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Discussion

Theoretical ecology has never been etiological: A reply to Donhauser

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In a recent article in these pages, Justin Donhauser draws a sharp contrast within theoretical ecology between 1) a teleological view which accepts "top down" causality to explain ecological network-level properties; and 2) an etiological view which seeks "bottom-up" or "efficient" causes of those phenomena (Donhauser, 2016, pp. 68–69).[1] Donhauser admirably succeeds in showing that several founders of ecological theory, including Lindeman (1942) and Hutchinson (1948), had "efficient" rather than "final" causality in mind. I believe, however, that Donhauser has not addressed, although he begins his paper by identifying, the concern critics often express about theory in ecology. Critics argue that empirical evidence fails to support the postulation of network-level ecological properties, such as the oscillations Donhauser describes. If network-level properties are not observed it is not important how they may be explained.

1. The principal criticism of ecological theory

Donhauser (p. 67) begins his article by helpfully and accurately citing a list of authors who 1) "have questioned whether the entities described in ecological theory exist in any meaningful sense at all" and 2) "have argued that theoretical ecological research is empirically unfounded (even empirically unfoundable)." Whether ecological networks and network-level properties exist, according to these critics, is an empirical question, although ecological theory treats it as if it were a conceptual one (Odenbaugh, 2007, p. 633). Gregory Cooper (2001), among other critics Donhauser cites, has expressed exasperation at the tendency of ecological theorists to argue their case on conceptual grounds, as if to show that ecological patterns might form or could arise is sufficient to demonstrate that they do form and do arise. To be sure, many of the kinds of properties theoreticians posit and mathematicians model are observable in principle; the critics contend, however, that these patterns or regularities are not observed in fact.

By saying that ecological theory has never been etiological, I mean that it has not presented empirical evidence of the causal forces it theorizes, such as density dependence, competitive exclusion, Lotka-Volterra predator-prey relations, the logistic relation of species abundance to resource limits, and the like. Hall (1988), whom Donhauser cites as one of many ecologists who believe that theoretical models are empirically unfounded, notes that they have been treated as if they are a priori true. "They are taught in virtually every introductory ecology course – often as 'basic truth'" even in the absence of empirical support for them. As Hall puts it, "biotic interactions seem to be recalcitrant to predictive models" (Hall, 1988, p. 10).

Donhauser correctly identifies behind the criticisms of theoretical ecology the view he attributes to the plant biologist Henry Gleason (1917, 1939) that "populations and communities are nothing but contingent collections of interacting organisms that continually change and do not exhibit any sort of observable network-level structure or dynamics" (p. 70) Many ecologists today agree with this assessment that organization or coherence at the community or network level is not found. John Lawton (1999) has argued that no general laws, rules, or patterns appear at the "community" level in ecology because contingent factors, which differ from place to place and time to time, overwhelm the kinds of forces or regularities that are of interest to theoreticians. According to Linquist (2015, p. 1105), "Lawton's paper has received an average of 37 citations per year since its publication, mostly endorsing his contingency thesis."

In a much-cited paper, Marc Lange (2005) provides a conceptually clear way to frame the criticism of theoretical ecology Hall and other critics Donhauser cites raise. Lange draws on a famous passage in which John Stuart Mill (1961, pp. 552–553) distinguishes between "greater" and "lesser" causes that determine the level of the tides at any particular place. The level of the tides can be generally predicted on the basis of a few greater causes, in this case, the gravitational attraction of the sun and moon. Nevertheless, local circumstances, such as the way the sea bottom and shoreline are configured, the direction of the wind, etc., may constitute lesser or accidental or causes which may make the levels of the tides at any place differ somewhat from those predicted on the basis of lunar and solar gravitation alone. Often these local contingencies and

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[1] All page references to Donhauser refer to this article.

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particularities can be determined and factored in to a place-specific prediction, but it may also be the case that not all these contingencies may be known at a particular site. Mill concludes that because greater causes can be distinguished across environments from lesser ones, Tidology may be an inexact science, but is a science nonetheless. The gravitational forces on which the levels of the tides depend are strong, general, and wide-ranging enough that they can be distinguished in their efficiency from the incidental factors that vary place to place.

Philosophical critics, several of whom Donhauser cites, argue that unlike Tidology, ecology cannot distinguish between greater and lesser causes. The abundance and distribution of the tides – their levels at different places – result from the greater causes of solar and lunar gravitation with only slight variations attributable to local, incidental, and contingent factors. The abundance and distribution of plants and animals – their levels at different places – in contrast result from local, idiosyncratic, incidental, and circumstantial forces and conditions particular to a place and time. In ecology, according to these critics, there is no way to distinguish the signal from the noise, "no distinction to be drawn between the 'greater causes' and a host of petty, local, idiosyncratic influences that must be ascertained on a case-by-case basis" (Lange, 2005, p. 398). For this reason, critics such as Shrader-Frechette and McCoy (1993; see also Simberloff, 2004, 2006) argue that the science of ecology should be directed not toward theorizing patterns and regularities that do not exist but toward building a catalogue of case studies.

2. Oscillations – what oscillations?

Donhauser reports that in a founding paper in theoretical ecology, Hutchinson (1948) imagined the kinds of patterns that could possibly arise if self-regulatory processes governed ecological networks. Hutchinson then constructed in conceptual terms the kinds of causes or "component-to-component" interactions which could in a mathematical sense explain those patterns. According to Donhauser, Hutchinson argued that "typical component-to-component interactions are the 'mechanisms' that jointly produce observable correlated changes and oscillations in nutrient and population abundances" (p. 71). It is true that Hutchinson argued that if certain theoretical assumptions about ecological interactions were correct, "oscillating systems should be found frequently in nature" (Hutchinson, 1948, p. 242). He was circumspect, in fact, diffident, however, on the question whether oscillating systems are frequently found in nature. Indeed, he called putative cases "highly exceptional" and wrote, "Practically no cases can as yet be placed in their proper categories in the theoretical scheme."

Donhauser draws a conceptual diagram of nutrient and species interactions, such as prey-predator relations, as a double wavy line with harmonic periodicities (p. 71). He writes that the wavy lines are not derived from any data set; "I've made up the values," he says. The critics of theoretical ecology to whom Donhauser responds argue essentially that had to make up the values since there are no data sets – no sustained empirical evidence – that could serve the purpose. As Donhauser points out, Hutchinson conceptually reconstructed how observable cyclical dynamics may or could possibly arise amid ecological phenomena, but Hutchinson did not contend that these observable cyclical dynamics had widely been observed. Donhauser does not claim these oscillations are in fact observed. He does not refer to any relevant data set because there is none; otherwise, he would not have to resort to making the values up.

To say that the kinds of oscillations Donhauser illustrates are not observed in nature may seem to be an overstatement. Yet this is practically the consensus among empirically-minded field ecologists. According to Peterson (2013), standard textbook examples of predator-prey oscillations, such as that between lynx and hare, have been thoroughly debunked (see also Gilpin, 1973; Botkin, 1990; for review see Sagoff, 2016). Botkin (2016 , p. 182)has written that over a career of searching the scientific literature, he never found a case where the mathematical idea behind oscillations worked (likewise Turchin, 2001, p. 24). Peterson (2013) wrote that "no serious student of predation believes the model suitably depicts the real world." Weiner (1995, p. 155) has written that there are virtually no examples in nature of oscillations of the sort Lotka-Volterra models would predict. "Yet, despite the lack of support for the core prediction of the Lotka-Volterra predator-prey models, they remain a staple of mathematical ecology."

Field biologists involved with the introduction of wolves to control elk and moose report that predator and prey populations vary independently and individualistically, each for contingent reasons particular to a place and time, rather than in relation to each other. In other words, there is no way to differentiate between greater and lesser causes in the relative population dynamics of these species. Vucetich, Smith, Stahler, and Ranta (2005; see also Smith, Peterson, & Houston, 2003), on the basis of data associated with the introduction of wolves to control elk populations in Yellowstone National Park, concluded that the influence of wolf on elk abundance was no greater than that of weather-related factors, such as snowfall, temperature, and precipitation, the hunting of elk outside the park, predation by bears, and other contingencies. Lotka-Volterra oscillation models leave researchers clueless about the contingent causes that matter case by case in the real world.

Similar results have been reported with respect to the influence of wolf on moose populations (Garrott et al., 2005) including the careful observation of wolf-moose interactions over 60 years at Isle Royale, which has been described as one of a few landmark studies capable of testing the integration of top predators as structuring agents in ecological systems (Sergio et al., 2014, p. 1236). According to the Isle Royale Research Project Websites, "The most important events in the history of Isle Royale wolves and moose have been essentially unpredictable events—disease, tick outbreaks, severe winters, and immigrant wolves." Wolves seem to have no more effect on moose populations, and vice versa, than any of a myriad lesser, contingent, and accidental causes (Montgomery, Vucetich, Roloff, Bump, & Peterson, 2014; Nelson, Vucetich, Peterson, & Vucetich, 2011). Predator populations are at most one "lesser" cause among many factors in the regulation of prey populations, and vice-versa.

Donhauser in his paper uses the term "network-level" 26 times; he speaks of "ecological network-level dynamics; " "ecological network-level phenomena; " and "network level structure." The critics to whom he responds, however, deny that network-level phenomena, such as oscillations, are observed. If network-level properties have been observed, there must be an empirical literature documenting their occurrence, but it is elusive. The literature of theoretical ecology presents what may be hundreds of conceptual and mathematical analyses of how observable network-level dynamics, structures, phenomena, etc. could occur as a result of component-to-component interactions. The critics to whom Donhauser responds do not doubt this. Rather, they question the extent to which observable network-level phenomena are actually observed.

Donhauser lists Worster (1990) among the articles to which he responds. According to Worster, rather than revealing network-level structures, processes, or dynamics, nature is "full of seemingly random events that elude our models of how things are supposed to work." It is a "landscape of patches, big and little, patches of all textures and colors, a patchwork quilt of living things, changing continually through time and space, responding to an