

AN ECOSYSTEM VIEW OF LINKS BETWEEN PEST SPECIES AND SERVICES

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ABSTRACT: An ecosystem approach to understanding the effects of biological invaders and pests can shed new light on the state of ecosystem services and how they are changing. Pests – undesirable, mainly non-native, species – are a major focus of both research and management efforts. Most of these efforts have been directed at eradicating pests or reducing their local abundance, often with the aim of maintaining indigenous biodiversity. Interest is also growing in whether pest management can mitigate the impacts of non-native species on ecosystems and ecosystem services. This chapter uses New Zealand and international literature to provide an ecosystem view and examples of pest impacts in ecosystems. Recent progress in linking functional traits, species, ecosystem processes, and services provides optimism for ongoing rapid progress in the prediction and management of ecosystem services.

Key words: biological invasions, ecosystem processes, management, multiple outcomes, non-native species, pathogens, pest animal species, weeds.

BACKGROUND

What are pests?

Pests are commonly considered simply as undesirable species (e.g. Harper 1977). This broad definition means pest species span phylogenetic boundaries – they comprise plants, bacteria, vertebrates, insects and fungi. In addition, ‘undesirable’ is a value-laden term. Sometimes pest species have undesirable effects that are well characterised (e.g. tuberculosis in animals), whereas in other cases desirability is in the eye of the beholder (e.g. some garden weeds are also edible greens).

Knowledge of pest species and their effects on ecosystem services is particularly important to New Zealand for several reasons. First, more than half the flora comprises non-native plant species, and many of these species are weeds (‘pest plants’); this is high by global standards. Second, some pest species such as mammalian herbivores were absent from New Zealand until the anthropocene, and have thus received much attention and management aimed at understanding and mitigating their effects on vegetation that did not co-evolve with mammalian herbivores. Third, New Zealand’s border biosecurity is among the strongest in the world, partly because of a desire to prevent more pests from establishing. Other reasons exist, but these three illustrate the size of the problem pest species cause in New Zealand. More comprehensive treatments can be found in Craig et al. (2000), Williams and West (2000), King (2005), Allen and Lee (2006), and Kelly and Sullivan (2010).

Scope of this chapter

The chapter starts with an ecosystem view of pest species, presenting well-documented examples in the form of biological invasions by non-native species. This ecosystem perspective differs from earlier ‘pest regulation’ approaches, which mainly address pathogens and diseases of crops and livestock (e.g. UK NEA 2011). The chapter then gives examples of the impacts of pests in ecosystems, and how these species can be managed to mitigate those impacts. This is not a comprehensive review of pests in New Zealand; instead, the chapter provides an ecosystem view for understanding the effects of pest species on ecosystem services and highlights the evidence needed to demonstrate effects of pest species on the condition and trends of ecosystem services.

PESTS AS DRIVERS OF ECOSYSTEM CHANGE

Interest in the effects of global change drivers on terrestrial

ecosystems has rapidly produced a large literature on how carbon dioxide enrichment, land-use change, nitrogen (N) deposition, and climate change affect diversity, ecological communities, and ecosystem processes (e.g. Wardle 2002; De Vries et al. 2006). One such major driver is biological invasions, but until recently this has received relatively little attention (e.g. Vitousek et al. 1997). This is despite growing evidence that a wide range of invasive organisms can strongly alter ecosystem processes (e.g. Levine et al. 2003; Wardle et al. 2007; Liao et al. 2008; Vilà et al. 2011). For example, non-native invasive species can transform ecosystems at the landscape level 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 of the best documented examples of these invaders include Dutch elm disease and chestnut blight in eastern US forests (Lovett et al. 2006a); *Phytophthora*-induced forest dieback syndromes in Australia, the US and central Europe (Condeso and Meentemeyer 2007); and invasive mammals in Australia and New Zealand (King 2005; Allen and Lee 2006). Pests can also be native species. For example, the early-successional shrub tutu (*Coriaria arborea*) is poisonous to stock and can cause tutin poisoning in honey, while the endemic native moth *Wiseana cervinata* is a pest in pastures (Barlow et al. 1986). Thus, although the examples below primarily treat pests as undesirable non-native species, the same principles apply to ‘undesirable’ native species (see a very informative recent review of this topic by Simberloff et al. (2012b)).

Because the number, distribution and abundance of invasive species are increasing in New Zealand (Kelly and Sullivan 2010), there is an immediate need to broaden our understanding of how biological invasions and pest species affect ecosystems and the services they provide. One approach is to consider the effects of a pest on resources, other species and the abiotic environment. These general factors regulate energy flow and nutrient cycling, determine ecosystem properties and processes, and ultimately can be used to understand many ecosystem services. This complex topic is not reviewed here, but is discussed in the original Millennium Ecosystem Assessment’s (2005) conceptual model, which links species and ecosystem processes to various ecosystem services; more recent publications (e.g. UK NEA 2011) refine this model. Another approach to understanding the general effects of pest species builds on this model by comparing differences in effects among trophic levels (Peltzer et al. 2010). This has also been used to determine the most likely effects of

species in general in ecosystems (e.g. Zavaleta et al. 2001; Wardle 2002; Strayer et al. 2006; Peltzer et al. 2010). Pest species from different trophic groups are generally thought to have contrasting but predictable effects in ecosystems (Figure 1); some examples of this are provided below.

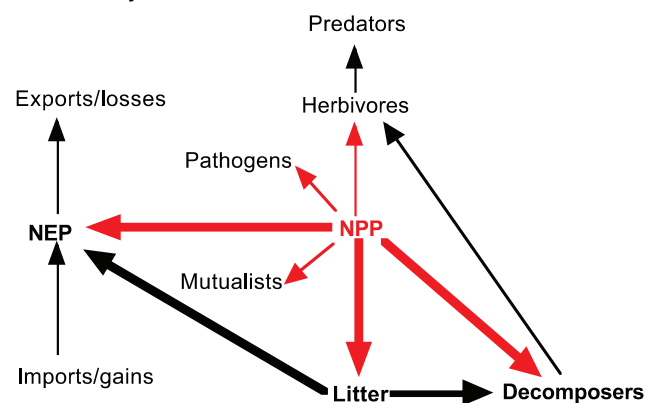
Pest plants

Pest plants (weeds) are primary producers, and thus affect ecosystem primary production directly through their own photosynthesis and respiration, and indirectly by affecting decomposition and nutrient fluxes (De Deyn et al. 2008; Figure 1A). Weeds are widely thought to be more productive than co-occurring native species because of a coordinated set of functional traits associated with rapid nutrient uptake, tissue turnover and growth, 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). Furthermore, litter from invaders is often more easily decomposed (e.g. Allison and Vitousek 2004; Litton et al. 2008; Kurokawa et al. 2010), potentially resulting in higher nutrient availability and primary production but also faster loss of organic matter from the ecosystem. The net effects of these processes could either increase or decrease ecosystem processes such as net carbon (C) sequestration. In general, the importance of indirect effects – for example, impacts mediated through intermediate species – is less well understood (Ellison et al. 2005; Didham et al. 2007; Sax et al. 2007). For example, weeds may influence the relative performance of other species, leading to successional pathways different from those in similar systems dominated by native plant species (e.g. Sullivan et al. 2007; Dickie et al. 2011). In addition, weed effects in ecosystems are context-dependent (i.e. can depend on local conditions or species pools) and can interact with abiotic factors such as climate (e.g. Jackson et al. 2002; Wilson and Pinno 2013); this suggests that broader, cross-system primary data are needed if meaningful generalisations are to be developed.

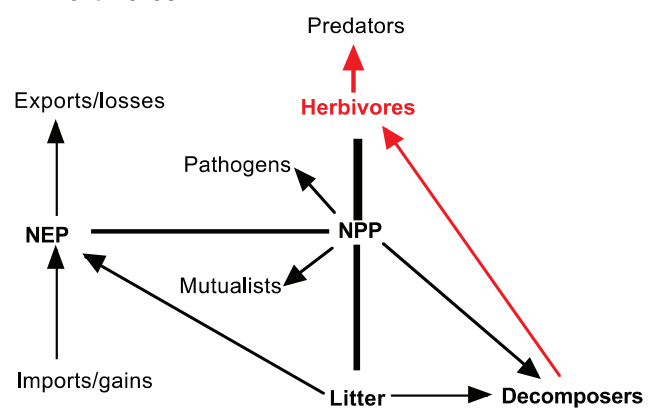
Pest herbivores

The direct effects of mammalian herbivore pests on forests through the consumption of seeds, cambium, roots, or foliage have been relatively well studied. For example, defoliation of the forest canopy by brushtail possums in New Zealand has been extensively studied (e.g. Campbell 1990; Bellingham et al. 1999; Cowan 2001, 2005; Nugent et al. 2001; Gormley et al. 2012). 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 and other ecosystem processes (Waring and Schlesinger 1985; Peltzer et al. 2010). Furthermore, introduced herbivores can also indirectly affect soil C and nutrients by altering 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 below-ground C sequestration. Globally, some of the best studied examples of this are for pest ungulates in New Zealand forests (e.g. Wardle et al. 2001; Bardgett and Wardle 2003; De Deyn et al. 2008). In the longer term, the direct and indirect effects of herbivory change both the structure (e.g. biomass) and composition (e.g. plant and soil biotic community) of vegetation, soils and ecosystem processes (Figure 1B).

A. Primary Producers



B. Herbivores



C. Pathogens

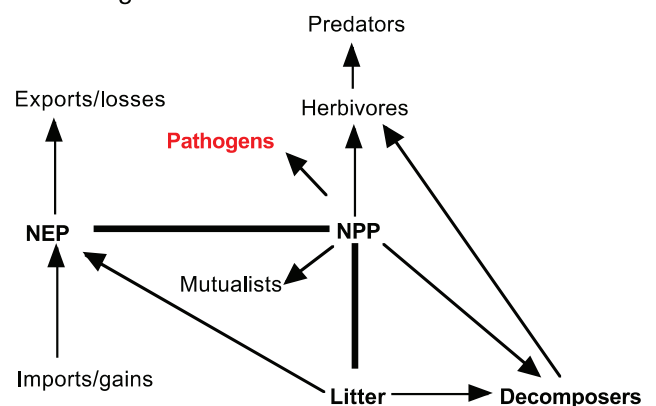


FIGURE 1 Summary of energy (biological carbon, C) flows through various ecosystem trophic levels. Individual panels depict the predicted major pathways of influence, for pest species from different trophic levels, on ecosystem C changes. Width of arrow depicts the relative importance of a pathway with respect to C flow. Most effects of trophic groups on NEP (net ecosystem production) are mediated indirectly through primary producers (NPP). External gains and losses of C represent subsidies or losses to an ecosystem of C via non-biological activities such as fire or atmospheric deposition. Pathogens and mutualists are ‘special cases’: they can modulate NPP with minimal C consumption. Although differences in energy flow is depicted here to illustrate differences between pests of different trophic status, analogous relationships can be constructed for other ecosystem properties or processes. (Modified from Peltzer et al. 2010.)

Pest pathogens and mutualists

Pathogens or invertebrates directly damage tissues or leaves and indirectly change phenology, physiological processes (e.g. photosynthesis), and foliar C and nitrogen (N) dynamics (e.g. Brockerhoff et al. 2006; Lovett et al. 2006a; Schmitz 2008; Nability et al. 2009; Figure 1C). Although the damage caused to vegetation by invasive pests and pathogens is relatively well documented (e.g. Leibold et al. 2004; Brockerhoff et al. 2006; Loo 2009), the underlying mechanisms and effects on ecosystem processes are not. Both insect herbivores and plant pathogens can affect ecosystems: in the short term through damage to host species, and in the longer term through changes in species performance or composition. Similarly, pest species can form important mutualistic interactions either with the hosts of other pests or with resident native species. The best-documented examples include changes in pollination, reproductive output, seed dispersal, N fixation, and soil nutrient uptake by canopy trees and early-successional plant species (e.g. Reinhart and Callaway 2006; Aizen et al. 2008). For example, invasive N-fixing plants often increase live biomass pools or accrete nutrients when suitable N-fixing mutualists (e.g. rhizobia) are available (e.g. Lafay and Burdon 2006; Parker et al. 2006). Similarly, invasive ectomycorrhizal fungi associated with tree roots may enhance nutrient uptake, growth, rates of biomass C accumulation, and plant establishment in new habitats (Reinhart and Callaway 2006; Dickie et al. 2010). In all of these cases, the magnitude of the effects will depend on the lethality of the pathogen or the benefits of the mutualist, the host specificity of the pest species, and the size of the contribution the host species makes to the ecosystem processes (e.g. Lovett et al. 2006a, b). Explicit tests of this hypothesis are rare but are recognised as an important avenue for future research efforts (e.g. Wardle et al. 2011).

HOW ARE IMPACTS IN ECOSYSTEMS MANIFESTED IN SERVICES?

Pest species affect ecosystem services by altering ecosystem properties and processes (Strayer 2012). The ecosystem impacts of individual species or, more recently, combinations of species have received growing interest internationally (Wardle et al. 2011; Cardinale et al. 2012). More generally, Parker et al. (1999) described the impact of non-native plant species as the product of abundance, distribution, and per capita effects. Distribution and abundance are the fundamental information for assessing the likely importance of any pest species. Per capita effects are somewhat more difficult to determine, and can include effects on resource abundance or quality, the presence or performance of other species, habitat quality or quantity, or disturbance regime. Despite the huge growth in studies of ecosystem impacts of invasive organisms in the past decade, few studies explicitly link these impacts to ecosystem services. In addition, a recent review of this literature by Hulme et al. (2013) demonstrates broad-scale biases in study organisms and in the evidence available to predict pest impacts on services.

Most literature on pest species does not take an ecosystem view, but instead provides fundamental information on the distribution, negative effects, ecology, or management of the species. Some studies go one step further by evaluating the effects of invasion or management of pest organisms on biological diversity, or on selected ecosystem properties or processes. For example, a search of the Web of Science (27 April 2013) using the key phrase: (pest or weed or pathogen) and (regulation or management) and “New Zealand” and (ecology or ecosystem or diversity

or service*) yielded 165 publications; of these, fewer than 5% report some aspect of an ecosystem process that could be used to derive an effect on services. More generally, a global review of literature showed that loss of native diversity had negative effects on primary production or decomposition that were comparable with other global drivers including drought, nutrient addition, carbon dioxide fertilisation, acidification, or increased ultraviolet radiation (Hooper et al. 2005, 2012). In summary, although the effects of pest organisms are expected to affect ecosystem services, evidence to demonstrate this is weak for all but a few well-characterised species and systems, both in New Zealand and internationally.

LINKS BETWEEN PEST MANAGEMENT AND ECOSYSTEM SERVICES

Pest management, particularly of environmental weeds, mammals, or biosecurity threats to primary production, is a major focus of science and conservation activities in New Zealand (e.g. Williams and West 2000; Parkes and Murphy 2003; Allen and Lee 2006; Clayton and Cowan 2010). This reflects the sheer size of the perceived problem of negative effects caused by introduced non-native species. For environmental weeds, this has led to either ‘species-led’ or ‘site-led’ management of weed species, depending on whether the goal of management is to eradicate a pest species or to protect a highly-valued site (e.g. Williams and West 2000). Although eradication is the ultimate goal of pest management, this is rarely achieved, for several reasons, for example low species detectability, limited resources for control efforts, or pest reinvasion (e.g. Kettenring and Adams 2011; Panetta et al. 2011). Therefore, most management reduces either the distribution or abundance of pests, with a coincident reduction of impact (*sensu* Parker et al. 1999).

In many cases, the most direct negative impact mitigated by pest management is a decline in biodiversity. Pests can influence several aspects of diversity, including species, functional, or phylogenetic diversity. This has led to the view that controlling invasive species should benefit diversity, but the underpinning research often lags behind management or policy needs (e.g. Hyvönen et al. 2007; Burrows et al. 2008; Simberloff et al. 2012a; Hulme et al. 2013). Understanding the implications of invasive species and their management on diversity, ecosystem processes or services requires answers to several questions. Do biological invaders cause important changes in diversity or ecosystem processes (either positive or negative) compared to other drivers? How might these effects be mitigated by management? How might pest species or invaded systems best be prioritised for management? These issues are complex and covered more thoroughly elsewhere (e.g. Hulme 2006; Gordon et al. 2008; Strayer 2012).

Invasion by a non-native organism occurs in three main stages, and the corresponding management opportunities are border interception, prevention of establishment and spread, and eradication of naturalised populations (Hobbs and Humphries 1995; Hulme et al. 2008). Furthermore, for non-native naturalised species, weed and pest risk assessment systems (including those based on expert opinion) have been developed to prioritise pest species thought to have detrimental effects (e.g. Williams and West 2000; Daehler et al. 2004; Caley et al. 2006). Because the impacts of invaders increase with increases in their distribution, abundance, per-capita effects (Parker et al. 1999; Strayer 2012), and divergence in function from native species (i.e. ‘functional distinctiveness’, Wardle et al. 2011), high priority pest species

typically comprise species that can dominate systems and have unique effects. Consequently, these species, with their potentially widespread naturalised populations, form the target of most pest management aimed at maintaining or enhancing ecosystem processes or services.

Some of the best-documented pest management is of introduced ungulate herbivores in New Zealand. For example, 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; they rapidly became overabundant and are now subjected to widespread control (e.g. Allen and Lee 2006). Exclusion studies (fencing to keep ungulates out) generally show an increase in the density of palatable understorey shrubs inside fenced areas and usually an increase in unpalatable understorey shrubs outside (e.g. Mason et al. 2010; see Forsyth et al. (2002) for a review of 'palatable' species). However, 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 they suggested this variability resulted from the multiple processes that regulate soil C storage (see also Bardgett and Wardle 2003). Whether introduced mammalian herbivores increase or decrease C sequestration in forest ecosystems will probably depend on the context, which will include the stage of forest development, soil fertility, and functional traits of the dominant tree species (Bardgett and Wardle 2003; Mason et al. 2010). In addition, direct C losses from herbivory by introduced deer in New Zealand are likely to currently affect less than 1% of forest C stocks. However, this seemingly small, short-term effect belies the potential long-term effects of deer on C sequestration and other ecosystem processes or services, because this herbivory can alter successional trajectories, reduce recruitment of tree species, and shift the relative dominance of canopy species towards unpalatable species (Coomes et al. 2003; Burrows et al. 2008). These findings support the recent recognition that the impacts of non-native species are idiosyncratic and can vary with duration of establishment (e.g. Strayer et al. 2006; Vilà et al. 2011; Hulme et al. 2013).

Most management involves reducing the local abundance of an invader to minimise impacts at relatively small spatial scales (Coomes et al. 2003; Hulme 2006). Consequently, the spatial scales of invader effects and management actions are often mismatched, and this indicates a need to find ways to manage invaders over wide areas. This can be resolved in part through large-scale and long-term primary data collection, in combination with modelling (e.g. Gormley et al. 2012; Mason et al. 2012; Dymond et al. 2013; Ausseil et al. 2013; Caplat et al. in press). This approach can substantially improve our knowledge of pest impacts on ecosystem processes and can also determine the effectiveness of management for influencing ecosystem services; however, efforts must be prioritised; robust, quantitative approaches for scaling up impacts and the outcomes of management are rapidly emerging in the literature. For example, plant functional traits and ecosystem processes have been explicitly linked to scale up species' impacts to landscape-level ecosystem services (e.g. Lavorel and Grigulus 2012; Hulme et al. 2013).

Complex outcomes of pests and their management

An unresolved issue that illustrates the complexities involved

with managing pest species for ecosystem services is whether effects on biological diversity are congruent with services (e.g. Wardle et al. 2007; Dickie et al. 2011); in other words, if a pest is managed to mitigate its negative effects on diversity, do ecosystem services improve? For example, Dickie et al. (2011) demonstrated that when Corsican pine (*Pinus nigra*) invaded native tussock grassland there was a complex trade-off between C sequestration, soil nutrient available, and diversity. Specifically, C storage increased linearly with pine invasion, but the response of diversity was non-linear and differed among trophic groups (e.g. plant diversity was positively unimodal, or maximal, part way through the invasion). These results were nearly identical for succession (invasion) by the native shrub kānuka (*Kunzea ericoides*). In this case, optimal management for both diversity and C would not aim to produce uninvaded grassland or closed-canopy forest, but would aim for some intermediate stage.

Another complex problem concerns the non-target effects of pest management. This is a controversial topic, only mentioned superficially here. New Zealand is a world leader in both research and management of some pest organisms, and the eradication of pest mammals from islands exemplifies this (Courchamp et al. 2003). However, this management can involve the controversial large-scale use of biocides including sodium monofluoroacetate (1080) for possums (e.g. Innes and Barker 1999; Eason et al. 2011), and anticoagulants for rodents (e.g. Eason et al. 2002; Spurr et al. 2005; Hoare and Hare 2006). The negative effects of these biocides on native species or valued game species (e.g. red deer) have generated intense debate over their costs and benefits; however, their effects on ecosystem services have only recently been recognised and have not yet entered the debate. For example, does reduction in pest animal numbers also increase supporting services such as soil retention or net primary production? What remains unresolved is whether taking an ecosystem view, or explicitly managing for ecosystem services rather than pest control per se, alters the balance of costs and benefits or affects potential conflicts arising from these management activities. These examples highlight the potential conflicts and compromises that can arise when pests are managed for multiple purposes including biodiversity and ecosystem services.

NEXT STEPS

Ecosystem services represent a typical 'global commons' issue. Consequently, if ecosystem services are to be improved or optimised in the face of uncertainties in the importance and magnitude of pest species impacts, well-informed management at regional to national scales will be necessary. On one hand, the abundance and distribution of many pest species have increased and will probably continue to increase, resulting in larger and more widespread ecosystem impacts (Kelly and Sullivan 2010). On the other hand, an ecosystem view of pest species and their impacts on services provides new approaches for understanding and managing pests so their future impacts can be minimised. This view necessarily includes knowledge about the likely trajectories and ecosystem processes of novel ecosystems (Hobbs et al. 2006, 2009; Seastedt et al. 2008; Mascaro et al. 2012), when to retain pest species for the restoration of services (e.g. Callaway et al. 2000; D'Antonio and Meyerson 2002), and how to manage conflicts over multiple objectives and services (e.g. Pressey et al. 2007; Liu et al. 2011). In addition, an ecosystem services approach can better explain the benefits of pest management to the public.

The following sections summarise principles or approaches

that could answer important questions about how pest management can most effectively influence ecosystem services.

Where is pest management most important?

Determining which systems are prioritised for management will depend on two things: the ecosystem services of interest, and which systems are most likely to respond to pest management. For example, where the aim is to improve C sequestration, forest systems recently disturbed and dominated by palatable woody species will probably deliver the greatest benefits from ungulate pest management (Burrows et al. 2008; Mason et al. 2010).

For how long should pest management be monitored?

Most management efforts, or monitoring of responses to management, are too short to evaluate meaningful ecosystem responses. Most studies measure pest impacts and responses to management for less than 2 years, but 5–10 years or longer is more appropriate for evaluating the impacts of non-native species on ecosystems or on supporting, regulating or provisioning ecosystem services (Brown et al. 2004; Strayer et al. 2006; Tanentzap et al. 2009; Vilà et al. 2011).

How should differing management objectives be reconciled?

Management for one objective, typically biodiversity maintenance, may not be congruent with other objectives, including multiple services. This requires an approach that explicitly recognises conflicts among multiple objectives, accepts the need to minimise these conflicts (Bennett et al. 2009; Nelson et al. 2009; Mason et al. 2012), and requires goals to be explicitly prioritised. More optimistically, this approach could also demonstrate additional, previously unrecognised benefits from pest management (e.g. Pejchar and Mooney 2009).

How do invasions interact with other drivers of change?

Biological invasions represent one of the most important and pervasive agents of global environmental change (Vitousek et al. 1997; Mack et al. 2000; Tyljanakis et al. 2008), and because these invasions and their impacts are increasing, there is an immediate need to broaden our understanding of how they influence ecosystem processes and services (Hulme et al. 2013). However, biological invaders interact with other drivers of global change such as altered land use, disturbance regimes and abiotic factors; in other words, many invasive organisms take advantage of ‘game-changing’ anthropogenic changes to ecosystems (MacDougall and Turkington 2005; Didham et al. 2005; Tyljanakis et al. 2008; Bauer 2012). Information on these other factors is necessary for evaluating the relative importance of pest species on ecosystem services.

Fundamental information is still needed

Even the longest established and most widespread pest species in New Zealand continue to expand their geographic range and local abundance (e.g. Scotch broom, wilding conifers), so their long-term ecosystem impacts are increasing; this is exacerbated by cumulative effects (Parker et al. 1999; Strayer 2012). Although coordinated efforts to quantify the distribution and abundance of (woody) vegetation have been developed (Coomes et al. 2002; Allen et al. 2003; Lee et al. 2005), no similar efforts exist for non-native species, nor have they been attempted for key ecosystem properties. However, these would be enormously useful for assessing condition and trends in ecosystem services, including soil natural capital (e.g. Dominati et al. 2010; Robinson and Lebron 2010; Robinson et al. 2013). Such large-scale data

collection would also help prioritise management goals for invasive species and ecosystems.

An ecosystem approach to understanding the effects of biological invaders and pests can shed new light on the state of ecosystem services and how they are changing. This approach may be particularly apposite for supporting services (e.g. nutrient and water cycling, primary production), but it is also relevant for some provisioning (e.g. food and fibre, fresh water) and regulating services (e.g. soil erosion, disease regulation, pollination). Moreover, ‘pests’ are by definition valued less than ‘non-pests’ and are considered undesirable, so the obvious links to cultural services should be further developed. Recent progress in linking functional traits, species, and ecosystem processes and services (e.g. Diaz et al. 2007; Lavorel et al. 2011; Lavorel and Grigulus 2012) provides optimism for ongoing and rapid progress in the prediction and management of ecosystem services.

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