested in the ecological boundaries of the assemblages inhabiting a region of the Namadgi National Park, we take a census of the local populations in that region and map out the causal structure they are related to.

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

Biodiverse Communities. Particularly important kinds of communities are those that conserve biodiversity. Often communities are conserved by protecting populations indexically relevant to some charismatic fauna. But we may also wish to specifically target preserving the populations that constitute biodiversity. There are many different biological features that can represent biodiversity, including species functions, morphology, phylogenetic diversity, and so forth. But for whatever features count toward biodiversity, we can identify the combination of populations that best represent these features and therefore represent biodiversity in a particular area. Then using the

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indexical communities procedure, we can find the ecological features relevant to the preservation of biodiversity. This causal structure is critical to minimize biodiversity loss from secondary extinctions (Dunne and Williams 2009).

Phenomenological Communities. People experience ecological communities as hikers, birders, hunters, and participants within these systems. Environmentalists and the public often have an interest in preserving particular assemblages that are familiar from their experience of the wild. Phenomenological communities are the midsized ecological objects that people think of when they are asked if we should preserve ecosystems. But these entities are referentially underdetermined; people struggle to describe the particular features of this system in a precise way or give an account of their extent past arbitrary boundaries. We can clarify the description of phenomenological communities through using indexical communities. Typically phenomenological communities are described through reference to assemblages including charismatic mammals, audible birdlife, visually stimulating angiosperms, and imposing trees. To fix the reference of such local assemblages we include in the starting set the phenomenologically prominent populations in a local area. For example, if you want to find the community of a blue gum forest, you include blue gums, lyrebirds, and waratahs and identify the populations relevant to them. By then building in the populations that maintain the experientially salient aspects of wildlife, we can identify the condition for preserving the environment the public immediately desires. This directly speaks to the practice of conserving ecological communities described by legislation. The Blakely's Red Gum Grassy Woodland is a legally protected endangered community.[7] This community is identified by a list of tree species and understory plants that are "commonly associated" with the community. Indexical communities are able to represent this unique assemblage and the way the law describes it, indexed to a set of populations.

I have no doubt that there will be other ways of and reasons for describing other starting sets for indexical communities. By allowing the starting set to be determined by the interested parties, we are able to tailor the indexical community to fulfill both the epistemic and normative roles that community ecology and conservation science require. This is a significant step forward; ecological communities as they are described by ecological sciences and the public appear to diverge, but the presented conceptual system allows for us to both describe their differences and unify them in a single explanatory system.

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

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

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

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

Some ecological assemblages may not feature any robust causal relations or outputs. In these cases they will not be machine or ensemble robust. These systems are better explained at the level of populations, with little reference to their local neighbors. In these cases ecological communities are not vin-

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dicated as units worthy of unique investigation in themselves. Instead we would be better off studying autoecology, the dynamics of particular populations.

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

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

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