

**IJEE SOAPBOX:  
PRINCE KROPOTKIN MEETS  
THE HUTCHINSONIAN NICHE**



ROBERT D. HOLT  
*Department of Biology*  
*University of Florida, Gainesville, Florida 32611-8525, USA*

Siberia in the winter is among the harshest ecosystems on earth, or so it must have seemed to the Russian nobleman Prince Petr Kropotkin back in the 19th century as he wandered in his scientific expeditions, winding through that seemingly endless wilderness of dark brooding forest and treacherous bog. In the course of his personal evolution from a privileged member of the elite, to an advocate for the oppressed peasantry and industrial workers and Russia's foremost anarchist-communist, he published a provocative work, *Mutual Aid* (1902, reprinted 2005), reflecting on natural and human systems, and the drivers of evolution in both. He drew upon his observations of animal and human life in Siberia to counter the grim world view of the social Darwinists, who asserted that the raw competitive struggle of individual against individual was the prime driver of evolution. Kropotkin believed his observations in Siberia showed that individual struggle against the forces of the environment was inadequate to explain persistence in that brutal realm, and that cooperation, rather than competition, must be an essential force in evolution (Gould, 1977, provides a fine essay on Kropotkin).

Evolutionary biologists have made vast strides since Kropotkin's day in understanding both competition and cooperation through the lenses of natural selection (Dugatkin, 2006), and have developed a nuanced world-view that encompasses both. The wildebeest of east Africa traverse the savanna in great herds, and Cape hunting dogs chase their prey down in packs, because herding and cooperative tactics are for each species respectively effective strategies that over the course of evolution have out-competed alternative non-cooperative strategies. In a hierarchical view of natural selection, competition at one level in the hierarchy can be abetted by cooperation at a lower level. Maynard Smith and Szathmari (1998) have argued that the molding of cooperative units—from the cell itself, to multicellular organisms, to social groups—should be viewed as fueling the most dramatic transitions in the history of life.

---

E-mail: rdholt@zoo.ufl.edu

*The IJEE Soapbox* provides an informal forum for leading ecologists and evolutionary biologists to expound on issues that they find particularly exciting, thought provoking, and novel.

Robert D. Holt is our first invited *IJEE Soapbox* essayist. Bob is Professor of Biology and Arthur R. Marshall, Jr., Chair in Ecology at the University of Florida, and is one of the foremost theoreticians in ecology and evolutionary biology. His research focuses on theoretical and conceptual issues at the population and community levels of ecological organization and on linking ecology with evolutionary biology. Bob is best known for his pioneering work on apparent competition, multispecies interactions in food webs (community modules) in time and space, and the evolution of niche conservatism.

In this essay, I reflect on how community ecology seems to be going through a comparable intellectual transformation, also involving the interplay of competition and (in a sense) “cooperation” among species. To place this transformation into context, it is important to go back to the basics of the core motivating questions of the discipline. Understanding the forces that govern the coexistence of species in communities is arguably *the* central problem in community ecology. G.E. Hutchinson (1959) famously asked “Why are there so many kinds of animals?” Answering this question has engaged many of the finest minds in ecology, including Hutchinson and his student Robert MacArthur, and their many intellectual descendants.

To boil down a large and subtle literature (see Holt, 2001) into a near-caricature of itself, the canonical answer focuses on *competition*, in a broad sense. To understand the ecological lineaments of diversity, one must understand how species partition resources by type, across space, or through time (Schoener, 1974, viz., “mechanisms of coexistence”, sensu Kotler and Brown, 1988) and also how some species steal or seize resources from other species in food webs (including parasitism, predation, and herbivory). [Trophic interactions are akin to resource competition, as in a certain sense a predator and its prey “compete” for the same packet of nutrient and energy. It just so happens that this packet comprises the body of the unfortunate prey individual.] Resource partitioning can be modulated by factors such as disturbance, strong intraspecific density dependence, direct interference, and dispersal. Food web interactions themselves can inflate or constrain coexistence from resource partitioning (Kotler and Holt, 1989, e.g., via modifying the “fitness equalization” dimensions of coexistence, see Chesson, 2000), and predation also provides prey with alternative modes of partitioning the world that can explain diversity maintenance at lower trophic levels (e.g., species may segregate in “enemy-free” space; Holt and Lawton, 1994; Chesson and Kuang, 2008).

In an abstract environmental space, where the axes are, e.g., temperature, resource availabilities, or natural enemy abundances, one can identify combinations of abundances at which each interacting species just meets its requirements—its zero net growth isocline, or ZNGI (Chase and Leibold, 2003)—delineating key dimensions of its Hutchinsonian niche (Hutchinson, 1978). A necessary condition for competitive coexistence in a local community is that the ZNGIs of different species cross, so each species has a combination of resources, predator abundances, etc., at which it is superior, in that its numbers can grow when rare, but the other species cannot. If species do not coexist locally, they may still coexist regionally, but the realized niche of the species—that range of resource conditions and sites it actually occupies, rather than potentially utilizes—will be smaller than its fundamental niche (Hutchinson, 1978).

So competition and food web interactions—antagonistic interactions between species—have historically provided the building blocks for the conceptual architecture of theoretical community ecology. All basic textbooks in ecology include nuggets of competition theory and predator–prey models, and these themes predominate in major advanced texts as well. The emphasis in ecology on the ceaseless struggle among species for a limited pie of resources goes back to Charles Darwin, who in his famous wedge metaphor likened nature to a space completely occupied by tightly fitting wedges. If a

species—a new wedge—is hammered in, others must shrink in size or be squeezed out. Much of the edifice of theoretical ecology puts quantitative teeth into Darwin's wedge image of the world. For instance, if wedges cannot overlap, and there is a minimal size to each wedge, the maximal number of species a community can contain is the size of the entire surface, divided by the size of each wedge (MacArthur, 1972).

But it is becoming increasingly clear that this vivid and fruitful view of how communities are put together misses key dimensions of ecological reality. There is a groundswell of interest among ecologists these days in themes such as facilitation (Brooker et al., 2008; Bulleri et al., 2008), mutualism, ecological engineering (Jones et al., 1997; Cuddington et al., 2007), and niche construction (Odling-Smee et al., 2004; Donohue 2005), which collectively highlight vital interactions in many communities not captured by the wedge view of the world. Ecologists have begun to focus on the imprint of positive interactions among species on community organization, from local scales such as intertidal zonation patterns (e.g., Bertness et al., 1999) to the grand sweep of macroevolution (e.g., Valiente-Banuet et al., 2006; Jablonski, 2008).

Facilitation has been defined as “encounters between organisms that benefit at least one of the participants and cause harm to neither” (Bruno et al., 2003, p. 120). Mutualisms are reciprocal facilitations. Ecological engineering can imply facilitation (e.g., leaf shelters after abandonment by their creators can provide refuge to many arthropod species, Fukui, 2001) although sometimes engineering involves negative interactions as well (e.g., Daleo et al., 2006). One can usefully define facilitation more broadly to include indirect as well as direct interactions, and I use this more expansive meaning in this essay. Bruno et al. (2003) suggest that a serious consideration of facilitation requires a reevaluation of many foundational predictions and paradigms in ecology. For instance, given facilitation, a species' realized niche can exceed its fundamental niche. As a concrete example where such a reexamination of fundamental premises may be needed, consider annual plants. A sophisticated body of theory exists characterizing coexistence of annuals competing for space and resources (e.g., Levine and Rees, 2004; Turnbull et al., 2007). Yet in some environments, experimental manipulation shows that annuals can experience strong interspecific facilitation, such as nurse plant effects, in a highly species- and life-stage-specific fashion (Lortie and Turkington, 2008). The detailed mechanisms of such facilitation are unclear, but empirically they are clearly quite important, and so could strongly influence the maintenance of species diversity.

The word “mechanisms” here is important. The reason competition theory and food web modeling comprise such a rich body of ecological ideas is that they rest on clear mechanisms expressed in quantitative terms, e.g., competition for space leads to logistic-like density dependence, and type II functional responses permits unstable dynamics and hence temporal partitioning of a single biotic resource. A full understanding of coexistence requires one to pay close attention to the quantitative expression of feedback effects between consumers and their environment. MacArthur (1970, 1972) showed that given simplifying assumptions, one could express resource competition between species using the classical Lotka–Volterra competition model. But the competition coefficients include rates of resource renewal, as well as consumption rates—not just overlap, but

impact. Traditional treatments of resource partitioning neglect one half of the fundamental duality in the coexistence question: for species to stably coexist, it does not suffice for them to differ in resource use, they also must differ in how they in turn affect their resources (Leibold, 1995). In effect, for two competing species to coexist in a durable equilibrium, each must have a larger impact on the resource it most requires (Chase and Leibold, 2003). Thus, competitive coexistence involves more than resource partitioning—it reflects as well feedbacks between organisms and their environment.

In like manner, a fully formed theory of community ecology wholeheartedly embracing facilitation and other positive interactions must include the careful articulation of specific mechanisms of organism–environment feedbacks. Brooker et al. (2008, p. 27) recently noted that “developments in facilitation modeling are at an early stage”. Despite increasing empirical literature documenting facilitation (Lortie, 2007, reports more than 1000 papers), there is still a striking dearth of ecological theory explicitly tailored to examine the interplay of facilitation and competition in a framework applicable to realistic empirical systems (Bruno et al., 2003), and relatively few attempts to characterize mechanisms of facilitation quantitatively. But recently, a number of steps have been taken towards the development of such theory.

Standard community theory based on competition and trophic interactions already embodies a number of mechanisms of facilitative and mutualistic interactions, emerging as indirect interactions in communities (Miller, 1994), and it is useful to briefly reflect on these. A bit of folk wisdom encapsulates one widespread mechanism for emergent facilitation: “The enemy of my enemy is my friend.” Within a trophic level, multi-species competitive interactions can lead to indirect facilitation (Levine 1976, 1999; Vandermeer, 1980). If A competes strongly with B, and B strongly with C, but A only weakly with C, then A indirectly facilitates C. Brooker et al. (2008) suggest such indirect facilitation is particularly likely where non-transitive competitive interactions involve multiple limiting resources. Competition at one trophic level can also alter the sign of the net relationship between species at other trophic levels. For instance, if two predators feeding on two prey species overlap in their diets, one might expect the predators to compete. But if the prey themselves directly compete, the predators might actually be net mutualists (Levine, 1976; Vandermeer 1980). The small body of theory on such mechanisms leading to indirect facilitation has to date focused on small perturbations near equilibria. Abrams and Nakajima (2007) have recently cautioned that in some cases, facilitation disappears when one considers large perturbations, or systems which never settle into equilibrium. So the jury is still out as to how significant this modality of facilitation will be in determining community organization. Another variation on the theme of “the enemy of my enemy is my friend” is a trophic cascade, where a consumer benefits species two (or more) trophic steps below by reducing the abundance or activity of natural enemies of those species. Trophic cascades—indirect, reciprocal facilitations—are dominant features of many ecosystems. For instance, blue crabs in salt marshes of eastern North America keep in check herbivorous snails, which, freed of predation and left to their own devices, devastate marsh grasses and leave in their wake little but barren mudflats (Silliman and Bertness, 2002; Silliman et al., 2005). Many

plants strengthen trophic cascades with evolved devices (e.g., domatia, nectaries, attractant volatile chemicals) that attract or sustain predators, thereby reducing the impact of herbivores (van Rijn and Sabelis, 2005; Dicke and Vet, 1999).

Other familiar and empirically well-grounded examples of emergent facilitation are found in multispecies predator–prey theory. Indirect mutualism between alternative prey can arise when a generalist predator is constrained in its numerical response (e.g., due to territoriality) and has a saturating functional response, or switches among prey species (Holt, 1977). This effect appears to explain dramatic natural phenomena, such as community-level masting in southeast Asian dipterocarp forests, and the synchronized emergence in vast numbers of three species of the periodical cicada *Magicicada* (*M. septendecim*, *M. cassini*, and *M. septendecula*) every 13 or 17 years at different locales in eastern North America (Lloyd and Dybas, 1966). Different prey species perceive different samples of the environment, and trans-specific cues can be utilized to help minimize predation. This interspecific pooling of information (along with advantages in foraging, Monkkonen et al., 1996) helps explain mixed-species flocks of birds moving across landscapes fraught with risk (Monkkonen et al., 1996). In northern winters, bird-watchers yearn to come across such flocks, since otherwise one may wander through silent woods for an entire day and see nary a bird. On a trail in the thick, dark, dank understory of a neotropical rain forest, one can tromp mid-day for hours upon sweating hours and see nothing, then stumble across a diverse mixed-species flock traversing the forest, an explosion of activity, with ant-wrens and foliage-gleaners and flycatchers flitting in and out of view, a maddening mélange of brief glimpses and then—gone! Mutual facilitation is key to the organization of these bird communities.

Feedback through resources can transform an interaction that on its face should be competition into neutral interactions or even facilitation. De Roos et al. (2008) have shown that emergent facilitation can arise from the interplay of stage structure and density dependence in a shared prey. The basic idea is that density dependence in maturation from juveniles to adult strongly influences the fraction of the population found in each stage. If juveniles compete strongly and adults do not, juveniles may comprise the bulk of the prey population, because maturation is slow and mortality occurs before reproduction. Adult prey may then be scarce. A predator specialized on juvenile prey relaxes density dependence, speeds development, and so can boost the abundance of adults, thus indirectly facilitating a predator specialized to adults. This emergent facilitation may be so strong that removing one predator entails extinction of the other. Bonsall and Holt (2003) likewise argued that stage structure feedbacks through labile rates of development can facilitate coexistence of alternative hosts sharing a parasitoid, and Roy and Holt (2008) demonstrated that predation upon a prey species with acquired immunity to a pathogen can actually boost pathogen prevalence—given density dependence. The reason is that killing immune prey can lead to compensatory increases in reproduction in remaining individuals, boosting the supply rate of fresh, susceptible hosts available for infection.

The above mechanisms of facilitation are already immanent in existing population community theory. Others (and those that have been the greater focus of the recent

flurry of interest in facilitation) arise from effects organisms have on the abiotic environment. Many of these require the development of new theory. For instance, high in the rocky intertidal of the Gulf of Main, algal canopies ameliorate physical stresses (reducing temperature and evaporative water loss) to the benefits of many understory species (though not all). By contrast, in the low intertidal, the canopy shelters consumers, so the net effect of the canopy shifts to neutrality, or even negative (Bertness et al., 1999). A quantitative model of this would need to characterize how a given biomass and architecture of algae translates into the abiotic variables that influence “stress” for understory creatures. There are two complementary directions that theory should take to incorporate such effects of organisms via abiotic variables: phenomenological models, and mechanistic models.

As with the classical Lotka–Volterra competition model, we need sensible phenomenological models for facilitation that express demographic rates in each species as a direct function of the density of itself and other species. Early forays in this direction included models of mutualism (Vandermeer and Boucher, 1978) and positive feedbacks in ecological systems (DeAngelis et al., 1986). More recently, Thompson et al. (2006) have developed models for demographically open populations of mutualists (which with little modification apply to asymmetrical facilitation). The models are based on plausible assumptions, such as saturating effects on increasing recruitment with the density of the partner. Phenomenological models are useful because they can be used as building blocks to address a wide range of questions (see, e.g., Travis et al., 2006; Kefi et al., 2007; Vellend, 2008). For instance, in an interesting contribution, Gross (2008) has revisited the classical model of exploitative competition for a single resource, and shown that given cross-species amelioration of mortality (e.g., due to reduction in stress), multiple species can coexist. In effect, each species adds a new dimension to Hutchinsonian niche space, providing additional routes to coexistence.

Although phenomenological models are useful, theory development should not stop there. I think a more determined effort needs to be made to develop mechanistic models of facilitation. Exploitative competition theory has been greatly enriched by a firm focus on the mechanics of resource consumption and renewal (Tilman, 1987; Grover, 1997). My sense of the empirical literature on facilitation is that there is a great deal of contingency in that whether or not facilitation is found depends on many poorly-understood details of specific species and their abiotic settings. As an example, if shading promotes plant facilitation in arid environments, a physical model of how plant size and form determine the light and thermal environment of seedlings could be used to place the nurse effect phenomenon on a more mechanistic footing and provide insights into this contingency. A fine example of a mechanistic model of facilitation and competition is provided by Gilad et al. (2007), who examine interactions between plants in arid environment using a model explicitly of the dynamics of a soil water pool. Plants compete for water via uptake, but also facilitate each other by increasing infiltration rates of rainfall into the soil. With this mechanistic model in hand, one can now make more explicit predictions, for instance, as to how the balance between facilitation and competition might shift with soil properties, or in changing climates. I suspect we are on the verge of seeing a prolif-

eration of many specific models, such as this, tailored to particular positive interactions, which can provide a firm mechanistic foundation for facilitation theory. More broadly, I also have a hunch that direct and indirect facilitation will prove to play a significant and as yet poorly understood role in the maintenance, as well as temporal and spatial structuring, of biodiversity.

Imagine that in a few years, Prince Kropotkin (much to his and our surprise) has been brought back to life, and along with other modern Russian ecologists takes part in a scientific expedition into the Siberian taiga and tundra. It is a little warmer than he remembers, but still a pretty harsh place to spend time. As Kropotkin listens to his companions reflecting on the patterns they see, he might hear surprising echoes of his thoughts, blended with reminders of his social Darwinist foes. Many ecological patterns in the Siberian landscape clearly involve strong antagonistic interactions, such as replacements of early successional species after fires with woody plants, and explosive outbreaks of foliage-stripping insects. There will also be doubtless impressive examples of intraspecific cooperation, as in the hunts of wolves for their prey. But alongside these classical ecological patterns, considerable weight will be given to forces of direct and indirect facilitation and mutualisms among species. Effective wolf predation may help forest regeneration by keeping vertebrate herbivores scarce and nervous, and the physical architecture and biomass of the plants may in turn define the landscape of fear within which the deadly predator-prey game plays out. The distribution of soil mycorrhizae may help explain habitat specialization by plants, the tiny mosses of the forest floor may provide refuge to countless collembolans and tiny beetles, the behavior of thrushes and other berry- and seed-eating birds may drive the rate of recovery of vegetation to disturbance, and the abundance of these birds may in turn reflect the productivity of these plants. Emphasizing the importance of such positive interactions in natural communities and ecosystems need not at all imply the world view of Gaia (with strains of “Kumbaya” humming softly in the background), but rather reflects the subtle interplay of positive and negative interactions in weaving the current fabric of life emerging from the Darwinian struggle. That is reality, and Prince Kropotkin got a hint of it.

#### ACKNOWLEDGMENTS

I thank Mark Bertness and Brian Silliman for helpful conversations about facilitation, and the University of Florida Foundation for its support.

#### REFERENCES

- Abrams, P.A., Nakajima, M. 2007. Does competition between resources change the competition between their consumers to mutualism? Variations on two themes by Vandermeer. *American Naturalist* 170: 744–757.
- Bertness, M.D., Leonard, G.H., Levine, J.M., Schmidt, P.R., Ingraham, A.O. 1999. Testing the relative contribution of positive and negative interactions in rocky intertidal communities. *Ecology* 80: 2711–2726.

- Bonsall, M.B., Holt, R.D. 2003. The effects of enrichment on the dynamics of apparent competitive interactions in stage-structured systems. *American Naturalist* 162: 780–795.
- Brooker, R.W., Maestre, F.T., Callaway, R.C., et al. 2008. Facilitation in plant communities: the past, the present and the future. *Journal of Ecology* 96: 18–34.
- Bruno, J.F., Stachowicz, J.J., Bertness, M.D. 2003. Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution* 18: 119–125.
- Bulleri, F., Bruno, J.F., Benedetti-Cecchi, L. 2008. Beyond competition: incorporating positive interactions between species to predict ecosystem invisibility. *PLoS Biology* 6: 1136–1140.
- Chase, J.M., Leibold, M.A. 2003. Ecological niches: linking classical and contemporary approaches. University of Chicago Press, Chicago, IL.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.
- Chesson, P., Kuang, J.J. 2008. The interaction between predation and competition. *Nature* 456: 235–238.
- Crespi, B.J. 2004. Vicious circles: positive feedback in major evolutionary and ecological transitions. *Trends in Ecology and Evolution* 19: 627–633.
- Cuddington, K., Byers, J.B., Wilson, W.G., Hastings, A., eds. 2007. *Ecosystem engineers: plants to protists*. Academic Press, San Diego, CA.
- Daleo, P., Escapa, M., Alberti, J., Iribarne, O.O. 2006. Negative effects of an autogenic ecosystem engineer: interactions between coralline turf and an ephemeral green alga. *Marine Ecology Progress Series* 315: 67–73.
- DeAngelis, D.L., Post, W.M., Travis, C.C. 1986. Positive feedbacks in natural systems. *Biomathematics Series*, Vol. 15. Springer, Berlin.
- De Roos, A.M., Schellekens, T., Van Kooten, T., Persson, L. 2008. Stage-specific predator species help each other to persist while competing for a single prey. *Proceedings of the National Academy of Sciences USA* 105: 13930–13935.
- Dicke, M., Vet, L.E.M. 1999. Plant–carnivore interactions: evolutionary and ecological consequences for plant, herbivore and carnivore. In: Olff, H., Brown, V.K., Drent, R.H., eds. *Herbivores: between plants and predators*. Blackwell Science, Oxford, pp. 483–520.
- Donohue, K. 2005. Niche construction through phenological plasticity: life history dynamics and ecological consequences. *New Phytologist* 166: 83–92.
- Dugatkin, L. 2006. *The altruism equation: seven scientists search for the origins of goodness*. Princeton University Press, Princeton, NJ.
- Fukui, A. 2001. Indirect interactions mediated by leaf shelters in animal–plant communities. *Population Ecology* 43: 31–40.
- Gilad, E., Shachak, M., Meron, E. 2007. Dynamics and spatial organization of plant communities in water-limited systems. *Theoretical Population Biology* 72: 214–230.
- Gould, S.J. 1997. Kropotkin was no crackpot. *Natural History* 106: 12–21.
- Gross, K. 2008. Positive interactions among competitors can produce species-rich communities. *Ecology Letters* 11: 929–936.
- Grover, J.P. 1997. *Resource competition*. Chapman and Hall, London, UK.
- Holt, R.D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12: 197–229.
- Holt, R.D. 2001. Coexistence of species. In: Levin, S., ed. *The encyclopedia of biodiversity*. Academic Press, San Diego, Vol. 5, pp. 413–426.
- Holt, R.D., Lawton, J.H. 1994. The ecological consequences of shared natural enemies. *Annual Review of Ecology and Systematics* 25:495–520.



- Hutchinson, G.E. 1959. Homage to Santa Rosalia or why are there so many kinds of animals? *The American Naturalist* 104:413-423.
- Hutchinson, G.E. 1978. *An introduction to population ecology*. Yale University Press, New Haven, CT.
- Jablonski, D. 2008. Biotic interactions and macroevolution: extensions and mismatches across scales and levels. *Evolution* 62: 715–739.
- Jones, C.G., Lawton, J.H., Shachak, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78: 1946–1957.
- Kefi, S., Rietkerk, M., van Baalen, M., Loreau, M. 2007. Local facilitation, bistability and transitions in arid ecosystems. *Theoretical Population Biology* 71: 367–379.
- Kotler, B.P., Brown, J.S. 1988. Environmental heterogeneity and the coexistence of desert rodents. *Annual Review of Ecology and Systematics* 19: 281–307.
- Kotler, B.P., Holt, R.D. 1989. Predation and competition—the interaction of two types of species interactions. *Oikos* 54: 256–260.
- Leibold, M.A. 1995. The niche concept revisited: mechanistic models and community context. *Ecology* 76: 1371–1382.
- Kropotkin, P. 1902 (reprinted 2005). *Mutual aid: a factor of evolution*. Porter Sargent Publishers, Boston, MA.
- Levine, J.M. 1999. Indirect facilitation: evidence and predictions from a riparian community. *Ecology* 80: 1762–1769.
- Levine, J.M., Rees, M. 2004. Effects of temporal variability on rare plant persistence in annual systems. *American Naturalist* 164: 350–363.
- Levine, S.H. 1976. Competitive interactions in ecosystems. *American Naturalist* 110: 903–910.
- Lloyd, M., Dybas, H.S. 1966. Periodical cicada problem. I. Population ecology. *Evolution* 20: 133–149.
- Lortie, C. 2007. An ecological tardy: the implications of facilitation through evolutionary time. *Trends in Ecology and Evolution* 22: 627–630.
- Lortie, C.J., Turkington, R. 2008. Species-specific positive effects in an annual plant community. *Oikos* 117: 1511–1521.
- MacArthur, R.H. 1970. Species packing and competitive equilibria for many species. *Theoretical Population Biology* 1: 1–11.
- MacArthur, R.H. 1972. *Geographical ecology*. Harper & Row, New York.
- Maynard Smith, J., Szathmari, E. 1998. *The major transitions in evolution*. Oxford University Press, Oxford, UK.
- Miller, T.E. 1994. Direct and indirect species interactions in an early old-field plant community. *American Naturalist* 143: 1007–1025.
- Monkkonen, M., Forsman, J.T., Helle, P. 1996. Mixed-species foraging aggregations and hetero-specific attraction in boreal bird communities. *Oikos* 77: 127–136.
- Odling-Smee, F.J., Laland, K.N., Feldman, M.W. 2004. *Niche construction: the neglected process in evolution*. Princeton University Press, Princeton, NJ.
- Roy, M., Holt, R.D. 2008. Effects of predation on host-pathogen dynamics in SIR models. *Theoretical Population Biology* 73: 319–331.
- Schoener, T.W. 1974. Resource partitioning in ecological communities. *Science* 185: 27–39.
- Silliman, B., Bertness, M. 2002. A trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences, USA* 99: 10500–10505.
- Silliman, B., van de Koppel, J., Bertness, M.D., Stanton, L., Mendelssohn, I.A. 2005. Drought, snails, and large-scale die-off of southern U.S. salt marshes. *Science* 310: 1803–1806.

- Thompson, A., Nisbet, R., Schmitt, R. 2006. Dynamics of mutualist populations that are demographically open. *Journal of Animal Ecology* 75: 1239–1251.
- Tilman, D. 1987 The importance of the mechanisms of interspecific competition. *American Naturalist* 129: 768–774.
- Travis, J.M.J., Brooker, R.W., Clark, E.J., Dytham, C. 2006. The distribution of positive and negative species interactions across environmental gradients in a dual-lattice model. *Journal of Theoretical Biology* 241: 896–902.
- Turnbull, L.A., Coomes, D.A., Purves, D.W., Rees, M. 2007. How spatial structure alters population and community dynamics in a natural plant community. *Journal of Ecology* 95: 79–89.
- Valiente-Banuet, A., Vital, A., Verdu, M., Callaway, R.M. 2006. Modern Quaternary plant lineages promote diversity through facilitation of ancient Tertiary lineages. *Proceedings of the National Academy of Sciences, USA* 103: 16812–16817.
- Valiente-Banuet, A., Verdu, M. 2007. Facilitation can increase the phylogenetic diversity of plant communities. *Ecology Letters* 10: 1029–1036.
- Vandermeer, J.H., Boucher, D. 1978. Varieties of mutualistic interaction in population models. *Journal of Theoretical Biology* 74: 549–558.
- Vandermeer, J.H. 1980. Indirect mutualism: variations on a theme by Stephen Levine. *American Naturalist* 116: 440–448.
- van Rijn, P.C.J., Sabelis, M.W. 2005. Impact of plant-provided food on herbivore–carnivore dynamics. In: Wackers, F.L., van Rooy, P.C.J., Bruin, J., eds. *Plant-provided food for carnivorous insects*. Cambridge University Press, pp. 224–266.
- Vellend, M. 2008. Effects of diversity on diversity: consequences of competition and facilitation. *Oikos* 117: 1075–1085.