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SYNTHESIS: LESSONS FROM DISPARATE ECOSYSTEM ENGINEERS

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The chapters in this section illustrate that the precise effects of ecosystem engineers can be highly system specific, but the ecosystem engineering concept reveals commonalities in engineering-related processes. The intricacies of an insect tying leaves together (Lill and Marquis) and an isopod collapsing salt marsh banks (Talley and Crooks) can readily be viewed as distinctly disparate examples, yet both have community-level effects initiated by alteration of physical structure. The idiosyncratic details of these examples are certainly important in their own right for providing insight into individual systems; however, examining a diversity of examples provides unique opportunities for gaining general insights and unifying theories. Here I draw out five major messages that are reflected in these chapters and evaluate some implications for future directions for the study of ecosystem engineers.

First, one distinct benefit in considering many different ecosystem engineers in side-by-side case studies is the identification of the unique advantages that different systems may offer for examining different lines of research questions. For example, the shelter-building insects described by Lill and Marquis and the soil-tilling earthworms described by Lavelle clearly alter the physical structure of habitat in important ways, but are often overlooked because of their small size. It is the small size of these engineers, however, that makes them easy to manipulate and replicate in experiments. Because most ecosystem engineering studies are observational, systems such as these may provide valuable insight into the mechanisms behind engineering outcomes. Similarly, some systems are more heavily influenced by broad physical forces than others allowing for examination of the interactions between engineering and external, often larger-scale processes. Wave energy, for instance, influenced the engineering potential of bioeroding isopods (Talley and Crooks).

Second, and perhaps most notably, the various examples in the chapters underscore that the temporal scale of the engineering and the persistence of the engineered aspects differs greatly between systems (Hastings et al. 2007). In temperate regions the structural changes of leaf tiers are cast aside when leaves are shed by deciduous trees every autumn. In contrast, the chemical and salinity changes to soil deposited by iceplant often persist for years even after the plant itself is removed (Molinari et al.). As Molinari et al. further emphasize, differences in the spatial scale of ecosystem engineering can also be apparent. On a small scale, invasive ecosystem engineers can exact great physical changes resulting in lower (Molinari et al.) or higher (Talley and Crooks) species richness. If the engineering skews the environment heavily enough, higher richness could especially be due to an increase in exotic species. At larger scales, a mosaic of engineered and unengineered habitat is likely in many cases to lead to high regional-scale species richness due to enhanced habitat heterogeneity. However, in extreme cases of engineering, like iceplant, where almost all species were excluded underneath it, low species richness can still result at large scales. Thus, although we see a common thread of engineers altering the physical environment and enhancing environmental heterogeneity, the resultant community effects are determined largely from the scale at which environmental heterogeneity affects biodiversity for a particular group of species as well as the baseline richness of unmodified habitats (Tews et al. 2004, Wright et al. 2006).

Third, physical, structural modification remains one of the most clear-cut examples of ecosystem engineering. Such modification is easily identified and has obvious effects on subsequent biotic interactions within a community. For example the effect of certain earthworm species to mesh soil particles into solid macroaggregated structures has direct consequences for nutrient distributions to plants. In other cases, like the bioeroding isopods, the structural modification may be so drastic that a habitat is completely converted to another habitat type.

Although any changes to the abiotic environment could be thought of as engineering, if such changes occur due to trophic, assimilatory, or even competitive purposes they may be better characterized with existing ecological terminology and frameworks like energy flow, metabolism, or allelopathy. For example, a filter-feeding mollusc could increase water clarity by removing plankton or sediment from the water column. Although the effect on water clarity may be the same, the removal of plankton is trophic while sediment removal is engineering. Placing the emphasis of ecosystem engineering on the process (filtration of sediment) as opposed to the consequence (water clarity) is important because it helps to indicate which ecological theories (e.g., ecosystem engineering, food webs) might be most applicable in a given instance. In this instance, dynamic feedbacks of the predator feeding on its planktonic prey and subsequent community-level consequences will surely differ from those arising from interactions of predators and nonliving sediment particles. What makes ecologists' task both difficult and compelling is that species may often be influential due to a mixture of engineering and biotic interactions. However, Talley and Crooks make a clear case that, from a management perspective, the bioeroding isopods are important mostly in nontrophic ways. Thus an explicit ecosystem engineering framework in and of itself would be particularly helpful to management applications in this system.

An emphasis on the processes behind ecosystem engineering can lead to some grey areas. In particular, it can sometimes be difficult to categorize chemical changes to an ecosystem. For example, are chemical inputs by iceplant into the soil best examined with an engineering framework or with alleopathy or Lotka-Volterra competition models? Ultimately the distinction between ecosystem engineering and biotic interactions that yield similar environmental effects (like filtration or alleopathy) may depend on the perspective and needs of the practitioner and which framework is easiest and most efficient to apply. In the case of iceplant, the clearest examples of chemical engineering may be through its spatially and temporally extended abiotic influence via inorganic chemicals (e.g., salt). Legacy effects of salt or chemicals that persist after an ecosystem engineer is removed might also be effectively framed as ecosystem engineering since there is no intentional competitive target of these lingering abiotic changes.

Fourth, for most ecologists who deal with contemporary systems, the paleontologic examples of Marenco and Bottjer depicting some of the earliest forms of engineering are intriguing. Specifically, the soft-bottom bioturbating–aerating species they describe opened up a new third dimension of habitat for marine infauna. By providing a broader temporal view, such paleontological evidence provocatively implies that ecosystem engineering may have important ramifications for evolutionary processes, particularly the appearance of novel functional groups of organisms. That is, if ecosystem engineers facilitate use of a completely novel habitat, they can catalyze new modes of life. It would be a tantalizing exercise to try to identify the explosive radiations of species throughout time and determine how many may have been attributable to novel ecosystem engineers facilitating expansion into previously uninhabited ecological niches. Such novel ecosystem engineers that began engineering in a new way or in a new habitat that physics alone could not engineer effectively may have been critical catalysts in the radiation of lifestyles and life-forms.

Fifth, two of the chapters in this section (Molinari et al and Talley and Crooks) dealt predominantly with ecosystem engineers in their non-native environments. Although ecosystem engineers typically function as engineers in both their native and introduced environments, when they are introduced to a new environment, ecosystem engineers may become more abundant or we may simply have a tendency to notice the engineering effects more in a place where the effects are novel. Invasive ecosystem engineers will often have unique traits (Crooks 2002), unless they happen to be structurally identical to a native species, e.g., one tree species replacing another. The large community changes that can often occur in an environment where an ecosystem engineer is introduced stem from the fact that the native ~~biota is~~ not adapted to the newly engineered abiotic conditions. Even if native species survive the direct alterations, the abiotic playing field, which provides the context upon which all biotic interactions are dependent, may be severely skewed. These disturbances may therefore erase a native species' prior advantage of local environmental adaptation accrued over evolutionary time, giving non-native species equal or better opportunity to compete their way into the community (Byers 2002). As opposed to direct anthropogenic disturbances, the modification of historic, environmental conditions by introduced ecosystem engineers may be particularly enhanced because, once established, they chronically alter the environment. This is one reason the removal of invasive ecosystem engineers is frequently a top priority in restoration efforts (Byers et al. 2006, Byers in press).

In summary, the scientific literature has an increasing number of clear examples of ecosystem engineers (Wright and Jones 2006). The most convincing of these are cases where engineering effects far outweigh effects from biotic interactions. Burrowing isopods and beavers are certainly part of food webs, but their largest impacts on the communities are through their engineering activities. Even though the effects of ecosystem engineers on their communities can be pervasive and extreme, there is still no widely used, off-the-shelf theoretical approach to study these effects that is analogous to the concepts and models available for studying predation and competition. Mutualism theory is a partial inroad in this direction (Bruno et al. 2003), and some progress has recently been made with explicit ecosystem engineering models (Gurney and Lawton 1996, Cuddington and Hastings 2004; Wilson and Wright, Cuddington and Hastings, Meron et al. ~~this book~~). Ecosystem engineering, with its dynamic components of organisms affecting physical structure and consequent feedbacks on the engineers and their communities, would benefit from full development of analytical, conceptual, and theoretical approach in ecology (Jones et al. 1994, Gurney and Lawton 1996, Cuddington and Hastings 2004).

Generalizing types of ecosystem engineering would greatly aid such a development of a full theoretical and conceptual treatment because one of the impediments may be that each case of ecosystem engineering has been viewed as idiosyncratic, to be addressed on a case-by-case basis. In describing the paleo explosion of bioturbators–aerators as an important, engineering life form, Marenco and Bottjer have provided an example of how we could meaningfully categorize engineers according to their functional alterations of the environment. Examples of other major categories of species that share overarching similarities of engineering effects may include the following: flow modifiers, habitat modifiers, and biogeochemical modifiers (Gutierrez et al. 2003). Identifying common, unifying groups of ecosystem engineers is a challenging, yet potentially fruitful pursuit for ecologists (Gutierrez et al. 2003). Because some ecosystem engineers, including the ones in this section, span multiple categories, the category applied may depend on which affected species one cares about. For example, earthworms modify both habitat and nutrient flows. For ground-dwelling insects the habitat modification may likely be the most important aspect, because aggregations and disaggregations of soil structures have a profound influence on certain other belowground species. However, for plants, the worms' role as nutrient distributors is likely to be a large one. In any event, such classification schemes would likely be welcomed by theoreticians seeking to develop general models for particular suites of engineers, or empiricists looking for common patterns across systems. The development of sound classifications is perhaps one of the most important needs to advance a generalized, unified study of ecosystem engineers.

REFERENCES

Bruno, J.F., Stachowicz, J.J., and Bertness, M.D. (2003). Inclusion of facilitation into ecological theory. *Trends in Ecology & Evolution* 18:119–125.

Byers, J.E. (2002). Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos* 97:449–458.

Byers, J.E. (in press). Invasive animals in marshes: Biological agents of change. In ~~*Anthropogenic modification of North American Salt Marshes: Causes, consequences, and Recommendations*~~, B.R. Silliman, ~~M.D. Bertness, and~~ E.D. Grosholz, Eds. University of California Press. 3

Byers, J.E., Cuddington, K., Jones, C.G., Talley, T.S., Hastings, A., Lambrinos, J.G., Crooks, J.A., and Wilson, W.G. (2006). Using ecosystem engineers to restore ecological systems. *Trends in Ecology & Evolution* 21:493–500.

Crooks, J.A. (2002). Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. *Oikos* 97:153–166.

Cuddintgon, K., and Hastings, A. (2004). Invasive engineers. *Ecological Modelling* 178:335–347.

Gurney, W.S.C., and Lawton, J.H. (1996). The population dynamics of ecosystem engineers. *Oikos,* 76(2):273–283.

Gutierrez, J.L., Jones, C.G., Strayer, D.L., and Iribarne, O.O. (2003). Mollusks as ecosystem engineers: The role of shell production in aquatic habitats. *Oikos* 101:79–90.

Hastings, A., Byers, J.E., Crooks, J., Cuddington, K., Jones, C., Lambrinos, J., Talley, T., and Wilson, W. (~~in press~~). Ecosystem engineering in space and time. *Ecology Letters*.

Jones, C.G., Lawton, J.H., and Shachak, M. (1994). Organisms as ecosystem engineers. *Oikos* 69:373–386.

Tews, J., Brose, U., Grimm, V., Tielborger, K., Wichmann, M.C., Schwager, M., and Jeltsch, F. (2004). Animal species diversity driven by habitat heterogeneity/diversity: The importance of keystone structures. *Journal of Biogeography* 31:79–92.

Wright, J.P., and Jones, C.G. (2006). The concept of organisms as ecosystem engineers ten years on: Progress, limitations, and challenges. *Bioscience* 56(3):203–209.

Wright, J.P., Jones, C.G., Boeken, B., and Shachak, M. (2006). Predictability of ecosystem engineering effects on species richness across environmental variability and spatial scales. *Journal of Ecology* 94(4):815–824.

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