Biol Theory (2011) 6:203–210
DOI 10.1007/s13752-012-0027-5

THEMATIC ISSUE ARTICLE: CULTURAL NICHE CONSTRUCTION

Legacy Effects: The Persistent Impact of Ecological Interactions

Kim Cuddington

Received: 9 March 2012 / Accepted: 29 May 2012 / Published online: 19 July 2012

Abstract The term "legacy effect" has been used in ecology since the early 1990s by authors studying plant succession, invasive-plant impacts, herbivory impacts, ecosystem engineering, and human land-use impacts. Although there is some variability in usage, the term is normally used to describe impacts of a species on abiotic or biotic features of ecosystems that persist for a long time after the species has been extirpated or ceased activity and which have an effect on other species. For example, human agricultural activities may have a legacy effect on soil structure and vegetative communities that lasts for centuries and which alters current communities. The concept may be related to the idea of ecological inheritance in evolutionary biology but would refer only to a subset of the features of this concept. In particular, legacy effects could refer to those kinds of ecological inheritance where a physical or biological change in ecosystem state is caused by one species, where this change persists after the extirpation of the causal species and alters selection pressure of another species much later in time.

Keywords Ecological inheritance · Ecosystem engineering · Legacy effects · Niche construction · Succession

In much the same way that *ecosystem engineering* forms the ecological counterpart to the evolutionary concept of niche construction, the concept of *legacy effects* is related to the notion of ecological inheritance. However, whereas ecosystem engineering and niche construction have had a similar degree of conceptual development in their respective fields, legacy effects have been defined only loosely in the ecological literature. Here I clarify the concept as it is used in ecology and then relate it to ecological inheritance (see also Odling-Smee and Laland 2012, this issue). I present this material for a nonspecialist audience, working on the assumption that some concepts that are quite familiar to ecologists may be novel to those working in evolution, or even more distantly, human cultural evolution. I begin by discussing some of the various definitions and examples of legacy effects in the ecology literature, then present my own synthetic version. Finally, I use this definition to describe the relationships between legacy effects and ecological inheritance.

Legacy Effect as Used in the Ecological Literature

The term legacy effect appears to have entered the scientific literature in the late 1980s or early 1990s (e.g., Molina and Amaranthus 1991; Simard 1995). Since its first appearance, the term has become more frequent, but perhaps not more so than would be expected given the leaps in the number of publications generally. References are found in five major areas of study: secondary succession, effects of invasive-plant species, effects of past herbivory events, ecosystem engineering, and human impacts on land use. I examine each of these below.

Biological Legacies and Secondary Succession

One of the first uses of the term legacy effect was associated with work on succession, which is the process whereby plants and animals colonize areas that have little

K. Cuddington (✉)
Department of Biology, University of Waterloo, Waterloo, ON, Canada
e-mail: kcudding@uwaterloo.ca

or no biological material either because the regions are newly formed (e.g., new land revealed by glacial retreat) or because they have recently suffered some major disturbance (e.g., clear cutting). Many authors describe the legacy effects of plants on soil properties that affect succession (e.g., Molina and Amaranthus 1991; Perry et al. 2008). Plants can alter the abiotic and biotic components of the soil ecosystem through a variety of processes. These effects may indirectly facilitate or inhibit the growth of other plants. If the effect is long lasting, it may affect the rate and direction of succession. Two types of effects that alter the impacts of soil processes on plant-community dynamics are the persistence of soil communities through large disturbance and the alteration of soil communities by early successional plants: those species that colonize an area immediately after disturbance.

Ecologists working with soils invoked the term legacy effects to describe the heritage of mycorrhizal organisms and soil nutrients left behind in forest soils even after areas are clear-cut or burned. The relationship between terrestrial vegetation and soil fungi is perhaps unappreciated by those outside this field of study. In short, approximately 80 % of terrestrial plants depend on mycorrhizal fungi for nutrient uptake and soil–water relationships (Wang and Qiu 2006). In one of the earliest works to invoke the concept of legacy effect, Molina and Amaranthus (1991) describe studies that show the "lasting beneficial legacy effect of rhizosphere organisms" in the soil, and note that this legacy supports rapid colonization by pioneering plants in secondary succession.

Perry, in his influential texts (Perry 1994; Perry et al. 2008), expands and amplifies this idea. In related early references (e.g., Simard 1995, a student of Perry), the definition of legacy effect is given formally as anything inherited from a previous ecosystem that influences the successional trajectory of the system. In a more recent text, Perry et al. (2008) define a legacy as anything handed down from a predisturbance ecosystem, including both legacies of human land use and biological legacies that are ubiquitous features of natural disturbances. Later in the text, the component of a biological legacy is described as a broad concept that includes anything of biological origin that persists through disturbance and maintains ecosystems and landscapes on given trajectories. Examples include soil communities, soil aggregates and organic matter, soil chemistry, dead wood, living plants and vegetation patches, seeds in the soil seed bank, and living roots from which new plants may sprout.

In recent years, legacy effect has been invoked to describe the effects of early successional plant species on subsequent vegetative communities (e.g., Densmore 2005; van de Voorde et al. 2011). Kardol et al. (2007) suggest that the legacy effects of early succession species can have long-lasting impacts and further note that plant-community dynamics at any later stages of ecosystem development may be determined by soil-community influences from the past.

It seems clear that these two groups of authors are giving the term legacy effect slightly different implications, despite the shared idea of a long-lasting impact on the soil ecosystem. Given this last point, it is worth discussing here the two historical models of succession and their relation to this definition. Two foundational models of succession had opposing viewpoints regarding the temporal dynamics of terrestrial plant communities. Clements (1916) described the vegetative community as a large superorganism on a fixed trajectory of development toward a particular end state, the climax community, which has a particular physiognomic form and ecosystem dynamics determined by large-scale climatic conditions. That is, Clements described the changes in species diversity, physical structure, and nutrient dynamics of a region over time as undergoing a fixed set of developmental stages, similar in some respects to the journey of a baby through youth and adulthood. In opposition, Gleason (1917) described succession as a historically contingent process whose outcome depends on chance events of colonization. The random occurrence of a few successfully germinating seeds of one species could lead to a completely different forest endpoint for one site compared to another that did not experience this chance event.

In Perry et al.'s (2008) definition, legacy effect is employed to explain similar endpoints in successional processes. Legacy effects are described as overwhelming the influence of chance events. That is, we may end up with the same forest communities during successional development because of the influence of long-lasting biological effects that direct ecological interactions. Therefore, legacy effects reduce the impact of chance events as well as the probability that secondary succession on a site is a historically contingent process. This addendum to the definition of legacy effect seems undesirable in that it pairs a mechanism, a long-lasting influence of ecological interactions, with a particular outcome, the maintenance of a climax community. And as demonstrated by Kardol et al. (2007) and others, legacy effects on soils may sometimes operate in exactly the opposite fashion: they increase the influence of chance colonization events early on in the successional process.

As we shall see, in other fields of study legacy effects are employed to describe ecological outcomes that are considered anomalous compared to other regions and are explained by invoking historical contingency. I will suggest that the ultimate impact of a legacy effect is relatively unrelated to its definition. To clarify, legacy effects are described as long-lasting impacts of ecological interactions, but the direction of that impact (e.g., maintaining a particular successional trajectory or disrupting it), is unimportant to the definition.

Long-Lasting Impacts of Invasive Plants

In the last decade, several authors have described the legacy effect of invasive-plant species on soils and, subsequently, on other vegetation (e.g., Davis et al. 2005; Jordan et al. 2011). It is clear that the impact of invasive plants through direct competitive interactions can be separated from their legacy impacts. Heneghan et al. (2006) distinguish between direct impacts of invasive-plant species (e.g., reduction in light) and indirect impacts (e.g., alteration in the availability of a limiting soil resource such as nitrogen). They note that indirect impacts may last quite a long time after the removal of the invasive species. Similarly, Grman and Suding (2010) distinguish between legacies and competitive effects, in that legacies last after the removal of the causal plant species. Elgersma et al. (2011) found that after 2 years of manipulating vegetation, there was essentially no effect of the current vegetation on soil microbial communities. Instead, microbial communities were determined by past vegetative communities, and they influenced current plants.

Grman and Suding (2010) offer a lucid account of the possible impacts of invasive plants on soil processes, where such plants may alter soils through (1) feedbacks between plants and soil pathogens or mutualists (e.g., Kourtev et al. 2002), (2) the release of allopathic compounds that accumulate and affect other plants or soil microorganisms (e.g., Orr et al. 2005), and (3) changes in resource availability or nutrient cycling (e.g., Mack and D'Antonio 2003). This last mechanism operates through competitive effects, but it is considered to be a legacy effect if it persists after the removal of the causal species.

In this context, many authors use the term legacy effect as synonymous with time lag. Lett and Knapp (2005) find no impact of an invasive shrub on soil resource availability but nevertheless describe the lag in the recovery of native graminoids after shrub removal as a legacy effect. They note that the lag seems to be caused through the loss of graminoid rhizomes in the area previously occupied by the shrub, an effect that might otherwise be described as a time lag in the recovery from competitive exclusion. In fact, even the concept of "long duration" is not essential to the use of the term legacy effect by some authors. Grman and Suding (2010) describe soil impacts from invasive species that occur within a single year as a legacy effect because these effects persist after species removal.

In addition, some authors describe as legacy effects chance abiotic events that alter subsequent vegetative dynamics. Davis and Pelsor (2001), for example, describe an impact on rainfall that altered competitive impacts between vegetative species over a 12-month period as a legacy effect. In my view, this type of event does not contain the essence of the concept, the persistent effect of a species now absent from the system, and is better described as the effect of historical contingency.

Taking the literature on invasive plants as a whole, Grman and Suding summarize the usage of the term legacy effects as those impacts that persist after removal of the causal species. However, it seems likely that we can exclude those impacts that are caused (a) merely by a time lag in the recovery from direct competition and (b) directly by chance abiotic events rather than through the agency of some organism.

Ghost of Herbivory Past

Ecologists investigating the influence of past herbivory events often use the term legacy effect when describing long-term consequences (e.g., Carson et al. 2005). Most recently, Nuttle et al. (2011) demonstrate that high densities of white-tailed deer at a time when logged forest patches were just recovering had long-term consequences not only for the current forest composition and physical structure but also for herbivorous insects and, consequently, for bird density and diversity. The authors describe this intense herbivory during a short time period (10 years) as a biological legacy because it has significant and measurable impacts two decades later and will continue to impact the region until the trees are replaced by natural processes (over 100 years).

It could be claimed that this kind of effect is simply an indirect trophic effect that requires no additional concepts for explanation. Indirect effects occur in communities linked by feeding or resource relations, where the behavior or population growth of one species affects the population growth of another species, even though the two are not directly connected in a predator–prey or competitive relationship. A classic example is that of the trophic cascade. In a simple food chain where a predator consumes a herbivore, which in turn consumes a plant species, an increase in predator density will increase plant biomass, even though the two are not directly linked. The predator will reduce the density of the herbivore, which will release the plant species from this check on its growth. The widespread loss of top predators and resulting trophic cascades have been invoked to explain landscape changes in ecosystems from lake clarity to the decline in woody vegetation (Estes et al. 2011).

Such indirect effects may take time to appear because of the linkage through many species, as the response of each species will take time to occur and then to propagate through the community web. Therefore, it could be argued that what has been described as a legacy effect is merely an indirect effect. The reason that the effect still persists in the absence of the originating species is a consequence of the time lag associated with indirect effects. That is, it could be suggested that there is no explanatory advantage in labeling these historical herbivory effects as legacy effects when they can be well accounted for in the standard terminology of indirect effects. This seems to be a reasonable argument when the effects of the trophic interaction can be anticipated through an existing model of trophic linkages. If, for example, all players of the potential community web are present, one could predict an increase in unpalatable vegetation at the expense of tastier species because of heavy deer grazing, the resulting impact on caterpillar density, and the subsequent decrease in bird diversity found by Nuttle et al. (2011). Moreover, if one modeled the interactions, one could also predict the time scales of these indirect effects and their likely persistence times. It is a slightly trickier proposition when one does not have prior knowledge of the previous existence of species or when interactions between species are nontrophic. It is clear, however, that indirect effects are a more general category than legacy effects.

Ecosystem Engineering and Legacy Effects

Hastings et al. (2007) define the legacy effect of an ecosystem engineer as the persistence of engineered aspects of the environment and the effects that still result when this engineer is dead or absent. They provide the example of a beaver dam, which deteriorates in the absence of beaver but which leads to the formation of a beaver meadow that can persist for nearly a century and which is rarely converted back to the original forested riparian zone. Other examples include effects of high herbivore density that alter the physical structure or processes of the environment and subsequently have a long-lasting impact on communities downstream in the timeline. Bowman et al. (2010) describe how large populations of feral buffalo in the 1980s created channels that allowed the ingress of saltwater to freshwater floodplains. Salination of the flood plains, combined with sea-level rise, is then shown to have contributed to the retreat of a *Melaleuca* swamp forest. Thus, buffalo movement patterns had a legacy effect on the swamp forest.

Other indirect effects of herbivory may arise by means of a reduction in an engineering species. Huntzinger et al. (2011) describe the impact of vole exclusion on lupine shrubs as determining the population density of land snails. The soils underneath lupines provide aestivation sites for the snails. Herbivory by voles reduced the density of these shrubs. The effect of voles on snails, however, was unexpectedly long lasting. Reductions of lupine density, a shrub that lives on average 5 years in this environment, were still visible 4–6 years later after vole-exclusion enclosures fully or partially failed.

It is clear that the usage of the concept of legacy effects in the ecosystem engineering literature includes these impacts on the abiotic environment as well as impacts on species density or community composition. These effects of ecosystem impacts are not accommodated in a description of indirect effects in standard food-web models of communities, although perhaps they could be described as indirect effects in more accommodating interaction webs. The main required component of the definition appears to be that of a long-term interspecific impact of a species no longer present in the system. However, if the definition includes the idea that the causal species is no longer present, it becomes difficult to see how the term legacy effect can simultaneously be invoked in studies of human impacts on natural systems.

Human Land Use and Our Environmental Legacy

One major area of research in ecology deals with effects of prior human land uses on ecosystem dynamics. Human activities such as forestry, agriculture, modification of natural disturbance regimes (e.g., control of fire and flood), manipulation of animal populations, urbanization, and release of chemical compounds through mining activities or industry can all have large effects on natural communities and ecosystems. All these activities may have impacts that persist for centuries after cessation and are often so widespread across broad areas that they are overlooked. For example, although most observers would recognize that the corn and soybean fields of Ohio are highly manipulated human-made environments, an unskilled observer might imagine that the northeastern U.S. forests are now a natural environment that is representative of the forest prior to widespread clearing. In fact, the species, soils, and nutrient cycling of these forests are a consequence of past human actions and have only a passing resemblance to the previous forest environment. In an influential review, Foster et al. (2003) note that ecologists now recognize that site history determines the structure and function of ecosystems and is therefore an integral part of ecological science. In a recent contribution, Martin et al. (2011) describe the recognition of legacy effects from historical land use as an important conceptual advance in ecology.

Most of the work in this field, like that in other studies of legacy effects, deals with soil dynamics following land use change. Perry et al. (2008) identify human land use as a source of legacy effects that profoundly influence successional patterns over centuries or even permanently. Flinn and Vellend (2005) found that the impact of past land uses on vegetation could equal or override the effects of topography, soils, subsequent disturbance, and current management. Models of nutrient cycling indicate that human land use can alter terrestrial nutrient budgets of soils for long periods. For example, Aber et al. (1997) predicted that forest harvest would cause changes in nitrogen cycling that would take more than two centuries to recover, defining a legacy effect as the time over which past disturbance can affect nutrient cycling. In grassland environments, plow horizons may persist for hundreds of years, and changes in phosphorous, carbon, and nitrogen imposed by agriculture can last for centuries after use and greatly affect the productivity of subsequent vegetation (McLauchlan 2006). Other agricultural uses can also cause long-lasting impacts. For example, soil compaction in forests caused by heavy livestock grazing can last for over 30 years and inhibit plant growth and seedling establishment (Bassett et al. 2005; Sharrow 2007).

The history of terrestrial land use also has profound impacts on aquatic environments. For example, Harding et al. (1998) found that the diversity of Appalachian stream invertebrates could not be predicted from current land use. There was no difference in invertebrate diversity between forested and clear-cut areas. However, watershed land use 50 years earlier was a good predictor. Martin et al. (2011) demonstrate that a consideration of historical land use, and the time since these uses, improved the fit of models predicting lake chemistry.

Definitions of legacy effects from this body of literature focus on the perhaps unexpected long-term persistence of effects. Martin et al. (2011), for example, define legacy effects as those continuing beyond some expected or perceived temporal endpoint. However, the idea of the causal agent being a species no longer present in the system is not integral to the definition of legacy effects as it is used in here. Instead, the legacy effects of past land use refer to persistence of effects of past actions of humans which have now ceased.

Legacy Effects: The Definition

Taken together, the various contexts in which ecologists use the term legacy effects suggest that the underlying common factor is one of long-term persistence of some biological activity that has since ceased. Although there are a few uses where the referred-to legacy is of purely abiotic origin (e.g., Davis and Pelsor 2001), most references deal with the effects of the direct activity of live organisms that persist after death, removal, or dispersal of the organism, or, especially in the case of human land use, the cessation of such activities. These effects may relate to community composition, physical structures, chemical or physical properties of substrates or waters, or nutrient concentrations or cycling.

Therefore, *we can define a legacy effect as an indirect effect that persists for a long time period in the absence of the causal species, or after this species has ceased the causal activity*. The impact of species A on the ecosystem or community persists for a long period after the particular activity of A that caused the impact has ceased (or A is no longer present in the system) and affects another species or group of species, C, downstream in the timeline (Fig. 1). The most common example of a legacy effect in the ecology literature would be the case where species A alters the soil structure or community, such that the alterations persist long enough after the extirpation of A to substantially alter the dynamics of species C, which did not exist in the system at the same time as A. However, the concept is general enough to include examples from other types of systems. A legacy effect is most likely to occur through soil processes because of the slow rate of change of this component of ecosystems. Note that this definition excludes cases where there is a long-term impact of a direct effect. For example, Lett and Knapp's (2005) description of the slow recovery of grass species after the removal of an invasive shrub would not be a legacy effect but merely a time lag in recovery rate, probably attributable to the reproductive rate of the grass species.

Legacy Effects and Ecological Inheritance

In the same way that ecosystem engineering may be the ecological equivalent of niche construction, legacy effects may be the equivalent of a related concept in the

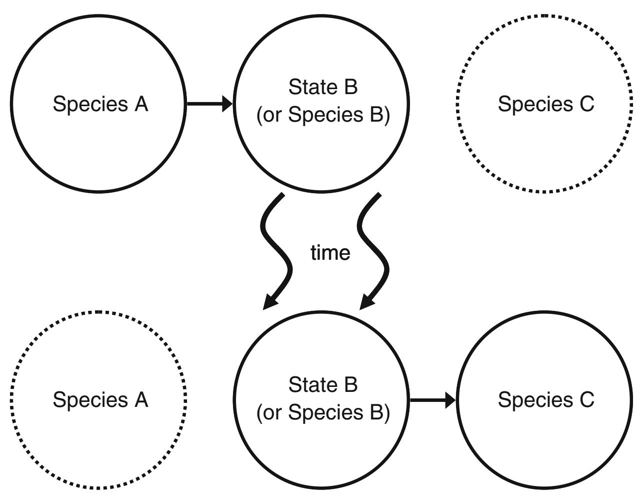

Fig. 1 Schematic representation of legacy effects. At one point in time, species A affects the environmental conditions (ecosystem engineering link) or the abundance of species B (trophic link). This alteration in species B affects species C, which may or may not be present in the system at the time of initial impact (indicated by the *dotted lines*), at a later time. The effect occurs at this later time (perhaps much later), even though species A is no longer present or the particular activity of A has ceased (as indicated by the *dotted lines*)

evolutionary literature, ecological inheritance. In the evolutionary literature, theoretical work suggests that legated effects of niche construction (ecological inheritance) can have important impacts on evolutionary dynamics (Laland et al. 1996, 1999; Lehmann 2007, 2008). Moreover, some authors have used legacy effects in the systems described here to study selection (Pregitzer et al. 2010). However, there seems to be less similarity between the latter pair of concepts than the former.

In his original definition of ecological inheritance, Odling-Smee (1988) described it as an inheritance transmitted from ancestors to successors via the external environment. He indicated that ecological inheritance has two components, one directed by the niche-constructing outputs of ancestral organisms and a second that is independent of the niche-constructing outputs of all ancestral organisms and arises in the remainder of the environment. His examples included the inheritance of breeding territories from parents to offspring, helpers in the Florida scrub jay, and potato washing in the macaque. However, Odling-Smee also noted that physical environmental modifications can be transmitted among organisms of different species as well as between generations and that offspring can modify their parents' environment.

In their paper in this issue, Odling-Smee and Laland (2012) again note that ecological inheritance is not always transmitted by genetic relatives. Moreover, they also suggest that ecological inheritance is related to the idea that environmental modification causing niche construction may persist long enough to impact many subsequent generations and perhaps even persist over geological time. Here, the important point is that these long-term effects of niche construction alter the selective environment for organisms downstream in the timeline.

The concept of legacy effect in ecology similarly includes the idea that effects may persist for long periods. However, there appears to be a difference in the described temporal dynamics. For example, Odling-Smee and Laland (2012, this issue) refer to changes in the environment that are built on by generation after generation of organisms of the same species. This example seems at odds with the idea of legacy effects, where the causal organism is now absent from the system or has ceased activity. In addition, with few exceptions, legacy effects are used to refer to indirect interspecific interactions rather than to intraspecific effects. The definition offered by Perry et al. (2008), which includes the seedbank and living plants in the concept of legacy effects, is clearly an outlier in the usage of this term. Mullineaux et al. (2009), when describing the dynamics of deep-sea vent communities, more accurately use the term "legacy individuals" to refer to those organisms that survive a large disturbance and subsequently influence community development.

Finally Odling-Smee and Laland (2012, this issue) note that they had previously modeled ecological inheritance as exclusively a physical resource (Laland et al. 1996, 1999), but this restriction is unnecessary and reduces the explanatory power of the concept. The inclusion of altered species compositions as a possible ecological inheritance also seems commensurate with legacy effects. However, for Odling-Smee and Laland, ecological inheritance easily includes the inheritance of information, such as that related to human culture, as well as the transmission of physical environmental effects and alterations in species communities. It is at this point that we begin to see a major divergence between the ecological concept of legacy effects and the evolutionary idea of ecological inheritance.

Within the ecology literature, the inheritance of mating territories or of behavioral changes is not included in the concept of legacy effects. That is not to say that ecologists are unaware of the large impacts of such relationships. However, these effects are described in the more specialized language of behavioral ecology and are separated from the idea of time-lagged impacts of biotic modification of ecosystems. There may be good reason for this distinction.

Like ecologists, Odling-Smee and Laland recognize that there are differences between the legacy of physical effects and the transfer of algorithmic information. However, they emphasize the similarities rather than the differences between these differing modes of inheritance. They choose to group the idea of property legacies and algorithmic inheritance in order to describe the similar importance of genetic information, algorithmic information, and modified environmental states for selection. The problem with this rhetorical device is that there are different modes of transmission for genetic and algorithmic information as compared to the simple transmission of ecosystem states. Primarily, all algorithm information, not just genetic information, requires transcription and therefore is prone to recombination and error in transmission. In comparison, the long-term persistence of alterations to ecosystems, as with the transfer of physical objects, is not necessarily dependent on transcription processes.

To take an extended example, when my mother gives me a handwritten recipe for Christmas pudding, I may or may not accurately decipher her handwriting regarding the amount of sugar, or I may spontaneously substitute dried cherries for raisins. In the same way, novel genetic inheritance is created by a combination of recombination and transcription error. On the other hand, when I inherit a gold locket from my mother, there is no error or recombination in that form of transmission, although there will most certainly be physical deterioration over time. One may think that the situation is more complex if I inherit a living system, such as a farm. After all, the organisms on a farm possess genetic information. However, the distinction is that the mode of transmission of property does not in itself alter what is being passed on. That is, there is not necessarily genetic or algorithmic transcription involved in this physical inheritance of property.

Applying the analysis more carefully to ecological inheritance in humans, we see that in much the same way that genetic recombination can lead to novel solutions to evolutionary pressures, algorithmic information can be combined or altered to yield innovations. Trivially, one could reflect on the fusion of various culinary traditions. Compare this, however, with the transmission of environmentally modified physical environments. The classic Banaue rice terraces of the Philippines carved out by Ifugao peoples 2000–3000 years ago clearly represent an environment with modified selection pressures, but their inheritance, unless combined with changing algorithmic information or abiotic pressures, cannot result in a changed product being passed on to the next generation. Therefore, while the end impact may be similar, i.e., modification of ecological or evolutionary outcomes, the mechanism of transmission admits dynamics in one case that are not possible in the other. This distinction will certainly be important in the accurate prediction of ecological or evolutionary dynamics caused by persistent environmental modification.

Conclusion

In conclusion, it seems possible, then, that a subset of legacy effects in ecology could map onto a particular component of the large group of mechanisms described as ecological inheritance. That is, legacy effects would correspond to those cases of ecological inheritance where physical or biological alterations of an ecosystem, caused by a species no longer present or acting in the system, persist for long enough to alter the selection environment for another species. However, legacy effects would not include those cases where ecological inheritance is invoked to describe transmittance of algorithmic information.

References

Aber JD, Ollinger SV, Dricoll CT (1997) Modeling nitrogen saturation in forest ecosystems in response to land use and atmospheric deposition. Ecol Model 101:61–78

Bassett IE, Simcock RC, Mitchell ND (2005) Consequences of soil compaction for seedling establishment: implications for natural regeneration and restoration. Austral Ecol 30:827–833

Bowman DMJS, Prior LD, de Little SC (2010) Retreating Melaleuca swamp forests in Kakadu National Park: evidence of synergistic effects of climate change and past feral buffalo impacts. Austral Ecol 35:898–905

Carson WP, Banta JA, Royo AA, Kirschbaum C (2005) Plant communities growing on boulders in the Allegheny National Forest: evidence for boulders as refugia from deer and as a bioassay of overbrowsing. Nat Area J 25:10–18

Clements F (1916) Plant succession. Publication 242. Carnegie Institute of Washington, Washington, DC

Davis MA, Pelsor M (2001) Experimental support for a resource-based mechanistic model of invasiblity. Ecol Lett 4:421–428

Davis MA, Bier L, Bushelle E, Diegel C, Johnson A, Kujala B (2005) Non-indigenous grasses impede woody succession. Plant Ecol 178:249–264

Densmore RV (2005) Succession on subalpine placer mine spoil: effects of revegetation with *Alnus viridis*, Alaska, USA. Arct Antarct Alp Res 37:297–303

Elgersma KJ, Ehrenfeld JG, Yu S, Vor T (2011) Legacy effects overwhelm the short-term effects of exotic plant invasion and restoration on soil microbial community structure, enzyme activities, and nitrogen cycling. Oecologia 167:733–745

Estes JA, Terborgh J, Brashares JS, Power ME, Berger J et al (2011) Trophic downgrading of planet Earth. Science 333:301–306

Flinn KM, Vellend M (2005) Recovery of forest plant communities in post-agricultural landscapes. Front Ecol Environ 3:243–250

Foster D, Swanson F, Aber J, Burke I, Brokaw N, Tilman D, Knapp A (2003) The importance of land-use legacies to ecology and conservation. Bioscience 53:77–88

Gleason HA (1917) The structure and development of plant association. Bull Torrey Bot Club 53:7–26

Grman E, Suding KN (2010) Within-year soil legacies contribute to strong priority effects of exotics on native California grassland communities. Restor Ecol 18:664–670

Harding JS, Benfield EF, Bolstad PV, Helfman GS, Jones EBD III (1998) Stream biodiversity: the ghost of land use past. Proc Nat Acad Sci 95:14843–14847

Hastings A, Byers JE, Crooks JA, Cuddington K, Jones CG, Lambrinos JG, Talley TS, Wilson WG (2007) Ecosystem engineering in space and time. Ecol Lett 10:153–164

Heneghan L, Fatemi F, Umek L, Grady K, Fagen K, Workman M (2006) The invasive shrub European buckthorn (*Rhamnus cathartica*, L.) alters soil properties in midwestern U.S. woodlands. Appl Soil Ecol 32:142–148

Huntzinger M, Karban R, Maron JL (2011) Small mammals cause non-trophic effects on habitat and associated snails in a native system. Oecologia 167:1085–1091

Jordan NR, Larson DL, Huerd SC (2011) Evidence of qualitative differences between soil-occupancy effects of invasive vs. native grassland plant species. Invas Plant Sci Manage 4:11–21

Kardol P, Cornips NJ, van Kempen MML, Bakx-Schotman JMT, van der Pitten WH (2007) Microbe-mediated plant-soil feedback causes historical contingency effects in plant community assembly. Ecol Monogr 77:147–162

Kourtev PS, Ehrenfeld JG, Haggblom M (2002) Exotic plant species alter the microbial community structure and function in the soil. Ecology 83:3152–3166

Laland KN, Odling-Smee FJ, Feldman MW (1996) The evolutionary consequences of niche construction. J Evol Biol 9:293–316

Laland KN, Odling-Smee FJ, Feldman MW (1999) Evolutionary consequences of niche construction and their implications for ecology. Proc Nat Acad Sci 96:10242–10247

Lehmann L (2007) The evolution of trans-generational altruism: kin selection meets niche construction. J Evol Biol 20:181–189

Lehmann L (2008) The adaptive dynamics of niche constructing traits in spatially subdivided populations: evolving posthumous extended phenotypes. Evolution 62:549–566

Lett MS, Knapp AK (2005) Woody plant encroachment and removal in mesic grassland: production and composition responses of herbaceous vegetation. Am Midl Nat 153:217–231

Mack MC, D'Antonio CM (2003) Exotic grasses alter controls over soil nitrogen dynamics in a Hawaiian woodland. Ecol Appl 13:154–166

Martin SL, Hayes DB, Rutledge DT, Hyndman DW (2011) The land-use legacy effect: adding temporal context to lake chemistry. Limnol Oceanogr 56:2363–2370

McLauchlan K (2006) The nature and longevity of agricultural impacts on soil carbon and nutrients: a review. Ecosystems 9:1364–1382

Molina R, Amaranthus M (1991) Rhizosphere biology: ecological linkages between soil processes, plant growth, and community dynamics. US Department of Agriculture, Forest Service Intermountain Research Station, General Technical Report 280

Mullineaux LS, Micheli F, Peterson CH, Lenihan HS, Markus N (2009) Imprint of past environmental regimes on structure and succession of a deep-sea hydrothermal vent community. Oecologia 161:387–400

Nuttle T, Yerger EH, Stoleson SH, Ristau TE (2011) Legacy of top-down herbivore pressure ricochets back up multiple trophic levels in forest canopies over 30 years. Ecosphere 2(1):Article 4

Odling-Smee FJ, Laland KN (2012) Ecological inheritance and cultural inheritance: what are they and how do they differ? Biol Theory 6. doi:10.1007/s13752-012-0030-x

Olding-Smee FJ (1988) Niche-constructing phenotypes. In: Plotkin H (ed) The role of behavior in evolution. MIT Press, Cambridge, pp 73–132

Orr SP, Rudgers JA, Clay K (2005) Invasive plants can inhibit native tree seedlings: testing potential allelopathic mechanisms. Plant Ecol 181:153–165

Perry DA (1994) Forest ecosystems. John Hopkins University Press, Baltimore

Perry DA, Oren R, Hart SC (2008) Forest ecosystems, 2nd edn. John Hopkins University Press, Baltimore

Pregitzer C, Bailey J, Hart S, Schweitzer J (2010) Soils as agents of selection: feedbacks between plants and soils alter seedling survival and performance. Evol Ecol 24:1045–1059

Sharrow SH (2007) Soil compaction by grazing livestock in silvopastures as evidenced by changes in soil physical properties. Agroforest Sys 71:215–223

Simard SW (1995) Interspecific carbon transfer in ectomycorrhizal tree species mixtures. PhD dissertation, Department of Forest Science, Oregon State University, Corvallis

van de Voorde TFJ, van der Putten WH, Bezemer TM (2011) Intra- and interspecific plant–soil interactions, soil legacies and priority effects during old-field succession. J Ecol 99:945–953

Wang B, Qiu Y-L (2006) Phylogenetic distribution and evolution of mycorrhizas in land plants. Mycorrhiza 16:299–363