Ecological Interdependence via Constraints

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Although ecological theory has historically focused on negative interactions among populations, like competition and predation, ecologists and conservation biologists highlight the significance of interdependence. It is not clear, however, what is asserted in the causal hypothesis that one population is interdependent on others. This essay argues that the most informative causal regularities for representing dependencies are those connecting populations through environmental constraint variables. Interdependence among populations can thus be understood as constraint-mediated dependency relations connected in a circuit.

1. The Puzzle of Interdependence. Living things do not always make life easy for one another. Ecology, as the science of how dynamic sets of living things hang together or fail to, has struggled from the beginning to describe how living things support and depend on one another. Although in common usage the word "ecological" can connote positive relationships with other parts of nature, ecologists have arguably found it easier to characterize relationships among living things that are at least partly negative. The most canonical and enduring models in ecology have been models of population growth and (where populations interact) competition and predation. Just as physics moved into models of fluid dynamics only after developing comparably more straightforward models of mechanics, models characterizing facilitation have been later arrivals in the discipline's development.

In one of the first works of modern European ecology, "Politia Naturae," translated into English in 1781 as "On the Police of Nature" (although perhaps better rendered as "The Polity of Nature"), Linnaeus summarizes the

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†Thanks to Roberta Millstein, Alkistis Elliott-Graves, and Steven Peck for the PSA symposium and the associated discussions that inspired this article. Their comments, together with those of several symposium attendees and two anonymous referees, helped substantially with reining it in.

Philosophy of Science, 85 (December 2018) pp. 1115–1126. 0031-8248/2018/8505-0030$10.00
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https://doi.org/10.1086/700600 Published online by Cambridge University Press

interactions of living things in a way that puts conflict in sharp focus. In this dissertation defended by his student C. D. Wilcke in 1760, Linnaeus characterizes the implications of exponential population growth in the face of finite resources in a way that would later be echoed by Thomas Malthus and Charles Darwin. "Where the population increases too much," Linnaeus writes, "concord and the necessities of life decrease, and envy and malignancy towards neighbors abound. Thus it is a war of all against all!" (Egerton 2007, 84). A century later, Charles Darwin echoes this framing of species interactions in *Origin*, remarking that "battle within battle must ever be recurring with varying success" (1859, 73). Gause (1934) quotes the same line in his first paragraph.

At the same time, the idea that living things are everywhere interdependent has been expressed by ecologists from the beginning. Linnaeus, notwithstanding "war of all of against all," described every species as dependent on some others. He characterizes the dependency of plants on animals this way: "Vegetables . . . are destined always to preserve their number of species. To obtain this end, generation, nutrition and proportion are necessary. Animals seem created to assist in effecting these three purposes" (Wilcke 1781, 159–60). Darwin later portrays the plants and animals in his iconic "entangled bank" at the end of *Origin* as "dependent on each other in so complex a manner" (1859, 489).

More recently, the idea that interdependence is a central causal relationship connecting populations has been a tenet of Conservation Biology, which emerged from ecology in the early 1980s. In one of that field's foundational documents, "What Is Conservation Biology?" (1985), Michael Soulé presents the idea that "species are interdependent" as the first corollary of the first "postulate" of this young discipline. The interdependence of species follows from Soulé's "evolutionary," "functional" postulate that "many of the species that constitute natural communities are the products of coevolutionary processes" (729). That is, their interdependence has arisen as a consequence of evolution having "tuned" each species to others. As they have evolved, each species has specialized to varying degrees in using others in particular ways, like as hosts or as prey. Describing patterns of interdependence therefore becomes an essential project for biology aimed at supporting conservation efforts.

Indeed, the concept of interdependence precedes the emergence of Conservation Biology in the US conservation movement. Roberta Millstein has characterized forester Aldo Leopold's understanding of the interdependence of populations in what he called a "land community," an interesting hybrid of ways communities and ecosystems are each often described. Millstein has suggested how interdependence characterized by Leopold derives from Charles Elton's animal ecology and provides structure to land communities (Leopold 1939; Millstein 2018). The land community and the interdepen-

https://doi.org/10.1086/700600 Published online by Cambridge University Press

dence it foregrounds have in turn been foundational for both the conservation movement and anglophone environmental ethics.

However, when people or parts of a body or a machine are interdependent, we generally consider it pathological for them to be warring with one another. The idea that they would normally be warring seems contradictory. Autoimmune diseases are pathological in part because they involve normally interdependent parts fighting one another. And so, ecology faces a puzzle. Ecological systems seem to be governed by interactions—competition, consumption, predation, and parasitism—with negative effects on individuals and populations: diminished fitness, death, extirpation, and extinction. And yet, not only are populations dependent on the others they use, they are somehow interdependent. If so, dependence relations cannot flow only one way, like from animals to plants to microorganisms, but instead must be connected back in a circuit. And yet it is not obvious that populations depend on their predators or parasites.

2. What Should a Causal Model of Interdependence Model? One sense in which populations clearly do depend on their predators is the sense in which the value of a variable can be dependent on others. Populations depend on others just by virtue of their numbers being affected by them. But this sense of "depend" does not exhaust the ecological meaning of "interdependence." The ecological usage involves if not direct reciprocation then at least indirect influence. Moreover, it involves survival or persistence of populations in some respect. If a virus were to destroy all life, it might depend on its hosts but not vice versa. Although the population sizes of hosts would depend on the virus's abundance and activity, the host populations would not (in this simple example) depend on the viruses to survive. Nonetheless, "dependence" and "interdependence" are sometimes used in ecology in the survival-independent sense. The concept of dependency in "density dependence," one of the most familiar ideas in ecology, is variable-type dependency.

However, ecologists and conservation biologists often use "dependence" and "interdependence" in the narrower sense, referring to what requirements populations have for survival. Describing the kinds and intensities of threats to populations, Noss (1994) notes that "longleaf pine (*Pinus palustris*) depends on frequent, low-intensity fires to prepare a seedbed of exposed mineral soil and to drive out competing hardwoods" (906). Elsewhere, survival-relevant dependency is on another population. Anstett, Hossaert-McKey, and McKey (1997) use "dependence" this way in an article titled "Modeling the Persistence of Small Populations of Strongly Interdependent Species: Figs and Fig Wasps." They characterize the services provided by figs and fig wasps to one another, and the relevance of those services to their population viability, specifically in terms of the populations' vulnerability to extirpation. At mini-

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mum, to say what can be conserved or what size constitutes a minimum viable population in various conditions (Shaffer 1981), for instance, one needs to know what a population depends on for survival.

Yet, ecological knowledge is increasingly knowledge of network relationships, beyond simply knowledge of pair-wise interactions. Bascompte (2009) writes "More recently, ecologists have studied interactions beyond predator-prey webs to include mutually beneficial interactions, such as those between plants and their animal pollinators or seed dispersers. These interactions play a major role in the generation and maintenance of biodiversity on Earth . . . and organize communities around a network of mutual dependences" (417). Some ecological phenomena such as metapopulation dynamics and the "influence of multiple local populations in shaping genetic variability" become visible only in a network (and not in a pair-wise) representation of ecological systems (418). In turn, understanding the persistence conditions of networks requires understanding the ways that their members are mutually supporting. Knowledge about how networks persist or fail to persist therefore requires knowledge of interdependence in the narrower, survival-relevant sense.

But what does it mean to describe populations as interdependent? Interdependence can be understood as a causal relationship or set of relationships, but it is not obvious what is entailed by the causal hypothesis that some set of things is interdependent. For example, a maximal kind of interdependence among parts could involve each of the parts needing to be precisely in its present state for every one of the other parts to exist. Moreover, not only the loss of any one part but also any part changing could be sufficient to disrupt or eliminate all the other parts. This set of causal relationships could be weakened along a series of dimensions: not every part might be essential, and their present states might be able to vary. And indeed, ecological systems are dynamic in this way. Populations arrive and disappear and change in myriad ways. Given the dynamic nature of ecological systems, this maximal, static interdependence does not appear to be an ecologically relevant kind of interdependence. So, my question, then, is what kind of causal structure should be understood as being attributed when a set of populations is hypothesized to be ecologically interdependent.

In asking what a claim about interdependence might involve causally, I mean to outline a causal model for thinking about interdependence, not to provide a reductive, metaphysical account of causation itself. Concluding a recent overview, Paul and Hall (2013) write that "after surveying the literature in some depth, we conclude that, as yet, there is no reasonably successful conceptual analysis of a philosophical causal concept" or a unified theory of causation and, indeed, that the prospects for one are dim (249). Without trying to fill that gap, philosophers of science can yet analyze what causal claims do and do not say about certain systems, and, for example, Wood-

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ward's (2003) influential work can be understood as undertaking this project for a range of scientific claims (Paul and Hall 2013, 18).

One way to assess what interdependence should involve is to consider maximal and minimal accounts of interdependence among populations.[1] On the minimal side, Hubbell (2006) recommends ignoring specific causal relations. He suggests that many general ecological patterns often taken to be explainable by relationships between species may be able to be explained instead by ecological drift, random dispersal, and speciation. Given successes at predicting biodiversity through a general model of just those factors, the Unified Neutral Theory can shift the burden of proof to any theory seeking to explain patterns in terms of species' differences and relative functional roles (Hubbell 2006). An implication of the null hypothesis suggested by this model is that species do not depend significantly on particular other species, although they might depend on a number of other species in aggregate, because many species are more functionally equivalent than generally appreciated. Accounts of "community assembly rules" (Cody and Diamond 1975) have competed with the Unified Neutral Theory for several decades as explanations for local biodiversity. The presence of a species in a community, in view of community assembly models, has primarily to do with its finding an open niche, a place in functional space where it is not outcompeted. Although neutral theory and community-assembly approaches work from opposite assumptions about the significance of species functioning, they do not differ much with respect to interdependence.

Even current models that ignore interdependence, like Hubbell's Neutral Theory does, stop short of denying its presence. Moreover, they do not deny its relevance to phenomena of interest to some ecologists. Rather, they doubt its relevance to accurately predicting some variables of interest, especially species richness. For purposes other than generating predictions, however, and when other dependent variables are of interest, modeling dependency relations can be essential. Accurately predicting the fates of particular populations, as conservation biologists especially are keen to do, requires considering dependency. The upshot is that it is consistent to observe that prominent, current predictive models can do without interdependence and, at the same time, that dependency and interdependence can occur among populations. Minimalist or eliminativist approaches do not offer reasons to conclude that dependency and interdependence are illusory.

On the other, maximalist extreme, in terms of the relative importance of interdependence to representing community dynamics, are the community-of-

1. Ecologists have also hypothesized the interdependence of other units, like ecosystems with other ecosystems, as in Loreau, Mouquet, and Holt (2003). I limit the current discussion to populations.

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interest and superorganism concepts of ecological communities developed by early twentieth-century ecologists Stephen Forbes (1925) and Frederic Clements (1916). Forbes's (1925) limnological study of several lakes in Illinois and Wisconsin persuaded him that the populations living in a lake form an organic complex, one whose character or "sensibility" is "expressed by the fact that whatever affects any species belonging to it, must have its influence of some sort upon the whole assemblage" (537). His chief example is the Black Bass:

> In the dietary of this fish I find, at different ages of the individual, fishes of great variety, representing all the important orders of that class; insects in considerable number, especially the various water-bugs and larvae of day-flies; fresh-water shrimps; and a great multitude of Entomostraca of many species and genera. The fish is therefore directly dependent upon all these classes for its existence. Next, looking to the food of the species which the bass has eaten, and upon which it is therefore indirectly dependent, I find that one kind of the fishes taken feeds upon mud, algae, and Entomostraca, and another upon nearly every animal substance in the water, including mollusks and decomposing organic matter. The insects taken by the bass, themselves take other insects and small Crustacea. The crawfishes are nearly omnivorous, and of the other crustaceans some eat Entomostraca and some algae and Protoza. At only the second step, therefore, we find our bass brought into dependence upon nearly every class of animals in the water. (547–48)

That is, the diet alone of the Black Bass is illustrative of how a single population can be dependent on nearly all others, forming what he concludes is a "community of interest." Community relations in Forbes's lake are dependency relations, as each population's interests depend on those of nearly all others.

Forbes's vision of a single, shared interest created by the mutual dependency of the diverse parts of a biological entity resembles Clements's stressing that vegetation communities resemble organisms. Writing about the idealized plant community type that he called formations, Clements offers that "it is felt that the earlier concept of the formation as a complex organism with a characteristic development and structure in harmony with a particular habitat is not only fully justified, but that it also represents the only complete and adequate view of vegetation" (1916, iii). In *The Theory of Ecological Communities*, one of this year's most discussed ecology books, Mark Vellend interprets Clements's organismic analogy in terms of strong, physiological interdependence: "Frederic Clements (1916), an American plant ecologist, . . . held that a community was an integrated entity within which species were as interdependent as organs in a human body" (Vellend 2016, 21). Similarly, ecologist Jurek Kolasa interprets both Forbes and Clements

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this way: "Forbes preceded Clements in emphasizing interdependence of components, boundedness, and the equilibrial nature of ecological systems" (Kolasa 2011, 29). A century later, their theories remain exemplars for current ecologists of commitment to strong interdependence.

The point of considering maximalist characterizations of interdependence is to consider what kind of causal relations are needed to capture what they posit (at least to the degree that what they posit is biologically plausible). The superorganism idea, that populations are integrated with one another in an intricate physiology similar to an individual animal's, is biologically dubious. And indeed, contra Vellend (2016), Clements intended the comparison of ecological communities to be with organisms significantly less physiologically complex than animals (Hagen 1988). Both Forbes's and Clements's accounts of community relations contain the idea that the presence of some populations facilitates the presence of other populations and that some of this facilitation is not optional for the facilitated species; some populations need some others in some ways. But in what ways?

Here the answer is perhaps a little more surprising. Clements understands all survival-relevant relationships among populations in a successional community (or "sere") as both indirect and indifferent to taxonomic identity (Eliot 2011, 75–76, 99). "Indirectness" means here that direct causal connections are not supposed or required. In explanations of the presence, absence, or abundance of some plant population, no other plant (or its properties) is ever cited by Clements (1916) as an unmediated cause. Rather, the mechanism through which the presence and activities of plant populations affect other populations is the modification of environmental variables. These include the availability of water, light, nutrients, and substrates for growth. Consequently, what Clements describes plants as depending on is not other species per se but rather that the values of a suite of variables are within particular ranges (like that there is neither too much nor too little nitrogen or water). "Indifference to identity" here means that plant populations do not "care"—in that their fitness and survival are not affected—which species they affect or are affected by. While the presence or absence of certain species is often an important cause of the success or failure of others, a Cinnamon Fern can thrive in a range of degrees of shade, whether the shade is produced by oaks or elms or indeed by a roof. Similarly, Forbes's lakes form deeply interdependent "communities of interest" despite that "every element is either hostile or indifferent to every other," and here the indifference is partly, although not entirely, to identity, along with welfare (Forbes 1925, 550).

Therefore, since causal indirectness and taxonomic indifference are features of the causal interdependence relationships described by these theories that are still benchmark accounts of maximal interdependence, a causal model of interdependence should not build in causal directness or taxonomic preference as necessary for interdependence.

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This is not to say that dependencies never connect two specific sets of species. Coevolution, although it operates on many relationships that are not mutualistic, has produced some less indifferent relationships between both free-living species and symbionts (Futuyma 2009, 178). However, mutualisms resulting from coevolution may still be indirect and taxonomically indifferent. Although they may be more fragile, as when a species relies on some one specific species for a necessary and irreplaceable resource or service, even these relationships are taxonomically indifferent by virtue of being evolved. Essential species can always in principle be swapped for others, through further evolution, if not always in practice. Consequently, mutualisms represent a special case of interdependence, one that can be accommodated by a broader account that allows indirect interdependence and indifference to identity (although cases of nonmutualistic interdependence cannot always be accounted for by an exposition that does not allow those). So, mutual dependence should not be built into a definition of interdependence.

In sum, a causal model of ecological interdependence should characterize pair-wise interdependence but not assume that interdependence is pairwise. It should make it possible to represent networks of populations as interdependent. But it should not assume or require taxonomically specific or direct, unmediated causal relationships.

3. A Causal Model of Dependency. To characterize ecological interdependence, we can begin with ecological dependency. Here is a case. Red Knot (*Calidris canutus*) is a bird species, a sandpiper that breeds in the high Arctic. The *rufa* population that migrates from the Canadian Arctic to the eastern United States, then to Brazil and Patagonia, depends on Horseshoe Crabs (*Limulus polyphemus*). On their annual southbound migration, Red Knots require nutrients and energy they acquire by eating Horseshoe Crab eggs at stopover sites around the Delaware Bay, before making a long trip over water to Brazil (Baker et al. 2013). Where Horseshoe Crab eggs are scarce around the Delaware Bay, so are Red Knots (Karpanty et al. 2006). The *rufa* Red Knot population depends on the Delaware Bay region's Horseshoe Crab population.

To say that a Red Knot population depends on a Horseshoe Crab population suggests that were Horseshoe Crabs not present, Red Knots could not be either, or not for long. Their population would be driven to zero. That is, if Horseshoe Crabs decline, that causes Red Knots to decline to zero. (If Horseshoe Crabs do not decline, Red Knots may or may not decline, conditional on many other variables including what else they depend on.) Generalizing on this, to assert that population *A* depends on population *B* might be to express the causal regularity that a decline in *B* would cause the extirpation of *A*.

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Such a formulation will be true for many instances of dependency. But it falls short as a general account, considered against fruitful accounts of how causal generalizations in biology can be robust and explanatory. If we interpret "Horseshoe Crab decline causes Red Knot decline" as a universally quantified generalization—in the form, that is, traditionally attributed to laws—it lacks stability. Mitchell (2002) understands the stability of such generalizations as "a measure of the range of conditions that are required for the relationship described by the law to hold" (346). This standard permits treating as explanatory even generalizations considerably less stable than (her example) Mendel's law of segregation. But the range of stability of the Red Knot–Horseshoe Crab dependency is extremely limited. Not only is it evolutionarily contingent (sensu Beatty 1995), it is thoroughly contingent on biogeographical history. Indeed, the *rufa* population may be the only Red Knots that depend on Horseshoe Crabs. The *roselaari* population, which migrates down the west coast of North America, feeds primarily on eggs of grunion—a fish—on its migratory stopovers (Carmona et al. 2011; Baker et al. 2013). Consequently, the Red Knot–Horseshoe Crab causal generalization holds for an individual population for a period of evolutionary and biogeographical history but probably nowhere else.

As an alternative to Mitchell's approach, Woodward and Hitchcock (2003) construe such causal generalizations as existentially quantified rather than universally quantified and recommend assessing their range of invariance. By "invariance" they mean holding true across a certain range of possible changes. For the Red Knots depending on Horseshoe Crabs, an existential construal fits better than construal as a universal generalization that may have only one instance. And there are indeed possible changes in the Atlantic Horseshoe Crab population that could affect the *rufa* Red Knot population. Consequently, while it is possible on this construal to understand the relationship as causal, its explanatory power is extremely weak, if explanatory power varies with degree of invariance over counterfactual conditions. Horseshoe Crab populations generally do not limit Red Knot populations. An adequate causal characterization of dependency should achieve more generality than the existential construal yields, if evolutionarily and biogeographically contingent dependencies like this are typical.

To achieve more generality, an adequate causal characterization of dependency should focus on the causal variables with informative invariance. The key to doing so lies in recalling that even the maximalist accounts of interdependence treated dependent populations as indifferent to taxonomic identity and connected indirectly. The invariance or stability of dependency relations can be increased by introducing a variable of a different sort: an environmental constraint. Environments constrain populations, and dependencies are created by ways environments can be modified to make survival

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possible. Populations then come to depend on the modifying agents, which can include other populations.

Ecological dependency can thus be conceptualized as a relationship between two kinds of constraints and something that can modify them. The two kinds of constraints are (1) a population's needs (as a function of individual organisms' needs), which are equivalently constraints on the conditions under which it can survive or persist, and (2) environmental variables that become constraints relative to actual or possible populations of organisms. For example, a Cinnamon Fern can thrive only in a certain range of light conditions; it requires some light with properties of sunlight, but it cannot handle much. The range of available sunlight in a forest environment constrains fern populations. But other populations can impede constraints. Oak trees, through their presence or absence and condition, can modify the amount of sunlight available. They interfere with the sunlight that would otherwise be too much for ferns, constraining them out of existence. Similarly, Red Knots on migration are constrained by the availability of digestible sources of energy. Horseshoe Crabs, releasing eggs, interfere with that constraint.

To express the improved ecological dependency relationship more formally: population *A* depends on population *B* if and only if *E* is an environmental variable constraining *A*, and *B* changes *E* in such a way that *E* cannot drive *A* to zero. In other words, the size of *B* and its influence on *E* are sufficient to prevent *E* from eliminating *A*. This is consistent with there being a population (or other agents) *C* that could also prevent *E* from extirpating *A*. Accordingly, "*A* depends on *B*" for populations *A* and *B* is always a contingent claim with a truth-value relative to a particular space/time or situation in evolutionary and biogeographical history.

Introducing the mediating constraint variable makes it possible to see where the necessitation enters the dependency relationship in contrast with what is contingent. The necessity arises in the power of constraints to extirpate populations. This is the aspect of the dependency relationship closest to what Waters (1998) describes as causal regularity. The values of environmental variables necessarily affect organisms with certain internal makeups. The other features of the regularity, including which agent inhibits the constraint, are contingent to varying degrees.

4. Interdependence Again. Given this definition of ecological dependency, an account of ecological interdependence follows easily: population *A* is interdependent with population *B* if and only if *A* is depending on *B*, and *B* is connected back to *A* in a circuit, via a series of dependencies. The boundaries of networks of interdependence are the limits of sets of populations connected circuit-wise.

One virtue of this way of expressing interdependence is that it easily integrates with depictions of interdependence extending to abiotic elements, as

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Millstein (2018) points out that Leopold's does. Given the centrality of environmental variables to dependency, the causal responsibility of nonliving parts of ecological systems, as they affect those systems, can be highlighted without shifting to new kinds of relationships.

For the same reason, this account also sidesteps traditional criticisms of accounts of interdependence like Forbes's, Clements's, and Leopold's. Each of these authors can be read—accurately or not—as privileging members of historically interdependent communities as irreplaceable. This apparent privileging has been read as xenophobic or unreasonably hostile to immigrant species and, at the same time, naive about the rapid biogeographical reshuffling that characterizes our contemporary world. But we can observe that ferns depend on chestnut trees, even as we accept that as chestnuts disappear, planted oaks or even awnings and roofs might potentially play the chestnut's former role. The degree to which new species can integrate into existing communities is a function of how well they interact with environmental constraints.

Let us return to the opening puzzle that early biologists like Linnaeus and later Forbes struggled with. How should we understand causal relationships among populations where they are simultaneously "warring" and situated in a mutual interdependence? Presentations of interdependence from Linnaeus to Forbes to Leopold have emphasized trophic (or consumption and food-web) relationships, at least in presenting interdependence. An account of interdependence built on constraints and environmental variables makes it easier to conceptualize populations as more than consumers and competitors. The environmental variables whose values organisms depend on to make their lives are tremendously diverse, and the ways in which organisms can depend on each other are as diverse as the ways that they can affect those variables.

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