

Pâslaru, Viorel (2018) "Mechanisms in ecology", in Stuart Glennan, Phyllis Illari (eds.), *The Rutledge Handbook of Mechanisms and Mechanical Philosophy*. London and New York: Routledge, 348-361.

<https://www.routledge.com/The-Routledge-Handbook-of-Mechanisms-and-Mechanical-Philosophy-1st-Edition/Glennan-Illari/p/book/9781138841697>

Chapter 32.

Mechanisms in Ecology¹

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Abstract

New mechanistic philosophy has not examined explanations in ecology although they are based extensively on describing mechanisms responsible for phenomena under scrutiny. This chapter uses the example of research on the shrub *Lonicera maackii* (Amur honeysuckle) to scrutinize individual-level mechanisms that are generally accepted and used in ecology and confronts them with the minimal account of mechanisms. Individual-level mechanisms are for a phenomenon, are hierarchical, and absent entities play a role in their functioning. They are distinguished by the role played by properties in determining activities and organization. The chapter also considers the experimental methods for discovery of individual-level mechanisms, the possibility of group-level mechanisms in ecology, and suggests further research problems.

I. Introduction

Genetics, cell biology and molecular biology offered to philosophers of science sufficient examples to challenge the logical empiricist view on scientific inquiry as a search for laws of nature and scientific explanation as subsumption of phenomena under laws.

Those areas of biology indicated instead that scientific inquiry is a search for mechanisms and explanation is a matter of describing them (see Chapters 1 and 24). The resulting new mechanistic philosophy of science offered various accounts of mechanisms whose common assumptions are articulated by this formulation of a minimal mechanism:

A mechanism for a phenomenon consists of entities (or parts) whose activities and interactions are organized so as to be responsible for the phenomenon (see Chapter 1).

Mechanisms are real and local complex systems or processes that are responsible for the phenomena scientists study. Mechanisms produce phenomena in virtue of their parts that are organized and engage in activities or interact. For example, a heart is a mechanism for pumping blood. It produces this phenomenon due to its parts right and left ventricles, right and left aortas, and the valves. They perform activities, such as the right ventricle contracting and pushing the blood into the pulmonary trunk, while the valves open and close. Parts and activities are organized. Blood is collected in the right atrium first, but not in the left atrium, and the tricuspid valve opens toward the apex of the heart, but not toward its top. Mechanistic approach is reductionist in that it explains properties and activities of the whole in terms of properties and activities of its lower-level parts. That walls of the heart contract is explained by referring to three layers of cardiac muscles and to the intercalated disks that enable direct transmission of electrical impulses between cells, which also shows that mechanisms are hierarchical. The mechanistic approach acknowledges the complexity of real systems and examines mechanisms in their contexts. Accordingly, operation of the heart mechanism is considered in the context of the thorax, its interaction with the diaphragm, the lungs and the system of blood vessels.

Mechanistic philosophers of biology have not examined mechanisms in ecology, which is important to do since they are ubiquitous, as a simple search of ecology publications can reveal, ecology is part of biology, and ecological mechanisms might be different from the rest. I use the case of the invasive shrub *Lonicera maackii* (Amur honeysuckle) to examine mechanisms at the level of individuals. I explore then the case of mechanisms involving groups of organisms. First, a brief on what is ecology.

II. What is Ecology?

Ecology is not environmentalism and its focus is not environmental problems and the effects of human impact on the environment. Ecology is a discipline of biology that studies the world of plants and animals, including humans, and is widely understood as “*the scientific study of the interactions that define the distribution and abundance of*

organisms” (Krebs 2008, 5). Distribution is the place in nature where organisms are found, while abundance is their number in an area. Distribution and abundance are two facets of the same phenomenon and the factors that affect the former could also influence the latter. The factors that determine the distribution and abundance of organisms fall into two categories: biotic and abiotic. Biotic factors comprise interactions between organisms, such as predation, or competition. Abiotic factors comprise influences of the environment on organisms, such as temperature, availability of light or water, its pH, or the nature of the ground.

Distribution and abundance are examined at various levels of increasing complexity and integration, but of decreasing understanding: populations, communities, ecosystems, landscapes, and biosphere. To explain phenomena of distribution and abundance at one level, ecologists typically seek explanatory mechanisms at lower levels. For example, behavioral and physiological mechanisms operating at the individual level are sought to explain changes in a population. Because its area of investigation spans so many levels, ecology neighbors with multiple sciences. It draws on physiological and behavioral studies of individual organisms, as well as on meteorology, geology, and geochemistry for its explanations (Krebs 2008). Ernest Haeckel introduced the term *ecology* in 1869, but ecological research and interest predate this date, making it one of the oldest disciplines of biology.

III. An Example of Individual-Level Ecological Mechanisms

Research on the competitive success of the invasive shrub *Lonicera maackii* (Amur honeysuckle)² against native plants illustrates how ecologists examine and conceive of mechanisms at the individual level and their effects at macro scale.

Specimens of the shrub were introduced to the U.S. in 1898 to the New York Botanical Garden. From there, humans further dispersed shrub specimens to serve as ornament or to stabilize soil. Furthermore, birds, deer, and small mammals consume the seeds of the shrub and drop them with feces at various locations, which helped the invasive plant establish throughout vast areas of the midwestern U.S.

L. maackii dominates native plants in competition for light and suppresses their growth because it has a dense canopy, is able to produce numerous stem shoots and grow

rapidly in habitats with different light regimens. When grown in understory, *L. maackii* maximizes height gain and allocates energy to continuous production of basal long shoots and consequently has a lower canopy width, fewer shoot ends, and a smaller diameter of basal stems. Should more light become available, which happens when a patch of forest is cleared, say, by a fallen tree, the shrub stops producing basal long shoots and starts producing long shoots at higher levels in the canopy, develops wider canopies, and produces more leaves. Compared to indigenous shrub species, *L. maackii* is able to equal or exceed the maximum stem growth, higher stomatal density and thickness of leaves, higher leaf number, area, and mass in low-light conditions, but exceeds such a performance in high-light conditions that occur following disturbances in forests. Under both light conditions, *L. maackii* allocates more energy to branch and leaf mass growth and this allows it to overgrow the slow-growing native shrubs. The shrub is fully able to regenerate after the first clipping both in open-growth and in forested areas. It leafs two to three weeks before the native plants and drops the leaves four-to-six weeks later than the native plants, and can be observed as late as December. Its leaves are also freeze-resistant and are not damaged by spring bouts of cold, in contrast to the native species. Seedlings establish throughout a variety of light conditions, and even those that were suppressed due to clumped seed input can survive and replace adult shrubs. All these features endow the plant with a dense canopy that decreases light availability to the ground, suppressing the growth of other plants.

In addition to outcompeting native plants for light, *L. maackii* dominates below-ground competition for nutrients and water. Its roots cover a wider area close to the surface, which allows it to deprive neighboring plants of water and nutrients, suppressing their growth. Additionally, it suppresses the growth of native plants by means of chemicals in a process called allelopathy. Leaves produce thirteen mildly acidic toxic compounds that inhibit or delay germination of seeds, or alter size, survival, and architecture (number of branches and bolts) of native plants and deter generalist herbivores from consuming its leaves. Roots produce similar chemicals, but they have milder inhibiting effects on neighboring plants. Chemicals released into the ground from decomposing leaves and by roots modify soil and leaf microbial communities, altering ecosystem function and processes.

Ecologists research above and below ground competition, as well as allelopathy as separate mechanisms, yet none of them is solely responsible for the competitive success of *L. maackii*. Since they act jointly, I suggest representing the separate descriptions in an integrated account (Figure 32.1), which will also facilitate the forthcoming philosophical examination of these mechanisms.

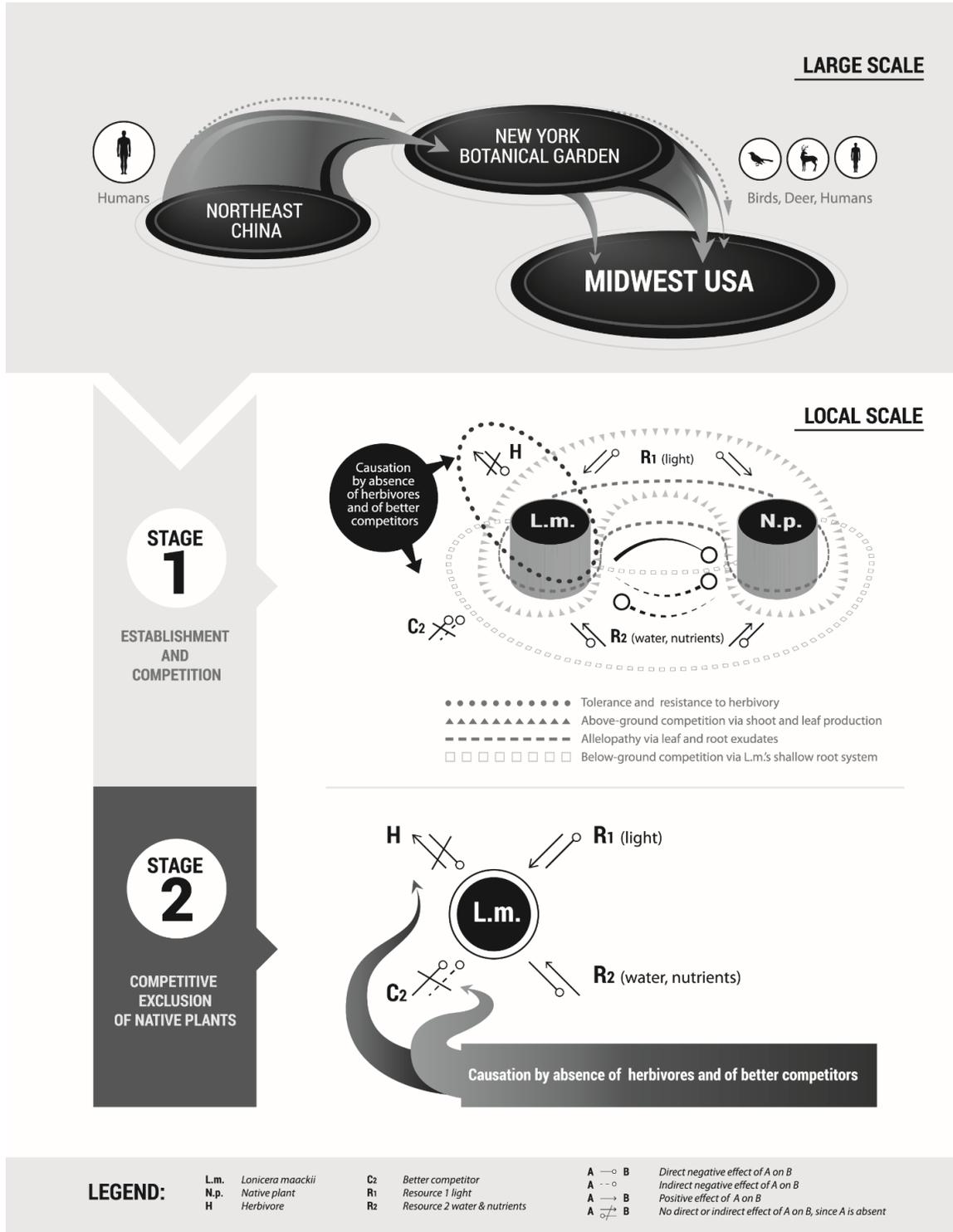


Figure 32.1 Integrated representation of the mechanisms of competitive success of *L. maackii*. Dispersal mechanisms at the large scale consist of activities of humans and animals transporting specimens and seeds of *L. maackii* at large distances. At the local scale, the mechanisms responsible for the competitive success of *L. maackii* and the

elimination of native flora are causation by absence of herbivores and of better competitors, the mechanisms of above ground competition for light, of below ground competition of nutrients, of allelopathy via leaf and root exudates, and of tolerance and resistance to herbivory. Drawing by the author.

IV. Individual-Level Mechanisms in Philosophical Focus

Ecological Mechanisms and the Minimal Account. Individual-level ecological mechanisms satisfy most, but not all features of the minimal account of mechanisms and their particularities contribute toward the general examination of mechanisms.

Several decades after the introduction of *L. maackii* to the U.S., it became clear that it is not an innocent shrub that beautifies landscapes, but a shrub that efficiently suppresses and eliminates native plants. This phenomenon of suppression and elimination of native flora required explanation that ecologists formulated from the beginning not in terms of laws, ecological or otherwise, but in terms of mechanisms. And so they articulated the mechanism of competition for light, of belowground competition for water and nutrients, and the mechanism of allelopathy, which were meant to account entirely for the elimination of native flora or offer partial explanations of that phenomenon. Accordingly, ecological mechanisms, just like in other areas of biology, are mechanisms for a phenomenon and are formulated to explain it.

Ecologists often characterize individual-level mechanisms as consisting of individual organisms with certain properties doing certain activities. In Gause's (1934) account of the mechanism of competition, the components are the individual cells of yeast differentiated by the property tolerance to alcohol. Alcohol produced by *S. kephir* is more toxic to *S. cerevisiae* than vice versa, the latter being eliminated. *L. maackii* is representative of cases in which the phenomenon cannot be explained by reference to a property of the individual organism and its activity, but to several properties and activities that engage different parts of the same organism. Accordingly, it is parts of organism that are entities in various mechanisms. The roots of *L. maackii* are components of the mechanism for below-ground competition, while its shoots and leaves are parts of the mechanism for above-ground competition, not the individual plant, although it is

necessary for the roots, shoots and leaves to function. The case of *L. maackii* helps stress that entities that appear simple are in fact composites of many parts that function in different mechanisms.

The composite nature of the organism *L. maackii* makes the mechanism of competition between this invasive plant and native species hierarchical. Its lower-level components are the mechanism of competition for light, the below-ground mechanism of competition for nutrients, the mechanism of allelopathy, and the mechanism of tolerance and resistance to herbivores. Each of these mechanisms is made up of parts at lower levels that are also investigated. The mechanism of competition for light consists of leaves and branches, with specific properties and performing activities. Shrubs that grow in understory have long shoots of a small diameter, fewer shoot ends, and a low canopy width. Since leaves are a key component of this mechanism, their properties are closely studied. Ecologists examine their higher stomatal density and thickness, their number per stem, area, mass, and their photosynthetic performance in low-light conditions compared to native species. The mechanism of photosynthesis that allows *L. maackii* to thrive in low-light conditions and the mechanism for longer leaf duration in *L. maackii* are a lower-level component of the mechanism of competition for light.

Hierarchical organization of ecological mechanisms shows some entities can be components in several mechanisms. Leaves and roots, in addition to being parts of the mechanisms of above-ground and respectively below-ground competition, are also components in the mechanism of allelopathy. Leaves produce toxic compounds that, once they reach the ground with falling leaves, inhibit the germination of seeds of native species, while roots produce metabolites that inhibit the growth of roots of native species. The outcome is the same in both cases: native species are prevented from growing. Descriptions of the mechanism of allelopathy include chemical analyses of the allelochemicals that leaves and roots produce.

Furthermore, ecological mechanisms do not have clear boundaries and what identifies them is the operational unification of components of different sizes. For example, the boundaries of the mechanism of competition for light are set by the operational unification of the parts of different sizes: shoots and leaves of individuals of species involved and light.

The explanatory role played by absent entities is another feature that, while not unique to ecological mechanisms, is very important. According to the Enemy Release Hypothesis, one of the hypotheses formulated to explain the success of *L. maackii*, the shrub spreads well in new environments *because* its traditional predators are absent. Similarly, it is not subject to intense competition, for there are no competitors that could challenge it. Ecologists consider the absent predators and competitors in light of the assumption that all species are parts of food webs and have predators and competitors that control their growth where the absence of either of them is a cause of a species' growth. Had either a predator or competitor been present, the dynamics of the species would have been different. Ecologists treat absent predators and competitors as possible causes that could influence the phenomenon under scrutiny, and as such they are part of the mechanistic account of the phenomenon along with the detailed descriptions of actual entities. This is not a departure from the realism of mechanistic philosophy, since the absent predators and competitors are not abstractions or fictions, but real organisms that happen not to be present in the habitat under scrutiny. It indicates, however, that the counterfactual account of causation is necessary for thinking about causation in mechanisms. The list of absent causes could also include other instances of causation by absence involving abiotic or biotic factors. Absence of sunlight explains the absence of shade-intolerant plants, and absence of water explains the presence of drought-resistant plants and the absence of drought-intolerant ones. The absence of an entity is not sufficient by itself to account for the phenomenon. The other components of the mechanism are required.

What Distinguishes Ecological Mechanisms. The central role of properties, the diminished role of organization and the relationship between the two, which I scrutinize next, are features that distinguish ecological mechanisms, yet neither the minimal account of mechanism nor the dominant conceptions of mechanism examine them closely or stress them enough.

Given the ontic dualism of MDC's conception, entities and activities take center stage in their characterization of mechanisms, and properties seem subordinated and only briefly acknowledged as bases of activities (Machamer, Darden, and Craver 2000). In Glennan's latest work causal powers or capacities perform the metaphysical role that

properties have relative to activities in MDC's characterization (Glennan 2014). The minimal account of mechanisms does not either thoroughly examine the role of properties in mechanisms. However, if the philosophy of mechanisms is to do justice to ecology, one has to emphasize the properties of entities. Ecologists are explicit about the importance of properties in characterization of mechanisms:

Perhaps I should clarify what I mean by mechanism. The mechanistic basis for population ecology is provided by the properties of entities one hierarchical level lower than populations, that is, by the behavior and physiology of individual organisms (Turchin 1999, 156).

And it is this focus on traits that defines ecology's subdisciplines of functional ecology and physiological ecology (Shipley 2010). In ecological context, properties of entities are the actual traits of organs, individuals, populations and communities that ecologists measure, rather than the not-yet-manifested capacities. And focus on properties is necessary to better understand the activities of organisms. *L. maackii* chemically suppresses the growth of native plants. To understand this activity, ecologists performed an analysis at the molecular level of the chemicals and confirmed experimentally their inhibitory effect (Cipollini et al. 2008). In other instances, description of properties amounts to a description of causes of an organism's impact, or of distribution and abundance. Variety of canopy shapes, i.e., leaf-forms, growth forms and heights of plants, accounts for better use of the three-dimensional space and, consequently, better light interception (Tremmel and Bazzaz 1993). Tolerance to high soil salinity and to deficiency of oxygen in water logged soils is a cause of the presence of the grass *Juncus gerardi* in those areas of marshes that are flooded regularly, while intolerance of the shrub *Iva frutescens* to those conditions explains its presence on the terrestrial borders of marshes that are not flooded (Bertness and Hacker 1994).

“Organization is the least controversial element in any characterization of mechanisms,” yet how to understand organization is not a trivial matter and it has not been discussed extensively (Illari and Williamson 2012, 127). The consensus in the literature is that along with entities and activities, organization is a necessary condition for a mechanism to be able to produce the phenomenon for which it is responsible. As a condition different from entities and activities, organization is generally treated as

something that can be changed actually or in principle by a human or natural agent: should the same entities and activities be organized differently, they would produce a different phenomenon (Illari and Williamson 2012, 127). This view on organization is a version of what Glennan (2014) calls induced organization and that is different from affinitive organization. This distinction between induced and affinitive organization helps address the nature of organization in ecological mechanisms.

In induced organization, the host, to use Glennan's example, determines how guests are seated at a dinner party. Induced organization is thus imposed upon entities and/or activities by the agent, human or nature, determining the organization of the mechanism. Such changes to the organization of mechanisms can be found in biogeography. A human or natural agent can change the distance between an island and its source region or change the arrangement of islands in an archipelago. Nature accomplishes this by means of tectonic changes, while humans by modifying the landscape, as in the case of land-based islands. Changing the distance between islands and their source region modifies the number of species present on an island (Pâslaru 2014).

One could further analyze induced organization and add that it can be changed by either adding or removing components. That is, the host could invite additional guests, or disinvite some if they fail to behave properly. Humans induced the organization of entities—plant species—at the New York Botanical Garden when they introduced a new component: *L. maackii*. Likewise, humans induce the organization of ecological communities when they decide to remove *L. maackii* because it behaves as an invasive species and suppresses native plants.

Affinitive organization depends upon affinities, or properties of entities and/or activities. The latter are organized as they are because of their properties. In induced organization, the host, to use Glennan's example, determines how guests are seated at a dinner party. In affinitive organization, guests find their own seats based on their affinities—friends, family, football fans, etc (Glennan 2014). An illustration of this is the organization of the mechanism of dispersal of seeds of *L. maackii*. It involves the interaction between birds, deer, and small mammals with the shrub's seeds and it was not induced, but resulted from affinities of the entities and their activities. Birds consume

seeds because of their nutritious value and taste, and spread them to other places, where they can germinate even after they had passed through the digestive tract of birds. No agent induced the interaction between birds, seeds and germination of the latter. Their properties determined them to interact and organization emerged as a result. The mechanism of competition for light appears organized: *L. maackii* leafs out before native plants and suppresses their growth by depriving them of light. Leafing at a certain time in the spring is a property of *L. maackii* that it will show regardless of where and in what plant community it is planted. Similarly, succession, another central ecological process, shows organization. An area is colonized in a certain order by species belonging to certain functional types. Properties of species determine the order of colonization. Soil-fixing plants establish first, and then trees, herbivores and carnivores. Even if an herbivore were introduced first, it could not get established in the absence of plants suitable for consumption. These examples indicate that affinitive organization is restrictive. It restricts an entity's interactions. They also indicate that properties of components limit induced organization and, more generally, "[a]ll mechanistic organization depends to some degree upon the existence of affinities—as parts must have the capacities to interact with other parts" (Glennan 2014). One cannot just organize differently the same entities and activities to get a different phenomenon. Trading the location of *L. maackii*'s canopy with that of its roots will produce no meaningful ecological phenomenon. The shrub will simply die. Whether induced organizations persist, also depends on the properties of entities. *L. maackii* was able to establish in New York, as well as throughout the Midwest, because of its properties and activities. Had it not been a good competitor for light, or a producer of allelochemicals, it would have been limited to the grounds of botanical gardens.

As in the case of non-hierarchical organization, properties determine hierarchical organization. Toxic compounds produced by leaves and roots of *L. maackii* cannot be a component of the mechanism of competition for light and occupy the same level with leaves of native species, because the compounds do not have the geometrical and material properties necessary to diminish the amount of light reaching native plants. And roots cannot be part of this mechanism, since their properties are such that they can only subsist in the ground. Therefore, the hierarchical organization is a product of the

properties of entities and activities and one cannot induce a different hierarchical organization of a mechanism by reshuffling its components. Instead, one has to introduce different entities which, however, could destroy the mechanism.

The stronger metaphysical finding of the foregoing examination is that inductive organization is on a par with properties in determining the functioning of mechanisms. Affinitive organization is a product of entities interacting in a certain manner in virtue of their properties. In mechanisms embodying affinitive organization, their organization is an epiphenomenon. Organization is not the central element that determines how entities and activities produce phenomena, but the properties of entities and activities are. This implies that to change the organization of a mechanism, one has to change the entities and their activities. Only changing the spatial or temporal organization, while preserving the components unaltered is rarely possible.

Experimental Methods for Mechanism Discovery. Experimental techniques in ecology exemplify a variety of experimental designs that have been identified by New Mechanists as strategies of mechanism discovery. Some experiments test the causal relevance of an entity, property, activity, or organizational characteristic. Others examine the activity or the entity that mediate between a cause and its effects, and are called by-what-activity and by-what-entity experiments, respectively (Craver and Darden 2013; see also Chapter 19). Experiments examining multilevel mechanisms are bottom-up or top-down experiments, using the analytic or the synthetic strategies, respectively (Bechtel and Richardson 1993, 20). Alternatively, one intervenes on the start conditions to produce the explanandum phenomenon and examines the behavior of the putative components (Craver and Darden 2013, 128). Ecologists' quest to identify mechanisms illustrates all of the foregoing experiments.

Cipollini et al. (2008) did by-what-entity experiments when they identified the thirteen phenolic compounds contained in the leaves of *L. maackii*, and then singled out the four chemicals (including their formulas) that have an allelopathic effect. They did by-what-activity experiments when they determined how the identified chemicals impact the growth of other plants by inhibiting seed germination, and deter the foraging behavior of herbivorous insects. Additionally, one could identify in ecology by-what-property

experiments that detect the property of an entity or activity that is solely responsible for or is necessary for the production of a phenomenon. Such is the experiment of Luken and Mattimiro (1991) of clipping off repeatedly for four years all stems at the top of the base of forest- and open-grown *L. maackii*. The experiment determined the shrub has the property of being resilient under stress, i.e., it is able to resprout in different habitats.

Ecologists also perform experiments to test for causal relevance. Luken et al. (1997) created large gaps in the shrub thicket to determine whether increasing light availability by removing the shrub enhances establishment of understory plants. This is an experiment that tests the causal relevance of shrub removal to enhancing abundance of understory plants. Similarly, Cipollini et al. (2008) tested the causal relevance of leaf metabolites in suppressing the growth of other plants. The experiment of Luken et al. (1997) illustrates bottom-up stimulation experiments. They exposed *L. maackii* and *L. benzoin* to increasing levels of light (0%, 25%, 100%) to simulate disturbance regimes that increase light availability. Typically, stimulation experiments examine putative components. However, light was not a putative component, but its level of causal efficacy, that Luken et al. examined, was. Bottom-up interference experiments in ecology decrease to various levels an abiotic or biotic component. An entire population of organisms could be removed, or parts of the organism, or the amount of an abiotic component could be decreased. For example, *L. maackii* was removed in some experiments to examine how its absence increases species richness (Gould and Gorchov 2000), in others only half of a plants' leaves were removed, and the strength of nitrogen fertilization was halved (Lieurance and Cipollini 2013).

Top-down experiments also are common. Based on the hypothesis that leachate of *L. maackii* affects other species, Watling et al. (2011) created artificial pools in which tadpoles were exposed to water containing leachate and to non-contaminated water. This experimental strategy was also used to investigate the mechanistic relationship between various levels of species diversity and ecosystem processes. In light of hypotheses about the role of species diversity in ecosystem processes, Naeem et al. (1994) created various communities in laboratory conditions, while Tilman et al. (2006) assembled them in field experiments. Instead of examining the behavior of specific components as the system is activated, ecologists focused on how species diversity produces ecosystem processes and

compared them with ecosystem processes that are produced by an actual system of similarly varying species diversity.

It is not always possible to manipulate components of a mechanism, or manipulation might not change the component in the same way as natural factors do. Additionally, manipulation might not be sufficient to assess the magnitude of the indirect effects correlated with the component from its direct ones. In such cases, some ecologists use path analysis and structural equation modeling (SEM) to identify causal relationships making up mechanisms (Pâslaru 2015). Mitchell (1992, 1994) used these methods to identify the “underlying causal mechanisms” responsible for the reproductive success of flowering plants given plant traits and pollinator behavior. The first step in the use of SEM is to conjecture causal relationships among variables based on available knowledge about the phenomenon in question and to formulate a path model incorporating hypothesized causal relationships. The proposed model then tested for fit with available data. Should the model not fit the data, one can change some paths of the model in light of a new hypothesis about the underlying causal mechanism and re-test the model (Figure 32.2). If deemed necessary, one could study the lower-level mechanisms that produce the causal relations between two variables.

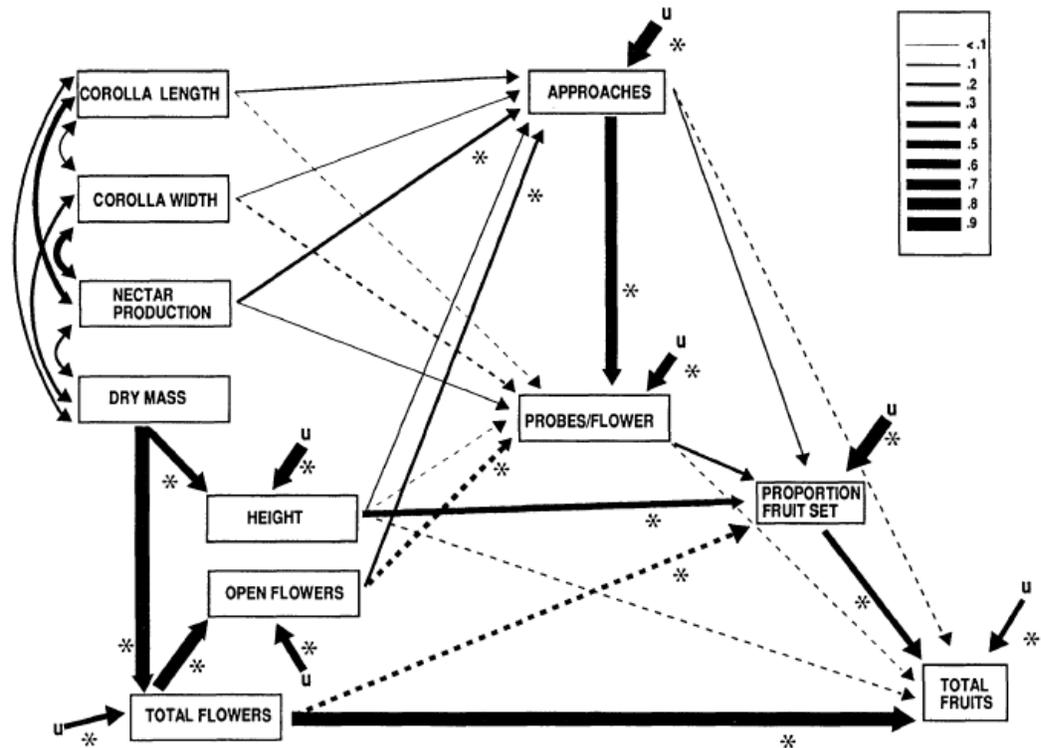


FIG. 2.—Solved path diagram for model A for the Almont population. *Solid lines* denote positive effects; *dashed lines* denote negative effects. Width of each line is proportional to the strength of the relationship (see legend), and paths differing significantly ($P < .05$) from zero are indicated with an *asterisk*. Actual values for path coefficients appear in table 2.

Figure 32.2. Final causal model of the causal relationships between reproductive success of flowering plants given plant traits and pollinator behavior. From Mitchell (1994, 879). Reprinted by permission of The University of Chicago Press.

IV. Mechanisms Above the Individual-Level

Ecologists generally accept individual-level mechanisms, but some question the existence of mechanisms involving populations. A frequent objection states that explaining population dynamics in terms of abundances or density-dependence is a phenomenological approach, and, therefore, unsatisfactory (Tilman 1987, Turchin 1999). Mechanisms are found exclusively at the individual level; at the population level one finds only summaries of interactions among individuals, which are necessary, since it is not possible to follow the interactions among individual organisms (Turchin 1999). However, other ecologists affirm the existence of mechanisms at various levels beyond

individuals, as I show below. Given ecologists' disagreement on this issue, further research is required.

The case for mechanisms involving populations could be made based on Millstein's (2006) argument for natural selection being a population-level causal process and her (2009) argument for populations as individuals. First, I offer some clarifications. Populations are groups of individuals of the same species. Since ecologists describe mechanisms that involve groups of organisms of different species, or of the same species, I prefer the term group-level mechanisms, instead of population-level, to cover both cases. Groups have properties that are different from those of individuals. The latter have properties that do not apply to groups: they have skeletons, physiological systems, organs, and engage in specific behaviors, e.g., feeding or mating. Groups are characterized by frequency, density, growth rate, generation, age structure, and diversity, properties that arise only when there is a collection of individuals. Group-level mechanisms contain causal relations that are best understood according to the counterfactual and manipulability accounts of causation. For example, 'If one systematically manipulates the density of a population to change the annual fecundity, then variation in population density is the cause of variation in annual fecundity.' Groups are the components in such mechanisms. They are organized spatially and temporally and changes in the properties of one component bring about changes in the properties of another component.

An example of group-level mechanisms is what Palmer et al. (2000) call the hypothetical mechanism by which diverse terrestrial and aquatic plant communities may increase biodiversity in aquatic sediments (see Figure 32.3). Its components are not individual organisms, but groups of organisms of various species. For example, component microbial diversity groups together populations of microbes of different species. Its property diversity is the number of species to which microbes belong and the functional identity of those species. In addition to groups of organisms as components, this mechanism features as component a property: temporal stability of detrital pool. Components of the mechanism are linked causally in the sense of the manipulability perspective on causation. Changing the number of species, say, by decreasing them, or eliminating certain species of functional importance changes the number and functional

identity of species present in the sediment. And the presence of a component is responsible for the presence of another one, for e.g., diverse riparian assemblages are partly responsible for the presence of dissolved organic carbon resources. While components appear organized in how they are causally interrelated, they do not perform any activity. This example and ecologists' use of the term *mechanism* suggest viewing group-level mechanisms as causal networks.

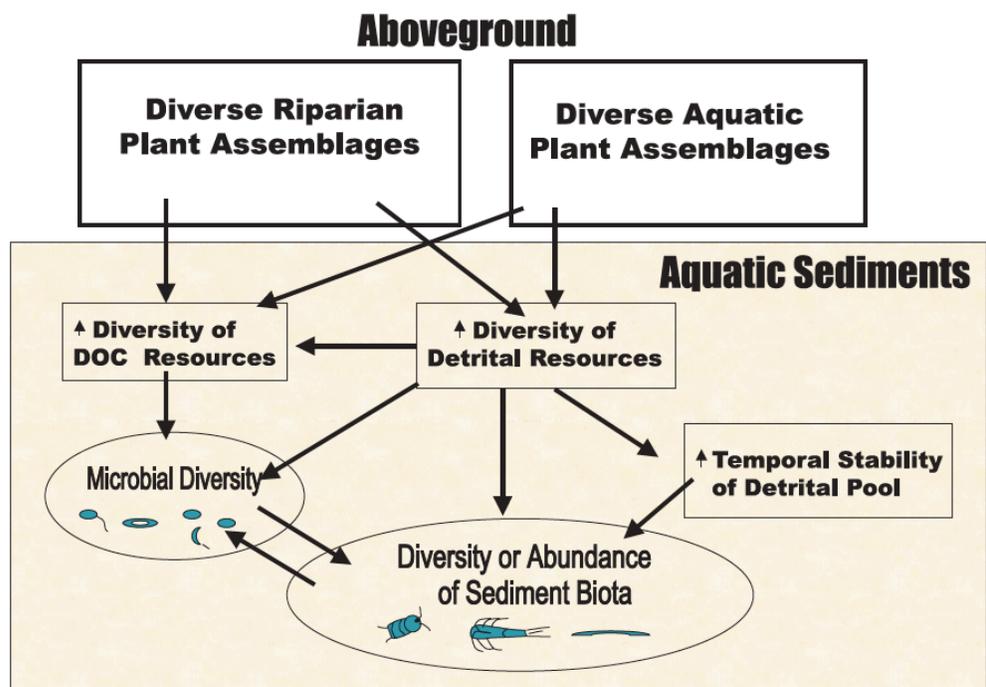


Figure 4. Hypothetical mechanisms by which diverse terrestrial (riparian) and aquatic plant communities may lead to an increase in the biodiversity in aquatic sediments. DOC: dissolved organic carbon; stability of detrital pool: temporal constancy in detrital food availability for consumers; diversity of detrital resources: number of different types of organic matter contributing to the detrital pool (e.g., leaf species that are chemically and structurally different); microbial diversity: number of functional or genetic groups of bacteria, fungi, and protozoans. Goose Creek (photo) in northern Virginia is typical of a healthy mid-Atlantic stream with high diversity of aquatic invertebrates and fish. Photo: David Hinkle.

Figure 32.3. Graph of a group-level mechanism. From Palmer et al (2000, 1069), Linkages between Aquatic Sediment Biota and Life Above Sediments as Potential Drivers of Biodiversity and Ecological Processes. *BioScience* 50 (12):1062-1075; published by Oxford University Press for The American Institute of Biological Sciences. Reprinted by permission of Oxford University Press.

Description of this group-level mechanism is not sufficient to provide a satisfactory explanation of the phenomenon biodiversity in aquatic sediments, because

Palmer et al. require a description of the lower level mechanisms underlying the group-level mechanism. Even if the group-level mechanism is explanatorily insufficient, it appears to be necessary to provide the context for individual-level mechanisms producing the upper-level causal relations.

Increased population size mechanism was proposed to explain the macro-scale relationship between the amount of energy that an assemblage of species receives and the number of species it contains. Adding energy increases population size that in turn reduces its extinction risk, and since populations are of different species, this increases the number of species of the assemblage (Evans, Warren, and Gaston 2005). This seems to be a group-level mechanism in which components energy and populations are linked causally so as to produce the phenomenon the number of species in an assemblage. However, it can be viewed as a phenomenological description, the mechanism being at the individual level. Increased amounts of energy allow individual organisms to grow and reproduce, which amounts to increase in population size. Since there are organisms of different species, increasing the amount of energy increases population size of all species, which results in the community containing a greater number of species compared to the situation when less energy is available. This interpretation of increased population size mechanism indicates that at least some group-level mechanisms are reducible to individual-level mechanisms. Ecologists' reason for speaking about mechanisms is methodological: "[i]t is neither profitable nor necessary ... to try to explain all macroscopic phenomena in terms of the mechanisms at lower levels" (Brown 1995, 155).

Elements of group-level mechanisms irreducible to individual-level mechanism appear in the mechanisms responsible for population regulation. This phenomenon occurs in populations fluctuating around a mean. Regulation happens when the per capita growth rate of the population is influenced by density-dependence. If the density of a population in an area is high, population growth is restricted, but it is amplified if the density is low (Rockwood 2015, 70-71). One of the proposed mechanisms to account for population regulation is crowding. In it, the frequency or intensity of interactions among individuals or with predators or parasites increases as population density increases, resulting in a lower fecundity for the population (Rodenhouse et al. 2003). As population density decreases, the frequency of interactions decreases, resulting in higher fecundity followed

by population increase. And so the population fluctuates around a mean. However, interactions among individuals, which constitute the individual-level mechanism of crowding, are insufficient to explain population regulation, because they occur at various densities. To account for population regulation, they have to be related to changes in population density, yet it is a property of a group-level component. This indicates that contrary to what ecologists claim, crowding is not a strictly individual-level mechanism but one that involves both individual- and group-level components.

V. Conclusion

Description of mechanisms is a central way of delivering explanations in ecology, especially at the individual-level, where they could be characterized as follows:

An individual-level mechanism for a phenomenon in ecology consists of entities, biotic or abiotic, that perform specific activities and are organized in certain ways by virtue of their properties such that they are responsible for the phenomenon.

These mechanisms show the importance of properties in determining activities and organization. The category of entities also comprises those entities that are absent, but could be present, and their absence coupled with existing entities is relevant for the functioning of the mechanism.

While the nature of group-level mechanisms is less clear, and additional research is needed, it can be concluded based on ecologists' use of the term mechanism that some of them are causal networks of group-level components and properties, while others offer useful methodological approaches despite being reducible to individual-level mechanisms.

Since ecology studies phenomena on various levels of integration above individuals and groups, further research should address the nature of mechanisms ecologists describe at those levels and their relationship with mechanisms at other levels, and answer this question: are there mechanisms specific for each level, or are they just variations of the individual- and group-level mechanisms examined above? I conjecture the latter to be the case.

Notes:

¹I am thankful to Dragoş Popa-Miu for helping me improve figure 32.1 and to Marilyn Marx for refining the English expression of this text. Hanley Sustainability Institute at the University of Dayton supported financially part of the research for this project.

² Summary of the research is based on the review by McNeish and McEwan (in press).

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