Understanding Leopold's Concept of "Interdependence" for Environmental Ethics and Conservation Biology

Roberta L. Millstein*†

Aldo Leopold's land ethic, an extremely influential view in environmental ethics and conservation biology, is committed to the claim that interdependence between humans, other species, and abiotic entities plays a central role in our ethical responsibilities. Thus, a robust understanding of "interdependence" is necessary for evaluating the viability of the land ethic and related views, including ecological ones. I characterize and defend a Leopoldian concept of "interdependence," arguing that it ought to include both negative and positive causal relations. I also show that strength and type of interdependence can vary with time, space, and context.

The new science of ecology . . . is daily uncovering a web of interdependencies so intricate as to amaze—were he here—even Darwin himself, who, of all men, should have the least cause to tremble before the veil. (Unpublished note from Aldo Leopold, 1935, quoted in Meine 2010, 359)

1. Introduction. Aldo Leopold, a twentieth-century forester, wildlife ecologist, conservationist, and professor, has been extremely influential in environmental ethics and conservation biology. Thus, it is not unusual to see claims like, "[Leopold's] view of the moral consideration of the land-community is the starting point for almost all discussions of environmental ethics" (Katz 1996, 235) or "today many conservation biologists see themselves as heirs

*To contact the author, please write to: Department of Philosophy, University of California, Davis, One Shields Ave., Davis, CA 95616; e-mail: RLMillstein@UCDavis.edu. †Thanks to Chris Eliot, Alkistis Elliott-Graves, Curt Meine, Steve Peck, Tami Schneider, Julianne Warren, and the Griesemer/Millstein Lab for helpful comments.

Philosophy of Science, 85 (December 2018) pp. 1127–1139. 0031-8248/2018/8505-0031\$10.00 Copyright 2018 by the Philosophy of Science Association. All rights reserved.

of Leopold's legacy to restore ethics and value to the science of conservation" (Van Dyke 2008, 41).

Yet Leopold is seldom seen as a figure for philosophers of science to examine, in part, I believe, because he is seen as an ethicist (which he was not) rather than a scientist (which he was). Philosophers mostly know him for "The Land Ethic," one essay from *A Sand County Almanac*, published post-humously in 1949. This is unfortunate. Leopold published over 500 works during his lifetime, containing groundbreaking ideas concerning forestry, agriculture, wildlife management, and more (Meine 2010). His conceptual frameworks were similarly innovative, especially regarding the related ideas of land community (biotic community), land health (stability), and interdependence. A scientist as influential as Leopold would typically have had his work analyzed by philosophers of science, with the goal of enhancing our understanding of contemporary science and science policy.

To begin to fill this lacuna in Leopold scholarship, I analyze Leopold's concept of interdependence to help shed light on contemporary environmental ethics and conservation biology. Importantly, interdependence formed the central basis for Leopold's ascription of moral consideration to land communities (Millstein 2015): "All ethics so far evolved rest upon a single premise: that the individual is a member of a community of interdependent parts. . . . The land ethic simply enlarges the boundaries of the community to include soils, waters, plants, and animals, or collectively: the land" (Leopold 1949, 203-4; emphasis added). Granted, Leopold was neither the originator of the concept of interdependence nor its sole explicator; his views on interdependence were influenced by Charles Darwin (Millstein 2015) and Charles Elton (Warren 2013), and Leopold influenced prominent ecologists like Eugene Odum (Craige 2002). But Leopold's land ethic specifically has had a strong influence on both environmental ethics and conservation biology (and related fields, such as forestry, wildlife management, and restoration ecology). This has given rise to a family of land-ethic-influenced approaches that view land communities (roughly, biotic communities or ecosystems; see Millstein, forthcoming) as morally considerable. Since interdependence is at the core of the land ethic, Leopold's ideas are essential for understanding the concept of interdependence in this family of approaches, both among those who accept a version of the land ethic and among those whose views are the result of a more diffuse Leopoldian influence.

I begin with an overview of Leopold's conception of interdependence. This prompts a series of questions: Are humans included in the community of interdependent parts? Does interdependence consist only of "positive" causal interactions, or are "negative" interactions included as well? What makes an interaction "positive" or "negative"? What entities are the causal interactions between, and what do they have effects on? The answers to these questions lead to some interim suggestions for how we should understand inter-

dependence. I then respond to two possible objections, wherein I elaborate and defend the concept of interdependence further. I conclude with a proposal for the concept of interdependence for environmental ethics and conservation biology.

2. Leopold's Concept of "Interdependence." By the end of his life, Leopold was characterizing interdependence in terms of food chains, or "lines of dependency for food and other services" (1949, 215). His notion of a food chain—the sequence of stages in the transmission of food, established by evolution (Leopold 1942/1999)—is tied to his conception of a land pyramid, where "each successive layer depends on those below it for food and often for other services, and each in turn furnishes food and services to those above" (Leopold 1949, 215). An example food chain is a squirrel that drops an acorn, which feeds a quail, which feeds a horned owl, which feeds a parasite (Leopold 1942/1999). But there are "chains of dependency" in addition to those involving food: "The oak grows not only acorns; it grows fuel, browse, hollow dens, leaves, and shade on which many species depend for food and cover or other services" (Leopold 1942/1999, 205). The land pyramid, Leopold states, contains a "tangle" or "maze" of all these types of chains.

Moreover, it is not just biotic components that form these interdependencies; indeed, soil is at the base of Leopold's land pyramid, and he saw plants such as oak trees as dependent on soil, with all food chains ultimately returning some of their matter and energy back to soil. I return to the topic of the interdependence of abiotic components below.

2.1. Are Humans Interdependent with Other Members of the Land Community? Leopold states explicitly that humans and their agricultural products are parts of these food chains and are thus interdependent with other biotic and abiotic elements: "Each species, including ourselves, is a link in many chains. The deer eats a hundred plants other than oak, and the cow a hundred plants other than corn. Both, then, are links in a hundred chains" (1949, 215). But some environmental ethicists have challenged this claim of human interdependence: "We are undoubtedly dependent on them, but in what ways are ecosystems dependent on us? Their independence from us is not like the independence of parents from offspring who can later reciprocate love and other mutual activities that can develop into interdependency. We play no such role in any ecosystem; we seem genuinely superfluous to ecosystem functioning" (Ouderkirk 2002, 6; see also Taylor 1981).

Here, Ouderkirk seems to imply that interdependence is only about positive interactions—reciprocal, mutually beneficial interactions. But humans sometimes have positive effects on other organisms. For example, humans have positive effects on corn, sheep, squirrels, rats, and pigeons—or at least on their population sizes. And some of these organisms have positive effects

on us—again, at least on our population sizes, with corn, for example, serving as a staple in many human diets.¹

Recent scientific findings corroborate Leopold's view that humans are interdependent with other organisms. For example, Thomas, Simcox, and Clarke (2009) show that *Maculinea arion* (large blue butterfly) had adapted to a single host-ant species that was affected by human-initiated grazing practices. Restoring those human-initiated grazing practices reversed the decline of the butterfly. More generally, Sullivan, Bird, and Perry (2017) argue that other organisms have been genetically adapted, via natural selection, to the presence of humans.

2.2. Does "Interdependence" Result Only from Positive Interactions? Even if one grants that humans can have positive effects on other species, a further question needs settling, namely, does interdependence really only include positive, mutually beneficial interactions? Ecologists typically identify a variety of causal interactions by their positive and negative effects, for example,

- competition—negative for both sides
- amensalism—negative on one side, neutral on the other
- parasitism, predation—positive on one side, negative on the other
- commensalism—positive on one side, neutral on the other
- mutualism—positive for both sides

Ouderkirk's suggestion seems to be that of these types of causal interactions, only the mutualistic ones exhibit "interdependence." Humans might have parasitic, competitive, or even commensalistic interactions with other organisms, but on Ouderkirk's picture, these would not amount to "interdependence." Relatedly, Eliot (2011) seems to imply that competitive interactions in particular are not dependence relations.

However, Leopold's sense of interdependence explicitly considered all these causal interactions, both positive and negative, to exhibit interdependence. In the key for a diagram entitled "Lines of Dependency (Food Chains) in a Community"—a diagram in which he is illustrating relations between the domains of the human and biological sciences—Leopold indicates that the "lines of dependency" can be predations, exploitations, services, or parasitisms (1942, 488). Indeed, one of the examples of interdependency that Leopold returned to frequently was the predator-prey relationship between wolves and deer (Leopold 1943). Furthermore, in discussing the "lines of dependence of the examples of dependence of the predator-prey relationship between wolves and deer (Leopold 1943).

^{1.} One might be further concerned that humans are not as crucial for the rest of the land community as other species are; see Millstein (2015) for a response to this concern.

dency" in "The Land Ethic," Leopold states that the land pyramid's "functioning depends on the co-operation and *competition* of its diverse parts" (1949, 215; emphasis added).

But perhaps defenders of Ouderkirk's view would think that Leopold should not have included both positive and negative causal interactions in his concept of interdependence—that his conception of interdependence was muddled or confused. However, Leopold was right to consider that both negative and positive causal interactions can give rise to interdependence, for two reasons.

First, interactions cannot always be definitively characterized as "positive" or "negative." Organisms can simultaneously exhibit negative and positive interactions, as when vascular plants compete for limited resources at the same time that they provide each other structural support (Harley and Bertness 1996). Or they can be positive in one context but negative in a different context, for example, yeast strains changing from mutualistic to competitive, depending on the amount of freely available amino acid in the environment (Hoek et al. 2016)—an abiotic component.

Second, causal interactions might be negative in one sense but positive in a different sense, especially when one varies the time scale. Consider Leopold's own example of wolves and deer on the Kaibab plateau in Arizona (Leopold 1943; see also Young 2002). Initially, one might reasonably say that wolves had a negative effect on deer predating on them and thus reducing their population size. But then wolves were eliminated from the Kaibab—deliberately extirpated through a government-sponsored killing program—and the deer populations exploded in size. So, one might think that removing the wolves had a positive effect on the deer. However, ultimately, without wolves keeping the deer populations in check, the deer ate much of the available foliage, and so they starved to death. Their population sizes crashed. Thus, wolves arguably had a positive effect on deer; in the presence of wolves, the deer were healthier and able to maintain a more stable, yet smaller, population size.

These considerations suggest not only that was Leopold right to include negative interactions in his concept of interdependence but also that the variability and context dependence of these interactions shows that rigidly classifying them as "negative" and "positive" can be problematic.

2.3. What Constitutes a "Negative" or "Positive" Causal Interaction? Moreover, the wolf-deer-foliage Kaibab example, by contrasting the health of individual deer with the control of deer population size, raises two questions: First, what do ecologists mean that some interactions are "negative" and some "positive"? Second, are the interactions negative for organisms, populations, or the whole land community? The answers to these questions often go unspecified. And those who do specify disagree. For example,

Odum (1971) specifies that positive interactions result in population growth, whereas negative interactions produce a population decrease. Brooker and Callaghan (1998), however, characterize positive interactions as the increased "performance" of organisms, such as increased size, whereas negative interactions result in the decreased "performance" of organisms. So, in both cases, whether a causal interaction is characterized as positive or negative has to do with the effect or outcome of the causal interaction (and is thus not really about the type of causal interaction). But Odum considers the effects on populations, whereas Brooker and Callaghan consider the effects on organisms. And, of course, the relevant sorts of effects are different as well: increased numbers in the former cases, increased "performance" in the latter.

However, the case of the Kaibab shows why sometimes "performance" does not correlate with population growth: the individual deer are healthier when their population sizes are smaller. So, the effect of the wolves on the deer (the result of a predator-prey relation) cannot be unequivocally characterized as "positive" or "negative." It was positive for the individual organisms but negative for the population.

One possible response to the discrepancy between meanings of "positive" and "negative" interactions would be to limit them to refer only to effects on population size. That stipulation would be consistent with the focus of population ecology.² But the case of the Kaibab also shows that whether wolves positively or negatively affect deer population sizes depends on the time scale and other populations present (in this case, whether there was foliage for deer to eat), since ultimately the deer population crashed without wolves. So, limiting our understanding of "positive" and "negative" to populations would only go so far in removing ambiguity. Recall that predation is typically characterized as "positive" for the predator and "negative" for the prey; the case of the Kaibab shows why this characterization is misleading.

Furthermore, there may be reason for "interdependence" to be broader than just the causal interactions between populations of different species studied by ecologists. Consider that Leopold's concept of interdependence included effects not just on the biotic components of land communities but also on the abiotic ones.

In a lecture in 1941, Leopold gave the following extended example of interdependence in which abiotic components play a key role. In Leopold's example, a Wisconsin farmer wants more cows. To have more cows, he has to have more corn and pasture, so he clears a slope—but he clears it too high. As a result, formerly small watercourses are now cut by gullies. These carry soil (and thus fertility) away; there is also flooding. The floods result in a loss

^{2.} See Molles (2015) for an alternative approach in which "positive" interactions are those that increase the fitness of individual organisms.

of lowland pasture, the suffocation of trout, and the destruction of highways and railroads. Leopold asks, "who suffers?" His answer is that the farmer suffers; the farmer loses soil fertility, runs out of firewood, and is forced to buy coal. The neighbors below the farmer also suffer because they lose land and possibly buildings. Taxpayers suffer because they must pay for the flood damage in higher taxes and prices. Fishers suffer because they have no trout to fish; their choice is to fish carp or stay home. But it is not just humans who suffer. Wildflowers and partridge are extirpated from the area because they can only live in unpastured woods. Woodcocks are similarly evicted because they inhabit only timbered streams. And so on. Ultimately, the chain of events leads to more rural slums and abandoned farms.

Leopold concludes: "This chain of evils, arising from one abuse affects all resources. The penalties of abuse are both economic and esthetic. They hit all people. Hence, I speak of the unity of land, and say that all parts of the land, including ourselves, prosper or decline together" (1941). The richness of Leopold's example shows what we would be missing if interdependence were only to include the effects on the sizes of populations. The effects on abiotic components, and their subsequent effects on other components, are central to chain of events. Moreover, not all important effects are populational ones; some are economic or aesthetic. Even some populational effects, such as reduction in the trout population, would be overlooked because they are not the direct result of population interactions. However, they are the direct result of interactions between the trout and abiotic components (water and soil in the form of mud). Finally, the flourishing of various populations, such as partridges, depends on the farmer not engaging in certain types of negative interactions. So, negative interactions are an important part of the story too. Thus, positive and negative effects on organisms, populations, and abiotic components are all relevant to interdependence.

Note that Leopold also emphasized that the health of the land as a whole was something that could be benefited or harmed.³ According to Leopold, "Health expresses the cooperation of the interdependent parts: soil, water, plants, animals, and people; it implies collective self-renewal and collective self maintenance" (1942/1991, 300). Again, recent studies have shown Leopold's prescience (or perhaps it would be better to say a remarkable insight) on this point. For example, reintroducing wolves to Yellowstone has produced not only a variety of positive effects on other species but also changes that "appear to represent the early stage of a recovering ecosystem"; further changes resulting from wolf reintroduction "could represent an important improvement in food resources and physical habitat for an array of wildlife

^{3.} See Warren (2013) for an extended and helpful analysis of Leopold's understanding of "land health." See McShane (2004) for an argument that ecosystems can be literally healthy.

species" and "could also help improve [Yellowstone's] resiliency relative to any ongoing or impending changes in climate" (Beschta and Ripple 2012, 137). Thus, effects on land communities, considered holistically, are part of interdependence as well.

Finally, although I have emphasized in this section that what makes a causal interaction "positive" or "negative" in this context are the types of effects on the entities involved rather than the types of causes, it is also worth considering which entities the interactions are between. Clearly and unproblematically, there are interactions between organisms of the same species and of different species, both direct and indirect (i.e., mediated through abiotic components). Perhaps more metaphysically challenging is the question whether populations of different species can interact qua populations. Attempting to answer that metaphysical question would take this article off on a large tangent (see Millstein [2013] for a defense of the idea), but I can make a few suggestive remarks toward the idea of populations interacting. Consider again the wolves reintroduced to Yellowstone. Laundré, Hernández, and Ripple (2010) argue that the behavior of the elk in Yellowstone has changed in the presence of the wolves, changing the amount, the location, and the type of plant consumed; they further suggest that this change is due to a fear of the risk of predation (a fear that, they argue, is present in many predatorprey interactions). But arguably, fear-inducing risk is present only when the wolves are of sufficient numbers for there actually to be a significant risk. Thus, the population size of the wolves and their behavior as a whole jointly change the behavior of the elk as a whole. Competitive interactions mediated by abiotic components are likewise plausibly populational interactions when there is a limited resource; for example, if a population of one species of plant sprouts before another, the first can often crowd out the second.

3. An Interim Account of "Interdependence." Thus, for a complete picture of the connections within a land community, interdependence needs to include different types of positive and negative effects and effects on more than just populations, including effects on abiotic components. It also needs to include humans, an essential part of Leopold's story. In short, interdependence is broader than the list of typical ecological interactions found in many textbooks (presented in sec. 2.2), and it includes causal interactions involving humans.

And perhaps a further lesson can be drawn from the story of the Wisconsin farmer. It would be a mistake to take an overly binary (or even trinary) approach toward understanding interdependence. Rather, one needs to consider the whole network, or web, of causal interactions, some of which are direct and some of which are indirect. For example, the farmer does not have a direct interaction with trout, but through a chain of causal interactions there is an indirect effect on trout. This makes the trout dependent on the farmer.

Furthermore, it may be that not all of the direct causal relationships are bidirectional, but they are all part of the same network of causes. Here it is also worth noting that Leopold (1942/1999, 1949) spoke of the land community as forming a *circuit*; typically, he was referring to the circuit from soil and back to soil, but the Wisconsin farmer example begins and ends with the farm, so it is generalizable. All these considerations point to the desirability of adopting a network understanding of interdependence.⁴ However, there are at least two possible objections to this Leopoldian conception of "interdependence."

3.1. Objection 1: The Leopoldian Conception of "Interdependence" Is Too Strong. One might worry that Leopold's claim for "unity" is too strong, given our contemporary understanding of the causal interconnections between biotic and abiotic entities on this planet. Is it really correct to say, as Leopold does, that "all parts of the land, including ourselves, prosper or decline together"?

Here it might seem as though Leopold is claiming something akin to what Jay Odenbaugh has recently dubbed as the "mantra" that "everything is connected to everything else" (Commoner 1971), which, Odenbaugh notes, seems to commit us to there being "simply one thing, the universe" (2010, 241).

In reply to this objection, it is important to recognize that Leopold need not be committed to this "mantra" or to there being only one planetary ecosystem ("Gaia" or the like); importantly, note that his example of the Wisconsin farmer is not a global one. Rather, his point may simply be that the interdependencies can be more extensive than we often realize, so that our fates are in fact tied to entities that we might not typically see ourselves as connected to. As Leopold stated, "There are two spiritual dangers in not owning a farm. One is the danger of supposing that breakfast comes from the grocery, and the other that heat comes from the furnace" (1949, 12). Some people might not think that farming (or mining) practices have much of an effect on them; Leopold's example shows that such thinking is mistaken.

It is also worth noting that the causal interactions that give rise to interdependencies do vary in strength and that those variations in strength can be used to circumscribe entities smaller than the universe or the planet (i.e., land communities; Millstein, forthcoming). Thus, one way of understanding Leopold's point might be to say that all parts of a land community, including ourselves, prosper or decline together. Of course, Leopold readily acknowledged that some land communities can adjust to large alterations (e.g., as found

^{4.} See Valiente-Banuet et al. (2014) for a present-day network approach to interdependence.

in Western Europe) even as others (e.g., the southwestern United States—recall the Dust Bowl, which Leopold lived through) cannot. The point is that because of the causal interactions between abiotic and biotic components, changes to one part of land community will cause changes in another, even if sometimes those changes might be small ones.

3.2. Objection 2: Not All Members of the Land Community "Need" Each Other. Still, there might be linguistic resistance to including negative causal interactions as "dependencies" if dependence is understood as "need." In particular, many organisms seem not to "need" humans—if anything, the opposite.

In response, it is important to recognize that "need" is only one way of understanding "dependence"; "dependence" can also be understand as "vulnerability" (Anstett, Hossaert-McKey, and McKey 1997). With vulnerability, it is easier to see why it is natural to include negative as well as positive causal interactions. Organisms can be harmed in a variety of ways by the causes they are exposed to and are therefore vulnerable.

The entities in Leopold's story of the Wisconsin farmer are all vulnerable and therefore all depend on each other. And organisms do "need" us not to do things that will negatively affect them.

Yet, in this essay I have emphasized that interdependencies are not only between biotic entities but between abiotic entities as well, and it might seemed strained, at best, to say that abiotic components of a land community are "vulnerable." There are at least two possible responses. One would be to try to make the case that abiotic components can indeed be vulnerable. For example, soil can be washed away or depleted of nutrients, air can become polluted, and water can become clogged or acidic, and these effects are due to the causal interactions between them and other components of the land community. Now perhaps these will be seen not as harms to the abiotic components themselves; perhaps they will only be seen as harms insofar as they harm biotic components, with "unhealthful" soil, air, and water being unhealthful just for the biotic organisms that depend on them or for the land community as a whole. I do not think I need to decide whether abiotic components can be literally harmed or only metaphorically harmed, with their harms serving as a proxy for harms to biotic components and their network of interconnections. Either abiotic components are vulnerable or they are "vulnerable"—both ways of understanding express the interdependency.

^{5.} This "adjustment" hints at an evolutionary dimension to Leopold's concept of interdependence, as does his inclusion of competition and the feedback between biotic and abiotic components. Unfortunately, I lack the space to further explore this important evolutionary dimension here. Thanks to Curt Meine, Steve Peck, and Alkistis Elliott-Graves for this point.

But should this line of argument still prove unpersuasive, one could abandon vulnerability altogether and understand "dependence" simply as "causal dependence," meaning just that B is dependent on A because changes in A produce changes in B.6 "Interdependence" involves at least this if not something further. There are causal interactions between components of the land community such that changes in one component produces changes in another. Here, abiotic components pose no special problem. For example, soils can provide the nutrients that allow certain types of plants to flourish; dead and decaying plants furnish nutrients back to the soil. Nutrient-poor soil, however, will not promote the flourishing of plants, and certain plants will deplete soils of nutrients more than they return them. Of course, not all relationships are reciprocal in this way; again, interdependencies are best seen as a function of the entire network of interacting components.

4. Conclusion. It remains to be shown how interdependence can form the basis for the moral considerability of land communities (biotic communities, ecosystems); I have not sought to defend that claim here. However, I hope to have shed some light on the concept of interdependence that underlies such claims in environmental ethics and conservation biology—and perhaps other areas of evolution and ecology as well, such as recent discussions of the holobiont—by clarifying, elaborating on, and defending Leopold's understanding of it.

Namely, interdependence, in the context of views that center on land communities (ecosystems, biotic communities), consists of a web (or network) of direct and indirect "negative" and "positive" causal interactions between organisms, populations, and abiotic components, including humans, yielding a variety of vulnerabilities in organisms, populations, and abiotic components (as well as land communities more holistically) with interactions that vary in strength and direction in time and in place.

REFERENCES

Anstett, Marie-Charlotte, Martine Hossaert-McKey, and Doyle McKey. 1997. "Modeling the Persistence of Small Populations of Strongly Interdependent Species: Figs and Fig Wasps." Conservation Biology 11 (1): 204–13.

Beschta, Robert L., and William J. Ripple. 2012. "Berry-Producing Shrub Characteristics following Wolf Reintroduction in Yellowstone National Park." Forest Ecology and Management 276:132–38.

6. Thanks to Rick Morris for this suggestion. Note that in using the phrase "causal dependence" I do not mean to invoke "causal dependence" accounts of causation specifically. The arguments in this article are meant to be noncommittal with respect to accounts of causation.

- Brooker, Rob W., and Terry V. Callaghan. 1998. "The Balance between Positive and Negative Plant Interactions and Its Relationship to Environmental Gradients: A Model." *Oikos* 81 (1): 196–207
- Commoner, Barry. 1971. *The Closing Circle: Nature, Man, and Technology*. New York: Knopf. Craige, Betty Jean. 2002. *Eugene Odum: Ecosystem Ecologist and Environmentalist*. Athens: University of Georgia Press.
- Eliot, Christopher H. 2011. "The Legend of Order and Chaos: Communities and Early Community Ecology." In *Handbook of the Philosophy of Science: Philosophy of Ecology*, ed. Kevin de-Laplante, Bryson Brown, and Kent A. Peacock, 49–108. Oxford: North-Holland.
- Harley, C. D. G., and M. D. Bertness. 1996. "Structural Interdependence: An Ecological Consequence of Morphological Responses to Crowding in Marsh Plants." Functional Ecology 10: 654–61
- Hoek, Tim A., Kevin Axelrod, Tommaso Biancalani, Eugene A. Yurtsev, Jinghui Liu, and Jeff Gore. 2016. "Resource Availability Modulates the Cooperative and Competitive Nature of a Microbial Cross-Feeding Mutualism." *PLoS Biology* 14 (8): e1002540.
- Katz, Eric. 1996. Nature as Subject: Human Obligation and Natural Community. London: Rowman & Littlefield.
- Laundré, John W., Lucina Hernández, and William J. Ripple. 2010. "The Landscape of Fear: Ecological Implications of Being Afraid." *Open Ecology Journal* 3:1–7.
- Leopold, Aldo. 1941. "Conservation of Natural Resources." The Aldo Leopold Archives, Lectures 1933–1947:949–50. Digital Collections, University of Wisconsin–Madison Library. http://digital.library.wisc.edu/1711.dl/AldoLeopold.
- ——. 1942. "The Role of Wildlife in a Liberal Education." In *Transactions of the Seventh North American Wildlife Conference*, 485–89. Washington, DC: American Wildlife Institute.
- 1942/1991. "Land-Use and Democracy." In *The River of the Mother of God and Other Essays by Aldo Leopold*, ed. Susan L. Flader and J. Baird Callicott, 295–300. Madison: University of Wisconsin Press.
- 1942/1999. "Biotic Land Use." In Aldo Leopold: For the Health of the Land: Previously Unpublished Essays and Other Writings, ed. J. Baird Callicott and Eric T. Freyfogle, 198–207. Washington, DC: Island.
- ——. 1943. "Deer Irruptions." Transactions of the Wisconsin Academy of Sciences, Arts, and Letters 35:351–66.
- ——. 1949. A Sand County Almanac and Sketches Here and There. New York: Oxford University Press.
- McShane, Katie. 2004. "Ecosystem Health." Environmental Ethics 26 (3): 227-45.
- Meine, Curt. 2010. Aldo Leopold: His Life and Work. Madison: University of Wisconsin Press.
- Millstein, Roberta L. 2013. "Natural Selection and Causal Productivity." In Mechanism and Causality in Biology and Economics, ed. Hsiang-Ke Chao, Szu-Ting Chen, and Roberta L. Millstein, 147–63. Dordrecht: Springer.
- ——. 2015. "Re-examining the Darwinian Basis for Aldo Leopold's Land Ethic." Ethics, Policy and Environment 18:301–17.
- Forthcoming. "Is Aldo Leopold's 'Land Community' an Individual?" In *Individuation across Experimental and Theoretical Sciences*, ed. Otávio Bueno, Ruey-Lin Chen, and Melinda B. Fagan. Oxford: Oxford University Press.
- Molles, Manuel C. 2015. Ecology: Concepts and Applications. Vol. 7. London: McGraw-Hill.
- Odenbaugh, Jay. 2010. "On the Very Idea of an Ecosystem." In *New Waves in Metaphysics*, ed. Allan Hazlett, 240–58. Basingstoke: Palgrave Macmillan.
- Odum, Eugene. P. 1971. Fundamentals of Ecology. 3rd ed. Philadelphia: Saunders.
- Ouderkirk, Wayne. 2002. "Introduction: Callicott and Environmental Philosophy." In *Land, Value, Community: Callicott and Environmental Philosophy*, ed. Wayne Ouderkirk and Jim Hill, 1–18. Albany, NY: SUNY Press.
- Sullivan, Alexis P., Douglas W. Bird, and George H. Perry. 2017. "Human Behaviour as a Long-Term Ecological Driver of Non-human Evolution." *Nature Ecology and Evolution* 1, art. 0065.
- Taylor, Paul. 1981. "The Ethics of Respect for Nature." Environmental Ethics 3:197–218.
- Thomas, Jeremy A., D. J. Simcox, and Ralph T. Clarke. 2009. "Successful Conservation of a Threatened *Maculinea Butterfly*." *Science* 325 (5936): 80–83.

- Valiente-Banuet, Alfonso, Elia Ramírez, Miguel Verdú, and Pedro Miramontes. 2014. "Plant Community Ecology." In *Frontiers in Ecology, Evolution and Complexity*, ed. Mariana Benítez, Octavio Miramontes, and Alfonso Valiente-Banuet. Ciudad de México: Coplt ArXives.
- Octavio Miramontes, and Alfonso Valiente-Banuet. Ciudad de México: Coplt ArXives.

 Van Dyke, Fred. 2008. Conservation Biology: Foundations, Concepts, Applications. Dordrecht: Springer.
- Warren, Julianne Lutz. 2013. Aldo Leopold's Odyssey: Rediscovering the Author of a Sand County Almanac. Washington, DC: Island.
- Young, Christian C. 2002. In the Absence of Predators: Conservation and Controversy on the Kaibab Plateau. Lincoln: University of Nebraska Press.