Forum

# The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management

Jane A. Catford [a,*], Curtis C. Daehler [b], Helen T. Murphy [c], Andy W. Sheppard [d], Britta D. Hardesty [c], David A. Westcott [c], Marcel Rejmánek [e], Peter J. Bellingham [f], Jan Pergl [g], Carol C. Horvitz [h], Philip E. Hulme [i]

[a] *School of Botany, The University of Melbourne, Vic 3010, Australia*
[b] *Botany Department, University of Hawai'i at Manoa, Honolulu, HI 96822, USA*
[c] *CSIRO Ecosystem Sciences, PO Box 780, Atherton, QLD 4883, Australia*
[d] *CSIRO Ecosystem Sciences, GPO Box 1700, Canberra, ACT 2601, Australia*
[e] *Department of Evolution and Ecology, University of California, Davis, CA 95616, USA*
[f] *Landcare Research, PO Box 40, Lincoln 7640, New Zealand*
[g] *Institute of Botany, Academy of Sciences of the Czech Republic, CZ-252 43 Pruhonice, Czech Republic*
[h] *Biology Department, University of Miami, PO Box 249118, Coral Gables, FL 33124, USA*
[i] *Bio-Protection Research Centre, Lincoln University, PO Box 84, Lincoln 7647, Canterbury, New Zealand*

## ARTICLE INFO

## ABSTRACT

The intermediate disturbance hypothesis (IDH) predicts a hump-shaped pattern between community diversity and disturbance, and is central to understanding patterns of species diversity. Here, we examine IDH in the context of alien plant invasions. IDH can offer insight into the role of disturbance in facilitating plant invasions and the effect of these invasions on floristic diversity.

Early stages of succession are most susceptible to invasion because resources and colonisation opportunities are elevated after disturbance. This trend is accentuated by human-mediated dispersal, a bias towards early successional species in the alien species pool, the tendency for fast-growing species to profit most from enemy release, and increased disturbance levels in human-modified habitats. Human disturbance, coupled with plant introductions, extends the diversity–disturbance curve and shifts peak diversity towards higher disturbance levels. However, invasive aliens can reduce native diversity at the community scale, especially in mid succession where competitive interactions structure communities. Certain invasive plants may have higher impacts because they overcome some life history tradeoffs as a result of their association with humans or novel evolutionary histories, e.g. enemy release. This may directly or indirectly (e.g. through plastic reallocation of resources from defence into growth) enable invasive plants to colonise earlier or persist into later stages of succession. By modifying disturbance regimes, invaders that transform the environment may also interfere with succession and precipitate low diversity communities. Low introduction rates of late successional species may currently limit impacts of aliens under infrequent disturbance.

IDH is a useful framework for understanding ecological communities. However, because of the novel evolutionary histories of alien species and the anthropogenic context in which they invade, disturbance levels that maximise total diversity in invaded communities can differ from those that maximise native diversity. Joint consideration of IDH and alien invasion patterns suggests a range of strategies can be used to manage diversity.

© 2011 Elsevier GmbH. All rights reserved.

## Introduction

The intermediate disturbance hypothesis (IDH; Paine and Vadas, 1969; Grime, 1973; Connell, 1978) is one of the fundamental hypotheses in ecology and has been implicated in structuring patterns of species richness in terrestrial and aquatic ecosystems across the globe (Shea et al., 2004). IDH proposes that

* Corresponding author. Tel.: +61 3 8344 5422; fax: +61 3 9348 1620.
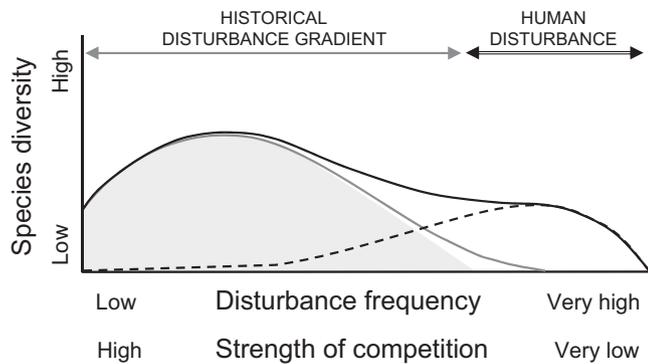*E-mail address:* catfordj@unimelb.edu.au (J.A. Catford).

**Fig. 1.** In early stages of invasion, the addition of alien species combined with human disturbance extends the IDH curve and augments species richness in high disturbance sites; it does not reduce native diversity. Early stages of invasion focus on colonisation and include introduction and naturalisation sensu Richardson et al. (2000). Grey shading indicates pre-invasion community species diversity under the historical disturbance regime; lines indicate diversity post-invasion and post-anthropogenic disturbance: solid black line, community diversity; dotted black line, alien diversity; solid grey line, native diversity.

the relationship between species richness/diversity and disturbance is hump-shaped such that intermediate levels of disturbance maintain the highest biological diversity in plant and animal communities. Although the pattern is widely observed, the mechanisms underlying IDH reflect the complex interplay between life-history, biotic interactions and historical disturbance regimes that will be particular to any one ecosystem (Menge and Sutherland, 1987). Disturbance also facilitates biological invasion, which can threaten native diversity (Hobbs and Huenneke, 1992; Pyšek and Richardson, 2006). As threats to biodiversity intensify (McKee et al., 2004) and rates of species invasion continue to rise (Hellmann et al., 2008; Hulme et al., 2009), effective ecological management requires detailed understanding of relationships among disturbance, invasion and diversity (Hulme, 2006).

The IDH hump-backed curve is most commonly attributed to the interplay between disturbance and tradeoffs in species' life history traits along successional gradients (Connell, 1978; Sheil and Burslem, 2003; Rejmánek et al., 2004; Shea et al., 2004). Low or reduced levels of disturbance will lead to low diversity through competitive exclusion and the dominance of long-lived species, while high or increased levels of disturbance will eliminate species incapable of rapid re-colonisation and growth (Huston, 1979). As a result, community diversity peaks at intermediate levels of disturbance causing a hump-shaped pattern (Fig. 1). We use this explanation of IDH (i.e. an emphasis on colonisation–competition tradeoffs) as the basis of our discussions because colonisation–competition tradeoffs are commonly invoked when considering IDH and are also thought to be particularly important for biological invasions (Seabloom et al., 2003). However, it should be noted that many other niche tradeoffs can potentially affect patterns of species diversity over time and space (e.g. competitive ability versus predator resistance, investment in reproduction versus survival, differential use of resources or tolerance to abiotic conditions; Stearns, 1989; Kneitel and Chase, 2004).

Although disturbance has been defined in different ways (Pickett and White, 1985; Mackey and Currie, 2000; Shea et al., 2004), here we view disturbance as any relatively discrete event that increases resource availability (e.g. nutrients, light) through the partial or total destruction of plant biomass (Grime, 1977; Connell, 1978). Under this definition, biotic interactions such as grazing are a form of disturbance, but competitive effects of alien plants are not considered as such because they do not result in the physical removal of plant biomass. Disturbance events can be

characterised by their duration, frequency, intensity, timing, spatial extent and variability (White and Pickett, 1985; Shea et al., 2004). While each of these disturbance parameters is ecologically important, for simplicity we concentrate only on disturbance frequency, or time since last disturbance. Time since disturbance relates to resource availability and stage of succession, and is thus associated with level of stress and strength of competition for resources (Fig. 1; Connell and Slatyer, 1977; Grime, 1977). IDH can apply to a single location followed over time or to a mosaic of habitat patches that are at different successional stages at one point in time (Shea et al., 2004); we focus on the former. IDH is most commonly applied to species richness, but it can also be applied to species and functional diversity (Mackey and Currie, 2001; Shea et al., 2004); here, we concentrate on species richness and species diversity. Despite decades of research on IDH, alien plant invasions have rarely been viewed in the context of IDH (cf. Hobbs and Huenneke, 1992; Kowarik, 2008). IDH can offer insight into the role of disturbance in facilitating biological invasions and the impact of alien plants on diversity and disturbance regimes.

In general, the life history strategies of alien and native plant species are constrained by similar tradeoffs (Leishman et al., 2010; Penuelas et al., 2010; cf. Huston and Smith, 1987; Funk and Vitousek, 2007). Alien and native species may thus be expected to respond in the same way to disturbance and succession. However, of the collection of native and alien species within a region, it is likely that the alien species will be better adapted to anthropogenic disturbance (Kowarik, 2008). The alien species pool may also contain species that have been released from natural enemies (Blumenthal et al., 2009) and belong to "novel" functional groups, which can prompt major biogeochemical changes and shifts in disturbance regimes and can alter the trajectory of secondary succession (Vitousek et al., 1987, 1997; Sullivan et al., 2007). Such differences between native and alien species can have important implications for understanding aliens' interactions with, and effects on, other species in a community.

In this paper, we consider the relationship between alien plant invasions and IDH by addressing two questions: in accordance with IDH, (1) at what disturbance frequencies is alien plant colonisation most likely and why, and (2) where along the disturbance continuum (at which successional stage) are alien plants likely to reduce community diversity and why? We use understanding of community and invasion ecology to answer these questions. We support our arguments with empirical evidence from a variety of terrestrial ecosystems and include disturbance types that range from livestock grazing to floods to volcanic eruptions (though much of the most relevant literature has focused on old-field successions). We conclude the paper by discussing implications and strategies for managing plant communities and how patterns of invasion might change in the future. In keeping with IDH, this paper focuses on invasion and the disturbance–diversity relationship, but we recognise that links between succession and invasion ecology are much broader (Davis et al., 2005).

## Question 1: In accordance with IDH, at what disturbance frequencies is alien plant colonisation most likely and why?

Frequently disturbed areas are most vulnerable to species invasion because resource availability is elevated, increasing the probability of successful colonisation and recruitment (Fig. 1). As depicted in models of succession (Connell and Slatyer, 1977), species richness in frequently disturbed areas is not limited by competition for (or tolerance of) limiting resources; instead, it reflects the ability of species to colonise, grow rapidly and withstand local environmental conditions (Huston and Smith, 1987). Conditions

following disturbance are particularly amenable to colonisation by both native and alien species, but there are several reasons why alien species are especially successful in these areas. The tendency for most alien species to successfully invade early successional systems can be attributed to their close association with humans, capacity to exploit human disturbance and their novel evolutionary histories, as described below.

Dominance of alien species that colonise soon after disturbance can be heightened when humans alter disturbance regimes, typically by elevating disturbance frequencies or introducing new forms of disturbance (Fig. 1; Hannah et al., 1995). Having evolved under historical disturbance conditions, native species may be poorly adapted to more frequent or novel forms of disturbance (Shea et al., 2004). For example, native species of Californian coastal sage scrub are well adapted to natural spring fires but are sensitive to human-mediated ploughing, grazing and autumn fires (Fleming et al., 2009). Subsequently, the "novel niches" at the high end of the disturbance gradient may be wholly occupied by alien species more tolerant of such conditions (Fig. 1; Moles et al., 2008). Even if some native species can tolerate modified disturbance regimes, alien species may greatly outnumber them and therefore dominate early successional systems. For example, in human-degraded riparian zones of the Hunter River, Australia there are 106 extant early successional alien plant species compared to 26 early successional native ones, and 33 native species associated with mid-late succession are now locally extinct (Kyle and Leishman, 2009). Even in naturally disturbed braided river systems of New Zealand, over 60% of plant species are naturalised aliens (Williams and Wiser, 2004).

Humans can increase the propagule pressure of alien species, and this is most advantageous in early succession where resource availability is high. As well as transporting alien species to the invaded range, humans (intentionally and unintentionally) help to move species around the landscape (Hodgkinson and Thompson, 1997). Species associated with human activities are thus likely to be dispersed more widely (Hulme, 2009), which extends the dispersal distance of alien species (Shea et al., 2004) in a way that may be unrelated to their natural dispersal abilities. Humans can also provide alien species with an advantage by planting them in high numbers in gardens, plantations or as agricultural crops (Lambdon et al., 2008; Essl et al., 2010). Consequently, they can become over-represented in the local species pool from which colonists are drawn, increasing the likelihood of alien plant establishment (Simberloff, 2009). The invasive grass, *Agropyron cristatum*, for example, can naturally only disperse over short distances (~5 m), so its invasion relies on its close proximity to abandoned fields where it was planted (Heidinga and Wilson, 2002) or accidental transportation associated with human activities. Many Pinaecae species (pine family) commonly colonise disturbed environments, but Pinaceae species used in plantation forestry are 2–4 times more likely to naturalise than those without commercial value (Essl et al., 2010).

Because alien species propagule pressure is high around areas of human activity (Pyšek et al., 2010), it is necessarily elevated around areas disturbed by humans. In various models of succession (Connell and Slatyer, 1977; Huston and Smith, 1987), rapid colonisation is considered important for occupying space in early succession. The ready supply of alien plant propagules close to disturbed areas may lead to "seed swamping" or earlier arrival of alien propagules post-disturbance, enabling alien species to colonise highly disturbed areas more rapidly than native species (see Huston and Smith, 1987). Human-driven increases in propagule pressure therefore provide a storage and dispersal advantage to alien species, with the greatest benefit occurring in low competition, high disturbance sites (Bellingham et al., 2005b).

These propagule pressure effects are often magnified by a "propagule bias" effect. Alien species are a non-random sample of the global species pool (Daehler, 1998) largely because most aliens are introduced (either deliberately or accidentally) through agriculture, forestry and horticulture (Lambdon et al., 2008; Essl et al., 2010). Many of these alien species possess traits that pre-adapt them to exploit disturbance (e.g. high relative growth rate, small seed size, low root–shoot ratios, Wilsey and Polley, 2006; van Kleunen et al., 2010) and be successful in the early stages of succession (Daehler, 2003). Aliens colonising sites with high resource availability often have higher specific leaf area, foliar nutrient content and photosynthetic capacity than native species, which results in faster growth and higher photosynthetic productivity (Leishman et al., 2007; Penuelas et al., 2010). Alien species tend to be positioned further along the leaf economics spectrum towards faster growth (Leishman et al., 2010; Penuelas et al., 2010; cf. Dawson et al., 2011 for an exception to this finding) and are well adapted to environments with high disturbance and resource availability.

These patterns in life history traits of aliens may partly stem from propagule bias, but they may also reflect that early successional species are more successful invaders than late successional species. Studies comparing the traits of invasive and non-invasive alien plant species can help to disentangle these patterns. Rejmánek and Richardson (1996) found that short juvenile period, small seed mass and short interval between large seed crops distinguished 12 invasive from 12 non-invasive pine species. These three traits are associated with early successional conditions in that they enable rapid population growth through early and consistent reproduction, high fecundity, long distance dispersal and high relative seedling growth rate (Rejmánek and Richardson, 1996). Supporting these findings, a meta-analysis that compared growth performance-related traits of 125 invasive and 196 non-invasive plant species revealed that mean trait values for invasive species were consistently higher than those of non-invasive ones (van Kleunen et al., 2010). These findings suggest that early successional characteristics associated with faster growth do predispose a species to becoming invasive.

Another explanation for the greater success of early successional alien species may lie in enemy release. Although not a universal finding (Chun et al., 2010), a reduction in herbivores and pathogens can lead to faster growth and a longer lifespan in the new environment. While enemy release should be beneficial to both early and late successional species, survivorship takes priority over growth as resource availability declines, so plants invest more in defence than productivity as succession progresses (Cates and Orians, 1975). Consequently, fast growing early successional species have more (and experience greater limitation from) natural enemies than late successional species (Davidson, 1993), so potentially lose more enemies (in absolute terms) when they leave their home range. As a result, they experience a greater effect of enemy release than stress-tolerant species characteristic of late succession (Blumenthal et al., 2009). The alien species fitness advantage associated with enemy release will therefore be higher in early successional communities (Blumenthal et al., 2009). This has been proposed as a potential explanation for the great success of many alien species in grasslands (Kulmatiski et al., 2008).

In summary, we hypothesise that early stages of succession characterised by frequent disturbance are most susceptible to colonisation by alien plants (Fig. 1). This is consistent with succession theory (Wilson, 1969), but is accentuated because of human-mediated dispersal advantages, the increased frequency of disturbance in human-modified habitats, and the apparent bias towards early successional species in the alien species pool. The tendency for early successional alien species to experience greater levels of enemy release than later successional species may provide
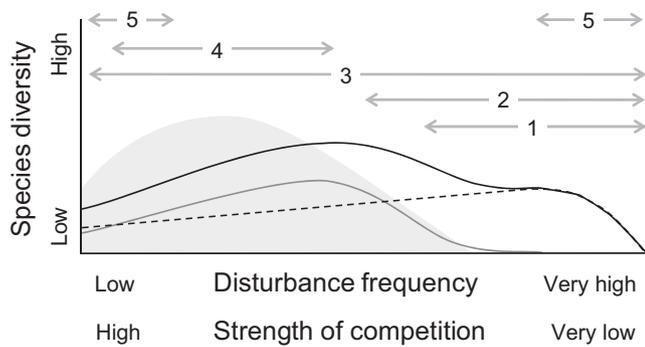
**Fig. 2.** Once established, invasive alien species able to persist into late successional stages may displace more than one native species causing a shift and reduction in peak diversity. Numbers indicate the mechanism that causes a reduction in diversity, 1: niche pre-emption, 2: apparent competition, 3: interference competition, 4: exploitative competition, 5: transformation of the environment; grey arrows indicate position along the disturbance gradient where mechanisms have greatest effect. Other details as in Fig. 1.

a further fitness advantage for early successional alien invaders. Although we contend that most alien species will colonise and establish in early succession, we note that many alien species can establish and persist into later stages of succession. As discussed below, alien species may also affect native species diversity (Fig. 2). While the hump-shaped curve remains, we predict that the concentration of colonising alien species at the high end of the disturbance spectrum can extend the diversity–disturbance gradient (Fig. 1). Patterns of native and alien species richness in vegetation relevés around Berlin, Germany support this prediction (Kowarik, 2008).

**Question 2: In accordance with IDH, where along the disturbance continuum are alien plants likely to reduce community diversity and why?**

Given that IDH relates to patterns of community richness/diversity, this is the currency with which we evaluate the impacts of alien species, particularly because such impacts are often of conservation concern (Vilà et al., 2011). However, we acknowledge that this is not the only effect of invasions, and that reductions in diversity need not result in local extinction (Davis, 2003), especially over the short-term.

We propose that there are five main ways in which alien species may reduce local diversity – through niche pre-emption, apparent competition, interference competition, exploitative competition and transformation of the environment. These mechanisms can occur at any point along a disturbance gradient, but some are likely to be more pronounced at particular stages of succession. Competition for resources, for instance, is most important in mid-late succession (Grime, 1977), so declines in diversity from exploitative competition are expected to be concentrated there (Fig. 2). In contrast, the composition of early successional communities is largely determined by colonisation probabilities (Foster et al., 2004), and interspecific interactions are correspondingly weak (as is often assumed in lottery models of community assembly, for example: Pacala and Tilman, 1994). As such, exploitative competition is less important, but alien species can reduce native plant diversity under high disturbance through niche pre-emption and apparent competition. We briefly discuss the five mechanisms below, and illustrate ways in which alien species can exploit these mechanisms and lead to diversity reductions at the community scale.

(1) *Niche pre-emption*
When the composition of a community is determined by a lottery, a bias towards alien species in the propagule pool would mean less representation by natives even if species do not interact (Sale, 1977). If alien species have faster growth rates or more efficient dispersal (human-mediated or not) than native colonists, alien species can colonise available microsites first, which will effectively pre-empt native species (Mwangi et al., 2007). Such displacement is unlikely to cause reductions in total plant diversity, but native diversity may decline, as observed following invasion of the alien annual geophyte *Oxalis pes-caprae* in Mediterranean olive groves (Vilà et al., 2006). As a result of its comparatively early and short-season phenology, *O. pes-caprae* has replaced vulnerable and endemic ruderal species and reduced native species diversity at these frequently disturbed sites. Niche pre-emption impacts patterns of species colonisation, so it will be most evident in, though not restricted to, early succession (Fig. 2).

(2) *Apparent competition*
If invasive alien species suffer less from generalist herbivores and pathogens than native species while simultaneously supporting larger populations of these herbivores and pathogens, this can result in apparent competition (Eppinga et al., 2006). If some individuals of native species are then replaced by individuals of the less enemy-constrained alien species, diversity can decline because of reductions in species evenness. Apparent competition can occur at anywhere along the disturbance gradient, but will likely have greatest impact in early succession where plant community composition is most likely to be shaped by natural enemies (reflecting the greater number of enemies in early succession; Blumenthal et al., 2009). In Californian grasslands, experimental addition of the alien annual forb, *Brassica nigra*, resulted in almost a ninefold increase in the consumer impact of small native mammals on native bunchgrass, *Nasella pulchra*, inhibiting *N. pulchra*'s establishment (Orrock et al., 2008).

(3) *Interference competition*
Alien colonists may inhibit native species recruitment and performance through interference competition, via such mechanisms as allelopathy (Vilà et al., 2006). Allelopathic or antimicrobial root exudates of alien species may more strongly suppress natives because native competitors are not adapted to them (Callaway and Ridenour, 2004). For example, phytotoxic root exudates of the invasive Eurasian forb, *Centaurea maculosa*, were found to markedly reduce the growth (height and leaf number) of native plant species in its invaded range in Montana, but not in its home range in Romania (Thorpe et al., 2009; cf. Weir et al., 2010). Interference competition can occur at all stages of succession, but it will likely have the highest impacts in mid succession where species richness is highest and stronger plant–plant interactions are expected (Fig. 2).

(4) *Exploitative competition*
Effects of exploitative competition will be most apparent in mid-late succession where resources become limiting and plant diversity is high (Fig. 2). If an alien species is more competitive than its native counterparts, it can co-opt more of the available resources leading to a decline in native species abundance or richness (White et al., 2006). In forest ecosystems, the species that pose the greatest threat to community structure and diversity are shade-tolerant species that persist or increase with succession (Martin et al., 2009). In a recent review, Martin et al. (2009) identified 139 invasive alien plant species established in North America that are shade-tolerant. These include *Acer platanoides* (Martin et al., 2010), *Lonicera tatrica* (Woods, 1993) and *Microstegium vimineum* (Flory and Clay, 2010); all of which are present in mid-late succession (Table 1). Unlike their native competitors, some alien shade-tolerant species are still able to achieve rapid growth despite

**Table 1**

Impacts of invasion on plant diversity: examples of alien plant species that invade early and mid-late stages of succession and displace one or more native species resulting in a reduction in native species diversity or community species diversity. Early succession: stage immediately following a disturbance that has high resource availability and high physical stress; characterised by short-lived species with high fecundity, long dispersal distances, fast growth rates and small stature. Mid-late succession: low physical stress; sere dominated by long-lived species able to effectively compete for, or tolerate, limiting resources (Grime, 1977; Huston and Smith, 1987).

| Alien species | Invaded system | Early successional | Mid-late successional | Native diversity reduction | Community diversity reduction | Description | References |
|---|---|---|---|---|---|---|---|
| *Oxalis pes-caprae* (annual geophyte) | Mediterrannean islands | X | | X | | Replaced vulnerable and endemic ruderal species | Vilà et al. (2006) |
| *Chrysanthemoides monilifera* subsp. *rotundata* (shrub) | Dunes, eastern Australia | X | | X | X | Native species richness reduced by 35–75% across a range of life forms in invaded sites | Mason and French (2008) |
| *Cinchona pubescens (tree)* | Uplands, Santa Cruz, Galápagos | X | | X | X | Over 50% decline in diversity and cover, but not richness, of native species | Jäger et al. (2009) |
| *Imperata cylindrical* (rhizomatous grass) | Longleaf pine flatwoods, Mississippi, USA. | | X | X | X | Reduced plot species richness by 60–80% within 3 years; by increasing shade, can displace shorter plants (i.e. most groundcover herbs) | Brewer (2008) |
| *Agropyron cristatum* (perennial grass) | North American prairie | X | X | X | X | Invades native prairie from abandoned agricultural fields; at 30% cover, reduces overall diversity by 35% (gamma and beta diversity both affected) | Heidinga and Wilson (2002) |
| *Taeniatherum caput-medusae* (annual grass) | North American sagebrush | | X | X | X | Plant diversity in heavily invaded sites reduced by 85% and richness by 60% compared with uninvaded sites. | Davies (2011) |
| *Microstegium vimineum* (grass) | Forest understoreys, USA | X | X | X | X | Reduced native plant species diversity by 38% within two years | Eschtruth and Battles (2009) and Flory and Clay (2010) |
| *Fallopia* spp. (rhizomatous herbs) | Europe | X | X | X | X | Reduce species diversity and alter community structure | Hejda et al. (2009) |
| *Tradescantia fluminensis* (clonal herb) | Forest understoreys, New Zealand | X | X | X | X | 10-fold reduction in tree seedling species richness in forest understoreys in invaded sites compared with uninvaded sites | Standish et al. (2001) |
| *Ligustrum robustum* subsp. *walkeri* (shrub) | La Réunion wet forests | X | X | X | X | At least 5 native species threatened with extinction | Lavergne et al. (1999) |
| *Lonicera tatarica* (shrubby honeysuckle) | woodlands, northeastern USA | X | X | X | X | In mesic stand with rich soil, herb cover and species richness and tree seedling density substantially depressed when *L. tatarica* cover > 30% | Woods (1993) |
| *Miconia calvescens* (tree) | Rainforests, Tahiti | X | X | X | X | Reduced fecundity of understorey trees; almost 50% of Tahiti's endemic species threatened with extinction | Meyer and Florence (1996) |
| *Triadica* (*Sapium*) *sebifera* (tree) | Louisiana forests, USA | X | X | X | X | Arresting succession from *Salix nigra* to *Nyssa aquatica-Taxodium distichum* forest in the Atchafalaya Basin | Rejmánek unpublished |

the low light conditions (Bellingham et al., 2005b; Martin et al., 2010). Fast growth rates are associated with competitive ability (Grime, 1977) and invasiveness (van Kleunen et al., 2010). The ability to maintain relatively high growth despite low light conditions will ensure that an invasive alien species can secure a greater share of resources and thus be highly invasive even in undisturbed forests. An advantage through exploitative competition is not necessarily limited to shade-tolerance: species differ in their tolerance to other resources, such as moisture and nutrients (Connell and Slatyer, 1977).

(5) *Transformation*

Some alien plants promote or inhibit disturbance by transforming the habitats they invade because of their growth form, ecology or life history characteristics (Richardson et al., 2000). By maximising or minimising the frequency of disturbance over a sequence of disturbance events, these species can attain an advantage over resident species by maintaining particular conditions or disturbance regimes. Among the best-known examples are alien grasses that alter fire regimes. A variety of alien C3 and C4 grasses have promoted fire in Hawaii, North, Central and South America, South Africa and Australia (D'Antonio and Vitousek, 1992). In northern Australia, savannas dominated by the alien grass *Andropogon gayanus* have a fuel load up to seven times higher than native grass savannas. The resultant increase in fire frequency and intensity causes tree mortality, reduces understorey diversity and promotes a self-sustaining grass-fire cycle (Rossiter et al., 2003). At the other end of the spectrum, highly competitive species can inhibit disturbance (e.g. *Ammophila arenaria* stabilises sand dunes: Buell et al., 1995) potentially preventing succession from being reset. Through positive feedbacks on disturbance, self-perpetuating monocultures, or near-monocultures, can form resulting in a flattened (and then a shortened) IDH curve. If an invasive alien species maintains conditions or a disturbance regime that did not exist previously, then the pre-invasion diversity–disturbance curve may no longer apply. This transformation might be interpreted as an alternate stable state, but it may be more accurately referred to as an alternate transient state (Fukami and Nakajima, 2011); its length of persistence is uncertain.

These five mechanisms are not limited to alien species, but alien species can potentially have a greater impact on community diversity than native species because of their novel evolutionary histories and association with humans; these may allow them to overcome life history tradeoffs that are associated with competition and colonisation. Longer-lived aliens that are expected to dominate later in succession may colonise earlier and in greater numbers because of frequent human-mediated dispersal and introduction. These species can displace shorter-lived species that are typically the most successful colonists after a disturbance. Instead of a gradual change from shorter- to longer-lived species as the former die, species composition and diversity will then remain similar through early to mid succession and the associated peak in diversity at mid succession will decrease (Fig. 2). Elevated propagule pressure can also help early successional alien species to persist into later stages of succession.

On arrival in a new range, alien species may lose specialist and generalist enemies (Keane and Crawley, 2002), they may form new symbiotic relationships (Mitchell et al., 2006) and their allelopathic chemicals may become "novel weapons" that more effectively suppress competitors (Callaway and Ridenour, 2004). As with human-mediated dispersal and increased propagule pressure, these altered dynamics may allow some alien species to establish

or persist in conditions to which they are otherwise poorly adapted (Table 2; DeWalt et al., 2004; Martin et al., 2010).

Focusing on enemy release, early successional species that are released from natural enemies may be able to persist into later stages of succession (DeWalt, 2005; Kulmatiski et al., 2008). If late-successional species are released from enemies against which they normally invest resources for defence, they may re-allocate these resources towards development of faster growth rates and seed production (Joshi and Vrieling, 2005); this would enable them to colonise a greater number of sites in early succession (Blumenthal et al., 2009). For example, *A. platanoides*, an invasive tree in the US, is able to maintain high growth rates under low light (Martin et al., 2010). In its introduced range, *A. platanoides* suffers three times less herbivory than it its native range (Adams et al., 2009), and it experiences less herbivore attack than a native congener (Cincotta et al., 2009). As well as high physiological plasticity (Martin et al., 2010), the ability of this species to occupy and maintain high growth rates in a variety of environmental conditions may partly relate to enemy release. The invasive shrub *Clidemia hirta* similarly benefits from reduced herbivory in its introduced range enabling it to invade forest understoreys where it is not normally found in its native range, as well as the open habitats that it usually occupies (DeWalt et al., 2004).

Together, the five mechanisms discussed above can potentially reduce diversity at any point along the (historical) disturbance gradient (Fig. 2). Depending on the number of alien colonists and the degree to which disturbance frequencies have been elevated, invasion may result in a bimodal hump-shaped curve. It seems more likely, however, that the unimodal curve will remain, with peak diversity reduced. The greatest losses in diversity will occur in mid-late succession where diversity and competition are high (Fig. 2). To date, there has only been a modest amount of evidence to support this prediction. This may reflect that there has been insufficient time to witness competitive impacts of invasive species on diversity (Davis, 2003), particularly in relatively undisturbed environments where invasion is necessarily slower and also less frequently examined (Martin et al., 2009). However, impacts of some mid-late successional alien species are increasingly being documented. The alien perennial grass *Agropyron cristatum* invades undisturbed mixed-grass prairie in the northern Great Plains of Canada and reduces species richness by c. 70% and species diversity by 45% (Christian and Wilson, 1999). Grasslands dominated by this alien grass are stable for decades and experience little reciprocal invasion by native species (Heidinga and Wilson, 2002). The shade tolerant alien tree *Miconia calvescens* invades Tahitian rainforests (Meyer and Florence, 1996) and by intercepting light, its dense canopies have reduced the fecundity and reproductive capacity of two endemic understorey trees (*Psychotria speciosa* and *Psychotria tahitensis*, Meyer et al., 2003). It has been predicted that, without intervention, up to 50 of Tahiti's 107 endemic plant species may go extinct as a result of this single alien species (Meyer and Florence, 1996).

Summarizing the impacts of invaders on the IDH curve (Fig. 2), we suggest that colonists in early successional communities may impact native diversity through apparent competition and niche pre-emption, but this will result in the smallest reduction in diversity (typically a one-for-one displacement). We predict that mid-late successional invasions will have a larger impact on native diversity (potentially a one-for-many displacement), being driven by exploitative competition and the ability of alien species to circumvent some evolutionary tradeoffs. In the case of species that transform the environment, we propose that the greatest reduction in diversity will also occur in mid-late succession but diversity will be affected across all successional stages. By altering disturbance regimes, this subset of species seems to fundamentally interfere

**Table 2**
Examples of some invasive alien species that may alter the appearance of IDH curve and the mechanisms by which they do so: (a) species that circumvent some life history tradeoffs, and (b) species that alter the frequency of disturbance inhibiting succession.

| Alien species | Mechanism for altering IDH prediction | Ecosystem | References |
|---|---|---|---|
| **(a) Avoid evolutionary tradeoff** | | | |
| *Acer platanoides* (tree) | Enemy release; high physiological plasticity; shade tolerance | Forests, USA | Adams et al. (2009) and Martin et al. (2010) |
| *Bischofia javanica* (tree) | High physiological plasticity; shade tolerance; rapid growth | Wet forests, oceanic islands, Japan | Hata et al. (2006) |
| *Clidemia hirta* (shrub) | Enemy release; shade tolerance | Forest understoreys, Hawaii | DeWalt et al. (2004) |
| *Ligustrum robustrum* subsp. *walkeri* (tree) | Shade tolerance; rapid growth | Wet forests, La Réunion | Lavergne et al. (1999) |
| *Miconia calvescens* (tree) | Enemy release; shade tolerance; ruderal characteristics, e.g. fast growth rates, prolific seed production, efficient dispersal | Wet forests, Tahiti | Meyer and Florence (1996) |
| *Microstegium vimineum* (grass) | Enemy release; high propagule pressure; high physiological plasticity; shade tolerance | Forest understoreys, USA | Eschtruth and Battles (2009) and Flory and Clay (2010) |
| *Pittosporum undulatum* (tree) | High physiological plasticity; shade tolerance; rapid growth | Wet forests, Jamaica | Bellingham et al. (2005b) |
| **(b) Transform environment in their favour** | | | |
| *Ammophila arenaria* (grass) | Decrease soil disturbance | Coastal dunes, California, USA | Buell et al. (1995) |
| *Andropogon gayanus* (grass) | Increase fire frequency: higher fuel load increases fire frequency and intensity | Tropical savannas, Australia | Rossiter et al. (2003) |
| *Mimosa pigra* (shrub) | Decrease fire frequency | Wetlands, northern Australia | Lonsdale and Miller (1993) |
| Multiple grass species | Increase fire frequency: promote self-sustaining grass-fire cycle | Multiple ecosystems, worldwide | D'Antonio and Vitousek (1992) |

with the process of succession. While they typically maintain communities at either very late or early stages of succession, over time species that transform ecosystems may affect community composition at all successional stages by shifting disturbance frequencies in a particular direction, decoupling the relationship between disturbance and diversity in the invaded ecosystems. When extended to evolutionary timeframes though (and assuming no further invasion by other transformers), other species in the area will likely adapt to a transformed system, but this process of rebuilding diversity is slow.

Empirical evidence (cited above) supports various elements of our integration of IDH and alien plant invasion (Figs. 1 and 2). However, field surveys along disturbance gradients will help to provide more rigorous tests of our predicted patterns. Manipulative studies will be required to assess the validity of specific mechanisms. This is no small task, but many useful experiments could be carried out within a context of adaptive management. Ultimately, we expect our framework to be valuable for informing biodiversity management.

## Discussion

### Management implications

In light of the mechanisms and impacts of invasion, there appear to be four main approaches for responding to and managing invasion: do nothing; control introduction and manage the propagule of supply alien and native species; manage environmental conditions; and manage invasive species populations. These approaches are not mutually exclusive and a combination of strategies will likely be required.

(1) *Do nothing – let succession take its course*

Supporting the notion that alien species tend to be early successional colonists, several studies have shown that the proportion of alien species significantly decreases with time since disturbance (Bellingham et al., 2005a; Murphy et al., 2008). Active restoration of invaded areas by removal of alien species immediately following disturbance may therefore be unnecessary (Dewine and Cooper, 2008), and can even be counterproductive (D'Antonio and Meyerson, 2002). In fact, alien plants able to tolerate anthropogenic increases in disturbance may play a valuable role in secondary succession and ecosystem restoration (Ewel and Putz, 2004), particularly if the native species pool is impoverished because of anthropogenic activities. However, there are several arguments against this as outlined below.

Alien plant species that colonise and dominate soon after disturbance can alter ecosystem function and properties and can potentially alter successional pathways (Vitousek et al., 1987; Peltzer et al., 2009), even though the alien species may be relatively short-lived and subsequently replaced by native species (Sullivan et al., 2007). Although the success of many alien species seems to relate to early successional characteristics, some invasive species can outcompete functionally similar native species and persist and dominate over long periods of time (Christian and Wilson, 1999). It has been hypothesised that alien species establish in high disturbance areas first and, from there, they can adapt to and colonise sites with different environmental conditions (Clark and Johnston, 2011). And, of course, not all alien species are early successional species that will be replaced over time; some are long-lived *K*-strategists that are highly competitive, can invade undisturbed areas and can persist for decades (Wilsey et al., 2009; van Kleunen et al., 2010).

(2) *Control introduction and manage propagule supply*

Preventing the introduction and establishment of invasive alien species will obviously be the most effective management strategy. Weed risk assessment approaches used in quarantine and biosecurity are typically based on alien species' life history traits, environmental preferences and a species' current weed status in other countries, but they rarely assess the likely impact of an invasive plant (Hulme, 2012). We have argued that species invading mid-successional seres tend to have the greatest impact on diversity and these species might have several distinguishing characteristics that can be included in weed risk assessments. For example, species that achieve success through

exploitative competition can be identified based on their tolerance to low resource availability combined with traits such as high physiological plasticity, high fecundity, ability to reach reproductive maturity early, ability to resprout, a large seed-bank, fast growth rate, and/or release from enemies (Meyer and Florence, 1996; Bellingham et al., 2005b; Martin et al., 2010; van Kleunen et al., 2010). The trait values of alien species should be considered relative to the recipient community with the idea that the more novel a functional group to which an alien species belongs, the greater the potential impact (Callaway and Ridenour, 2004; Brewer, 2008).

To reduce the establishment of alien species and impacts of niche pre-emption, reducing propagule pressure of alien species and increasing the propagule supply of native species could tilt the balance towards native species (or at least put them on a more level playing field). Sources of alien species propagules could be reduced by e.g. preventing urbanisation close to nature reserves (von der Lippe and Kowarik, 2008; cf. Teo et al., 2003), managing botanic garden and crop/plantation species in vicinity of important ecosystems (Hulme, 2011), and focusing control efforts on reducing spread from alien invasion hotspots (Ibáñez et al., 2009). Native species suitable for direct sowing should be selected based on their traits and ability to establish and persist under the current environmental conditions (Funk et al., 2008; Moles et al., 2008). This approach will be particularly valuable (and effective) in systems that have experienced environmental modification and those in early succession where colonisation opportunities are at their highest, including alien-dominated systems (Christian and Wilson, 1999; Davis and Pelsor, 2001).

(3) *Manage environmental conditions*

In situations where the relative abundance of alien species has increased following environmental modification (Catford et al., 2011), it may be more effective to target the cause of the problem (e.g. altered disturbance regimes) than attempt to manage plant populations directly, i.e. the symptom (MacDougall and Turkington, 2005; Hulme, 2006). For example, the invasive grass *Cortaderia jubata* is the only species in the local species pool capable of growing along severely eroded road cuts in California (Fig. 3). Rather than applying herbicide to control *C. jubata*, it would be more effective to reduce the disturbance frequency by stabilising the soil; this would provide suitable conditions for a greater range of species, including natives (M. Rejmánek, unpublished).

The ability of some alien species to modify environmental conditions in their favour means that these species have

the greatest potential to alter the character and function of an ecosystem. If management is committed and sustained, directly targeting the environmental parameter that these species change may be a useful control technique, as seen in control burns of the alien fire-suppressing species *Mimosa pigra* in Australia (Lonsdale and Miller, 1993). The addition of carbon-rich substrates may reduce the legacy of high N in soils colonised by nitrogen-fixing aliens, and activated charcoal may be used to neutralise impacts of harmful allelochemicals (Hulme, 2006). However, such management actions may be hard to execute (e.g. promoting fire), may have non-target impacts, and – unless the target species is eradicated – may be futile over the long term as the species will continue to modify the habitat. Modifying aspects of the environment that these species do not actively change may warrant exploration. For example, altering river flow regimes (e.g. higher water table, earlier spring floods) may inhibit growth and germination of the alien *Impatiens glandulifera* in riparian zones in Europe (Tickner et al., 2001), though it may come at the cost of inhibiting native species or facilitating other alien species (Hulme and Bremner, 2006).

(4) *Manage invasive species populations to reduce their impact*

For some highly invasive species, it may be more effective to focus on weed control techniques that directly target their populations. Traditional control techniques like herbicide use and mechanical removal may help to alleviate the competitive effects of some species and limit further spread. Highly invasive, competitive species that have experienced enemy release may be suitable targets for biological control; fast-growing species typically benefit the most from enemy release (Blumenthal et al., 2009), so they should be a priority.

*Future trends*

Global increases in international trade and changes to trading routes will bring new species to different areas (Hulme, 2009), and demands of industry for different plant types will ensure that species with a increasing variety of life history traits are introduced. Even tropical forests, which are typically considered more resistant to invasion than other ecosystems, are likely to experience increased numbers of alien species as forestry practices shift to planting shade-tolerant alien species that can persist in lower light environments characteristic of late succession (Fine, 2002). If the propagule bias towards early successional species is reduced in the future, many more alien species will be able to occupy late successional stages and the potential for new negative impacts will



**Fig. 3.** *Cortaderia jubata* (Pampas grass) growing along severely eroded road cuttings in coastal areas of California, USA. This apomictic South American species establishes under very high disturbance frequencies that native species cannot tolerate. When herbicides are used to kill *C. jubata*, more erosion follows precipitating further invasion. Source: M. Rejmánek

increase. Even if all species introductions ceased today, impacts would nevertheless continue to rise (Essl et al., 2011). In addition to the lag-phase common to many plant invasions (Aikio et al., 2010), the slower rate of absolute invasion by late successional species means that many alien species already introduced into ecosystems may have gone unnoticed. This trend is exacerbated by the dearth of invasion research in late successional communities (Martin et al., 2009).

While most alien species appear to respond in much the same way as native species, a crucial fraction of the alien species pool can significantly affect the ecosystems they invade (Christian and Wilson, 1999; Liao et al., 2008). As ecosystems are increasingly altered through biological invasions and environmental modification (Hobbs et al., 2006), potential differences between alien and native species' effects on ecological processes must continue to be examined. There is already empirical evidence to suggest that the novel evolutionary histories of alien species affect the way community diversity is maintained, and that diversity is maintained at a lower level than in communities made up of coevolved native species (Wilsey et al., 2009; Penuelas et al., 2010).

The scenarios and examples explored in this paper illustrate that IDH is a useful framework for understanding ecological communities and for highlighting ways in which alien species can affect diversity across a broad range of systems. However, because of the novel evolutionary histories of alien species and the anthropogenic context in which they invade, disturbance levels that maximise total diversity in invaded communities may differ from those that maximise native diversity. In particular, alien plants that can overcome some life history tradeoffs and those that transform disturbance regimes may alter the hump-shaped curve that IDH predicts. With increasing rates of invasion (Hulme et al., 2009) and the advent of novel ecosystems (Hobbs et al., 2006), the role and response of these species in community dynamics should be a research priority.

## Acknowledgements

## References

Adams, J., Fang, W., Callaway, R., Cipollini, D., Newell, E., 2009. A cross-continental test of the Enemy Release Hypothesis: leaf herbivory on *Acer platanoides* (L.) is three times lower in North America than in its native Europe. Biol. Invasions 11, 1005–1016.
Aikio, S., Duncan, R.P., Hulme, P.E., 2010. Lag-phases in alien plant invasions: separating the facts from the artefacts. Oikos 119, 370–378.
Bellingham, P.J., Peltzer, D.A., Walker, L.R., 2005a. Contrasting impacts of a native and an invasive exotic shrub on flood-plain succession. J. Veg. Sci. 16, 135–142.
Bellingham, P.J., Tanner, E.V.J., Healey, J.R., 2005b. Hurricane disturbance accelerates invasion by the alien tree *Pittosporum undulatum* in Jamaican montane rain forests. J. Veg. Sci. 16, 675–684.
Blumenthal, D., Mitchell, C.E., Pyšek, P., Jarošík, V., 2009. Synergy between pathogen release and resource availability in plant invasion. Proc. Natl. Acad. Sci. U. S. A. 106, 7899–7904.
Brewer, S., 2008. Declines in plant species richness and endemic plant species in longleaf pine savannas invaded by *Imperata cylindrica*. Biol. Invasions 10, 1257–1264.

Buell, A.C., Pickart, A.J., Stuart, J.D., 1995. Introduction history and invasion patterns of *Ammophila arenaria* on the north coast of California. Conserv. Biol. 9, 1587–1593.
Callaway, R.M., Ridenour, W.M., 2004. Novel weapons: invasive success and the evolution of increased competitive ability. Front. Ecol. Environ. 2, 436–443.
Cates, R.G., Orians, G.H., 1975. Successional status and the palatability of plants to generalized herbivores. Ecology 56, 410–418.
Catford, J.A., Downes, B.J., Gippel, C.J., Vesk, P.A., 2011. Flow regulation reduces native plant cover and facilitates exotic invasion in riparian wetlands. J. Appl. Ecol. 48, 432–442.
Christian, J.M., Wilson, S.D., 1999. Long-term ecosystem impacts of an introduced grass in the northern Great Plains. Ecology 80, 2397–2407.
Chun, Y.J., van Kleunen, M., Dawson, W., 2010. The role of enemy release, tolerance and resistance in plant invasions: linking damage to performance. Ecol. Lett. 13, 937–946.
Cincotta, C., Adams, J., Holzapfel, C., 2009. Testing the enemy release hypothesis: a comparison of foliar insect herbivory of the exotic Norway maple (*Acer platanoides* L.) and the native sugar maple (*A. saccharum* L.). Biol. Invasions 11, 379–388.
Clark, G.F., Johnston, E.L., 2011. Temporal change in the diversity–invasibility relationship in the presence of a disturbance regime. Ecol. Lett. 14, 52–57.
Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302–1310.
Connell, J.H., Slatyer, R.O., 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111, 1119–1144.
D'Antonio, C., Meyerson, L.A., 2002. Exotic plant species as problems and solutions in ecological restoration: a synthesis. Restor. Ecol. 10, 703–713.
D'Antonio, C.M., Vitousek, P.M., 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. Annu. Rev. Ecol. Syst. 23, 63–87.
Daehler, C.C., 1998. The taxonomic distribution of invasive angiosperm plants: ecological insights and comparison to agricultural weeds. Biol. Conserv. 84, 167–180.
Daehler, C.C., 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. Annu. Rev. Ecol. Syst. 34, 183–211.
Davidson, D.W., 1993. The effects of herbivory and granivory on terrestrial plant succession. Oikos 68, 23–35.
Davies, K., 2011. Plant community diversity and native plant abundance decline with increasing abundance of an exotic annual grass. Oecologia 167, 481–491.
Davis, M.A., 2003. Biotic globalization: does competition from introduced species threaten biodiversity? Bioscience 53, 481–489.
Davis, M.A., Pelsor, M., 2001. Experimental support for a resource-based mechanistic model of invasibility. Ecol. Lett. 4, 421–428.
Davis, M.A., Pergl, J., Truscott, A.-M., Kollmann, J., Bakker, J.P., Domenech, R., Prach, K., Prieur-Richard, A.-H., Veeneklaas, R.M., Pysek, P., del Moral, R., Hobbs, R.J., Collins, S.L.A., Pickett, S.T., Reich, P.B., 2005. Vegetation change: a reunifying concept in plant ecology. Perspect. Plant Ecol. 7, 69–76.
Dawson, W., Burslem, D.F.R.P., Hulme, P.E., 2011. The comparative importance of species traits and introduction characteristics in tropical plant invasions. Divers. Distrib. 17, 1111–1121.
DeWalt, S.J., 2005. Effects of natural enemies on tropical woody-plant invasions. In: Burslem, D.F.R.P., Pinard, M., Hartley, S.E. (Eds.), Biotic Interactions in the Tropics. Cambridge University Press, Cambridge, UK, pp. 459–483.
DeWalt, S.J., Denslow, J.S., Ickes, K., 2004. Natural-enemy release facilitates habitat expansion of the invasive tripoical shrub *Climedia hirta*. Ecology 85, 471–483.
Dewine, J.M., Cooper, D.J., 2008. Canopy shade and the successional replacement of tamarisk by native box elder. J. Appl. Ecol. 45, 505–514.
Eppinga, M.B., Rietkerk, M., Dekker, S.C., Ruiter, P.C.D., Van der Putten, W.H., 2006. Accumulation of local pathogens: a new hypothesis to explain exotic plant invasions. Oikos 114, 168–176.
Eschtruth, A.K., Battles, J.J., 2009. Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. Ecol. Monogr. 79, 265–280.
Essl, F., Dullinger, S., Rabitsch, W., Hulme, P.E., Huelber, K., Jarošík, V., Kleinbauer, I., Krausmann, F., Kühn, I., Nentwig, W., Vilà, M., Genovesi, P., Gherardi, F., Desprez-Loustau, M.L., Roques, A., Pyšek, P., 2011. Socioeconomic legacy yields an invasion debt. Proc. Natl. Acad. Sci. U. S. A. 108, 203–207.
Essl, F., Moser, D., Dullinger, S., Mang, T., Hulme, P.E., 2010. Selection for commercial forestry determines global patterns of alien conifer invasions. Divers. Distrib. 16, 911–921.
Ewel, J.J., Putz, F.E., 2004. A place for alien species in ecosystem restoration. Front. Ecol. Environ. 2, 354–360.
Fine, P.V.A., 2002. The invasibility of tropical forests by exotic plants. J. Trop. Ecol. 18, 687–705.
Fleming, G.M., Diffendorfer, J.E., Zedler, P.H., 2009. The relative importance of disturbance and exotic-plant abundance in California coastal sage scrub. Ecol. Appl. 19, 2210–2227.
Flory, S.L., Clay, K., 2010. Non-native grass invasion alters native plant composition in experimental communities. Biol. Invasions 12, 1285–1294.
Foster, B.L., Dickson, T.L., Murphy, C.A., Karel, I.S., Smith, V.H., 2004. Propagule pools mediate community assembly and diversity-ecosystem regulation along a grassland productivity gradient. J. Ecol. 92, 435–449.

Fukami, T., Nakajima, M., 2011. Community assembly: alternative stable states or alternative transient states? Ecol. Lett. 14, 973–984.

Funk, J.L., Cleland, E.E., Suding, K.N., Zavaleta, E.S., 2008. Restoration through reassembly: plant traits and invasion resistance. Trends Ecol. Evol. 23, 695–703.

Funk, J.L., Vitousek, P.M., 2007. Resource-use efficiency and plant invasion in low-resource systems. Nature 446, 1079–1081.

Grime, J.P., 1973. Competitive exclusion in herbaceous vegetation. Nature 242, 344–347.

Grime, J.P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111, 1169–1194.

Hannah, L., Carr, J.L., Lankerani, A., 1995. Human disturbance and natural habitat: a biome level analysis of a global data set. Biodivers. Conserv. 4, 128–155.

Hata, K., Suzuki, J.-I., Kachi, N., Yamamura, Y., 2006. A 19-year study of the dynamics of an invasive alien tree, *Bischofia javanica*, on a subtropical oceanic island. Pac. Sci. 60, 455–470.

Heidinga, L., Wilson, S.D., 2002. The impact of an invading alien grass (*Agropyron cristatum*) on species turnover in native prairie. Divers. Distrib. 8, 249–258.

Hejda, M., Pyšek, P., Jarošík, V., 2009. Impact of invasive plants on the species richness, diversity and composition of invaded communities. J. Ecol. 97, 393–403.

Hellmann, J.J., Byers, J.E., Bierwagen, B.G., Dukes, J.S., 2008. Five potential consequences of climate change for invasive species. Conserv. Biol. 22, 534–543.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A., Epstein, P.R., Ewel, J.J., Klink, C.A., Lugo, A.E., Norton, D., Ojima, D., Richardson, D.M., Sanderson, E.W., Valladares, F., Vilà, M., Zamora, R., Zobel, M., 2006. Novel ecosystems: theoretical and management aspects of the new ecological world order. Global Ecol. Biogeogr. 15, 1–7.

Hobbs, R.J., Huenneke, L.F., 1992. Disturbance, diversity, and invasion: implications for conservation. Conserv. Biol. 6, 324–337.

Hodgkinson, D.J., Thompson, K., 1997. Plant dispersal: the role of man. J. Appl. Ecol. 34, 1484–1496.

Hulme, P., 2012. Weed risk assessment: a way forward or a waste of time? J. Appl. Ecol., doi:10.1111/j.1365-2664.2011.02069.x.

Hulme, P.E., 2006. Beyond control: wider implications for the management of biological invasions. J. Appl. Ecol. 43, 835–847.

Hulme, P.E., 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. J. Appl. Ecol. 46, 10–18.

Hulme, P.E., 2011. Addressing the threat to biodiversity from botanic gardens. Trends Ecol. Evol. 26, 168–174.

Hulme, P.E., Bremner, E.T., 2006. Assessing the impact of *Impatiens glandulifera* on riparian habitats: partitioning diversity components following species removal. J. Appl. Ecol. 43, 43–50.

Hulme, P.E., Pyšek, P., Nentwig, W., Vilà, M., 2009. Will threat of biological invasions unite the European Union? Science 324, 40–41.

Huston, M., Smith, T., 1987. Plant succession: life history and competition. Am. Nat. 130, 168–198.

Huston, M.A., 1979. A general hypothesis of species diversity. Am. Nat. 113, 81–101.

Ibáñez, I., Silander Jr., J.A., Allen, J.M., Treanor, S.A., Wilson, A., 2009. Identifying hotspots for plant invasions and forecasting focal points of further spread. J. Appl. Ecol. 46, 1219–1228.

Jäger, H., Kowarik, I., Tye, A., 2009. Destruction without extinction: long-term impacts of an invasive tree species on Galápagos highland vegetation. J. Ecol. 97, 1252–1263.

Joshi, J., Vrieling, K., 2005. The enemy release and EICA hypothesis revisited: incorporating the fundamental difference between specialist and generalist herbivores. Ecol. Lett. 8, 704–714.

Keane, R.M., Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. Trends Ecol. Evol. 17, 164–170.

Kowarik, I., 2008. On the role of alien species in urban flora and vegetation. In: Marzluff, J.M., Shulenberger, E., Endlicher, W., Alberti, M., Bradley, G., Ryan, C., Simon, U., ZumBrunnen, C. (Eds.), Urban Ecology: An International Perspective on the Interaction Between Humans and Nature. Springer, New York, pp. 321–338.

Kneitel, J.M., Chase, J.M., 2004. Trade-offs in community ecology: linking spatial scales and species coexistence. Ecol. Lett. 7, 69–80.

Kulmatiski, A., Beard, K.H., Stevens, J.R., Cobbold, S.M., 2008. Plant–soil feedbacks: a meta-analytical review. Ecol. Lett. 11, 980–992.

Kyle, G., Leishman, M.R., 2009. Functional trait differences between extant exotic, native and extinct native plants in the Hunter River, NSW: a potential tool in riparian rehabilitation. River Res. Appl. 25, 892–903.

Lambdon, P.W., Lloret, F., Hulme, P.E., 2008. How do introduction characteristics influence the invasion success of Mediterranean alien plants? Perspect. Plant Ecol. 10, 143–159.

Lavergne, C., Rameau, J.-C., Figier, J., 1999. The invasive woody weed *Ligustrum robustum* subsp. *walkeri* threatens native forests on La Réunion. Biol. Invasions 1, 377–392.

Leishman, M.R., Haslehurst, T., Ares, A., Baruch, Z., 2007. Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. New Phytol. 176, 635–643.

Leishman, M.R., Thomson, V.P., Cooke, J., 2010. Native and exotic invasive plants have fundamentally similar carbon capture strategies. J. Ecol. 98, 28–42.

Liao, C., Peng, R., Luo, Y., Zhou, X., Wu, X., Fang, C., Chen, J., Li, B., 2008. Altered ecosystem carbon and nitrogen cycles by plant invasion: a meta-analysis. New Phytol. 177, 706–714.

Lonsdale, W.M., Miller, I.L., 1993. Fire as a management tool for a tropical woody weed: *Mimosa pigra* in northern Australia. J. Environ. Manage. 39, 77–87.

MacDougall, A.S., Turkington, R., 2005. Are invasive species the drivers or passengers of change in degraded ecosystems? Ecology 86, 42–55.

Mackey, R.L., Currie, D.J., 2000. A re-examination of the expected effects of disturbance on diversity. Oikos 88, 483–493.

Mackey, R.L., Currie, D.J., 2001. The diversity–disturbance relationship: is it generally strong and peaked? Ecology 82, 3479–3492.

Martin, P.H., Canham, C.D., Kobe, R.K., 2010. Divergence from the growth–survival trade-off and extreme high growth rates drive patterns of exotic tree invasions in closed-canopy forests. J. Ecol. 98, 778–789.

Martin, P.H., Canham, C.D., Marks, P.L., 2009. Why forests appear resistant to exotic plant invasions: intentional introductions, stand dynamics, and the role of shade tolerance. Front. Ecol. Environ. 7, 142–149.

Mason, T.J., French, K., 2008. Impacts of a woody invader vary in different vegetation communities. Divers. Distrib. 14, 829–838.

McKee, J.K., Sciulli, P.W., Fooce, C.D., Waite, T.A., 2004. Forecasting global biodiversity threats associated with human population growth. Biol. Conserv. 115, 161–164.

Menge, B.A., Sutherland, J.P., 1987. Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. Am. Nat. 130, 730–757.

Meyer, J.-Y., Florence, J., 1996. Tahiti's native flora endangered by the invasion of *Miconia calvescens* DC. (Melastomataceae). J. Biogeogr. 23, 775–781.

Meyer, J.-Y., Florence, J., Tchung, V., 2003. Les Psychotria (Rubiacées) endémiques de Tahiti (Polynésie Française) menacés par l'invasion de *Miconia calvescens* (Mélastomatacées): statut, repartition, écologie, phénologie et protection. Révue d'Écologie (la Terre et la Vie) 58, 161–185.

Mitchell, C.E., Agrawal, A.A., Bever, J.D., Gilbert, G.S., Hufbauer, R.A., Klironomos, J.N., Maron, J.L., Morris, W.F., Parker, I.M., Power, A.G., Seabloom, E.W., Torchin, M.E., Vázquez, D.P., 2006. Biotic interactions and plant invasions. Ecol. Lett. 9, 726–740.

Moles, A.T., Gruber, M.A.M., Bonser, S.P., 2008. A new framework for predicting invasive plant species. J. Ecol. 96, 13–17.

Murphy, H.T., Metcalfe, D.J., Bradford, M.G., Ford, A.F., Galway, K.E., Sydes, T.A., Westcott, D.J., 2008. Recruitment dynamics of invasive species in rainforest habitats following Cyclone Larry. Aust. Ecol. 33, 495–502.

Mwangi, P.N., Schmitz, M., Scherber, C., Roscher, C., Schumacher, J., Scherer-Lorenzen, M., Weisser, W.W., Schmid, B., 2007. Niche pre-emption increases with species richness in experimental plant communities. J. Ecol. 95, 65–78.

Orrock, J.L., Witter, M.S., Reichman, O.J., 2008. Apparent competition with an exotic plant reduces native plant establishment. Ecology 89, 1168–1174.

Pacala, S.W., Tilman, D., 1994. Limiting similarity in mechanistic and spatial models of plant competition in heterogeneous environments. Am. Nat. 143, 222–257.

Paine, R.T., Vadas, R.L., 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. Limnol. Oceanogr. 14, 710–719.

Peltzer, D.A., Bellingham, P.J., Kurokawa, H., Walker, L.R., Wardle, D.A., Yeates, G.W., 2009. Punching above their weight: low-biomass non-native plant species alter soil properties during primary succession. Oikos 118, 1001–1014.

Penuelas, J., Sardans, J., Llusia, J., Owen, S.M., Carnicer, J., Giambelluca, T.W., Rezende, E.L., Waite, M., Niinemets, Ü., 2010. Faster returns on 'leaf economics' and different biogeochemical niche in invasive compared with native plant species. Glob. Change Biol. 16, 2171–2185.

Pickett, S.T.A., White, P.S., 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, London.

Pyšek, P., Jarošík, V., Hulme, P.E., Kühn, I., Wild, J., Arianoutsou, M., Bacher, S., Chiron, F., Didžiulis, V., Essl, F., Genovesi, P., Gherardi, F., Hejda, M., Kark, S., Lambdon, P.W., Desprez-Loustau, M.-L., Nentwig, W., Pergl, J., Poboljšaj, K., Rabitsch, W., Roques, A., Roy, D.B., Shirley, S., Solarz, W., Vilà, M., Winter, M., 2010. Disentangling the role of environmental and human pressures on biological invasions across Europe. Proc. Natl. Acad. Sci. U. S. A. 107, 12063–12064.

Pyšek, P., Richardson, D.M., 2006. The biogeography of naturalization in alien plants. J. Biogeogr. 33, 2040–2050.

Rejmánek, M., Rejmánková, E., Holzner, W., 2004. Species diversity of plant communities on calcareous screes: the role of intermediate disturbance. Preslia 76, 207–222.

Rejmánek, M., Richardson, D.M., 1996. What attributes make some plant species more invasive? Ecology 77, 1655–1661.

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D., West, C.J., 2000. Naturalization and invasion of alien plants: concepts and definitions. Divers. Distrib. 6, 93–107.

Rossiter, N.A., Setterfield, S.A., Douglas, M.M., Hutley, L.B., 2003. Testing the grass-fire cycle: alien grass invasion in the tropical savannas of northern Australia. Divers. Distrib. 9, 169.

Sale, P.F., 1977. Maintenance of high diversity in coral reef fish communities. Am. Nat. 111, 337–359.

Seabloom, E.W., Harpole, W.S., Reichman, O.J., Tilman, D., 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. Proc. Natl. Acad. Sci. U. S. A. 100, 13384–13389.

Shea, K., Roxburgh, S.H., Rauschert, E.S.J., 2004. Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. Ecol. Lett. 7, 491–508.

Sheil, D., Burslem, D.F.R.P., 2003. Disturbing hypotheses in tropical forests. Trends Ecol. Evol. 18, 18–26.

Simberloff, D., 2009. The role of propagule pressure in biological invasions. Annu. Rev. Ecol. Syst. 40, 81–102.

Standish, R.J., Williams, P.A., Robertson, A.W., 2001. The impact of an invasive weed *Tradescantia fluminensis* on native forest regeneration. J. Appl. Ecol. 38, 1253–1263.

Stearns, S.C., 1989. Trade-offs in life-history evolution. Funct. Ecol. 3, 259–268.

Sullivan, J.J., Williams, P.A., Timmins, S.M., 2007. Secondary forest succession differs through naturalised gorse and native kanuka near Wellington and Nelson. N. Z. J. Ecol. 31, 22–38.

Teo, D.H.L., Tan, H.T.W., Corlett, R.T., Wong, C.M., Lum, S.K.Y., 2003. Continental rain forest fragments in Singapore resist invasion by exotic plants. J. Biogeogr. 30, 305–310.

Thorpe, A.S., Thelen, G.C., Diaconu, A., Callaway, R.M., 2009. Root exudate is allelo-pathic in invaded community but not in native community: field evidence for the novel weapons hypothesis. J. Ecol. 97, 641–645.

Tickner, D.P., Angold, P.G., Gurnell, A.M., Mountford, J.O., Sparks, T., 2001. Hydrol-ogy as an influence on invasion: experimental investigations into competition between the alien *Impatiens glandulifera* and the native *Urtica dioica* in the UK. In: Brundu, G., Brock, J., Camarda, I., Child, L., Wade, M. (Eds.), Plant Invasions: Species Ecology and Ecosystem Management. Backhuys Publishers, Leiden, The Netherlands, pp. 159–168.

van Kleunen, M., Weber, E., Fischer, M., 2010. A meta-analysis of trait dif-ferences between invasive and non-invasive plant species. Ecol. Lett. 13, 235–245.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarošík, V., Maron, J.L., Pergl, J., Schaffner, U., Sun, Y., Pyšek, P., 2011. Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. Ecol. Lett. 14, 702–708.

Vilà, M., Tessier, M., Suehs, C.M., Brundu, G., Carta, L., Galinidis, A., Lambdon, P., Manca, M., Medail, F., Moragues, E., Traveset, A., Troumbis, A.Y., Hulme, P.E., 2006. Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. J. Biogeogr. 33, 853–861.

Vitousek, P.M., D'Antonio, C.M., Loope, L.L., Rejmánek, M., Westbrooks, R., 1997. Introduced species: a significant component of human-caused global change. N. Z. J. Ecol. 21, 1–16.

Vitousek, P.M., Walker, L.R., Whiteaker, L.D., Mueller-Dombois, D., Matson, P.A., 1987. Biological invasion by *Myrica faya* alters ecosystem development in Hawaii. Science 238, 802–804.

von der Lippe, M., Kowarik, I., 2008. Do cities export biodiversity? Traffic as dispersal vector across urban–rural gradients. Divers. Distrib. 14, 18–25.

Weir, T.L., Perry, L.G., Gilroy, S., Vivanco, J.M., 2010. The role of root exudates in rhizosphere interactions with plants and other organisms. Annu. Rev. Plant Biol.

White, E.M., Wilson, J.C., Clarke, A.R., 2006. Biotic indirect effects: a neglected con-cept in invasion biology. Divers. Distrib. 12, 443–455.

White, P.S., Pickett, S.T.A., 1985. Natural disturbance and patch dynamics. In: Pickett, S.T.A., White, P.S. (Eds.), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York, pp. 3–13.

Williams, P.A., Wiser, S., 2004. Determinants of regional and local patterns in the floras of braided riverbeds in New Zealand. J. Biogeogr. 31, 1–18.

Wilsey, B., Polley, W.H., 2006. Aboveground productivity and root–shoot allocation differ between native and introduced grass species. Oecologia 150, 300–309.

Wilsey, B.J., Teaschner, T.B., Daneshgar, P.P., Isbell, F.I., Polley, H.W., 2009. Biodiversity maintenance mechanisms differ between native and novel exotic-dominated communities. Ecol. Lett. 12, 432–442.

Wilson, E.O., 1969. The species equilibrium. Brookhaven Symposia in Biology 22, 38–47.

Woods, K.D., 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four new england forests. Am. Midl. Nat. 130, 62–74.