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Source: *Annual Review of Ecology, Evolution, and Systematics*, Vol. 41 (2010), pp. 59-80

Published by: Annual Reviews

Stable URL: <http://www.jstor.org/stable/27896214>

Accessed: 01-09-2017 13:39 UTC

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Ecosystem Consequences of Biological Invasions

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Annu. Rev. Ecol. Evol. Syst. 2010. 41:59–80

First published online as a Review in Advance on
July 27, 2010

The *Annual Review of Ecology, Evolution, and Systematics* is online at ecolsys.annualreviews.org

This article's doi:
10.1146/annurev-ecolsys-102209-144650

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1543-592X/10/1201-0059\$20.00

Key Words

biogeochemistry, ecosystem engineers, functional traits, nutrients, transformers

Abstract

Exotic species affect the biogeochemical pools and fluxes of materials and energy, thereby altering the fundamental structure and function of their ecosystems. Rapidly accumulating evidence from many species of both animal and plant invaders suggests that invasive species often increase pool sizes, particularly of biomass, and promote accelerated flux rates, but many exceptions can be found. Ecosystem dynamics are altered through a variety of interacting, mutually reinforcing mechanistic pathways, including species' resource acquisition traits; population densities; ability to engineer changes to physical environmental conditions; effects on disturbance, especially fire; regimes; the ability to structure habitat for other species; and their impact on food webs. Local factors of landscape setting, history, and other sources of disturbance constrain ecosystem responses to invasions. New research directions are suggested, including the need for whole-system budgets, the quantification of abundance-impact relationships for particular ecosystem processes, and a better exploration of food web impacts on ecosystem processes.

Mass balance:
accounts for all masses
of a given material in
an ecosystem, such
that any difference
between inputs and
outputs equals the
change in storage
within the ecosystem

INTRODUCTION

Impacts of non-native species are assessed at many scales, ranging from genetic and evolutionary changes in individual organisms to ecosystems and landscapes, reflecting the scope of effects that alter ecological integrity and ecosystem services (Charles & Dukes 2008, Pejchar & Mooney 2009). Nevertheless, the mechanisms and even the scope of impact continue to be debated (Davis 2009). This review concentrates on the ecosystem scale. In trying to establish what kinds of impacts exotic species may have on ecosystems, it is first necessary to define the scope of what is meant by ecosystem, as this word is freely used in many contexts. The question of impact also requires some definition, as this term is also broadly used to refer to a wide range of possible outcomes due to invasion. The goals of this review are to survey the mechanisms by which invasive species affect ecosystems and to ask whether specific pathways of effect are universally applicable to all types of invaders in all types of ecosystems, and whether invasive species alter ecosystems through mechanisms not found in uninvaded systems.

CONTEXT AND THEORY

Ecosystems, Impacts, and Mechanisms

Ecosystems. The term ecosystem is used in the ecological literature to refer to habitat types (e.g., “the lake ecosystem”), entirely biotic phenomena such as food webs, and the interacting set of organisms and resources in the abiotic environment (Tansley 1935). In this review, I focus on the latter definition and ask if and how invasive species alter pools, fluxes, and mass balances of materials and energy. Tansley’s definition requires examination not only of the biology of the organisms and the physico-chemical environment, but also the processes and mechanisms that connect organisms with each other as well as with the environment.

Ecosystem structures in terrestrial and aquatic ecosystems have many similarities, but also some notable differences. In terrestrial ecosystems, the plant-soil system involves a complex network of interactions and feedbacks (Ehrenfeld et al. 2005) and may function almost in isolation from the surrounding landscape (e.g., in ombrotrophic bogs). Terrestrial ecosystems receive inputs from the atmosphere, from bedrock, and from adjacent ecosystems. In aquatic systems, by contrast, separate subsystems are found within the water column, at the water-sediment interface, and within the sediments. All these components can exchange materials with each other, as well as with other ecosystems and the atmosphere. Water movements play an important structuring role, and the dynamics of sediments are as important as the dynamics of nutrients, oxygen, and carbon in determining aquatic ecosystem function. Thus, it may be that invasives alter aquatic and terrestrial ecosystems through different pathways.

Animals and plants may also affect ecosystems through different pathways. Plants directly interact with both the atmosphere through uptake of CO₂ and release of water vapor and with the soil or sediments through uptake of nutrients and water. In so doing, they alter the properties of these components of the physical environment. Plants defend themselves against enemies largely through tissue chemistry. Animals may interact with these components both indirectly, through their consumption of plants and deposition of waste materials, and directly, through their burrowing or attachment activities. Animals also may have separate behaviors for resource acquisition and for defense from predators, and these activities may differentially affect the physical environment and ecosystem processes. Thus, there is a potential for animal and plant invaders to affect ecosystem dynamics differently.

This review examines how exotic invasive species affect or change the physico-chemical environment, either directly or through their interactions with other organisms, and the ramifications

of these changes for both the rest of the biota and the abiotic environment. Purely biotic impacts of invasive species have been extensively and recently reviewed [e.g., mycorrhizae (Pringle et al. 2009), mutualists (Travaset & Richardson 2006), plant and soil pathogens (Parker & Gilbert 2004, Reinhart & Callaway 2006, van der Putten et al. 2007), plus many papers on particular groups of biota (e.g., Kenis et al. 2009, Sousa et al. 2009, Wallentinus & Nyberg 2007)]. I examine evidence for changes in pool sizes, flux rates within ecosystems (transfers among pools and transformations of element chemistries), and changes in both inputs to and outputs from ecosystems reflecting mass balance approaches to whole-system budgets. I use the term ecosystem processes to include all of the fluxes and transformations of materials within, into, and out of ecosystems, as well as the pool sizes of materials within biotic and abiotic components of the system.

Impacts. Studies of changes wrought in ecosystems by the presence of invasive exotic species range in scale from small, plot-scale studies of individual flux rates to landscape-scale transformations of extensive areas. Species that alter ecological conditions (biotic, abiotic, or both) over larger regions have been termed transformers (Richardson et al. 2000). However, species may change flux rates of materials but not necessarily greatly transform large areas. In this review, changes over all scales of space and time are considered.

Mechanisms. The analysis of ecosystem impacts by exotic species is related to the current theoretical explorations of the ways in which species affect ecosystem function (Hooper et al. 2005, Reiss et al. 2009). One set of theories addresses mechanisms by which individual species can have strong effects on their ecosystems and includes the concepts of ecosystem engineers (Cuddington et al. 2007), keystone species (Power et al. 1996), and foundation species (Ellison et al. 2005). A second branch addresses the complex of morphological, physiological, and chemical properties of individual species. For plants, these are referred to as functional traits, and they occupy a central role in explaining species-ecosystem relationships (Eviner & Chapin 2003, Gamfeldt & Hillebrand 2008, Hooper et al. 2005, Reiss et al. 2009). They also have figured strongly in recent explanations of exotic species impacts (Henderson et al. 2006, Levine et al. 2003, Raizada et al. 2008). Theories addressing the mechanisms by which animal species affect ecosystem function also invoke species traits (e.g., feeding or nesting behavior, often in combination with individual morphology, and social behavior or the tendency to form dense aggregations), but are not as well developed as a body of theory. A third body of theory commonly invoked to explain ecosystem impacts rests on concepts of food web structure and trophic cascades (Polis et al. 1999, Shurin et al. 2002).

Questions: What Does the Literature Currently Reveal about Ecosystem Impacts?

This review addresses two sets of topics:

1. What are the mechanisms by which exotic species affect ecosystem processes?
 - a. Are these the same set of mechanisms that have been identified for understanding native species' impacts on their ecosystems? Or, are there pathways of impact that appear to be unique to exotic invasions?
 - b. How similar are the mechanisms of ecosystem change in terrestrial and aquatic systems?
 - c. How similar are the mechanisms of ecosystem change resulting from plant versus animal invasions?

Ecosystem engineer:
a species that alters resource availability to other species through nontrophic behaviors or structures

Keystone species:
a species that has an effect on other species and/or on material fluxes out of proportion to its abundance, and through entirely biotic mechanisms

Foundation species:
a species whose physical structure determines the physical characteristics of a site through its abundance and/or particular characteristics

Functional traits:
characteristics of species that affect both their ability to use resources and their effects on those resources

Trophic cascade:
changes in abundances of lower-level consumers within a food web and primary producers in response to changing abundance of a top predator

2. What are the patterns of change to ecosystem processes resulting from invasions?
 - a. Do invasions cause changes to the inputs and outputs to ecosystems, altering total ecosystem stocks of materials?
 - b. Or, do invasions primarily alter pools and fluxes within ecosystems, without changing total stocks?

Finally, research needs are addressed.

MASS BALANCE AND ECOSYSTEM PROCESSES

Over the past decade, the number of papers that have documented changes in ecosystem processes and properties has mushroomed, as has the number of variables assessed. The following survey of pool sizes, internal fluxes, inputs and outputs reflects over 300 papers reporting on over 200 species.

Pool Size: Do Exotic Species Alter the Amounts and Distribution of Elements within Ecosystems?

Change in pool sizes has been examined in many studies of plant invasions. Liao et al. (2008), in a recent meta-analysis, found that plant invasions result in much higher pools of aboveground (133% higher) and belowground (5%) carbon (C), aboveground (85%) and belowground (112%) nitrogen (N), litter C (49%), soil C (7%), and soil N (19%). Similar trends have been suggested in other narrative reviews (Ehrenfeld 2003, Raizada et al. 2008). The relatively few papers addressing phosphorus (P) and cation pools also show trends of higher biomass and litter pools. However, Liao et al. (2008) noted that these overall patterns were variable among life forms and ecosystem types, and that high variability occurred in the relative differences of all pools. The many papers published subsequently are mostly in accord with these results; reports of higher plant and litter biomasses (often taken as proxies of C, N, and other nutrients) are more frequent than reports of lower amounts. Notably, some widespread grass invasions result in decreased pool sizes. For example, *Bromus tectorum* invasions into former shrublands have lower soil and biomass C stocks than do uninvaded shrublands, as a result of fire (Bradley et al. 2006); and *Agropyron cristatum* invasions in the northern Great Plains result in lower soil pools (by 25%) of both C and N, due to less root growth, although aboveground biomass pools are higher (Christian & Wilson 1999).

Nutrient pools in soil similarly increase more frequently than they decrease following plant invasions (Liao et al. 2008). Nitrogen and C pools are most frequently documented; and fewer studies address P and cations. Soil N pools are increased more with invasion by N-fixing plants than by nonfixers. Phosphorus pools tend to increase in soil (e.g., Duda et al. 2003, Hughes & Denslow 2005, Vanderhoeven et al. 2006), but decreases or absences of difference are also observed (Collins & Jose 2009, Martin et al. 2009, Scharfy et al. 2009). Cation pools frequently show both increases and decreases, as well as lack of difference. However, observations of changes in pool sizes can be site specific. For example, loosestrife (*Lythrum salicaria*) invasions elevate N pools in some sites (Fickbohm & Zhu 2006) but not in others (Mahaney et al. 2006). *Solidago gigantea* similarly alters soil pool sizes of N and P in some sites but not others (Scharfy et al. 2009, Vanderhoeven et al. 2006). Soil moisture, another important soil pool, is strongly affected by rooting depth of plants and season of active uptake (Enloe et al. 2004, Gerlach 2004, Potts et al. 2008, Williams & Baruch 2000). Exotic species can deplete soil moisture pools below levels observed under native species when their roots extend deeper than the native species or are active during different times of year.

Biomass pools in aquatic invasions also tend to increase, largely because many of the most prominent invaders are plants or invertebrates that form dense colonies [bivalves such as

Venerupis philippinarum, *Dreissena polymorpha*, *Crassostrea gigas*; polychaetes such as *Ficopomatus enigmaticus*; or algal beds such as *Caulerpa* spp. (Ruesink et al. 2006, Wallentinus & Nyberg 2007)]. Ruesink et al. (2006), for example, report increases of 250% in biomass associated with non-native oyster introductions. Excretion by animals is another pathway important in aquatic ecosystems; for example, excretion by tilapia (*Oreochromis niloticus*) increases water column N and P by up to 540% (Figueredo & Giani 2005), and excretion by apple snails (*Pomacea caniculata*) increases solution P more than tenfold (Carlsson et al. 2004). Similarly, the deposition of feces and pseudofeces by invasive bivalves concentrates nutrients at the benthic-water interface and in water adjacent to invasive populations (Hecky et al. 2004).

Bioturbation associated with exotic earthworms (e.g., Addison 2009, Bohlen et al. 2004, Eisenhauer et al. 2007, Hale et al. 2005) and ants (Cammeraat & Risch 2008, DeFauw et al. 2008, Lach & Hooper-Büi 2010) redistributes materials, changing pool sizes within portions of the soil. Decreased forest floor litter mass, decreased pools of nutrients in surface soils, and increased pools in lower soil layers typically occur. Animals also affect plant and soil pools through excretion; coqui frogs (*Eleutherodactylus coqui*) greatly increase nutrient pools in plant biomass and in litter (Beard et al. 2002). A third mechanism resulting from animal behavior is the accumulation of nutrients in soils behind dams built by invasive beavers (Anderson & Rosemond 2007).

Fluxes within Ecosystems: Do Exotic Species Alter Flux Rates among Pools and Transformation Rates of Materials within Ecosystems?

Within-system fluxes, like pool sizes, have received extensive attention in recent years. In terrestrial ecosystems affected by invasive plants, litter decomposition rates are on average 117% higher for exotic than co-occurring native species, and the higher litter masses imply higher element input rates to the soil (Liao et al. 2008). These patterns continue to be observed in many but not all recently published studies. Contrasting examples of equivalent or slower litter decomposition than natives often include grasses [e.g., *Holcus lanatus* (Bastow et al. 2008), *Spartina alterniflora* (Liao et al. 2007), *Aegilops triuncialis* (Drenovsky & Batten 2007), *Microstegium vimineum* (Ehrenfeld et al. 2001), *Bromus tectorum* (Ogle et al. 2003)], but also some broad-leaved species [such as *Robinia pseudoacacia* (Castro-Díez et al. 2009) and *Acer platanoides* leaves within streams (Reinhart & VandeVoort 2006)]. Invasive plant litter decomposes more quickly than native litter, usually because of higher chemical quality [lower C:N and/or lower lignin:N ratios (Liao et al. 2008)]. Rapidly decomposing litter of exotics also may facilitate more rapid decomposition of co-occurring native species (Ashton et al. 2005, Hughes & Uowolo 2006, Rodgers et al. 2008).

Animal invasions affect litter decomposition rates through several pathways. Direct consumption and displacement from the soil surface into the soil matrix and stimulation of microbial populations by earthworms are the most extensively studied pathways (Li et al. 2002). Worms also directly affect decomposition rates of material remaining on the surface, including fresh litter (Belote & Jones 2009) and deer pellets (Karberg & Lilleskov 2009). Invasive insect herbivores directly increase litter fluxes and alter the timing of their inputs to soil (Lovett et al. 2002, Stadler et al. 2006). Animals indirectly affect decomposition rates through their alteration of detritivore communities. Thus, invasive ants reduce or remove detritivore populations, causing decreases in decomposition and increases in litter pool sizes (Dunham & Mikheyev 2010, O'Dowd et al. 2003). Animal invasions also alter moisture and temperature controls on litter decomposition, as found for woolly adelgid (*Adelges tsugae*) invasions (Cobb et al. 2006). Finally, animal excretion, through its changes to litter nutrient pools, can accelerate decomposition rates, although such effects are not always observed (Beard et al. 2003, Sin et al. 2008, Tuttle et al. 2009).

Litter decomposition in aquatic habitats appears to be less strongly influenced by the chemistry of the litter than is the case for terrestrial systems. Several studies (e.g., Braatne et al. 2007, Harnes et al. 2009, Hladysz et al. 2009, Reinhart & VandeVoort 2006) have failed to find differences between decomposition rates of exotic and native litters within streams, although some studies do find differences (higher rates for exotics) in some sites (e.g., Lecerf et al. 2007). Aquatic invertebrate communities often change in composition in response to exotic litter, but decomposition rates do not necessarily change with altered community composition.

As with litter inputs and decomposition rates, N fluxes (N mineralization and nitrification) within terrestrial ecosystems affected by plant invasions tend to be increased by invasive plant species, as shown by Liao et al. (2008) and supported by many more recent studies. However, as with other ecosystem processes, complex patterns among fluxes and among species are frequently reported. For example, *Andropogon gayanus* stimulates increases in net N mineralization but inhibits nitrification (Rossiter-Rachor et al. 2009), *Solidago gigantea* has variable effects on N in different sites across Switzerland (Scharfy et al. 2009), and N-fixing species can vary in their effects on N cycling rates in different sites (Yelenik et al. 2007). Changes in litter decomposition rates do not necessarily correlate with N mineralization rates from the litter or in the soil; indeed, complex and context-dependent relationships between litter decomposition, soil respiration rates, and N mineralization rates in both soil and litter are frequently observed, defeating any attempt at easy summarization (e.g., Hughes & Uowolo 2006, Koutika et al. 2007, Mack & D'Antonio 2003).

The redistribution of elements within ecosystems is another important change in fluxes (deep soil to plant biomass and to the soil surface). Plants redistribute materials through uptake by deep roots and deposition of nutrient-enriched litter on the soil surface. For example, two invasive trees in deciduous forests, *Acer platanoides* and *Ailanthus altissima*, increase the concentrations of cations around individual trees more than do native species (Gómez-Aparicio & Canham 2008). Whether deep uptake of cations promotes faster weathering rates (and thus a net input to ecosystems) remains unknown. Animal-mediated redistribution of materials among soil horizons can stimulate changes in process rates such as soil respiration, N mineralization, and denitrification, although again, these changes are not always observed (Bohlen et al. 2004, Costello & Lamberti 2009, Eisenhauer et al. 2007).

Aquatic invasions also involve large-scale redistribution of materials, particularly net transfers from the water column to the sediment surface and changes in fluxes from the sediments to the sediment/water interface and/or the water column, as reviewed recently by Ruesink et al. (2005), Sousa et al. (2009), and Wallentinus & Nyberg (2007). Such large-scale changes have been well documented for zebra mussels (*Dreissena polymorpha*—Hecky et al. 2004; Strayer 1999, 2009), introduced oysters (*Venerupis philippinarum*—Bartoli et al. 2001), and slipper limpets (*Crepidula fornicata*—Martin et al. 2007, Ragueneau et al. 2005), as well as for dense beds of aquatic plants (e.g., *Zostera japonica*—Larned 2003 and *Caulerpa* spp.—Klein & Verlaque 2008). Extensive documentation of changes in food webs resulting from these invasions is rarely expanded to determine effects on element fluxes; the work of Miehl et al. (2009a,b) in showing how food web changes alter C flows subsequent to *Dreissena* invasions is a notable exception.

Inputs: Do Exotic Species Alter Nutrient Inputs into Ecosystems?

Carbon inputs to an ecosystem occur through photosynthetic fixation and, at the ecosystem scale, result in changes to net primary production (NPP). Extensive research has addressed differences in C physiology, nutrient use efficiency, and leaf C costs in exotic versus co-occurring native plants. Researchers commonly report higher C input rates for exotic plants (Baruch & Goldstein 1999, Funk & Vitousek 2007, Liao et al. 2008, Tecco et al. 2010, van Kleunen et al. 2010, and

many others). This literature supports the inference of higher C input rates to invaded ecosystems. However, patterns are, not surprisingly, complicated by conflicting results. Leishman et al. (2010) found no evidence of systematic differences in C physiology between native and exotic species in Australia, and Tecco et al. (2010) found that woody but not herbaceous species had higher resource acquisition abilities than did native species across habitats in Argentina. Whether differences in C capture always translate to higher NPP is often implied but not often demonstrated.

There are far fewer data available to evaluate changes to secondary production from invasive animal species. In aquatic systems, studies of invasive mudsnails (*Potamopyrgus antipodarum*, Hall et al. 2006) and invasive bivalves (Ruesink et al. 2006) report large increases in secondary production compared to the native species (4-fold to 250-fold increases). The high biomasses documented for invasive bivalves and other reef-forming aquatic invertebrates suggest high rates of secondary production, but few studies document these biomasses, report productivity rates, or compare production with uninvaded systems.

Invasions of exotic herbivorous insects decrease growth and biomass, but explicit quantifications of reductions in NPP are surprisingly rare (Kenis et al. 2009). In one of a few such studies, Nuckolls et al. (2009) found that *Adelges tsugae* invasions decreased both above- and belowground production and also caused a 20% decrease in soil respiration flux. In the most comprehensive study to date, Clark et al. (2010) used both biometric and eddy flux measurements to show that defoliation of oak-pine forests by gypsy moths (*Lymantria dispar*) resulted in a 41–55% reduction in net ecosystem exchange (net C uptake), depending on the percentage of oaks in the canopy. In oak stands completely defoliated during a severe outbreak, there was a net release of C (122 g C m⁻² year⁻¹ of uptake before defoliation, versus 203 g C m⁻² year⁻¹ release back to the atmosphere after defoliation). Undoubtedly, exotic insect pests cause large-scale reductions in C inputs, but the scope of such changes remains to be quantified.

Exotic species' impacts on N inputs are more difficult to evaluate. Nitrogen inputs must reflect either increases in N fixation or N inputs in water inflows, in dry deposition of reactive N, or through animal-mediated transport. Although the effects of invasive N-fixing plants have been widely discussed and reviewed, few of these studies actually quantify the change in net N inputs due to the addition of an N-fixing plant (Scherer-Lorenzen et al. 2008); indeed the seminal work of Vitousek and colleagues on *Morella faya* invasions in Hawaii remains one of the few quantifications of the amount of increase in N inputs (from 0.2 to 18 kg N ha⁻¹ year⁻¹) (Vitousek & Walker 1989). The available evidence indicates that N-fixation rates vary with the invader and site (Rodríguez-Echeverría et al. 2009, Yelenik et al. 2007). Nonsymbiotic N fixation is also poorly quantified, but responds to invasions in various ways. Animal invasions in aquatic habitats can enhance N fixation through differential grazing on algae (Arango et al. 2009). Plant invasions can increase nonsymbiotic fixation through stimulation of sediment and rhizosphere microbes [*Caulerpa taxifolia* in aquatic habitats (Chisholm & Moulin 2003) and some invasive grasses in terrestrial habitats (Williams & Baruch 2000)] and support of endophytes (*Sorghum halapense*, Rout & Chrzanowski 2009). Plant invasions may also decrease fixation rates through reductions in microbial habitat (Ley & D'Antonio 1998, Sperry et al. 2006). The role of changing N-fixation rates on ecosystem N budgets remains an open question, although the evidence suggests that invaders can change the abundance of N-fixing organisms of varying effectiveness through a variety of pathways, and at least some symbiotic N-fixing exotic plants do increase N pools in plants and soil (Rice et al. 2004).

Ecosystems that depend on animal-mediated inputs of nutrients from different adjacent or distant ecosystems (Polis et al. 1999) are particularly vulnerable to exotic species that disrupt those import mechanisms. This has been elegantly demonstrated in the case of islands on which ground-nesting sea bird populations have been greatly reduced by invasive predators. This reduces guano

inputs of marine-derived N and causes cascades of changes to soil and plant pools and fluxes (Croll et al. 2005, Fukami et al. 2006, Mulder et al. 2009). Although there are many other examples of trophic cascades induced by exotic animal invasions (e.g., Simberloff 2009, Snyder & Evans 2006, Zavaleta et al. 2001), the implications for ecosystem inputs and outputs of food web alterations are rarely examined.

In some aquatic animal invasions, transfers of material from the water column to the sediment surface affect nutrient flows between adjacent water bodies. The slipper limpet, *Crepidula fornicata*, creates a “silica pump” (Ragueneau et al. 2005), by which its suspension feeding removes up to 84% of riverine dissolved silica inputs to the Bay of Brest (France), which dramatically lowers both Si availability to pelagic diatoms and the Si flux from the enclosed bay to the adjacent coastal ocean. A similar “phosphorus shunt” has been described for zebra mussel invasions into the Great Lakes (Hecky et al. 2004), by which riverine inputs of P are diverted from lake waters to the benthos. These alterations of nutrient inputs depend on the dense populations and resulting high water filtration rates of colonial bivalves.

Outputs: Do Exotic Species Alter Nutrient Losses from Ecosystems?

Output mechanisms for materials include losses to the atmosphere as gaseous forms and as particulate forms as a result of erosion or fire, plus losses in water through leaching or surface flows. In terrestrial systems, soil and plant respiration are primary pathways of C loss. Soil respiration rates increase in some invaded systems (Litton et al. 2006, Marchante et al. 2008, Zou et al. 2006), depend on soil texture and water inputs in others (Huxman et al. 2004), and do not change with plant invasions in other cases (e.g., Scharfy et al. 2009). Earthworm effects on soil respiration are similarly variable with soil type, soil history, and species composition of the worm population (Fisk et al. 2004, Li et al. 2002).

Losses of N gases (NO , N_2O , N_2) through nitrification or denitrification have been only infrequently quantified with respect to plant invasions. There is some evidence that denitrification losses may decrease (*Bromus tectorum*, Evans et al. 2001) or increase (*Triadica sebifera*, Zou et al. 2006; *Typha x glauca*, Angeloni et al. 2006; *Morella faya*, Hall & Asner 2007; *Phragmites australis*, Windham & Ehrenfeld 2003), but some of these studies rely on laboratory incubations, measurements of denitrifier communities, or other proxy methods. Hall & Asner (2007) provided the best available estimate of ecosystem flux rates. They found that N_2O emissions were elevated by *M. faya*, but only in wet-mesic sites, not dry sites, and only when *M. faya* was the canopy dominant, not just isolated trees. Invasion increased N losses sevenfold and was correlated with both high N input rates from fixation and high NO_3 pools in the soil.

Animal invasions may also affect losses through denitrification by altering microbial community structure, activity, and the oxygen status of the environment. As with plant invasions, there is a paucity of clear evidence of the magnitude and generality of these effects, and rates from laboratory or small chambers are rarely extrapolated to ecosystem-scale budget estimates. Earthworm invasions may increase denitrification-based losses from both forest (Burtelow et al. 1998) and riparian (Costello & Lamberti 2009) soils, but again, not always (Bohlen et al. 2004). Invasive animals that alter soil oxygen status through bioturbation theoretically can alter denitrification rates, but there are very few good data to assess this speculation, aside from one observation of invasive aquatic polychaetes that decrease denitrification through increased oxygenation (Hietanen et al. 2007).

Another pathway of loss that has been surprisingly poorly studied is the expected losses through volatilization and particulate fluxes during fire (Nepstad 2002, Wan et al. 2001). Despite much attention to increases in fire frequency, particularly from exotic grasses (Brooks et al. 2004,

Davis 2009, Williams & Baruch 2000), there have been few efforts to quantify the effects of invasive plant-induced changes in fire regime on ecosystem N. In one of the few ecosystem-scale studies of fire-mediated N losses, Rossiter-Rachor et al. (2008, 2009) showed that invasion of *Andropogon gayanus* into Australian savannas results in 113% higher loss of N and other nutrients than from the native grasslands, and that the losses were proportional to exotic plant biomass. They pointed out that because the only N input, from rainfall, is low in this system ($2 \text{ kg N ha}^{-1} \text{ year}^{-1}$), the N lost to burning in invaded sites (up to $61.5 \text{ kg N ha}^{-1} \text{ year}^{-1}$ in high-intensity fires) would take about 10 years of inputs to replace. Thus, the high biomass of many invasive fire-promoting grasses probably leads to long-term losses of N from invaded grasslands and savannas. Exotic plant-mediated changes in fire regimes also result in C loss; in one site, *Bromus tectorum* converted a Western shrubland from C sink to C source (Bradley et al. 2006).

Leaching losses are similarly poorly known. Although many studies have demonstrated increased rates of nitrification and increased concentrations of nitrate within the soil, the possibility of higher leaching loss rates is not clearly addressed in the literature. Animal invasions can promote increased leaching indirectly by increasing nitrification while decreasing plant uptake. Such a pathway has been demonstrated for hemlock woolly adelgid (*Adelges tsugae*) infestations, which increase nitrate and cation concentrations in soil water sixfold over uninfested stands (Yorks et al. 2003). Exotic earthworms and ants may also increase leaching losses through increased nitrification coupled with increased soil porosity (Cammaraat & Risch 2008, Green et al. 1999), but these effects are site-specific (Bohlen et al. 2004) and not well quantified.

Water losses through evapotranspiration are among the best-documented output fluxes changed by invasion. The great increase in water flux rates associated with *Acacia* invasions in South Africa (Dye & Jarman 2004, Gorgens & van Wilgen 2004) and *Tamarix* invasions in the American Southwest (Shafroth et al. 2005) are well known, but other invasive plants also alter water fluxes through higher transpiration rates (e.g., Gerlach 2004, Potts et al. 2008). Animal invasions indirectly alter water fluxes by imposing stress on plants and by changing species composition, as has been demonstrated for *Adelges tsugae* invasions (Daley et al. 2007), and causing tree mortality (Ford & Vose 2007).

MECHANISMS OF ECOSYSTEM CHANGE

This survey suggests that the mechanisms by which individual species alter ecosystem processes include multiple pathways that are not only not mutually exclusive, but probably complementary.

Plant Functional Traits

Individual species traits are clearly implicated as a major pathway of ecosystem impact. Differences in morphological, chemical, and physiological traits are well documented for many plant invaders as a mechanism for change of some ecosystem processes (particularly NPP, litter decomposition, above- and belowground stocks of nutrients, and water use). In many but not all cases, invasive species have higher values of resource-acquisition traits, larger size, and/or higher growth rates, which imply higher pool sizes of C, N, etc. However, conclusions based on comparisons of traits depend heavily on the type of comparison. Contradictory patterns reported in some meta-analyses (Leishman et al. 2010, Tecco et al. 2010) are a warning that global patterns remain elusive and that comparative findings depend on the specifics of the comparison. Comparisons of plant traits have focused exclusively on terrestrial plants; trait analysis has yet to be extended to aquatic invasive plants. Moreover, the translation of trait differences to ecosystem-scale changes in pools and flux rates remains, in many cases, reasonable but unverified.

Phenology is not usually included in lists of functional plant traits, but clearly it is an important source of alterations to ecosystem processes. The production of high amounts of biomass or litter at certain times of year different from the native community affects the interlinked dynamics of C, nutrients, and water. Uptake rates, the activities of soil microbial communities that effect material transformations, and material use rates (e.g., transpiration, leaf area production) have been shown to change ecosystems solely through changes in timing of plant growth. Phenology may be as important as physiological or chemical traits as a driver of ecosystem change in invaded systems.

Several limitations to explanations of ecosystem differences based on plant traits should be pointed out. First, the amount of difference in particular traits required for an ecosystem-scale impact remains unknown for any trait. Indeed, it seems likely that the amount of difference in resource-acquisition traits required for ecosystem change vary both with the trait and with the ecological context. This caveat is supported by the many studies in which the same invader causes different effects on the same process at different sites (e.g., Dye & Jarman 2004, Koutika et al. 2007, Mack & D'Antonio 2003, Scharfy et al. 2009). Second, most studies compare heavily invaded versus uninvaded sites. Although this is an important first step in establishing the existence of impacts, it does not permit analysis of the quantitative issue of how much of a change in a functional trait is necessary in order to have an impact at the ecosystem level. Third, it is often not clear whether an ecosystem impact is a result of the difference in traits of individuals, or a difference resulting from higher densities of plants with similar resource use traits, or some combination of the two. Finally, as noted above, it is not clearly demonstrated that higher resource-related traits translate into increased resource pools or flux rates at the ecosystem level.

No comparable body of theory addresses trait differences for animals or animal invaders. Nevertheless, this survey suggests that such an approach might prove useful for understanding invasions. Certain behaviors, such as bioturbation, or the construction of large nest structures from plant biomass, or dense aggregations of individuals, are often associated with animals that create ecosystem change. A full consideration of the role of individual species traits in animals is beyond the scope of this review but may repay further analysis.

Keystones, Engineers, and Foundations: Disproportionate Effects of Species

All of the proposed pathways by which individual species affect ecosystems are exemplified by exotic species' impacts on ecosystem processes. Ecosystem engineering and physical habitat alteration are the most frequently cited mechanistic pathways of ecosystem change caused by exotics (Crooks 2002, Davis 2009). Both animals and plants have been identified as ecosystem engineers that cause changes to the abiotic environment through a variety of behaviors and individual traits. Physical environmental changes resulting from trophic behaviors are just as important, however, although these pathways are usually excluded from the definition of engineering. Trophic activities that change physical environments include filter feeding, herbivory-mediated changes in light penetration, and consumption of organic horizons (that is, worms). Plants alter physical environments through their size, morphology, and density. These properties affect light penetration, water flow and chemistry in both aquatic and soil environments, sediment deposition, and soil chemistry. Engineering concepts are more readily applied to animals than to plants, for which distinctions between trophic and nontrophic behaviors are irrelevant, as all growth involves resource acquisition. Indeed, in many of the cases examined, exotic species are altering ecosystems through combinations of trophic and nontrophic effects, so that they are both ecosystem engineers and keystone species.

Despite the emphasis on ecosystem engineering in the invasion literature, much of the literature on engineers describes biotic changes such as changes in species composition, rather than effects

on ecosystem processes. This is particularly the case for terrestrial engineers. In aquatic habitats, a long tradition in limnology of close attention to the role of water chemistry and nutrient fluxes has produced tighter connections between engineering and ecosystem processes, and examples of engineering are much better documented (e.g., Caraco & Cole 2002, Carlsson et al. 2004, Hecky et al. 2004, Hummel & Findlay 2006, Ragueneau et al. 2005, Scheffer et al. 2003, Strayer 2009).

Undoubtedly, species that act as engineers or keystones in their native range (e.g., beavers, earthworms, colonial bivalves, densely growing grasses) are very likely to carry out the same activities in an invaded range. For species that are not identified as engineers in their native range, the main issue may be an abundance-impact question: Do exotic species become engineers or keystones in an invaded range as a result of higher population densities than normally achieved in the native range? This question implies that in some cases, ecosystem engineering may follow as a consequence of unrelated mechanisms (such as enemy release) that allow a species to become much more abundant in the invaded than the native range.

Perhaps the most widespread and general form of engineering results from the higher biomasses of invasive populations, as documented above. Denser, taller plants in terrestrial environments alter light and moisture regimes, create thicker litter layers, and change habitats for all types of consumers. In aquatic environments, dense mats of plants or shell beds alter hydrodynamics, water-sediment fluxes, light penetration, and consumer food webs. Thus, exotic species alter ecosystems in part by becoming novel foundation species, which then engineer changes to the physical environment. This situation implies that ecosystem processes, namely high rates of C fixation and NPP or secondary production in the case of animals, can drive ecosystem engineering in a self-reinforcing feedback process. Furthermore, it supports the conclusion that all of the various pathways identified in the body of theory on diversity-ecosystem function help explain ecosystem impacts of exotics and overlap in their applicability.

Disturbance Regimes

As noted above, changes to fire regimes as a result of plant invasions have been widely documented (Brooks et al. 2004, D'Antonio et al. 1999, Pauchard et al. 2008), but few studies have produced whole-system budgets. Given the known effects of fire in mobilizing nutrients and promoting loss through various pathways (Wan et al. 2001), it might be expected that exotics that promote frequent fire also promote long-term decreases in nutrient stocks, a speculation supported by a few such analyses (Bradley et al. 2006, Rossiter-Rachor et al. 2008).

Exotic insect defoliation events are also frequently invoked as causes of ecosystem change and altered disturbance regimes. Increases in the frequency and intensity of defoliation events are associated with widespread changes in NPP, litter fluxes, water fluxes, and nutrient fluxes, as has been well illustrated for the two best-studied exotic defoliators [hemlock woolly adelgid (*Adelges tsugae*) and the gypsy moth (*Lymantria dispar*)] (Clark et al. 2010, Daley et al. 2007, Eshleman et al. 1998, Ford & Vose 2007, Jenkins et al. 1999, Orwig et al. 2008, Riscassi & Scanlon 2009, Schäfer et al. 2009, Stadler et al. 2005, Townsend et al. 2004). Environmental change caused by altered insect defoliation regimes promotes vegetation changes that can result in a state change in the plant community such as the permanent loss of hemlocks in adelgid-affected forests (Gandhi & Herms 2010), with the implication that such a state change will profoundly alter many ecosystem processes.

Other exotic-mediated alterations of physical disturbance are less well documented, particularly with respect to their impacts on ecosystem dynamics. Anecdotal evidence that invasive vines, such as *Pueraria montana* and *Celastrus orbiculatus*, increase tree death through overtopping is frequently cited (e.g., Webster et al. 2006), but there do not appear to be quantitative studies of changes to

tree-throw disturbance dynamics, nor to the ecosystem effects of such changes in disturbance regimes. Changes to flooding regimes have been ascribed to *Tamarix* spp. invasions (Tickner et al. 2001), but there are few data to evaluate the extent of flood frequency changes, and in no other riparian or stream invasions has the suggestion been made that the hydrological regime itself has been modified. In summary, both animals and plants can alter disturbance regimes with resulting changes to ecosystem processes, but few studies of disturbance regime changes quantify the changes to these processes.

Altered Food Webs

Changes in food web architecture provide another mechanism by which ecosystem processes are altered. Four pathways were found: (a) trophic cascades in which invasive predators reduce populations of consumers that transport nutrients between habitats, reducing inputs and altering within-system cycling; (b) invasive predators that alter the species composition and abundance of detritivores, altering litter decomposition rates (e.g., Beard et al. 2003); (c) invasive plants, whose litter is more or less palatable to detritivores than native species' litter (e.g., Bastow et al. 2008, Reinhart & VandeVoort 2006); and (d) exotic animal modification of detritivore habitats within soil or water, as seen for invasive ants and worms (e.g., Dunham & Mikheyev 2010, Eisenhauer et al. 2007) and zebra mussels (Michls et al. 2009a). However, changes to detritivore populations do not necessarily produce changes in litter decomposition or nutrient mineralization rates, and evidence that invertebrate communities are altered is more common than evidence that these changes result in altered rates of litter decomposition or nutrient fluxes.

CONCLUSIONS AND RESEARCH DIRECTIONS FOR THE FUTURE

Mechanisms of Impact on Ecosystem Processes

It is clear that invasive exotic species can alter ecosystem processes through a wide variety of mechanisms, over a variety of spatial and temporal scales and over a wide range of degree of impact. This survey of the burgeoning literature on the subject also shows that no one pathway of impact can account for all cases of ecosystem change. Indeed, multiple mechanisms can be identified in most, perhaps all, examples of ecosystem change. Specific mechanistic pathways, such as functional traits, ecosystem engineering, and altered disturbance regimes interact with each other and may reinforce each other to drive quasi-permanent state changes. Thus, in the continued search for mechanisms of impact of exotic species, a more promising direction of research should be to quantify and document pathways of interacting mechanisms, rather than to focus on single causative pathways as a "holy grail" of universal explanation (Simberloff 2010).

It is also clear from this literature that though some patterns may be frequently found (e.g., higher resource acquisition rates in exotic plants, increased N and C mineralization rates), these patterns are far from universal. Indeed, as noted above, there are many examples in which the same exotic species causes quite different impacts on ecosystem processes at different sites or at different times. This variability in effect emphasizes the importance of ecological context in understanding and anticipating impact to ecosystems. The assessment of impact also depends on the choice of system for comparison and the degree to which site history, other disturbances, and the physical setting of a site (e.g., soil type, geomorphologic setting, etc.) are taken into account. Furthermore, the quantitative amount of difference in the various traits between an invading species and the native species it replaces that is necessary to generate ecosystem impact is unknown.

Stoichiometry: the ratios of elements within organisms, populations, and environmental pools that affect resource acquisition and use

The data suggest that the most common pathways of impact of both plant and animal species are through changes, mostly increases, of biomass and alterations in the timing of growth and mortality. Higher biomasses of organisms necessarily reorganize fluxes of C, water, and nutrients because of stoichiometry and physiological requirements for resources. They similarly alter the physical environment by altering light penetration, temperature patterns, and the physical habitats available for detritivores and consumers, all of which can alter input and output fluxes. The ability of the invasive species to maintain high biomasses under the altered physical conditions suggests that positive feedback is present and important.

To date, no exotic species has been studied whose mechanism of impact differs qualitatively from that of native species or that cannot be understood through ecological theories developed for native species and uninvaded ecosystems. However, the fact that total ecosystem biomass frequently appears to increase does pose a challenge to researchers and theorists: What sets the biomass limits for an ecosystem, and what processes allow this limit to increase as a new species becomes established? The higher biomasses seen in many invasions suggest that ecosystem size, as measured in total C and circulating nutrient stocks, is set by ecological factors operating within broad, regional environmental constraints and is not strictly constrained by local limits. Invasions thus present an interesting opportunity for basic research: How do invading species promote changes to the inputs, outputs, and within-system fluxes that permit the total amount of biomass of an ecosystem to increase?

Are There General Patterns of Ecosystem Alteration?

It is clear that studies that quantify differences in individual flux rates and/or pool sizes greatly outnumber studies of input and output fluxes, and studies of whole-system mass balance budgets are rare indeed. Thus, it is unknown as yet whether exotics tend to alter the distribution of materials within ecosystems more or less frequently than they cause net gains or losses. Indeed, perhaps the largest piece of missing information necessary to evaluate the impacts of invasive species on ecosystem processes is the lack of whole-system budgets that use mass balance and stoichiometric theory (Stern & Elser 2002) as the basis for analysis. Understanding and management of other environmental problems, such as acid deposition, eutrophication, and CO₂ emissions, have depended on detailed whole-system budget analyses (Pace & Groffman 1998); exotic species invasions have not yet followed suit. The only case in which such comprehensive whole-system analyses have been conducted involves the effects of invasive woody plants on water budgets in South Africa (e.g., Gorgens & van Wilgen 2004), which has led to effective management at a country-wide scale (Marais & Wannenburgh 2008). Indeed, the lack of such a whole-system perspective makes it difficult to evaluate the significance of the documented changes in particular fluxes and pools and can lead to erroneous conclusions about the implications of differences in individual flux rates (as exemplified in Rout & Callaway 2009). It remains quite possible that changes in within-system fluxes do not result in net changes of inputs and outputs and the balance between them.

The importance of system-specific context in elucidating causative mechanisms of impact is another impediment to evaluating the generality of ecosystem alterations. In studies of both animal and plant invasions, site-specific factors, including soil type, hydrogeology, and a diverse range of habitat differences, result in contrasting patterns of change, or the lack thereof, by the same exotic species. Site history has also been invoked as a major modifying factor in determining ecosystem impacts of exotics (Didham et al. 2005, Kulmatiski et al. 2006). The prominence of both historical and site-specific factors in these and other studies suggests that a state-factor approach might be useful as a context for exploring ecosystem impacts. In soil science, state factors are widely understood to constrain patterns of soil development and function (Huggett 1998), and

this perspective has been adopted in the analysis of ecosystem processes in general (Chapin et al. 2002). From this perspective, it is not at all surprising that biotic changes resulting from invasions of both plants and animals should cause differing effects in different sites, depending on the status of the other state factors at those sites.

Finally, studies of N and C cycling dominate the literature. There are, strikingly, fewer studies of P and cation cycling. Altered pools and fluxes of cations figure prominently in some analyses of ecosystem change during invasion [see Gómez-Aparicio & Canham (2008) and Howard et al. (2004) for plant invasions, and Ragueneau et al. (2005) for aquatic animal invaders]. Because pH is often identified as a “master variable” through its control over the biogeochemistry of other materials, changes to cations, particularly calcium, may play a much larger role than has been recognized thus far and deserve increased attention.

Are There Fundamental Differences in the Pathways and Mechanisms by which Animals and Plants Affect Ecosystem Processes? Between Aquatic and Terrestrial Ecosystems?

Both plants and animals can be engineers, keystones, and foundation species. But plants affect ecosystem processes exclusively through their patterns of resource acquisition and growth, so that their ecophysiological and morphological traits provide a primary explanatory framework for their impacts on ecosystems. It is the density, morphology, and growth rate of plants that account for both changes to nutrient cycles and also the “transforming” accumulations of sediment that alter geomorphology and hydrology. In contrast, animals affect ecosystem processes through several separate pathways based on trophic and nontrophic characteristics and based on behaviors that may involve either or both sets of characteristics. Thus, beavers’ dam-building behavior is in support of both trophic activity (food supply) and nontrophic needs (protection from predators). Invasive bivalves affect ecosystems through the production of dense shell beds, which transform soft substrate into hard (nontrophic traits), but also through the intense water-filtering effects of dense populations (trophic traits). Animals affect ecosystems through consumption and also through excretion, a process with no analog in plant growth. Exotic predators affect ecosystems through trophic cascades, through removal of animal-mediated nutrient transport mechanisms and through differential predation of herbivores and detritivores. Therefore, animals affect ecosystem fluxes through a greater number of mechanistic pathways than do plants. The effects of animal invaders, particularly terrestrial animals, on ecosystem processes are subjects ripe for more detailed study.

Aquatic ecosystems have a tripartite structure (water, sediment/water interface, and sediments) and a great amount of physical transport within and between ecosystem compartments generated by moving water. This contrasts with the dual structure and relative immobility of terrestrial ecosystems. The greater importance of water flows as a structuring element of aquatic systems creates a different set of pools and fluxes that need to be considered. But these do not produce fundamental differences in the mechanisms by which individual species (in this case, invasive exotics) alter ecosystem function.

RESEARCH DIRECTIONS

Several clear research needs can be identified from this review.

1. Whole-ecosystem budgets based on mass balance approaches are needed in order to evaluate the importance and effects of changes in individual flux rates and also to evaluate the potential for changes that have social or economic consequences.

2. Quantification of the abundance-impact curves for particular fluxes and pool quantities needs to be determined. There are now a large number of studies demonstrating that heavily invaded and uninvaded systems differ for many components of all material cycles; there is virtually no information on how different a species needs to be in functional trait properties, and/or how different in abundance, in order to affect ecosystem processes.
3. A state factor approach developed for both terrestrial and aquatic systems might help explain how site history and site location (geology, topography, hydrology, water chemistry, etc.) constrain ecosystem responses to invasive species.
4. Extensive attention has been paid to C and N cycles and, to a lesser extent, water cycles; much less attention has been paid to P and cation cycling. These materials may be as important or more important than N in affecting ecosystem dynamics and deserve more study.
5. Numerous studies of animal invaders have been undertaken to demonstrate their role in changing species composition and in trophic cascades within communities. However, with relatively few exceptions, there is little knowledge about how food web alterations affect ecosystem processes.
6. Related to the previous recommendation, the role of animals as agents of input and output of materials deserves more attention, concerning both novel fluxes introduced by invading animals and changes to the activities of native animals caused by introduced predators or competitors.
7. Alterations to the stoichiometries within pools and fluxes have received little attention. Because stoichiometric relationships between resources and consumers (whether soil and water for producers, or producers for consumers, or both for detritivores) constrain both population dynamics and element fluxes, the effects of invasive species on element ratios need greater research attention.

SUMMARY POINTS

1. Invasive exotic species can alter ecosystem processes through a wide variety of mechanisms that complement each other, over a variety of spatial and temporal scales and over a wide range of degree of impact.
2. No one mechanism of impact can account for all cases of ecosystem change. Although ecosystem engineering, keystone species effects, and individual functional traits account for many of the observed impacts, none of these pathways is sufficient to account for all ecosystem changes, and most cases of ecosystem change involve multiple mechanisms.
3. Ecosystem consequences of exotic invasions are site- and comparison-specific, so that the same invasive species may have different effects in different locations.
4. The data suggest that the most common pathways of impact of both plant and animal species are through changes, mostly increases, of biomass and alterations in the timing of growth and mortality.

DISCLOSURE STATEMENT

The author is not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

ACKNOWLEDGMENTS

I thank B. Clough, K. Elgersma, M. Palta, L. Shappell, and A. Wen for comments on earlier drafts. I acknowledge support from the National Science Foundation (DEB-0309047) and the U.S. Department of Agriculture (grants USDA-CSREES-2002-353 and USDA-CSREES-2005-2221).

LITERATURE CITED

- Addison JA. 2009. Distribution and impacts of invasive earthworms in Canadian forest ecosystems. *Biol. Invasions* 11:59–79
- Anderson CB, Rosemond AD. 2007. Ecosystem engineering by invasive exotic beavers reduces in-stream diversity and enhances ecosystem function in Cape Horn, Chile. *Oecologia* 154:141–53
- Angeloni NL, Jankowski KJ, Tuchman NC, Kelly JJ. 2006. Effects of an invasive cattail species (*Typha x glauca*) on sediment nitrogen and microbial community composition in a freshwater wetland. *FEMS Microbiol. Lett.* 263:86–92
- Arango CP, Riley LA, Tank JL, Hall RO. 2009. Herbivory by an invasive snail increases nitrogen fixation in a nitrogen-limited stream. *Can. J. Fish. Aquat. Sci.* 66:1309–17
- Ashton IW, Hyatt L, Howe KM, Gurevitch J, Lerdau M. 2005. Invasive species accelerate decomposition and litter nitrogen loss in a mixed deciduous forest. *Ecol. Appl.* 15:1263–72
- Bartoli M, Nizzoli D, Viaroli P, Turolla E, Castaldelli G. 2001. Impact of *Tapes philippinarum* farming on nutrient dynamics and benthic respiration in the Sacca di Goro. *Hydrobiologia* 455:203–12
- Baruch Z, Goldstein G. 1999. Leaf construction cost, nutrient concentration, and net CO₂ assimilation of native and invasive species in Hawaii. *Oecologia* 122:183–92
- Bastow JL, Preisser EL, Strong DR. 2008. *Holcus lanatus* invasion slows decomposition through its interaction with a macroinvertebrate detritivore, *Porcellio scaber*. *Biol. Invasions* 10:191–99
- Beard KH, Eschtruth AK, Vogt KA, Vogt DJ, Scatena FN. 2003. The effects of the frog *Eleutherodactylus coqui* on invertebrates and ecosystem processes at two scales in the Luquillo Experimental Forest, Puerto Rico. *J. Trop. Ecol.* 19:607–17
- Beard KH, Vogt KA, Kulmatiski A. 2002. Top-down effects of a terrestrial frog on forest nutrient dynamics. *Oecologia* 133:583–93
- Belore RT, Jones RH. 2009. Tree leaf litter composition and nonnative earthworms influence plant invasion in experimental forest floor mesocosms. *Biol. Invasions* 11:1045–52
- Bohlen PJ, Pelletier DM, Groffman PM, Fahey TJ, Fisk MC. 2004. Influence of earthworm invasion on redistribution and retention of soil carbon and nitrogen in northern temperate forests. *Ecosystems* 7:13–27
- Braatne JH, Sullivan SMP, Chamberlain E. 2007. Leaf decomposition and stream macroinvertebrate colonization of Japanese knotweed, an invasive plant species. *Int. Rev. Hydrobiol.* 92:656–65
- Bradley BA, Houghton RA, Mustard JF, Hamburg SP. 2006. Invasive grass reduces aboveground carbon stocks in shrublands of the Western US. *Glob. Change Biol.* 12:1815–22
- Brooks ML, D'Antonio CM, Richardson DM, Grace JB, Keeley JE, et al. 2004. Effects of invasive alien plants on fire regimes. *BioScience* 54:677–88
- Burtelow AE, Bohlen PJ, Groffman PM. 1998. Influence of exotic earthworm invasion on soil organic matter, microbial biomass and denitrification potential in forest soils of the northeastern United States. *Appl. Soil Ecol.* 9:197–202
- Cammeraat ELH, Risch AC. 2008. The impact of ants on mineral soil properties and processes at different spatial scales. *J. Appl. Entomol.* 132:285–94
- Caraco NF, Cole JJ. 2002. Contrasting impacts of a native and alien macrophyte on dissolved oxygen in a large river. *Ecol. Appl.* 12:1496–509
- Carlsson OL, Brönmark C, Hansson L-A. 2004. Invading herbivory: the golden apple snail alters ecosystem functioning in Asian wetlands. *Ecology* 85:1575–80
- Castro-Díez P, González-Muñoz N, Alonso A, Gallardo A, Poorter L. 2009. Effects of exotic invasive trees on nitrogen cycling: a case study in Central Spain. *Biol. Invasions* 11:1973–86

- Chapin FSI, Matson PA, Mooney HA. 2002. *Terrestrial Ecosystems*. New York: Springer-Verlag
- Charles H, Dukes JS. 2008. Impacts of invasive species on ecosystem services. In *Biological Invasions*, ed. W Nentwig, pp. 217–38. Berlin: Springer
- Chisholm JRM, Moulin P. 2003. Stimulation of nitrogen fixation in refractory organic sediments by *Caulerpa taxifolia* (Chlorophyta). *Limnol. Oceanogr.* 48:787–94
- Christian JM, Wilson SD. 1999. Long-term ecosystem impacts of an introduced grass in the Northern Great plains. *Ecology* 80:2397–407
- Clark KL, Skowronski N, Hom J. 2010. Invasive insects impact forest carbon dynamics. *Glob. Change Biol.* 16:88–101
- Cobb RC, Orwig DA, Currie S. 2006. Decomposition of green foliage in eastern hemlock forests of southern New England impacted by hemlock woolly adelgid infestations. *Can. J. For. Res.* 36:1331–41
- Collins A, Jose S. 2009. *Imperata cylindrica*, an exotic invasive grass, changes soil chemical properties of forest ecosystems in the southeastern United States. In *Invasive Plants and Forest Ecosystems*, ed. RK Kohli, S Jose, HP Singh, DR Batish, pp. 237–50. Boca Raton, FL: CRC Press
- Costello DM, Lamberti GA. 2009. Biological and physical effects of non-native earthworms on nitrogen cycling in riparian soils. *Soil Biol. Biochem.* 41:2230–35
- Croll DA, Maron JL, Estes JA, Danner EM, Byrd GV. 2005. Introduced predators transform subarctic islands from grassland to tundra. *Science* 307:1959–61
- Crooks JA. 2002. Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97:153–66
- Cuddington K, Byers JE, Wilson WG, Hastings A, eds. 2007. *Ecosystem Engineers: Plants to Protists*. San Diego, CA: Academic/Elsevier. 405 pp.**
- Daley MJ, Phillips NG, Pettijohn C, Hadley JL. 2007. Water use by eastern hemlock (*Tsuga canadensis*) and black birch (*Betula lenta*): implications of effects of the hemlock woolly adelgid. *Can. J. For. Res.* 37:2031–40
- D'Antonio CM, Dudley TL, Mack MC. 1999. Disturbance and biological invasions: direct effects and feedbacks. In *Ecosystems of Disturbed Ground*, ed. LR Walker, pp. 413–52. Amsterdam: Elsevier
- Davis MA. 2009. *Invasion Biology*. Oxford, UK: Oxford Univ. Press. 264 pp.
- DeFauw SL, Vogt JT, Boykin DL. 2008. Influence of mound construction by red and hybrid imported fire ants on soil chemical properties and turfgrass in a sod production agroecosystem. *Insect. Soc.* 55:301–12
- Didham RK, Tylianakis JM, Hutchison MA, Ewers RM, Gemmell NJ. 2005. Are invasive species the drivers of ecological change? *Trends Ecol. Evol.* 20:470–74
- Drenovsky RE, Batten KM. 2007. Invasion by *Aegilops triuncialis* (barb goatgrass) slows carbon and nutrient cycling in a serpentine grassland. *Biol. Invasions* 9:107–16
- Duda JJ, Freeman CD, Emlen JM, Belnap J, Kitchen SG, et al. 2003. Differences in native soil ecology associated with invasion of the exotic annual chenopod, *Halogeton glomeratus*. *Biol. Fertil. Soils* 38:72–77
- Dunham AE, Mikheyev AS. 2010. Influence of an invasive ant on grazing and detrital communities and nutrient fluxes in a tropical forest. *Divers. Distrib.* 16:33–42
- Dye P, Jarman C. 2004. Water use by black wattle (*Acacia mearnsii*): implications for the link between removal of invading trees and catchment streamflow response. *S. Afr. J. Sci.* 100:40–44
- Ehrenfeld JG. 2003. Effect of exotic plant invasions on soil nutrient cycling processes. *Ecosystems* 6:503–23
- Ehrenfeld JG, Kourtev P, Huang W. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecol. Appl.* 11:1287–300
- Ehrenfeld JG, Ravit B, Elgersma K. 2005. Feedback in the plant-soil system. *Annu. Rev. Environ. Resour.* 30:75–115
- Eisenhauer N, Partsch S, Parkinson D, Scheu S. 2007. Invasion of a deciduous forest by earthworms: changes in soil chemistry, microflora, microarthropods and vegetation. *Soil Biol. Biochem.* 39:1099–110
- Ellison AM, Bank MS, Clinton BD, Colburn EA, Elliott K, et al. 2005. Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front. Ecol. Environ.* 3:479–86
- Enloe SF, DiTomaso JM, Orloff SB, Drake DJ. 2004. Soil water dynamics differ among rangeland plant communities dominated by yellow starthistle (*Centaurea solstitialis*), annual grasses, or perennial grasses. *Weed Sci.* 52:929–35
- Eshleman KN, Morgan RP, Webb JR, Deviney FA, Galloway JN. 1998. Temporal patterns of nitrogen leakage from mid-Appalachian forested watersheds: role of insect defoliation. *Water Resour. Res.* 34:2005–16

Provides a comprehensive analysis of ecosystem engineering that highlights many invasive species.

- Evans RD, Rimer R, Sperry L, Belnap J. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecol. Appl.* 11:1301–10
- Eviner VT, Chapin FSI. 2003. Functional matrix: a conceptual framework for predicting multiple plant effects on ecosystem processes. *Annu. Rev. Ecol. Evol. Syst.* 34:455–85
- Fickbohm SS, Zhu WX. 2006. Exotic purple loosestrife invasion of native cattail freshwater wetlands: effects on organic matter distribution and soil nitrogen cycling. *Appl. Soil Ecol.* 32:123–31
- Figueredo CC, Giani A. 2005. Ecological interactions between Nile tilapia (*Oreochromis niloticus*, L.) and the phytoplanktonic community of the Furnas Reservoir (Brazil). *Freshw. Biol.* 50:1391–403
- Fisk MC, Fahey TJ, Groffman PM, Bohlen PJ. 2004. Earthworm invasion, fine-root distributions, and soil respiration in north temperate forests. *Ecosystems* 7:55–62
- Ford CR, Vose JM. 2007. *Tsuga canadensis* (L.) Carr. mortality will impact hydrologic processes in southern Appalachian forest ecosystems. *Ecol. Appl.* 17:1156–67
- Fukami T, Wardle DA, Bellingham PJ, Mulder CPH, Towns DR, et al. 2006. Above- and below-ground impacts of introduced predators in seabird-dominated island ecosystems. *Ecol. Lett.* 9:1299–307
- Funk JL, Vitousek PM. 2007. Resource-use efficiency and plant invasion in low-resource systems. *Nature* 446:1079–81
- Gamfeldt L, Hillebrand H. 2008. Biodiversity effects on aquatic ecosystem functioning—maturation of a new paradigm. *Int. Rev. Hydrobiol.* 93:550–64
- Gandhi KJK, Herms DA. 2010. Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biol. Invasions* 12:389–405**
- Gerlach JD. 2004. The impacts of serial land-use changes and biological invasions on soil water resources in California, USA. *J. Arid Environ.* 57:365–79
- Gómez-Aparicio L, Canham CD. 2008. Neighborhood models of the effects of invasive tree species on ecosystem processes. *Ecol. Monogr.* 78:69–86
- Gorgens AHM, van Wilgen BW. 2004. Invasive alien plants and water resources in South Africa: current understanding, predictive ability and research challenges. *S. Afr. J. Sci.* 100:27–33
- Green WP, Pettry DE, Switzer RE. 1999. Structure and hydrology of mounds of the imported fire ants in the southeastern United States. *Geoderma* 93:1–17
- Hale CM, Frelich LE, Reich PB, Pastor J. 2005. Effects of European earthworm invasion on soil characteristics in northern hardwood forests of Minnesota, USA. *Ecosystems* 8:911–27
- Hall RO, Dybdahl MF, VanderLoop MC. 2006. Extremely high secondary production of introduced snails in rivers. *Ecol. Appl.* 16:1121–31
- Hall SJ, Asner GP. 2007. Biological invasion alters regional nitrogen-oxide emissions from tropical rainforests. *Glob. Change Biol.* 13:2143–60
- Harner MJ, Crenshaw CL, Abelho M, Stursova M, Shah JFF, Sinsabaugh RL. 2009. Decomposition of leaf litter from a native tree and an actinorhizal invasive across riparian habitats. *Ecol. Appl.* 19:1135–46
- Hecky RE, Smith REH, Barton DR, Guildford SJ, Taylor WD, et al. 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. *Can. J. Fish. Aquat. Sci.* 61:1285–93
- Henderson S, Dawson TP, Whittaker RJ. 2006. Progress in invasive plants research. *Prog. Phys. Geogr.* 30:25–46
- Hietanen S, Laine AO, Lukkari K. 2007. The complex effects of the invasive polychaetes *Marenzelleria* spp. on benthic nutrient dynamics. *J. Exp. Mar. Biol. Ecol.* 352:89–102
- Hladyz S, Gessner MO, Giller PS, Pozo J, Woodward G. 2009. Resource quality and stoichiometric constraints on stream ecosystem functioning. *Freshw. Biol.* 54:957–70
- Hooper DU, Chapin FS, Ewel JJ, Hector A, Inchausti P, et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.* 75:3–35
- Howard TG, Gurevitch J, Hyatt L, Carreiro M, Lerdau M. 2004. Forest invasibility in communities in southeastern New York. *Biol. Invasions* 6:393–410
- Huggett RJ. 1998. Soil chronosequences, soil development, and soil evolution: a critical review. *Catena* 32:155–72
- Hughes RF, Denslow JS. 2005. Invasion by a N₂-fixing tree alters function and structure in wet lowland forests of Hawaii. *Ecol. Appl.* 15:1615–28

- Hughes RF, Uowolo A. 2006. Impacts of *Falcataria moluccana* invasion on decomposition in Hawaiian lowland wet forests: the importance of stand-level controls. *Ecosystems* 9:977–91
- Hummel M, Findlay S. 2006. Effects of water chestnut (*Trapa natans*) beds on water chemistry in the tidal freshwater Hudson River. *Hydrobiologia* 559:169–81
- Huxman TE, Cable JM, Ignace DD, Eilts JA, English NB, et al. 2004. Response of net ecosystem gas exchange to a simulated precipitation pulse in a semiarid grassland: the role of native versus non-native grasses and soil texture. *Oecologia* 141:295–305
- Jenkins JC, Aber JD, Canham CD. 1999. Hemlock woolly adelgid impacts on community structure and N cycling rates in eastern hemlock forests. *Can. J. For. Res.* 29:630–45
- Karberg NJ, Lilleskov EA. 2009. White-tailed deer (*Odocoileus virginianus*) fecal pellet decomposition is accelerated by the invasive earthworm *Lumbricus terrestris*. *Biol. Invasions* 11:761–67
- Kenis M, Auger-Rozenberg M-A, Roques A, Timms L, Péré C, et al. 2009. Ecological effects of invasive alien insects. *Biol. Invasions* 11:21–45
- Klein J, Verlaque M. 2008. The *Caulerpa racemosa* invasion: a critical review. *Mar. Pollut. Bull.* 56:205–25
- Koutika LS, Vanderhoeven S, Chapuis-Lardy L, Dassonville N, Meerts P. 2007. Assessment of changes in soil organic matter after invasion by exotic plant species. *Biol. Fertil. Soils* 44:331–41
- Kulmatiski A, Beard KH, Stark JM. 2006. Soil history as a primary control on plant invasion in abandoned agricultural fields. *J. Appl. Ecol.* 43:868–76
- Lach L, Hooper-Bùi LM. 2010. Consequences of ant invasions. In *Ant Ecology*, ed. L Lach, CL Parr, KL Abbott, pp. 261–87. New York: Oxford Univ. Press
- Larned ST. 2003. Effects of the invasive, nonindigenous seagrass *Zostera japonica* on nutrient fluxes between the water column and benthos in a NE Pacific estuary. *Mar. Ecol. Prog. Ser.* 254:69–80
- Lecerf A, Patfield D, Boiche A, Riipinen MP, Chauvet E, Dobson M. 2007. Stream ecosystems respond to riparian invasion by Japanese knotweed (*Fallopia japonica*). *Can. J. Fish. Aquat. Sci.* 64:1273–83
- Leishman MR, Thomson VP, Cooke J. 2010. Native and exotic invasive plants have fundamentally similar carbon capture strategies. *J. Ecol.* 98:28–42
- Levine JM, Vila M, D'Antonio CM, Dukes JS, Grigulis K, Lavelle S. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proc. R. Soc. Lond. Ser. B* 270:775–81
- Ley RE, D'Antonio CM. 1998. Exotic grass invasion alters potential rates of N fixation in Hawaiian woodlands. *Oecologia* 113:179–87
- Li XY, Fisk MC, Fahey TJ, Bohlen PJ. 2002. Influence of earthworm invasion on soil microbial biomass and activity in a northern hardwood forest. *Soil Biol. Biochem.* 34:1929–37
- Liao C, Luo Y, Jiang L, Zhou X, Wu X, et al. 2007. Invasion of *Spartina alterniflora* enhanced ecosystem carbon and nitrogen stocks in the Yangtze Estuary, China. *Ecosystems* 10:1351–61
- Liao CZ, Peng RH, Luo YQ, Zhou XH, Wu XW, et al. 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. *New Phytol.* 177:706–14
- Litton CM, Sandquist DR, Cordell S. 2006. Effects of non-native grass invasion on aboveground carbon pools and tree population structure in a tropical dry forest of Hawaii. *For. Ecol. Manag.* 231:105–13
- Lovett GM, Christenson LM, Groffman PM, Jones CG, Hart JE, Mitchell MJ. 2002. Insect defoliation and nitrogen cycling in forests. *BioScience* 52:335–41
- Mack M, D'Antonio CM. 2003. Exotic grasses alter controls over soil nitrogen dynamics in a Hawaiian woodland. *Ecol. Appl.* 13:154–66
- Mahaney WM, Smemo KA, Yavitt JB. 2006. Impacts of *Lythrum salicaria* invasion on plant community and soil properties in two wetlands in central New York, USA. *Can. J. Bot.* 84:477–84
- Marais C, Wannenburgh AM. 2008. Restoration of water resources (natural capital) through the clearing of invasive alien plants from riparian areas in South Africa—costs and water benefits. *S. Afr. J. Bot.* 74:526–37
- Marchante E, Kjoller A, Struwe S, Freitas H. 2008. Short- and long-term impacts of *Acacia longifolia* invasion on the belowground processes of a Mediterranean coastal dune ecosystem. *Appl. Soil Ecol.* 40:210–17
- Martin MR, Tipping PW, Sickman JO. 2009. Invasion by an exotic tree alters above and belowground ecosystem components. *Biol. Invasions* 11:1883–94
- Martin S, Thouzeau G, Richard M, Chauvaud L, Jean F, Clavier J. 2007. Benthic community respiration in areas impacted by the invasive mollusk *Crepidula fornicata*. *Mar. Ecol. Prog. Ser.* 347:51–60

Provides the most comprehensive analysis of changes to specific pools and fluxes from plant invasions currently available.

- Miehls ALJ, Mason DM, Frank KA, Krause AE, Peacor SD, Taylor WW. 2009a. Invasive species impacts on ecosystem structure and function: a comparison of Oneida Lake, New York, USA, before and after zebra mussel invasion. *Ecol. Model.* 220:3194–209
- Miehls ALJ, Mason DM, Frank KA, Krause AE, Peacor SD, Taylor WW. 2009b. Invasive species impacts on ecosystem structure and function: a comparison of the Bay of Quinte, Canada, and Oneida Lake, USA, before and after zebra mussel invasion. *Ecol. Mod.* 220:3182–93
- Mulder CPH, Grant-Hoffman MN, Towns DR, Bellingham PJ, Wardle DA, et al. 2009. Direct and indirect effects of rats: Does rat eradication restore ecosystem functioning of New Zealand seabird islands? *Biol. Invasions* 11:1671–88
- Nepstad D. 2002. Forest fires: behavior and ecological effects. *Nature* 415:476
- Nuckolls AE, Wurzbarger N, Ford CR, Hendrick RL, Vose JM, Kloeppel BD. 2009. Hemlock declines rapidly with hemlock woolly adelgid infestation impacts on the carbon cycle of southern Appalachian forests. *Ecosystems* 12:179–90
- O'Dowd DJ, Green PT, Lake PS. 2003. Invasional 'meltdown' on an oceanic island. *Ecol. Lett.* 6:812–18
- Ogle SM, Reiners WA, Gerow KG. 2003. Impacts of exotic annual brome grasses (*Bromus* spp.) on ecosystem properties of northern mixed grass prairie. *Am. Midl. Nat.* 149:46–58
- Orwig DA, Cobb RC, D'Amato AW, Kizlinski ML, Foster DR. 2008. Multi-year ecosystem response to hemlock woolly adelgid infestation in southern New England forests. *Can. J. For. Res.* 38:834–43
- Pace ML, Groffman PM, eds. 1998. *Successes, Limitations, and Frontiers in Ecosystem Science*. New York: Springer. 499 pp.
- Parker IM, Gilbert GS. 2004. The evolutionary ecology of novel plant-pathogen interactions. *Annu. Rev. Ecol. Syst.* 35:675–700
- Pauchard A, Garcia RA, Pena E, Gonzalez C, Cavieres LA, Bustamante RO. 2008. Positive feedbacks between plant invasions and fire regimes: *Teline monspessulana* (L.) K. Koch (Fabaceae) in central Chile. *Biol. Invasions* 10:547–53
- Pejchar L, Mooney HA. 2009. Invasive species, ecosystem services and human well-being. *Trends Ecol. Evol.* 24:497–504
- Polis GA, Anderson WB, Holt RD. 1999. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. *Annu. Rev. Ecol. Syst.* 28:289–316
- Potts DL, Harpole WS, Goulden ML, Suding KN. 2008. The impact of invasion and subsequent removal of an exotic thistle, *Cynara cardunculus*, on CO₂ and H₂O vapor exchange in a coastal California grassland. *Biol. Invasions* 10:1073–84
- Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, et al. 1996. Challenges in the quest for keystones. *BioScience* 46:609–20
- Pringle A, Bever JD, Gardes M, Parrent JL, Rillig MC, Klironomos JN. 2009. Mycorrhizal symbioses and plant invasions. *Annu. Rev. Ecol. Syst.* 40:699–715
- Ragueneau O, Chauvaud L, Moriceau B, Leynaert A, Thouzeau G, et al. 2005. Biodeposition by an invasive suspension feeder impacts the biogeochemical cycle of Si in a coastal ecosystem (Bay of Brest, France). *Biogeochemistry* 75:19–41
- Raizada P, Raghubanshi AS, Singh JS. 2008. Impact of invasive alien plant species on soil processes: a review. *Proc. Natl. Acad. Sci. India B* 78:288–98
- Reinhart KO, Callaway RM. 2006. Soil biota and invasive plants. *New Phytol.* 170:445–57
- Reinhart KO, VandeVoort R. 2006. Effect of native and exotic leaf litter on macroinvertebrate communities and decomposition in a western Montana stream. *Divers. Distrib.* 12:776–81
- Reiss J, Bridle JR, Montoya JM, Woodward G. 2009. Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. Evol.* 24:505–14
- Richardson DM, Pysek P, Rejmanek M, Barbour MT, Panetta FD, West CJ. 2000. Naturalization and invasion of alien plants: concepts and definitions. *Divers. Distrib.* 6:93–107
- Rice SK, Westerman B, Federici R. 2004. Impacts of the exotic, nitrogen-fixing black locust (*Robinia pseudo-acacia*) on nitrogen cycling in a pine-oak ecosystem. *Plant Ecol.* 174:97–107
- Riscassi AL, Scanlon TM. 2009. Nitrate variability in hydrological flow paths for three mid-Appalachian forested watersheds following a large-scale defoliation. *J. Geophys. Res.* 114:G02009

- Rodgers VL, Wolfe BE, Werden LK, Finzi AC. 2008. The invasive species *Alliaria petiolata* (garlic mustard) increases soil nutrient availability in northern hardwood-conifer forests. *Oecologia* 157:459–71
- Rodriguez-Echeverria S, Crisóstomo JA, Nabais C, Freitas H. 2009. Belowground mutualists and the invasive ability of *Acacia longifolia* in coastal dunes of Portugal. *Biol. Invasions* 11:651–61
- Rossiter-Rachor NA, Setterfield SA, Douglas MM, Hutley LB, Cook GD. 2008. *Andropogon gayanus* (gamba grass) invasion increases fire-mediated nitrogen losses in the tropical savannas of northern Australia. *Ecosystems* 11:77–88
- Rossiter-Rachor NA, Setterfield SA, Douglas MM, Hutley LB, Cook GD, Schmidt S. 2009. Invasive *Andropogon gayanus* (gamba grass) is an ecosystem transformer of nitrogen relations in Australian savanna. *Ecol. Appl.* 19:1546–60
- Rout ME, Callaway RM. 2009. An invasive plant paradox. *Science* 324:734–35
- Rout ME, Chrzanowski TH. 2009. The invasive *Sorghum halepense* harbors endophytic N₂-fixing bacteria and alters soil biogeochemistry. *Plant Soil* 315:163–72
- Ruesink JL, Feist BE, Harvey CJ, Hong JS, Trimble AC, Wisheart LM. 2006. Changes in productivity associated with four introduced species: ecosystem transformation of a “pristine” estuary. *Mar. Ecol. Prog. Ser.* 311:203–15
- Ruesink JL, Lenihan HS, Trimble AC, Heiman KW, Micheli F, et al. 2005. Introduction of non-native oysters: ecosystem effects and restoration implications. *Annu. Rev. Ecol. Evol. Syst.* 36:643–89
- Schäfer KVR, Clark KL, Skowronski N, Hamerlynck EP. 2009. Impact of insect defoliation on forest carbon balance as assessed with a canopy assimilation model. *Glob. Change Biol.* 16(2):546–60
- Scharfy D, Eggenschwiler H, Venterink HO, Edwards PJ, Gusewell S. 2009. The invasive alien plant species *Solidago gigantea* alters ecosystem properties across habitats with differing fertility. *J. Veg. Sci.* 20:1072–85
- Scheffer M, Szabo S, Gragnani A, van Nes EH, Rinaldi S, et al. 2003. Floating plant dominance as a stable state. *Proc. Natl. Acad. Sci. USA* 100:4040–45
- Scherer-Lorenzen M, Olde Venterink H, Buschmann H. 2008. Nitrogen enrichment and plant invasions: the importance of nitrogen-fixing plants and anthropogenic eutrophication. In *Biological Invasions*, ed. W Nentwig, pp. 163–80. Berlin: Springer
- Shafroth PB, Cleverly JR, Dudley TL, Taylor JP, Van Riper C, et al. 2005. Control of *Tamarix* in the Western United States: implications for water salvage, wildlife use, and riparian restoration. *Environ. Manag.* 35:231–46
- Shurin JB, Borer ET, Seabloom EW, Anderson K, Blanchette CA, et al. 2002. A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.* 5:785–91
- Simberloff D. 2009. Rats are not the only introduced rodents producing ecosystem impacts on islands. *Biol. Invasions* 11:1735–42
- Simberloff D. 2010. Invasions of plant communities—more of the same, something very different, or both? *Am. Midl. Nat.* 163:219–32
- Sin H, Beard KH, Pitt WC. 2008. An invasive frog, *Eleutherodactylus coqui*, increases new leaf production and leaf litter decomposition rates through nutrient cycling in Hawaii. *Biol. Invasions* 10:335–45
- Snyder WE, Evans EW. 2006. Ecological effects of invasive arthropod generalist predators. *Annu. Rev. Ecol. Evol. Syst.* 37:95–122
- Sousa R, Gutierrez JL, Aldridge DC. 2009. Non-indigenous invasive bivalves as ecosystem engineers. *Biol. Invasions* 11:2367–85
- Sperry L, Belnap J, Evans RD. 2006. *Bromus tectorum* invasion alters nitrogen dynamics in an undisturbed arid grassland. *Ecology* 87:603–16
- Stadler B, Muller T, Orwig D. 2006. The ecology of energy and nutrient fluxes in hemlock forests invaded by hemlock woolly adelgid. *Ecology* 87:1792–804
- Stadler B, Muller T, Orwig D, Cobb R. 2005. Hemlock woolly adelgid in New England forests: canopy impacts transforming ecosystem processes and landscapes. *Ecosystems* 8:233–47
- Sterner RW, Elser JJ. 2002. *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. Princeton, NJ: Princeton Univ. Press
- Strayer DL. 1999. Transformation of freshwater ecosystems by bivalves. *BioScience* 49:19–28
- Strayer DL. 2009. Twenty years of zebra mussels: lessons from the mollusk that made headlines. *Front. Ecol. Environ.* 7:135–41

Overviews all types of marine invaders, with attention to chemical and physical changes.

Surveys invasive grass effects on ecosystem processes.

- Tansley AG. 1935. The use and abuse of vegetational concepts and terms. *Ecology* 16:204–307
- Tecco PA, Diaz S, Cabido M, Urcelay C. 2010. Functional traits of alien plants across contrasting climatic and land-use regimes: Do aliens join the locals or try harder than them? *J. Ecol.* 98:17–27
- Tickner DP, Angold PG, Gurnell AM, Mountford JO. 2001. Riparian plant invasions: hydrogeomorphological control and ecological impacts. *Prog. Phys. Geogr.* 25:22–52
- Townsend PA, Eshleman KN, Welcker C. 2004. Remote sensing of gypsy moth defoliation to assess variations in stream nitrogen concentrations. *Ecol. Appl.* 14:504–16
- Travaset A, Richardson DM. 2006. Biological invasions as disruptors of plant reproductive mutualisms. *Trends Ecol. Evol.* 21:208–16
- Tuttle NC, Beard KH, Pitt WC. 2009. Invasive litter, not an invasive insectivore, determines invertebrate communities in Hawaiian forests. *Biol. Invasions* 11:845–55
- Vanderhoeven S, Dassonville N, Chapuis-Lardy L, Hayez M, Meerts P. 2006. Impact of the invasive alien plant *Solidago gigantea* on primary productivity, plant nutrient content and soil mineral nutrient concentrations. *Plant Soil* 286:259–68
- van der Putten WH, Klironomos JN, Wardle DA. 2007. Microbial ecology of biological invasions. *ISME J.* 1:28–37
- van Kleunen M, Weber E, Fischer M. 2010. A meta-analysis of trait differences between invasive and noninvasive plant species. *Ecol. Lett.* 13:235–45
- Vitousek PM, Walker L. 1989. Biological invasion by *Myrica faya* in Hawai'i: plant demography, nitrogen fixation, ecosystem effects. *Ecol. Monogr.* 59:247–65
- Wallentinus I, Nyberg CD. 2007. Introduced marine organisms as habitat modifiers. *Mar. Pollut. Bull.* 55:323–32**
- Wan SQ, Hui DF, Luo YQ. 2001. Fire effects on nitrogen pools and dynamics in terrestrial ecosystems: a meta-analysis. *Ecol. Appl.* 11:1349–65
- Webster CR, Jenkins MA, Jose S. 2006. Woody invaders and the challenges they pose to forest ecosystems in the eastern United States. *J. For.* 104:366–74
- Williams DG, Baruch Z. 2000. African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. *Biol. Invasions* 2:123–40**
- Windham L, Ehrenfeld JG. 2003. Net impact of a plant invasion on nitrogen-cycling processes within a brackish tidal marsh. *Ecol. Appl.* 13:883–96
- Yelenik SG, Stock WD, Richardson DM. 2007. Functional group identity does not predict invader impacts: differential effects of nitrogen-fixing exotic plants on ecosystem function. *Biol. Invasions* 9:117–25
- Yorks TE, Leopold DJ, Raynal DJ. 2003. Effects of *Tsuga canadensis* mortality on soil water chemistry and understory vegetation: possible consequences of an invasive insect herbivore. *Can. J. For. Res.* 33:1525–37
- Zavaleta ES, Hobbs RJ, Mooney HA. 2001. Viewing invasive species removal in a whole-ecosystem context. *Trends Ecol. Evol.* 16:454–59
- Zou JW, Rogers WE, DeWalt SJ, Siemann E. 2006. The effect of Chinese tallow tree (*Sapium sebiferum*) ecotype on soil-plant system carbon and nitrogen processes. *Oecologia* 150:272–81