

REVIEW

Effects of biological invasions on forest carbon sequestration

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Abstract

There has been a rapidly developing literature on the effects of some of the major drivers of global change on carbon (C) sequestration, particularly carbon dioxide (CO₂) enrichment, land use change, nitrogen (N) deposition and climate change. However, remarkably little attention has been given to one major global change driver, namely biological invasions. This is despite growing evidence that invasive species can dramatically alter a range of aboveground and belowground ecosystem processes, including those that affect C sequestration. In this review, we assess the evidence for the impacts of biological invaders on forest C stocks and C sequestration by biological invaders. We first present case studies that highlight a range of invader impacts on C sequestration in forest ecosystems, and draw on examples that involve invasive primary producers, decomposers, herbivores, plant pathogens, mutualists and predators. We then develop a conceptual framework for assessing the effects of invasive species on C sequestration impacts more generally, by identifying the features of biological invaders and invaded ecosystems that are thought to most strongly regulate C in forests. Finally we assess the implications of managing invasive species on C sequestration. An important principle that emerges from this review is that the direct effects of invaders on forest C are often smaller and shorter-term than their indirect effects caused by altered nutrient availability, primary productivity or species composition, all of which regulate long-term C pools and fluxes. This review provides a conceptual basis for improving our general understanding of biological invaders on ecosystem C, but also points to a paucity of primary data that are needed to determine the quantitative effects of invaders on ecosystem processes that drive C sequestration.

Keywords: biological invasion, carbon sequestration, community structure, forest ecosystem processes, herbivory, invasive species, secondary succession, soil biota, trophic interactions

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Introduction

The effects of global change on terrestrial ecosystems have generated intense debate in scientific and policy arenas, and produced a rapidly developing literature, particularly on carbon dioxide (CO₂) enrichment, land use change, nitrogen (N) deposition and climate change (Schimel *et al.*, 2001; Wardle, 2002; Wright, 2005; De Vries *et al.*, 2006). Remarkably little attention has been given to one of these major drivers, namely biological invasions (e.g. Vitousek *et al.*, 1997). This is despite growing evidence that invaders can dramatically alter

ecosystem processes, including those that affect carbon (C) sequestration (e.g. Ehrenfeld, 2003; Levine *et al.*, 2003; Wardle *et al.*, 2007). Recent studies suggest that ecosystem C stocks are altered by a wide range of invasive organisms including plants (Jackson *et al.*, 2002; Bradley *et al.*, 2006; Litton *et al.*, 2006), earthworms (Frelich *et al.*, 2006), rats (Wardle *et al.*, 2007) and deer (Wardle *et al.*, 2001). With the ongoing global increase in the number, distribution and abundance of invasive species there is an immediate need to broaden our understanding of how biological invasions influence ecosystem C sequestration.

Forest ecosystems are a primary focus for C sequestration research and policy development because of their potentially high primary production and impor-

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tance to C stocks globally (Dixon *et al.*, 1994; Schlesinger, 1997; Houghton, 2005). Forests cover about 4 billion hectares or 30% of the Earth's land surface (Brunner & Godbold, 2007). However, evidence is accumulating that many forests are not at biomass equilibrium even at large spatial scales (e.g. Fan *et al.*, 1998; Luysaert *et al.*, 2008). As a consequence, international agreements, such as the Kyoto Protocol and Montreal Process, require signatory countries to both manage and monitor changes in C stocks in forest ecosystems (e.g. IPCC, 2008). Management of C sequestration in forests is an option for offsetting emissions and trading in C credits (e.g. Hyvönen *et al.*, 2007). We suggest that invasive species management has important implications for C sequestration in forests yet has been widely overlooked to date.

Invasive species can cause dramatic landscape-level transformations of forests by altering disturbance regimes, nutrient cycling and both above- and below-ground ecosystem properties (e.g. Mack *et al.*, 2000; Ehrenfeld, 2003; van der Putten *et al.*, 2007). Some well-documented examples include Dutch elm disease and chestnut blight in eastern US forests (Lovett *et al.*, 2006a), *Phytophthora*-induced forest dieback syndromes in Australia, the United States and central Europe (Condeso & Meentemeyer, 2007), and invasive mammals in Australia and New Zealand (Allen & Lee, 2006). However, the short- and long-term C sequestration effects of these biological invaders, representing different trophic levels, are poorly understood. Furthermore, the consequences for C sequestration of the invader will also depend on the attributes of the forest it invades (cf. Lovett *et al.*, 2006a). In this review, we first present case studies highlighting a range of invader impacts on C sequestration in forests, then develop a conceptual framework for assessing invasive species C sequestration impacts more generally, and finally summarize the implications for managing invasive species for C sequestration.

Case studies of effects of functionally different invaders on C sequestration

C sequestration is the difference between C input (gross primary productivity, GPP) and C loss (respiration, leaching, and disturbances e.g. from herbivory and fire) from an ecosystem (Lovett *et al.*, 2006b). This balance between C inputs and outputs can be directly influenced by invasive primary producers, consumers, mutualists, pathogens, and decomposers (Fig. 1) by altering C fixation, consumption and respiration. Recent studies have also demonstrated important indirect effects of biological invaders on C stocks through, for example, predation on native ecosystem engineers

(Wardle *et al.*, 2007) and altering the dominance of 'foundation' species (*sensu* Ellison *et al.*, 2005). Despite this growing literature, almost no studies have explicitly addressed the issue of whether biological invaders alter ecosystem C stocks and have quantified changes only in one or two pools of C (Liao *et al.*, 2008). Invasive species influence C sequestration both over short-term scales (weeks to years) by directly affecting rates of primary production or decomposition, and over long-term scales (decades and beyond) by causing compositional changes in the dominant tree species (e.g. Bunker *et al.*, 2007; see also Table 1). We illustrate direct and indirect effects over different time scales by considering the influence of contrasting biological invaders on C sequestration processes.

Primary producers

Invasive primary producers directly affect ecosystem NPP through their own photosynthesis and respiration, and indirectly through affecting decomposition processes and nutrient fluxes (De Deyn *et al.*, 2008; Fig. 2a). Invasive, non-native plants are widely thought to be more productive than co-occurring native species because of a coordinated set of functional traits that include relatively rapid growth and high foliar nutrient contents as well as the absence of enemies or pathogens from their home range (Sutherland, 2004; Mitchell *et al.*, 2006; Vile *et al.*, 2006; Leishman *et al.*, 2007; Blumenthal *et al.*, 2009; Peltzer *et al.*, 2009). Further, litter from invaders is often more decomposable than native species (e.g. Allison & Vitousek, 2004; Litton *et al.*, 2008), potentially resulting in higher nutrient availability and primary production but also more rapid loss of organic matter from the ecosystem compared with uninvaded systems; the net effects of these processes could either increase or decrease net C sequestration. The importance of indirect effects through interactions with other species from a range of trophic levels is less well understood (Ellison *et al.*, 2005; Didham *et al.*, 2007; Sax *et al.*, 2007).

The best-documented indirect effect of plant invaders on C stocks is via altered disturbance regimes. Invasive grasses have increased fire frequency or intensity in woody systems globally compared with uninvaded systems, including in the western United States, Hawai'i, Brazil, and Australia (D'Antonio & Vitousek, 1992; Hoffman *et al.*, 2004; Bradley *et al.*, 2006; Litton *et al.*, 2006). For example, invasion by the highly productive Gamba grass (*Andropogon gayanus*) into tropical savannas of northern Australia increases fire fuel loads seven-fold and fire intensities eight-fold compared with native-dominated systems (1.54 vs. 0.36 kg m⁻² and 15.7 vs. 2.1 MW m⁻² for invaded and native vegetation respectively; Rossiter

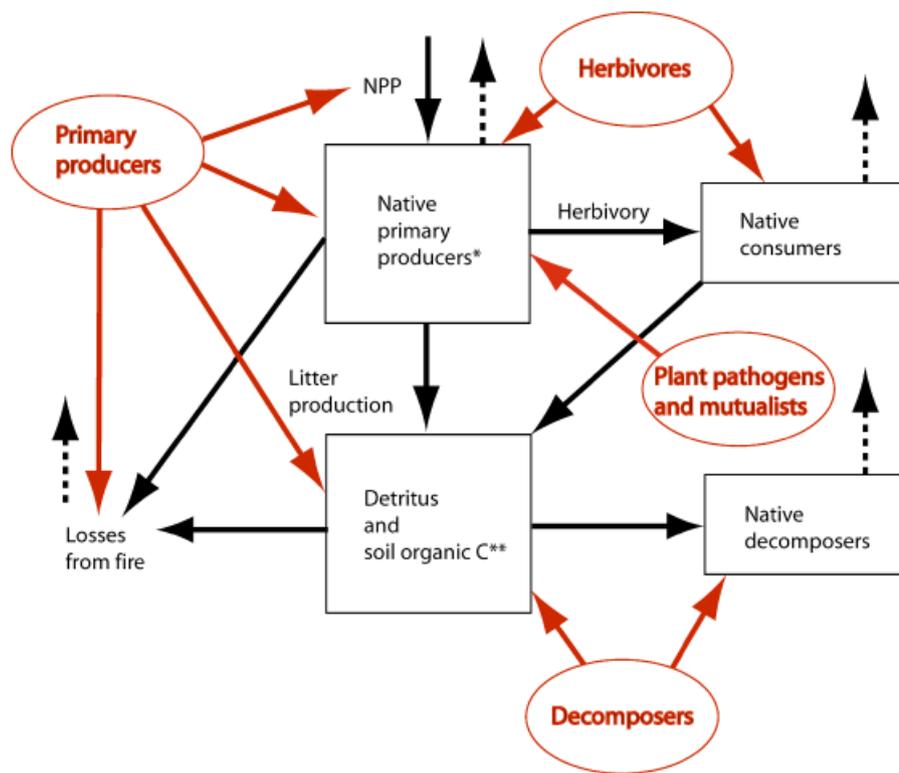


Fig. 1 Major pools (boxes) and fluxes (arrows) of carbon (C) in forest ecosystems. Dashed arrows represent losses to the atmosphere through respiration or combustion. Different trophic levels of invasive species (in red) affect different parts of the C cycle. Most C storage is in the pools marked with asterisks.

et al., 2003). Further, most trees survive fire intensities of 2.1 MW m^{-2} whereas more intense fires associated with Gamba grass increase large tree mortality ($>0.35 \text{ m DBH}$: diameter at breast height) and nearly eliminate small ($<0.10 \text{ m DBH}$) trees (Cook *et al.*, 2005). This results in a 2–25% decline in live tree C by single fires in addition to the nonbiological oxidation and loss of C. In contrast, C sequestration of uninvaded woodlands in neighbouring Queensland over 14 years was $0.37 \text{ t C ha}^{-1} \text{ yr}^{-1}$, a 9% gain in live tree C (Burrows *et al.*, 2002). Thus, increased fire intensity associated with Gamba grass invasion alters tree population size structures toward increasing dominance by intermediate-size trees, reducing current live-tree C stocks and the potential for future C sequestration.

Although the increasing distribution and abundance of invasive plant species globally is well documented, there are surprisingly few studies specifically addressing the long-term consequences for C sequestration (Strayer *et al.*, 2006; Ostertag *et al.*, 2009). In addition, invader effects on C sequestration can be context-dependent and interact with abiotic factors such as climatic regime (e.g. Jackson *et al.*, 2002) suggesting that broader, cross-system primary data are needed for the

development of meaningful generalizations (e.g. Biggs *et al.*, 2009).

Detritivores and decomposers

The soil microbial community and soil invertebrates regulate organic matter decomposition rates and thus C and nutrient fluxes, which in turn feed back to influence aboveground communities and primary productivity (Wardle *et al.*, 2004; Fig. 2b). There is an increasing awareness that belowground invaders, including detritivores and decomposers, can have wide-ranging effects in ecosystems and on other trophic levels both above- and belowground (De Deyn *et al.*, 2004; Yeates & Williams, 2006; van der Putten *et al.*, 2007).

One of the best documented invasions by soil organisms is that of burrowing earthworms (e.g. *Dendrobaena octaedra*, *Lumbricus terrestris*, and *L. rubellus*) into temperate forests of North America. Earthworms change soil processes by altering soil structure through burrowing and casting, processing litter and redistributing organic matter (Hale *et al.*, 2005; Hendrix *et al.*, 2008). These effects reduce the dominance of fungi (including mycorrhizal species) relative to bacteria in the soil, and

Table 1 Summary of distinguishing features and common direct and indirect effects on carbon (C) balance or sequestration by invasive species from different trophic levels (see also Figs 1 and 2)

Trophic level	Common pathways of influence on C balance		
	Direct effects	Indirect effects	Examples of functional traits
Primary producers	C fixation (NPP). Direct influence of C pools through litter quality and quantity, exudates, insolation, nutrient uptake, and hydrological processes. Respiration	Interactions with other trophic levels. Alteration of nutrient cycles. Habitat for other species. Can have major influence on physical disturbance regime (i.e. combustibility)	Photosynthetic rate (A_{\max}) Litter production Nutrient resorption proficiency Litter quality Fuel load for fires
Decomposers (microbes and detritivores)	Regulation of decomposition and soil. Alteration of physical soil structure and organic matter pools. Influence rates of detritus processing (e.g. includes saprophytic fungi, soil microbes, mesofauna, etc.). Respiration	Cascading effects in soil food webs. Alteration of nutrient cycling. Feedbacks to plant community composition and NPP	Exoenzyme production Bioperturbation Trophic position in soil food web Substrate specificity Assimilation efficiency
Herbivores	Consumption of NPP (can include generalist and specialist consumers (i.e. folivores, root feeders, stem feeders)) Respiration	Feedbacks with soil fertility. Diet choice can alter plant species composition and relative abundance, plant–soil feedbacks and long-term forest C balance. Regulation of plant C fixation rates. Alteration of C quality. Movement and recycling of nutrients (N, P, K)	Basal metabolic rate Mass Gut length Assimilation efficiency Host specificity Lethality to host
Pathogens	Consumption of NPP. Respiration. Specialised consumption of other trophic levels	Selective damage to hosts can alter plant species composition and relative dominance. Particularly well developed boom-bust cycles in insect herbivores alter temporal patterns of NPP, decomposition, etc.	Mode of action <i>Per capita</i> influence on host performance Population growth Host specificity Lethality to host
Mutualists	Alteration of NPP (both + and–). Respiration	Selective benefit can alter plant species composition and relative dominance. Most effects are mediated in conjunction with host species	Host specificity Enzyme secretion Nutrient uptake apparatus Per unit mass influence on host performance
Predators	Consumption of herbivores and other predators. Respiration	Top-down cascading trophic effects. Specialized consumption of other trophic levels can alter species composition and dominance	<i>Per capita</i> consumption Specificity for prey Assimilation rate

favor faster growing fungal taxa relative to slow growing ones (McLean & Parkinson, 2000); these changes would in turn be expected to lead to more rapid turnover of

microbial tissue and soil organic matter (Coleman *et al.*, 1983; Wardle, 2002). Further, invasive earthworms are well known to increase rates of nutrient cycling (notably

N and Ca) and depress the abundance and diversity of microarthropods (Scheu & Parkinson, 1994; Bohlen *et al.*, 2004a,b,c; Frelich *et al.*, 2006). Regeneration of both understory and canopy plant species can be suppressed by earthworm removal of surface organic layers; in some situations this can lead to promotion of small-seeded early successional low-biomass plant species rather than large-seeded late successional high-biomass species (Bohlen *et al.*, 2004b; Frelich *et al.*, 2006). Thus, earthworms cannot only affect long-term forest C balance through soil C loss but also by promoting low-biomass early successional tree species in some cases.

Invasive earthworms illustrate how invasive decomposers and detritivores may be expected to alter forest soil C directly through decomposition or litter consumption, and C sequestration indirectly via altered biogeochemical processes and complex interactions with species from other trophic levels. These effects can be generalized to invasive decomposers, and illustrate the crucial role that decomposers and detritivores have in controlling both energy flow and nutrient cycling in forest ecosystems that can strongly influence long-term C sequestration.

Mammalian herbivores

The direct effects of introduced herbivores on forests through the consumption of seeds, cambium, roots or foliage have been extensively studied. Introduced herbivores may increase canopy disturbance through, for example, felling of trees (e.g. beavers reintroduced to Finland and invasive in Chile: Harkonen, 1999; Jaksic *et al.*, 2002) and defoliation (e.g. brushtail possums in New Zealand: Nugent *et al.*, 2001). These direct effects can regulate recruitment, growth, and mortality of trees (e.g. Coomes *et al.*, 2003; Husheer *et al.*, 2006), with potentially important consequences for C sequestration (Waring & Schlesinger, 1985). Further, introduced herbivores can indirectly affect C in the soil through influencing the quantity and quality of resources returned to the soil, and several mechanisms have been proposed that can have either positive or negative consequences for net belowground C sequestration (e.g. Bardgett & Wardle, 2003; De Deyn *et al.*, 2008). In the longer term, the direct and indirect effects of herbivory drive both structural (e.g. biomass) and compositional (e.g. plant and soil biotic community) adjustments in forests and cause ongoing changes in forest ecosystem C stocks (Fig. 2c).

The consequences of excluding introduced mammalian herbivores (primarily deer and goats) have been studied in relatively intact natural forests throughout New Zealand (Wardle *et al.*, 2001). These mammals were first introduced 220 years ago when the forests

did not have large herbivores present; they rapidly became overabundant but are now subjected to widespread control (e.g. Allen & Lee, 2006). Over recent decades, exclusion studies generally show an increase in palatable understory shrub density inside fenced areas and usually an increase in unpalatable understory shrubs outside (e.g. Wardle *et al.*, 2001). Wardle *et al.* (2001) used a national network of exclosures to test the hypothesis that dominance of unpalatable plant species would reduce litter quality and decomposability, thereby increasing soil C storage. Instead they found that soil C responded idiosyncratically and suggested that this variability resulted from the multiple processes that regulate soil C storage (see Bardgett & Wardle, 2003). We know of no studies that have quantified the rates of C cycling processes involved here or whether these effects were caused by variation in C quality rather than quantity *per se*, and thus the underlying causes of idiosyncratic soil C responses to invasive herbivores.

The most profound effect of herbivores on forest C sequestration will occur when herbivory not only increases canopy disturbance, but also disrupts subsequent recovery of tree species. Whether introduced mammalian herbivores increase or decrease C sequestration in forest ecosystems will likely be context dependent, according to the stage of forest development, soil fertility, and functional traits of the dominant tree species (discussed in 'Features of forest ecosystem', see also Pastor & Post, 1986; Bardgett & Wardle, 2003).

Insect herbivores and plant pathogens

The impacts of insect pests and plant diseases on forest C sequestration include direct effects of increased tree mortality and decreased productivity as well as indirect effects that ramify through the ecosystem due to altered nutrient cycling, plant phenology, and species composition. For instance, the effects of defoliating insects on net primary productivity can be explained in terms of the direct effects of foliage removal, and indirect effects of changes in foliage phenology, physiological processes (e.g. photosynthesis), and foliar C and N dynamics (e.g. Brockerhoff *et al.*, 2006; Lovett *et al.*, 2006a; Schmitz, 2008; Nability *et al.*, 2009; Fig. 2d). While the damage caused to native forest ecosystems by invasive pests and pathogens is well documented (e.g. Liebhold *et al.*, 1995; Brockerhoff *et al.*, 2006; Loo, 2009), the underlying mechanisms and effects on C sequestration are not. Because insect herbivores and plant pathogens target primary producers, they will affect C sequestration in the short term through damage to host species, and in the longer term through changes in plant species composition. Many invasive pests and pathogens are

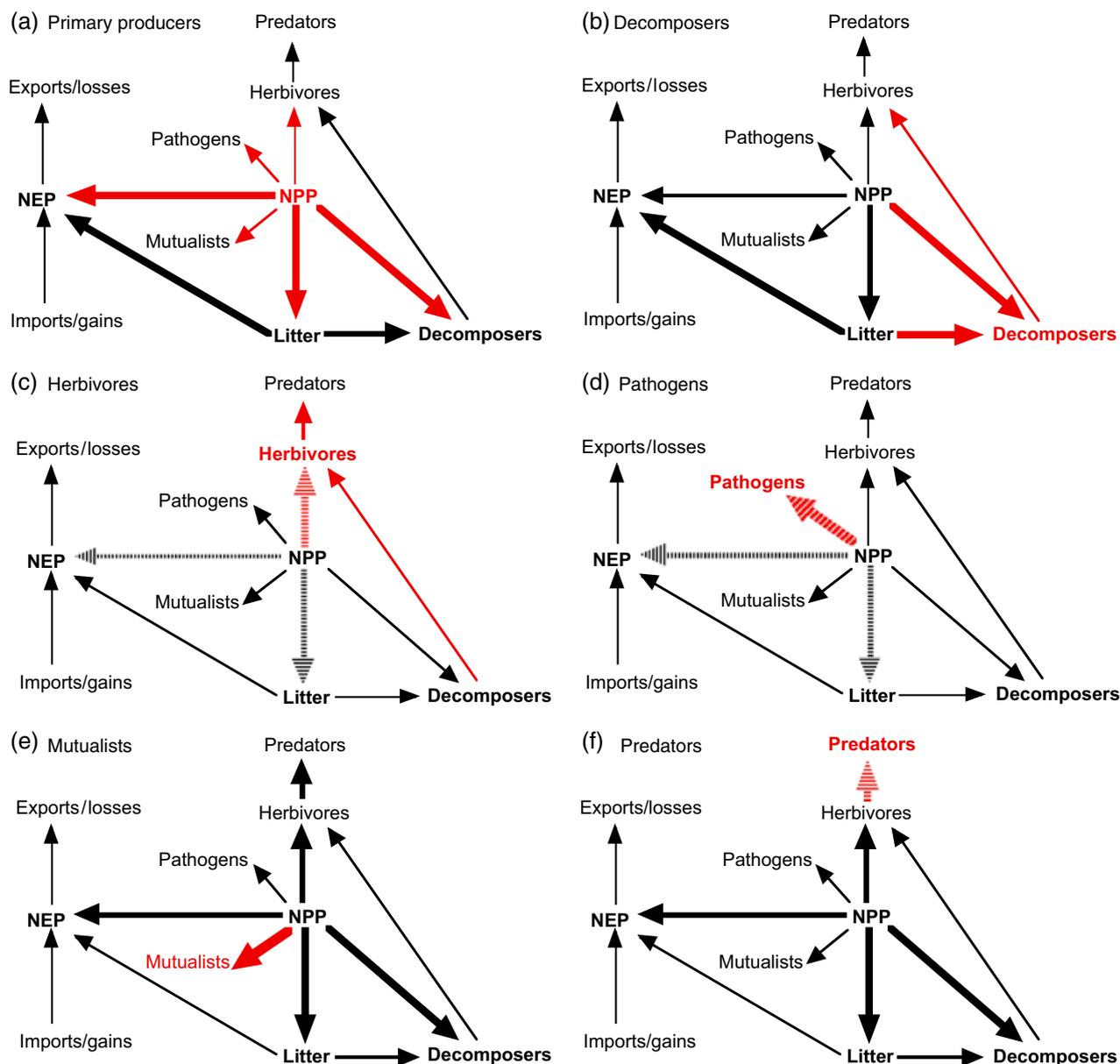


Fig. 2 Summary of energy [biological carbon (C)] flows through various forest ecosystem trophic levels. Individual panels depict the predicted major pathways of influence for invasive species from different trophic levels on ecosystem C changes. The direct effects of invaders are highlighted in red. Width of arrow depicts the relative importance of a pathway with respect to C flow; dashed arrows represent negative effects. Most effects of trophic groups on net ecosystem production (NEP) are mediated indirectly through primary producers (NPP). External gains and losses of C represent subsidies or losses to an ecosystem of C via nonbiological activities such as fire or atmospheric deposition. Pathogens and mutualists are 'special cases' in that they can modulate NPP with minimal C consumption. Modified from Lovett *et al.* (2006b).

specialists that target particular host species or genera, making them particularly effective at changing tree species composition.

One important example is the hemlock woolly adelgid (*Adelges tsugae*), a small, aphid-like insect from Asia that attacks two common species of hemlock (*Tsuga canadensis* and *Tsuga caroliniana*) in eastern North America. There appears to be little resistance to the insect,

which is expected to spread throughout the range of these hemlocks. Once infested, the trees undergo a rapid canopy decline (Orwig & Foster, 1998). This reduces GPP but increases the transmittance of solar irradiance to the forest floor, resulting in increased rates of decomposition and mineralization of soil organic matter (Jenkins *et al.*, 1999; Kizilinski *et al.*, 2002). Both reduced productivity and increased decomposition

reduce C storage in the short term (i.e. years to decades). However, hemlock is a slow-growing tree, and the species that replace it over decades to centuries are likely to be faster growing, leading to higher C sequestration rates in woody biomass. Thus, over the period of hemlock decline and its replacement by other species, we expect that ecosystem C stocks would first decline as large hemlock trees die and the forest floor begins to decompose more rapidly, and then increase rapidly as faster-growing trees revegetate the stand. Whether C stocks recover to its preinvaded state will depend upon characteristics of the trees that replace hemlock, particularly their woody biomass and litter decomposability.

We hypothesize that other pests and pathogens, including those that attack plant roots, will follow this general pattern: the initial disturbance will reduce the rate of C sequestration in the stand, and by killing trees and opening up the canopy to increase decomposition, will result in a short-term decrease in C pools. This could well be the case for invasive root pathogenic fungi such as *Phytophthora cinnamomi* and *Armillaria luteobubalina* which causes significant dieback of natural vegetation in Australia (Peters & Weste, 1997; Shearer *et al.*, 1998), and *Phytophthora ramorum* that causes death of a range of vascular plant species and serves as the agent of sudden oak death syndrome in California (Venette & Cohen, 2006). In all cases, the magnitude of effects will depend on the lethality and host specificity of the pest or pathogen, and the contribution the host species makes to the total ecosystem C (Lovett *et al.*, 2006a). An explicit test of this hypothesis has, however, is yet to be undertaken.

Mutualists

Invasive species can form important mutualistic interactions either with other invaders, or with resident native species. No work to date has explicitly considered the C consequences of these mutualistic relationships even though mutualistic invaders are known to alter pollination, reproductive output, seed dispersal, and soil nutrient uptake of canopy trees and early successional species (e.g. Stout *et al.*, 2002; Morales & Aizen, 2006; Reinhart & Callaway, 2006; Aizen *et al.*, 2008; Fig. 2e).

The best documented role of mutualists as biological invaders involves pollinators. Invasive 'buzz pollinating' insects such as honey bees (*Apis mellifera*) and bumble bees (*Bombus terrestris*) facilitate pollination, seed set, and fecundity, and ultimately increase recruitment rate of invasive plants in many systems (Huryn, 1997). For example, the globally invasive shrubs Scotch broom (*Cytisus scoparius*) and gorse (*Ulex europeaus*) are often pollinator limited, and bee pollination increases

seed production, rates of invasion and local abundance of these species (e.g. Parker, 1997; Stokes *et al.*, 2006) and their effects on forest succession (e.g. Sullivan *et al.*, 2007). Similarly, the invasion of the shrub *Lantana camara* in Australia is facilitated by honeybees (Goulson & Derwent, 2004). Mutualistic seed dispersers such as birds can also increase fecundity and promote invasion by weedy plants (e.g. Gosper *et al.*, 2005; Buckley *et al.*, 2006; Westcott *et al.*, 2008). Facilitated invasion of woody weeds by mutualistic pollinators or seed dispersers could potentially increase live biomass C leading to more rapid succession to high-biomass forest.

There is strong reason to believe that mutualisms may promote C sequestration in many instances. Invasive N-fixing plants often increase live biomass pools or accrete nutrients when suitable N-fixing mutualists are available (e.g. Lafay & Burdon, 2006; Parker *et al.*, 2006). Similarly, invasive ectomycorrhizal fungi associated with tree roots may enhance plant nutrient uptake, growth, rates of biomass C accumulation, and plant establishment in new habitats (Reinhart & Callaway, 2006), although there may also be costs caused by soil C depletion (e.g. Chapela *et al.*, 2001). Finally, invading mutualists can also disrupt existing mutualistic plant-animal interactions (Traveset & Richardson, 2006), although the effects of these interactions on C sequestration remain unknown. The impacts of invasive mutualists on forest C sequestration are expected to be strong but idiosyncratic because of the wide range of interactions, trophic levels, and functional groups involved.

Predators

There is increasing evidence that consumption of prey by top predators in terrestrial ecosystems can induce cascading effects on multiple lower trophic levels (Pace *et al.*, 1999; Terborgh *et al.*, 2001; Fukami *et al.*, 2006). This may in turn regulate resource input to the ecosystem, although relatively few studies have explicitly addressed this issue. There is some evidence that top predators, by affecting densities of their prey, can exert important indirect effects on both primary producers and decomposers (Letourneau & Dyer, 1998; Croll *et al.*, 2005; Wardle *et al.*, 2005). Given the critical role of these trophic levels in determining ecosystem C fluxes, it is plausible that top predators can indirectly influence C sequestration (Fig. 2g).

Effects of invasive predators on ecosystem C storage have been demonstrated for forested islands off the coast of northern New Zealand. Here, seabirds serve as ecosystem engineers by transporting resources from the ocean to the land, and through extensive soil burrowing during nesting. Some of these islands have

been invaded by rat species (notably *Rattus rattus* and *Rattus norvegicus*) during the past 150 years while others have not. When present, rats serve as predators of seabird eggs and chicks, severely reducing seabird densities. Wardle *et al.* (2007) measured ecosystem C storage for each of nine rat-invaded and nine uninvaded islands in this system (Fig. 2). The amount of C sequestered in live plant biomass (mostly trees) on the invaded islands was double that on the uninvaded islands. This was likely due to seabirds reducing tree biomass by damaging roots during burrowing, and the reversal of these effects by rat predation. Conversely, the amount of C sequestered in nonliving pools (e.g. soil organic matter) was 1.38 times greater on uninvaded than invaded islands, probably due to seabirds transporting organic matter from the ocean to the land. The net effect is that invaded islands have 1.37 times more total C stored than do noninvaded islands.

These types of effects are also likely to be important in other coastal forests, given the widespread influence of invasive predators on seabird populations throughout the world (Courchamp *et al.*, 2003). Further, there are many other situations in which invasive predators influence ecosystem level processes in forests. For example, invasive predatory ants can impair processing of forest litter by detritivorous prey (O'Dowd *et al.*, 2003), and invasive predatory wasps can greatly alter the structure of invertebrate food webs and potentially the processes that they drive (Beggs & Wardle, 2006). In summary, there is considerable potential for predators to control ecosystem C through top-down cascading effects on other trophic levels.

Framework from an ecosystem perspective

Features of both the invasive species and the forest ecosystem are important for understanding impacts of invaders on ecosystem C. There is a rapidly growing literature linking species features (i.e. functional traits or characteristics) to ecosystem properties including C sequestration (e.g. Eviner, 2003; Díaz *et al.*, 2004, 2007; Shipley *et al.*, 2006; De Deyn *et al.*, 2008). Thus, using functional traits to predict the effects of invaders based on their trophic position allows us to make general predictions about impacts on C rather than using a species-specific approach. A matrix of key features for both invasive species and the invaded system with respect to C sequestration is summarized in Table 1; these are discussed below.

Features of the invader

Trophic position of biological invaders is an important, primary discriminator of their effects on ecosystem C

(Table 1, Fig. 2). Each trophic level has its own specificity of influence on C sequestration, and this can be captured by a core of functional traits (Table 1, Fig. 2). Primary producers are the only group that directly influences C fixation through photosynthesis, and have major influences on live and detrital C pools through litter inputs and root exudates. Another important feature of primary producers is their role in influencing disturbance regimes, particularly through regulating the frequency and intensity of fire (e.g. D'Antonio & Vitousek, 1992). Decomposers represent a vast diversity of organisms, but their common distinguishing feature is their regulation of C fluxes of litter and detritus (i.e. heterotrophic respiration). In addition, decomposers have unique influences on nutrient cycling, soil physical structure, and organic matter through biochemical processing of detritus or soil organic matter (Wardle, 2002; Bohlen *et al.*, 2004b). The major distinguishing feature of many herbivores is selective disturbance (*sensu* Grime, 1979) of primary production through diet preference; this differs from environmental disturbance such as fire and wind in both the magnitude and specificity of damage (Crawley, 1983). Pathogens are treated here as a special case of herbivory for which consumption is highly selective, and for which damage done is disproportionate relative to their biomass. In addition, feedbacks between pathogens and their hosts are commonplace, and often display boom-bust cycles (Lovett *et al.*, 2006a). Similarly, mutualists primarily exert their influence on NPP through interactions with primary producers both directly by altering the ratio of C gains to losses for individual species, and indirectly by inducing longer-term changes in plant species composition or relative dominance (Traveset & Richardson, 2006). Finally, predators are unique in that their influence is through highly selective damage to lower trophic levels, and their effects on C sequestration are exerted via top-down trophic cascades (Wardle *et al.*, 2007). In summary, the mode of action differs for invaders from different trophic levels, although there are some consistent features of influence within trophic levels.

Although different trophic groups are expected to vary in their direct and indirect effects on ecosystem C, the importance of these effects is dictated by the distribution and abundance of species within these groups (Parker *et al.*, 1999; Liao *et al.*, 2008). As such the 'mass ratio hypothesis' of Grime (1998; see also Vile *et al.*, 2006) predicts that, all else being equal, widespread, high-biomass species will have larger impacts on ecosystem C than uncommon, low-biomass species. If this is the case then secondary discriminators that influence the impacts of invaders on C are their distribution and abundance. These generic features link

population vital rates (i.e. the capacity of an invader to occupy space and increase in abundance) with their direct and indirect effects on NPP. Although generality is sought here, there are instances when unusual or novel functional traits result in invaders having unexpectedly large influences in ecosystems (e.g. Peltzer *et al.*, 2009), for example, through disruption of interaction networks previously dominated by native species (e.g. disruption of native tree mycorrhizal mutualists by an invasive herb; Wolfe & Klironomos, 2005; Stinson *et al.*, 2006; see also Tylianakis *et al.*, 2008).

Several additional distinguishing features of invaders may influence NPP, and hence ecosystem C, including *per capita* processing rates, nutrient stoichiometry, and influence on nutrient availability or cycling (particularly of N and P). Functional traits can be used to quantify invader effects, link features with specific influences on C pools or fluxes, and compare effects among different invasive species. For example, increasing foliar nutrient contents of primary producers are associated with high rates of C fixation but also high litter quality resulting in more rapid decomposition and nutrient release (Wardle *et al.*, 2004). Further, even when traits between native and non-native plants are compared within functional groups (e.g. native vs. non-native N fixers), leaf and litter quality is still higher for non-natives (e.g. Leishman *et al.*, 2007; Peltzer *et al.*, 2009), suggesting that co-occurring native and non-native species should have different effects even within functional groups. Invasive plants can have deeper root systems than resident native species, thus allowing invaders greater access to water or nutrients (Hierro *et al.*, 2005). Similarly, N-fixing plants invading into communities of non-N-fixing species can access N in a way that native species cannot (Vitousek & Walker, 1989). Progress in understanding the variation of species' impacts both within and among trophic levels on C pools and fluxes can be made by linking functional traits with species-level impacts.

Features of forest ecosystem

The short- and long-term consequences of invasive species on C sequestration also depend on features of the invaded ecosystem, particularly forest community composition, structural dynamics, and environment (e.g. Jackson *et al.*, 2002). These features are often inter-related or interact to determine how a forest ecosystem responds to biological invasion. Invaders from different trophic levels will also respond differently to these features, as they have contrasting requirements in terms of resources and habitat.

Community composition can be thought of in terms of species dominance characteristics and species assem-

blages, and these are well known to vary greatly along environmental gradients. While it has been intensely debated as to which aspects of community composition confer resistance to invader effects on ecosystem functioning, including their trophic position (e.g. Hooper *et al.*, 2005; Cadotte *et al.*, 2006; Tylianakis *et al.*, 2008), it is clear that resident species matter. The most profound consequences of invasive species on C sequestration should occur when the dominant plant species (i.e. those having highest basal area, root biomass, leaf area, or litter production) are affected, thus influencing NPP and litter inputs in the short-term, and successional pathways in the long-term (Lovett *et al.*, 2006a; Sullivan *et al.*, 2007). These impacts are also likely to be greatest when the affected species dominates over extensive areas. For example, since chestnut blight invaded the USA, chestnut (*Castanea dentata*) has been reduced from a canopy dominant in eastern deciduous forests to an occasional understorey plant maintained by sprouting (Greller, 1988). Where invasive species (e.g. herbivores or pathogens) cause such dieback, we suggest that a principle control on C stocks will be the decay rate of woody debris and the ability of co-occurring trees to occupy the canopy space liberated by the decline of the affected species.

Forests are structurally dynamic because most are recovering from historical disturbances. Forest development thus provides an important context for understanding invasive species impacts on C sequestration. Disturbance is commonly considered to lower the resistance of ecosystems to invasive species through removal of resident species, increasing resource availability to invaders, and by providing a window of opportunity for invaders to establish (e.g. D'Antonio *et al.*, 1998; Davis *et al.*, 2000; Buckley *et al.*, 2007). The opportunities for invasive species to establish following disturbance can have long-term above- and below-ground consequences for C sequestration. This is particularly apparent where resident species have not experienced the type and intensity of disturbance to which the invaders are adapted. For example, invasive pine species have an ability to colonize and rapidly accumulate biomass C in many areas deforested by fire that is not shared by co-occurring native tree species (Benecke & Nordmeyer, 1982; Richardson, 1998; Ledgard, 2001). In the eastern United States, hemlock forests may get a double dose of invasive species, as opening of the canopies due to invasion by the hemlock woolly adelgid facilitates invasion by exotic plants (Eschtruth *et al.*, 2006), which in turn interact with native herbivores to control plant community composition (e.g. Baiser *et al.*, 2008). This is consistent with Simberloff & von Holle's (1999) 'invasional meltdown' hypothesis, and suggests that invasive species can have

synergistic effects on ecosystem properties. Long-term interactions among invasive and resident species during forest development will ultimately determine the C sequestration consequences of disturbance.

Environmental limits should place an overall distributional constraint on invasive species at a macro-scale, although many invasive species have yet to realize their distributional potential and hence impact. Abiotic environmental factors determine an invader's impact within that range, including the potential consequences for C sequestration. For example, climate, light availability (e.g. Maule *et al.*, 1995), and soil fertility (e.g. Wiser *et al.*, 1998) all can influence plant invasion success. With regard to invasive animals, invasive earthworms exhibit preferences in soil pH and organic matter whereas invasive deer prefer sites with greater soil N availability (Wardle, 2002). Bardgett & Wardle (2003) suggest fundamentally different effects of herbivores on ecosystem processes driving C dynamics in nutrient-replete or nutrient-limited ecosystems, which should also apply to invasive herbivores. Further, if invasive herbivores enter low-nutrient forests that are not adapted to herbivory, they can greatly increase tree mortality (Lovett *et al.*, 2006a). Thus, invaders both respond to and influence features of the invaded systems.

Implications for management

Forest ecosystems are managed for a range of purposes, which increasingly includes C sequestration (Noss, 2001; Luysaert *et al.*, 2008). Managing forests for C storage is driven by the need to offset CO₂ emissions from other sectors to reduce atmospheric CO₂ concentration and mitigate the rate of climate change (e.g. Hyvönen *et al.*, 2007; IPCC, 2008). Invasive species occupy forests in many parts of the world, and as most countries have an established bank of introduced species and receive new invaders through increasing global trade (e.g. Levine & D'Antonio, 2003), there is considerable potential for ongoing invasions. This has led policy makers to consider the control of invasive species as beneficial to C sequestration for emissions trading purposes, but the underpinning science or data are lagging behind policy needs (e.g. Hyvönen *et al.*, 2007; Burrows *et al.*, 2008). In order to understand the implications of invasive species management on forest C sequestration, three interlinked issues require urgent resolution. Firstly, are biological invaders likely to contribute significantly to forest C sequestration (either positively or negatively)? Secondly, can the effects of invaders on forest C be mitigated through management actions? Thirdly, can specific invaders, or invaded systems, be

prioritized for management action? These issues are discussed below.

Contribution of biological invaders

There are studies on the magnitude or importance of biological invasions on net changes in C stocks, but the data available demonstrate that either substantial C losses or gains are possible (Croll *et al.*, 2005; Wardle *et al.*, 2001, 2007; Ostertag *et al.*, 2009). If this turns out to be a general principle, then it cannot be assumed that the management of invasive species will result in C gains. Rather, management should focus on specific sites and conditions. For example, direct C losses from herbivory by introduced deer in New Zealand affect <1% of forest C stocks currently, but these seemingly small short-term effects on C stocks through consumption belie the important indirect long-term effects of deer on C sequestration including altered successional trajectories, reduced recruitment of tree species, and shifts in the relative dominance of canopy species toward unpalatable species (Coomes *et al.*, 2003; Burrows *et al.*, 2008). Our review demonstrates that the indirect effects of invasive species (e.g. alteration of soil C stocks, changes in tree species composition) that manifest themselves over longer time scales (i.e. decades to centuries) may be considerably more important than the short-term direct effects of invaders. Without knowing the long-term C trajectories of an invaded system, it will be difficult to demonstrate gains in C as a result of management. Thus large-scale and long-term primary data collection, in combination with modeling, are needed to advance our knowledge in this area to determine the effectiveness of management for sequestering C.

Potential to manage the effects of invaders

Management of invasive organisms occurs at three stages of the invasion process: border surveillance and interception, prevention of establishment and spread, and control of naturalized populations (Hobbs & Humphries, 1995; Hulme *et al.*, 2008). Furthermore, for the pool of non-native naturalized species, there are weed and pest risk assessment systems (including those based on expert opinion) for prioritizing the detrimental effects of invaders (e.g. Daehler *et al.*, 2004; Caley *et al.*, 2006). Management of most invaders for the purpose of maintaining or enhancing forest C stocks will operate on fully naturalized populations. The impacts of these invaders are driven by increasing distribution, abundance and effect (Parker *et al.*, 1999). Thus, invaders can significantly influence C sequestration through large effects at any spatial scale or through

small effects at large scales. Most invasive species likely fall into the latter category, and thus their impacts on C sequestration or emissions are usually difficult to detect or monitor. Most management involves reducing the local abundance of an invader in order to minimize impacts at relatively small spatial scales (Coomes *et al.*, 2003; Hulme, 2006), so there is often a mismatch in spatial scales of invader effects and management actions that need to be resolved. Further, if an invader causes a gain in C (e.g. as can occur for some invasive species of primary producers, mutualists and predators, Fig. 2), these gains may be lost after controlling the invader. Conversely, if an invader causes a loss in C (e.g. consumers and pathogens), there may be a gain in C after controlling the invader. Clearly the effectiveness of management in mitigating the effects of invaders and maximizing rates of C sequestration depends upon the reversibility of invasive species impacts (e.g. Coomes *et al.*, 2003). In summary, there is the potential to manage biological invaders for the purposes of forest C sequestration, but there is an urgent need for research on whether the C gains or losses resulting from biological invasions can be reversed through management. A corollary point is that the importation of new exotic species involves the risk, though not the certainty, of significant impacts on C sequestration. More research on the pathways by which species affect C dynamics will permit the risk to be better quantified than is possible at present.

It is worth noting that invasions can also themselves be consequences of global change. For example, many invaders can be considered the passengers of other agents of global change (*sensu* MacDougall & Turkington, 2005), and as such are merely beneficiaries of changed land-use, nutrient deposition rates, or disturbance regimes (Didham *et al.*, 2005; Tylianakis *et al.*, 2008). However, invaders can also alter ecosystems through their impacts and feedbacks on nutrient cycling, C flows and abundance of co-occurring species (see Wardle, 2002; Wolfe & Klironomos, 2005; Tylianakis *et al.*, 2008). Clearly, cause and effect need to be carefully disentangled in order to attribute changes in C sequestration specifically to management of any biological invader.

Framework for prioritizing actions

Although atmospheric CO₂ is a 'global commons' issue, well-informed management at landscape to national scales is essential to maximize the benefits of global C sequestration in forests to mitigate global change. There are particular challenges in demonstrating long-term additionality and increases in C storage from the control of invasive species against a backdrop of variability

associated with forest dynamics. We suggest those forest systems most likely to increase substantially in C sequestration following management of invasives have particular features: (a) that succession is dominated by few species that are strongly influenced by the invader, (b) that the invaded system represents relatively large geographic areas or vegetation classes, (c) that the total standing stock of C of the invaded system is low compared with potential stocks without the invader present, and (d) that the forest has high productivity with a large detrital C pools and slow rates of wood and litter decay. Further, it is also necessary that the invader can be controlled effectively (abundance reduced) by management options. Better understanding of these factors will help resolve the issue of location, timing, and spatial and temporal scales where management of invaders can influence C sequestration most effectively. These criteria will require large-scale data collection to resolve how to prioritize management amongst invasive species and invaded forest ecosystems; such research has recently been initiated for invasive mammals in New Zealand forests and shrublands (e.g. the New Zealand Department of Conservation Wild Animal Control for Emissions Management project; Allen & Carswell, 2008). Primary data of this type are also needed urgently to underpin policy development to encourage effective forest management, and to provide credibility for the efficacy of invasive species management as an option for offsetting greenhouse gas emissions and trading in C credits. For these purposes, we suggest that 5–10-year periods (the first commitment period of the Kyoto Protocol is 2008–2012) are often too short for assessment of changes in C stocks with an acceptable degree of uncertainty as this time period frequently represents only a small interval in the much longer lifespan of forest ecosystems. Further, it is important to recognize that management of C *per se* may not achieve other objectives such as conservation and maintenance of biodiversity (Schulze *et al.*, 2002). Careful consideration of the priorities for managing across a range of ecosystems services is necessary. Finally, we reiterate that biological invasions represent one of the most pervasive agents of global environmental change with major impacts (Vitousek *et al.*, 1997; Tylianakis *et al.*, 2008). With the ongoing increase in species invasions globally, there is an urgent need to broaden our understanding and determine the biotic and abiotic processes regulating the impacts of biological invasions on ecosystem C sequestration.

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