

What have exotic plant invasions taught us over the past 20 years?

Ragan M. Callaway and John L. Maron

Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA

Invasive organisms have become a focal interest in ecology, owing not only to the tremendous destruction that they can cause, but also because we do not yet understand fully how they change from being minor components of their native communities to dominant components of invaded communities. Here, we discuss our perceptions of how the study of exotic plant species has contributed to the changing face of ecology over the past 20 years. Research on invasive organisms has promoted synthetic efforts between fields that have historically operated in isolation. Most importantly, the study of invasions has resulted in significant intellectual shifts in the way that old paradigms are perceived by ecologists and have led us into new and uncharted territory.

Introduction

The 20-year lifespan of *TREE* corresponds with a booming economy of invasive research. Commented on by Charles Darwin in the *Origin of Species* [1], organized by Elton [2] and modernized by Mack *et al.* [3] and by Sax *et al.* [4], the study of invasive organisms is now a growth industry in ecology and evolution. Attempts to unravel the mystery of why some invasive species can undergo profound shifts in ecological fortune, from being minor components of their native communities to becoming overwhelming dominants of invaded communities (Figure 1), has catalyzed important advances in the disciplines of ecology and evolution.

Here, we discuss our subjective perspective on the changes wrought by the study of invasive organisms. The specific areas of research that we highlight reflect our own biases and focus specifically on insights gained from the study of exotic plant invasions (Box 1). Our treatment is by no means exhaustive, and our opinions on the past 20 years of progress are just that; opinions.

Evolutionary ecology

Evolutionary biologists have long recognized exotic plant introductions as an unprecedented biogeographical experiment in evolutionary biology. Well before the first publication of *TREE* in 1986, there was great interest in studying species introductions as a way to understand the evolutionary processes that are associated with the colonization of new environments. These early studies investigated the evolutionary potential of weeds, and

suggested that they undergo genetically based adaptation to conditions within their introduced range [4–6]. This initial interest from evolutionary biologists never fully caught on within the discipline, but the study of exotics caught fire with ecologists. Within ecology, increasing concern for the ecological causes and consequences of invasions emerged [3]. Part of the reason for this shift was practical; exotics continued to expand and alter native systems worldwide, and pressure mounted for an adequate response. However, the evolutionary dimension of invasions was ignored, in part, because the reigning paradigm at that time was that evolution occurred over millennia in natural field settings, and could not easily be studied in a realistic ecological context. Thus, rather than seeing exotics as model systems with which to study evolution, ecologists focused on the population and community ecology of invaders.

During the past decade, however, things have come full circle. Compelling evidence has accrued for evolution occurring in contemporary time spans (e.g. [7–10]). Much of this evidence has come from exotics, causing evolution to be considered more seriously within the ecological context of invasions [11–15]. Furthermore, exotics are increasingly appreciated as drivers of the evolutionary responses of native organisms [16,17]. A particularly dramatic example comes from recent work in Australia, where exotic cane toads *Bufo marinus*, which are larger than native toads, appear to have caused a genetically based increase in the gape size of native snakes [17].

This renewed interest in the role of evolution in exotic invasions has been fueled by empirical work on two fronts. First, an increasing number of biogeographical comparisons of native and exotic phenotypes with common-garden experiments suggest that exotics often have different genetically based phenotypes compared with native conspecifics [18]. Second, emerging research has pointed to the importance of hybridization as an evolutionary force in invasions [19,20]. On the conceptual side, newer hypotheses, particularly the evolution of increased competitive ability (EICA) [21], suggest that evolution is a viable mechanism promoting exotic success. Specifically, EICA predicts that exotics are successful because they have evolved greater size or fecundity in their introduced environments compared with environments in which they are native. This increased vigor is thought to be due to life-history tradeoffs, in which selection favors the loss of costly defense traits, thereby freeing resources that can be devoted to increased growth or fecundity [21]. For

Corresponding author: Callaway, R.M. (ray.callaway@mso.umt.edu).

Available online 11 May 2006

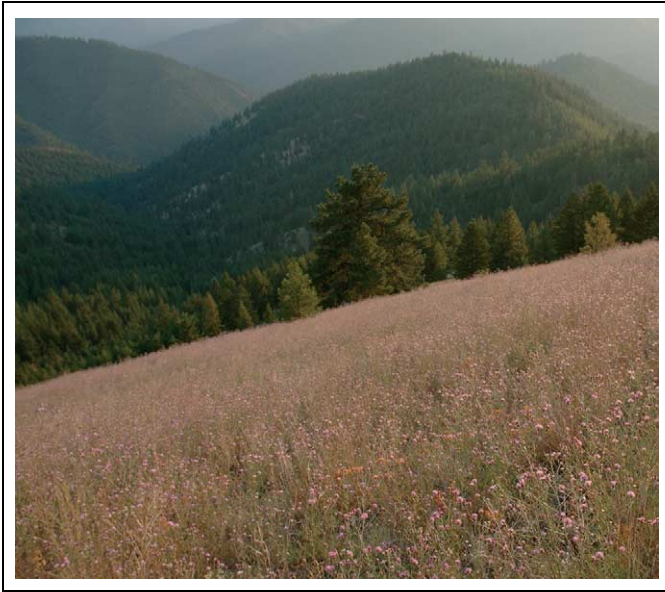


Figure 1. Knapweed *Centaurea maculosa*, one of the most destructive invasives in the USA, in the Bitterroot Mountains of Montana. Reproduced with permission from Giles C. Thelen.

example, North American genotypes of the invasive Asian tree *Sapium sebiferum* are larger but more poorly defended against herbivores than are Asian genotypes [22,23].

Communities

Coevolutionary relationships among species

Twenty years ago, a Gleasonian ‘individualistic’ (e.g. communities are merely the product of the species that happen to disperse to a particular area and that have shared adaptations to an abiotic environment [24]) perspective on the forces that organize plant communities had yet to be challenged. Today, processes that Gleason advocated as being important to community structure, such as chance colonization events, local adaptation and resource competition, are still viewed as significant, but a larger set of factors are appreciated as influencing community composition [25]. Facilitation, for example, has been shown to be an important determinant of community diversity [26]. Investigation of species-specific interactions among plants [27,28] and among soil microbes [29,30] have also revealed that balanced networks of indirect interactions can promote diversity.

The emerging view that these varied indirect interactions can exert a structuring force within

communities has been bolstered by research on exotics. Furthermore, the fact that some exotics occur at spectacularly greater abundance in recipient communities than in their native ones has been interpreted to be partially the result of broken evolutionary relations among plants [31–33]. For example, the invasive Eurasian plant *Centaurea diffusa* appears to have stronger allelopathic effects on North American plant species in invaded ranges than do Eurasian conspecifics in communities in the native range of *C. diffusa* [31]. If plant species commonly evolve in response to interspecific neighbors, it implies that non-individualistic processes must be accounted for in theories of community organization. In turn, this suggests that coevolutionary dynamics, which 20 years ago were considered to be difficult to define and of little relevance to community theory, are of greater importance to the organization of natural systems than was previously thought [34].

Interactions among plants

Over 20 years ago, Harper [35] had written off allelopathy (plant suppression of other plants through the release of biochemicals) as an experimentally intractable minor process. Recent biogeographical comparisons and synthesized genetic, molecular and field studies of invasive plants, however, have brought it back to the conceptual playing field [31–33,36–38]. Empirical evidence for stronger allelopathic effects of exotic European invaders on North American natives than on other European species points to the importance of coevolutionary relationships within plant communities [31,33,37,39,40]. For this reason, allelopathic interactions might be relatively weak in natural communities (but see [41–43]). Research on exotics has been key to the revival of research on biochemical interactions among plants in general.

Species saturation

Two decades ago, many ecologists thought that communities contained the maximum number of species that could be supported locally and that community assembly was governed primarily by strong competitive interactions among resident species. However, with increased interest in understanding the processes that affect invasion success, there has been a proliferation of work suggesting the importance of other factors. Experiments on community invasibility in grasslands have highlighted the importance of seed limitation in constraining community diversity, suggesting that plant assemblages are more open than was once thought. A particularly striking example of this was provided by Tilman [44], who demonstrated that adding seeds of new (but not necessarily exotic) species to intact grassland communities resulted in strong increases in species richness. Surprisingly, ameliorating seed limitation did not substantially reduce the cover of resident species. From a restoration perspective, research on exotics has suggested that the re-establishment of natives in heavily invaded grasslands is hindered by the lack of seeds, rather than by direct competitive dominance by resident exotics. For example, in heavily invaded Californian grasslands, Seabloom *et al.*

Box 1. Major advances in ecology and evolution resulting from research on invasives

- Improved understanding of rapid evolution.
- Improved understanding of coevolutionary dynamics in communities.
- Support for the potential impact of allelopathy on communities.
- Improved understanding of community assembly and the determinants of local diversity.
- Emphasis of the importance of top-down effects of specialist consumers on communities.
- Improved understanding the linkages between population, community and ecosystem ecology.

[45] found that native perennial grasses exerted strong competitive effects on annual exotics once recruitment limitation of natives was ameliorated through seed addition.

Other work, again with exotics, has reinforced the notion that communities are not saturated. Exotics might owe their success to the fact that they have novel functional attributes that enable them to access free resources that are not depleted by natives [46,47]. This implies that some native assemblages might be open to species that have unique functional attributes and can access niche space that is not inhabited by natives. For example, Farione *et al.* [47] showed that diverse assemblages containing species that overlapped with invaders in functional type resisted invasion better than did assemblages lacking species of particular functional types.

Plant–herbivore interactions

Since Hairston and colleague's 'green world' paper (which asserted that plant community productivity and composition was indirectly affected by cascading trophic interactions) [48], the extent to which consumers have substantial impacts on plant production has been hotly debated [49–52]. Over the past two decades, however, interest in consumer effects on plants has come from an entirely different group of researchers: those attempting to explain exotic plant success. Interest in Elton's [2] original idea (that some exotics owe their spectacular success to escape from specialist consumers) has expanded substantially. This is bringing renewed interest to long-standing questions regarding the role of consumers in vegetation dynamics. For example, the question of whether generalists versus specialists hold greater sway in impacting plant populations has become highly relevant. The extent to which native specialist herbivores might regulate native plant populations has also found renewed urgency, because understanding the potential for specialists to control their hosts is key to determining whether the practice of using specialists as biocontrols will be effective.

Classical biological control is based on the hypothesis that exotic plants become invaders in new environments by escaping natural specialist enemies that suppress them in their native range [53]. Thus, the strategy behind biocontrol is to reestablish top-down control by reintroducing the natural enemies of the invader into its new range. This has been the conceptual underpinning of classical biological control for over a hundred years and it continues to be today [54,55]. Over the past 20 years, biocontrol has garnered increased scrutiny. Louda *et al.* [56] found that a biocontrol insect, introduced to control an exotic thistle, now has substantial effects on a co-occurring native thistle. This has forced a healthy re-evaluation of biocontrol safety procedures and the potential effects of biocontrol releases on native food webs [57].

Plant–soil microbe interactions

Applied research on biocontrols and weeds has resulted in increased interest in herbivore effects on plants, and basic research over the past 20 years has revolutionized what we know about plant–soil microbe interactions. However,

as for plant–herbivore interactions, comparative studies of interactions between invasive plants and soil microbes are changing the ways in which we perceive communities.

Using techniques developed by Jim Bever [58] and Wim van der Putten and colleagues [59] to study feedback plant–soil microbe relationships, John Klironomos [60] found that rare plant species that are native to North America consistently demonstrated negative feedbacks with North American soil microbes, whereas abundant exotic and native plant species demonstrated positive feedbacks. Klironomos also provided evidence that the invasive species had escaped relatively host-specific pathogens in their homelands, but had connected with non-host-specific soil mutualists in their newly invaded lands. This finding reinforced the general theory that plant pathogens tended to be relatively host specific, whereas mutualists, such as arbuscular mycorrhizae, are not [61,62]. Klironomos' research was followed by several comparative biogeographical studies that have generally demonstrated more positive net effects of soil biota on invasive species in their new regions than in their native regions [63–66].

Ecosystems

Twenty years ago, just as evolutionary biology and ecology were often isolated from each other, so too were ecosystem ecology and population biology. Ecosystem ecologists approached their field from a systems perspective, often seeking to determine rates for processes that were thought of as 'black boxes'. At the same time, population ecologists were concerned with demography and population growth, ignoring the potential for these processes to feed back to, and to be affected by, ecosystem processes. However, the seminal work by Vitousek and colleagues on the exotic tree *Myrica faya*, first published in 1987, provided much of the impetus for bridging the gap between ecosystem and population ecology [67,68]. Their research elegantly demonstrated that a single exotic nitrogen-fixing tree could dramatically affect ecosystem processes, such as the total pool sizes of soil nitrogen and rates of soil nitrogen mineralization (i.e. microbial conversion of nitrogen to ammonium and nitrate). Vitousek and Walker [68] showed that *M. faya* significantly enriched nitrogen-limited volcanic soils with fixed nitrogen, thereby increasing the availability of soil nitrogen to other species in this system. More recently, Asner and Vitousek [69] demonstrated that areas heavily invaded and enriched by *M. faya* can significantly alter forest canopy chemistry.

Over the past few decades, an increasing number of studies on exotics have shown how single species can exert profound effects on ecosystems [70]. These effects can be diverse, including alteration of fire regimes [71,72], hydrological cycles [73,74], or nutrient cycles [75,76]. Not only has our understanding of linkages between single species and ecosystem dynamics increased owing to the study of exotics, but work on exotics that occupy the top, rather than bottom, of food webs has also highlighted novel routes by which exotic predators can have powerful indirect effects on ecosystems. For example, introduced foxes have dramatically altered plant productivity and composition across the Aleutian Archipelago of Alaska. By

reducing seabird populations, foxes have effectively thwarted the delivery of nutrients (in guano) from sea to land, thereby reducing nitrogen availability and plant productivity on fox-infested versus fox-free islands [77,78].

Conclusions

Apart from stimulating advances in several key areas of ecology, the rapid growth in invasion research over the past 20 years has helped catalyze a healthy fusion between fields and subdisciplines that have historically operated in isolation. Given that the success of exotics is often attributed to some change or release in a regulating factor in the new range that might constrain abundance in areas where plants are native, future advances are likely to come from comparative biogeographical experiments in which potential regulating factors are simultaneously manipulated in both the native and introduced range [79].

We predict that several areas in ecology are likely to undergo substantial conceptual changes owing to research on invasive species. First, until recently, ecologists have considered mainly how escape from specialist consumers might affect exotic success. We predict that future work on invasions will shed light on other enemies, particularly the importance of generalist herbivores as well as soil microbes as inhibitors of plant populations (e.g. [80]). Presently, we lack insight into the extent to which biogeographical differences in these divergent groups of consumers contribute to exotic success. In particular, work on soil microbes should enable ecologists to test the long standing assumption that 'everything is everywhere'; in other words that global dispersal of soil microbes overrides local evolution [81]. If regional evolutionary trajectories have a role in the microbial suppression of invaders at home but not away [39,66], we will have to re-think biogeographical theory as applied to soil biota.

Second, we predict that the next 20 years will see an increase in research on disturbance in the context of invasions. Disturbance is assumed to be a crucial driver of invasions, but biogeographical comparisons of disturbance effects will enable us to determine how similar invasion is to colonization. Third, with the increasing sophistication of molecular tools, we predict that the next 20 years will see great leaps in our ability to reconstruct the history of invasions and to determine the precise source of many invading populations. This is already occurring to a limited extent. Rapidly developing methods should also greatly enhance our understanding of how evolutionary events, such as changes in plant ploidy, contribute to successful range expansion. This, in turn, should increase our more general understanding of how sudden changes in ploidy can alter the evolutionary trajectory and ecological fortune of plants.

Fourth, it is likely that we will gain an enhanced appreciation for how multiple factors interact to influence plant population abundance and community organization. To date, work in native communities has tended to focus on single-factor explanations for plant success. Yet research on exotics will probably show that different factors (e.g. disturbance, propagule pressure and enemy release) often have strong interactive effects that

contribute to exotic success. Fifth, it seems quite likely that, when many exotics are investigated, researchers will find different causes for invader success. With increasing numbers of case studies, we should gain greater power to predict when and where particular processes might be important in affecting native populations and communities.

Finally, we predict that, on the 40th anniversary *TREE*, 20 years from now, the papers published on exotics that will be seen as most important will be those that not only illuminate the causes and consequences of exotic success, but also reveal fundamental and currently unknown truths about the functioning of native systems.

Acknowledgements

J.L.M. was supported by NSF grants OPP-0296208 and DEB-0296175 and from a fellowship from the Catalunya PIV while in residence at the Institut de Ciència i Tecnologia Ambientals, Universitat Autònoma de Barcelona. R.M.C. was supported by NSF grant DEB-0236061, NSF International Programs, DOD SERDP, USDA 04-JV-11222044-235, and USDA NRI 2003-01823.

References

- 1 Darwin, C. (1859) *On the Origin of Species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*, John Murray
- 2 Elton, C.S. (1958) *The Ecology of Invasions by Animals and Plants*, Methuen
- 3 Mack, R.N. *et al.* (2000) Biotic invasions: causes epidemiology, global consequences and control. *Ecol. Appl.* 10, 689–710
- 4 Sax, D.F. *et al.* (2005) *Species Invasions: Insights into Ecology, Evolution and Biogeography*, Sinauer
- 5 Baker, H.G. (1974) The evolution of weeds. *Annu. Rev. Ecol. Syst.* 5, 1–24
- 6 Baker, H.G. and Stebbins, G.L., eds (1965) *The Genetics of Colonizing Species*, Academic Press
- 7 Reznick, D.N. *et al.* (1997) Evaluation of the rate of evolution in natural populations of guppies (*Poecilia reticulata*). *Science* 275, 1934–1937
- 8 Huey, R.B. *et al.* (2000) Rapid evolution of a geographic cline in size in an introduced fly. *Science* 287, 308–309
- 9 Grant, P.R. and Grant, B.R. (2002) Unpredictable evolution in a 30-year study of Darwin's finches. *Science* 296, 707–711
- 10 Huey, R.B. *et al.* (2005) Using invasive species to study evolution: case studies with *Drosophila* and salmon. In *Species Invasions: Insights into Ecology, Evolution, and Biogeography* (Sax, D.F. *et al.*, eds), pp. 139–164, Sinauer
- 11 Bone, E. and Farres, A. (2001) Trends and rates of microevolution in plants. *Genetica* 112–113, 165–182
- 12 Lee, C.E. (2002) Evolutionary genetics of invasive species. *Trends Ecol. Evol.* 17, 386–391
- 13 Rice, K.J. and Emory, N.C. (2003) Managing microevolution: restoration in the face of global change. *Front. Ecol. Env.* 1, 469–478
- 14 Stockwell, C.A. *et al.* (2003) Contemporary evolution meets conservation biology. *Trends Ecol. Evol.* 18, 94–101
- 15 Maron, J.L. *et al.* (2004) Rapid evolution of an invasive plant. *Ecol. Monogr.* 74, 261–280
- 16 Carroll, S.P. *et al.* (1997) Genetic differentiation of fitness-associated traits among rapidly evolving populations of soapberry bug. *Evolution* 51, 1182–1188
- 17 Phillips, B.L. and Shine, R. (2004) Adapting to an invasive species: toxic cane toads induce morphological change in Australian snakes. *Proc. Natl. Acad. Sci. U. S. A.* 101, 17150–17155
- 18 Bossdorf, O. *et al.* (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia* 144, 1–11
- 19 Ellstrand, N.C. and Schierenbeck, K.A. (2000) Hybridization as a stimulus for the evolution of invasiveness in plants. *Proc. Natl. Acad. Sci. U. S. A.* 97, 7043–7050

- 20 Lambrinos, J.G. (2004) How interactions between ecology and evolution influence contemporary invasion dynamics. *Ecology* 85, 2061–2070
- 21 Blossey, B. and Nötzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *J. Ecol.* 83, 887–889
- 22 Siemann, E. and Rogers, W.E. (2001) Genetic differences in growth of an invasive tree species. *Ecol. Lett.* 4, 514–518
- 23 Siemann, E. and Rogers, W.E. (2003) Reduced resistance of invasive varieties of the alien tree *Sapium sebiferum* to a generalist herbivore. *Oecologia* 135, 451–457
- 24 Gleason, H.A. (1926) The individualistic concept of plant association. *Bull. Torrey Bot. Club* 53, 7–26
- 25 Lortie, C.J. *et al.* (2004) Rethinking plant community theory. *Oikos* 107, 433–438
- 26 Bruno, J.F. *et al.* (2003) Inclusion of facilitation into general ecological theory. *Trends Ecol. Evol.* 18, 119–125
- 27 Ehlers, B.K. and Thompson, J. (2004) Do co-occurring plant species adapt to one another? The response of *Bromus erectus* to the presence of different *Thymus vulgaris* chemotypes. *Oecologia* 141, 511–518
- 28 Iason, G.R. *et al.* (2005) Does chemical composition of individual Scots pine trees determine the biodiversity of their associated ground vegetation? *Ecol. Lett.* 8, 364–369
- 29 Czárán, T.L. *et al.* (2002) Chemical warfare between microbes promotes biodiversity. *Proc. Natl. Acad. Sci. U. S. A.* 99, 786–790
- 30 Kirkup, B.C. and Riley, M.A. (2004) Antibiotic-mediated antagonism leads to a bacterial game of rock–paper–scissors *in vivo*. *Nature* 428, 412–414
- 31 Callaway, R.M. and Aschehoug, E.T. (2000) Invasive plants versus their new and old neighbors: a mechanism for exotic invasion. *Science* 290, 521–523
- 32 Mallik, A.U. and Pellissier, F. (2000) Effects of *Vaccinium myrtillus* on spruce regeneration: testing the notion of coevolutionary significance of allelopathy. *J. Chem. Ecol.* 26, 2197–2209
- 33 Vivanco, J.M. *et al.* (2004) Biogeographical variation in community response to root allelochemistry: novel weapons and exotic invasion. *Ecol. Lett.* 7, 285–292
- 34 Thompson, J.N. (2005) *The Geographic Mosaic Theory of Coevolution*, University of Chicago Press
- 35 Harper, J.L. (1977) *Population Biology of Plants*, Academic Press
- 36 Czarnota, M.A. *et al.* (2001) Mode of action, localization of production, chemical nature, and activity of sorgoleone: a potent PSII inhibitor in *Sorghum* spp. root exudates. *Weed Tech* 15, 813–825
- 37 Bais, H.P. *et al.* (2003) Allelopathy and exotic plants: from genes to invasion. *Science* 301, 1377–1380
- 38 Hierro, J.L. and Callaway, R.M. (2003) Allelopathy and exotic plant invasion. *Plant Soil* 256, 25–39
- 39 Callaway, R.M. *et al.* (2005) Evolutionary trajectories in plant and soil microbial communities: *Centaurea* invasions and the geographic mosaic of coevolution. In *Species Invasions: Insights into Ecology, Evolution, and Biogeography* (Sax, D.F. *et al.*, eds), pp. 341–363, Sinauer
- 40 Callaway, R.M. and Ridenour, W.M. (2004) Novel weapons: a biochemically based hypothesis for invasive success and the evolution of increased competitive ability. *Front. Ecol. Env.* 2, 436–433
- 41 Webb, L.J. *et al.* (1967) A factor toxic to seedlings of the same species associated with living roots of the non-gregarious subtropical rain forest tree *Grevillea robusta*. *J. Appl. Ecol.* 4, 13–25
- 42 Schenck, J. *et al.* (1999) Spatial segregation of roots. *Adv. Ecol.* 28, 145–180
- 43 Bertin, C. *et al.* (2003) The role of root exudates and allelochemicals in the rhizosphere. *Plant Soil* 256, 67–83
- 44 Tilman, D. (1997) Community invasibility, recruitment limitation and grassland biodiversity. *Ecology* 78, 81–92
- 45 Seabloom, E.W. *et al.* (2003) Invasion, competitive dominance and native California grassland species. *Proc. Natl. Acad. Sci. U. S. A.* 100, 13384–13389
- 46 Shea, K. and Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends Ecol. Evol.* 17, 170–176
- 47 Fargione, J. *et al.* (2003) Community assembly and invasion: an experimental test of neutral versus niche processes. *Proc. Natl. Acad. Sci. U. S. A.* 100, 8916–8920
- 48 Hairston, N.G. *et al.* (1960) Community structure, population control, and competition. *Am. Nat.* 94, 421–425
- 49 Owen, D.F. and Wiegert, R.G. (1981) Mutualism between grasses and grazers: an evolutionary hypothesis. *Oikos* 36, 376–378
- 50 Belsky, A.J. (1986) Does herbivory benefit plants? A review of the evidence. *Am. Nat.* 127, 870–892
- 51 Crawley, M.J. (1989) Insect herbivores and plant population dynamics. *Annu. Rev. Entomol.* 34, 531–564
- 52 Louda, S.M. and Potvin, M.A. (1995) Effect of inflorescence-feeding insects on the demography and lifetime fitness of a native plant. *Ecology* 76, 229–245
- 53 Keane, R.M. and Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends Ecol. Evol.* 4, 164–170
- 54 Hajek, A.E. (2004) *Natural Enemies: An Introduction to Biological Control*, Cambridge University Press
- 55 Van Driesche, R.G. and Bellows, T.S. (1996) *Biological Control*, Kluwer Academic Press
- 56 Louda, S.M. (1997) Ecological effects of an insect introduced for the biological control of weeds. *Science* 277, 1088–1090
- 57 Pearson, D.E. and Callaway, R.M. (2003) Indirect effects of host-specific biocontrol agents. *Trends Ecol. Evol.* 18, 456–461
- 58 Bever, J.D. (1994) Feedback between plants and their soil communities in an old field community. *Ecology* 75, 1965–1977
- 59 Van der Putten, W.H. *et al.* (1993) Host-specific soil-borne diseases contribute to succession in foredune vegetation. *Nature* 362, 53–56
- 60 Klironomos, J.N. (2002) Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417, 67–70
- 61 Augspurger, C.K. (1990) Spatial patterns of damping-off disease during seedling recruitment in tropical forests. In *Pests, Pathogens, and Plant Communities* (Burdon, J.J. and Leather, S.R., eds), pp. 3–14, Blackwell Scientific
- 62 Streitwolf-Engel, R. *et al.* (1997) Clonal growth traits of two *Prunella* species are determined by co-occurring arbuscular mycorrhizal fungi from a calcareous grassland. *J. Ecol.* 85, 181–191
- 63 Reinhart, K.O. and Callaway, R.M. (2004) Soil biota facilitate exotic *Acer* invasions in Europe and North America. *Ecol. Appl.* 14, 1737–1745
- 64 Reinhart, K.O. *et al.* (2003) Plant–soil biota interactions and spatial distribution of black cherry in its native and invasive ranges. *Ecol. Lett.* 6, 1046–1050
- 65 Reinhart, K.O. *et al.* (2005) Soil feedback and pathogen activity in *Prunus serotina* throughout its native range. *J. Ecol.* 93, 890–898
- 66 Callaway, R.M. *et al.* (2004) Release from inhibitory soil biota in Europe may promote exotic plant invasion in North America. *Nature* 427, 731–733
- 67 Vitousek, P.M. *et al.* (1987) Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. *Science* 238, 802–804
- 68 Vitousek, P.M. and Walker, L.R. (1989) Biological invasion by *Myrica faya* in Hawaii: plant demography, nitrogen fixation, and ecosystem effects. *Ecol. Monogr.* 59, 247–265
- 69 Asner, G.P. and Vitousek, P.M. (2005) Remote analysis of biological invasion and biochemical change. *Proc. Natl. Acad. Sci.* 102, 4383–4386
- 70 Ehrenfeld, J.G. (2003) Effects of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6, 503–523
- 71 D'Antonio, C.M. (2000) Fire, plant invasions and global change. In *Invasive Species in a Changing World* (Mooney, H.A. and Hobbs, R.J., eds), pp. 65–93, Island Press
- 72 Brooks, M.L. *et al.* (2004) Effects of invasive alien plants on fire regimes. *Bioscience* 54, 677–688
- 73 Dyer, A.R. and Rice, K.J. (1999) Effect of competition on resource availability and growth of a California bunchgrass. *Ecology* 80, 2697–2710
- 74 Zavaleta, E. (2000) Valuing ecosystem services lost to *Tamarix* invasions in the United States. In *Invasive Species in a Changing World* (Mooney, H.A. and Hobbs, R.J., eds), pp. 261–300, Island Press
- 75 Stock, W.D. *et al.* (1995) Impacts of invading N₂-fixing *Acacia* species on patterns of nutrient cycling in two Cape ecosystems: evidence from soil incubation studies and ¹⁵N natural abundance values. *Oecologia* 101, 375–382
- 76 Ehrenfeld, J.G. *et al.* (2001) Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecol. Appl.* 11, 1287–1300

- 77 Croll, D.A. *et al.* (2005) Introduced predators transform subarctic islands from grassland to tundra. *Science* 307, 1959–1961
- 78 Maron, J.L. *et al.* (2006) An introduced predator transforms Aleutian Island plant communities by disrupting spatial subsidies. *Ecol. Monogr.* 76, 3–24
- 79 Hierro, J. *et al.* (2005) A biogeographical approach to plant invasion biology: the importance of studying exotics in their introduced and native range. *J. Ecol.* 93, 5–15
- 80 Parker, J.D. *et al.* (2006) Opposing effects of native and exotic herbivores on plant invasions. *Science* 311, 1459–1461
- 81 Whitfield, J. (2005) Is everything everywhere? *Science* 310, 961

Endeavour

the quarterly magazine for the history and philosophy of science

You can access *Endeavour* online via *ScienceDirect*, where you'll find a collection of beautifully illustrated articles on the history of science, book reviews and editorial comment.



featuring

Selling the silver: country house libraries and the history of science by Roger Gaskell and Patricia Fara

Carl Schmidt – a chemical tourist in Victorian Britain by R. Stefan Ross

The rise, fall and resurrection of group selection by M.E. Borello

Mary Anning: the fossilist as exegete by T.W. Goodhue

Caroline Herschel: 'the unquiet heart' by M. Hoskin

Science in the 19th-century zoo by Oliver Hochadel

The melancholy of anatomy by P. Fara

and coming soon

Etienne Geoffroy St-Hillaire, Napoleon's Egyptian campaign and a theory of everything by P. Humphries

Losing it in New Guinea: The voyage of HMS *Rattlesnake* by J. Goodman

The accidental conservationist by M.A. Andrei

Powering the porter brewery by J. Sumner

Female scientists in films by B.A. Jones

and much, much more . . .

Locate *Endeavour* on *ScienceDirect* (<http://www.sciencedirect.com>)