CENTENARY SYMPOSIUM SPECIAL FEATURE

Invasions: the trail behind, the path ahead, and a test of a disturbing idea

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Summary

1. We provide a brief overview of progress in our understanding of introduced plant species.

2. Three main conclusions emerge from our review: (i) Many lines of research, including the search for traits that make species good invaders, or that make ecosystems susceptible to invasion, are yielding idiosyncratic results. To move forward, we advocate a more synthetic approach that incorporates a range of different types of information about the introduced species and the communities and habitats they are invading. (ii) Given the growing evidence for the adaptive capacity of both introduced species and recipient communities, we need to consider the implications of the long-term presence of introduced species in our ecosystems. (iii) Several foundational ideas in invasion biology have become widely accepted without appropriate testing, or despite equivocal evidence from empirical tests. One such idea is the suggestion that disturbance facilitates invasion.

3. We use data from 200 sites around the world to provide a broad test of the hypothesis that invasions are better predicted by a change in disturbance regime than by disturbance *per se*. Neither disturbance nor change in disturbance regime explained more than 7% of the variation in the % of cover or species richness contributed by introduced species. However, change in disturbance regime was a significantly better predictor than was disturbance *per se*, explaining approximately twice as much variation as did disturbance.

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4. *Synthesis.* Disturbance is a weak predictor of invasion. To increase predictive power, we need to consider multiple variables (both intrinsic and extrinsic to the site) simultaneously. Variables that describe the changes sites have undergone may be particularly informative.

Introduction

We have come a long way in our understanding of introduced species in the century since publication of the *Journal of Ecology* began. One hundred years ago, introductions were widely celebrated, and acclimatization societies were busy 'enriching' the flora and fauna in many regions world-wide. Some of the more notable achievements of acclimatization societies include introducing starlings and house sparrows to the United States (in an attempt to introduce all the birds mentioned in Shakespeare's works to New York's Central Park; Marzluff *et al.* 2008), introducing brushtail possums to New Zealand (to establish a fur industry; Cowan 1992) and distributing ornamental plant species such as *Lantana camara* and *Miconia calvescens* to gardens world-wide (Meyer 1996; CRC Weed Management 2003). Many species (e.g. cane toads in Australia) were introduced as biocontrols, and many more species were introduced accidentally (e.g. zebra mussels). As a result of both intentional and unintentional introductions, introduced species now make up a substantial part of the vascular flora in most places (about half in Hawaii, New Zealand and the Cook Islands, 21% in Britain, 24% in Canada, 10–30% in several mainland USA states, 12.5% in Europe and 10% in Australia; Vitousek *et al.* 1996). The ecological and socio-economic costs of invasive species have become increasingly apparent. Introduced species are thought to be the second greatest threat to native diversity (at least in the US; Wilcove *et al.* 1998), and the combined annual costs of introduced species have been estimated to exceed US$336 billion for just the United States, United Kingdom, Australia, South Africa, India and Brazil (Pimentel *et al.* 2001).

The applied nature of invasion biology makes it attractive to researchers and funding agencies alike, and as a result, the field is enormous and progressing at great speed. Over 10 000 papers have been published in the field of invasion biology in the last 30 years (Gurevitch *et al.* 2011). In such a rapidly growing field, it is worthwhile to ask which lines of research are yielding important advances, whether there are important questions being overlooked, and whether there are areas where our efforts are yielding poor returns. In the first part of this paper, we aim to give an overview of progress in our understanding of invasion biology (particularly in relation to plants), highlighting some promising directions for future research and some areas that we believe could be scaled back.

The traits of successful invaders

Since Baker (1965, 1974) published his famous lists of the traits of the ideal weed, one of the most common lines of investigation in invasion biology has been the search for traits that might allow us to predict invasiveness. Being able to predict which species are likely to become problem invaders would allow us to exclude such species from import and to effectively target weed control resources while species are still in the early stages of invasion (Lodge 1993; Williamson & Fitter 1996; Sakai *et al.* 2001). However, the results of individual studies have been rather idiosyncratic (Pyšek & Richardson 2007), and researchers have increasingly used compilations such as vote counting studies, meta-analyses and global comparisons of traits to search for general trends. Compilations have shown that invasive species tend to have higher population growth rates, lower levels of herbivore damage, higher shoot/root ratios, lower survival, higher plasticity in many functional traits and higher specific leaf area than do non-invasive and/or native species (Daehler 2003; Hawkes 2007; Ramula *et al.* 2008; van Kleunen, Weber & Fischer 2010; Ordonez, Wright & Olff 2010; Davidson, Jennions & Nicotra 2011). There is also a positive relationship between abundance in the native range and abundance in the introduced range (Firn *et al.* 2011). However, different compilations have shown contradictory results for many crucial traits, including plant growth rate (Daehler 2003; van Kleunen, Weber & Fischer 2010), plant size (Hawkes 2007; van Kleunen, Weber & Fischer 2010; Ordonez, Wright & Olff 2010), fecundity (Daehler 2003; Mason *et al.* 2008) and seed mass (Mason *et al.* 2008; Ordonez, Wright & Olff 2010). Thus, although individual studies often present seemingly clear results, the larger picture is unfortunately still one of idiosyncrasy and inconsistency. Further, even when there are statistically significant differences in the mean values of traits, the high degree of overlap in trait distributions for native, introduced and invasive species (Ordonez, Wright & Olff 2010) means that it is not currently possible and will probably never be possible to predict which species are likely to become problem invaders on the basis of traits alone. We therefore suggest that this is one area of invasion biology that merits less attention in the future. While performing studies on additional traits or in new regions will give locally relevant information, additional comparisons of traits seem unlikely to move our understanding of invasion biology forward in any substantial way.

Propagule pressure

The available evidence suggests that high propagule pressure facilitates invasions (Von Holle & Simberloff 2005; Eschtruth & Battles 2009), and proxies for propagule pressure such as human population density and proximity are strong predictors of invasions (Pyšek *et al.* 2010; Vilà & Ibáñez 2011). However,

relatively few studies have quantified propagule pressure in introduced plants (Simberloff 2009). The often-overlooked importance of propagule pressure has been suggested as an explanation for the high level of idiosyncrasy observed in studies of invasions (Lockwood, Cassey & Blackburn 2005). The first priority for this field is to collect more empirical data on propagule pressure in different ecosystems. Studies that quantify the relationship between propagule pressure and invasion at large scales seems likely to yield interesting results, as do quantifications of the relative importance of propagule pressure under different circumstances.

The genetics of invasions

Small population sizes characteristic of introduced species in the early stages of invasion are predicted to restrict adaptive evolution by limiting additive genetic variance (i.e. variance that allows a population to respond to selection; Prentis et al. 2008). Genetic bottlenecks have been demonstrated in many invasive taxa. For example, 58 of 72 studies show lower genetic diversity in introduced populations than in native populations (Puillandre et al. 2008). However, rapid adaptive evolution has been repeatedly demonstrated in introduced populations, and the predicted reduction in genetic variance is frequently not observed (Lee 2002; Roman & Darling 2007; Simberloff 2009). For example, in a review of aquatic invasions (including algae, invertebrates and fish), populations in only 16 of 43 invasive species had reduced genetic diversity (Roman & Darling 2007). Why is this? High propagule pressure and repeated introductions can provide a supply of new genetic material and limit the reduction in genetic variance due to bottlenecks (Roman & Darling 2007; Prentis et al. 2008; Simberloff 2009). In addition, dominance and epistatic genetic variance can be converted into additive genetic variance through random genetic drift (Lee 2002; Turelli & Barton 2006). Increased additive genetic variance due to epistasis in populations that have passed through a bottleneck has been observed (e.g. Cheverud et al. 1999). However, it is unclear whether epistasis is generally important in adaptive evolution after population bottlenecks (Turelli & Barton 2006), nor are we aware of any instances of epistasis facilitating adaptation in invasive species.

Some pernicious invasive species are the hybrid offspring of non-weedy invasive species and native species (Rieseberg et al. 2007). Hybridization can increase the persistence and impact of introduced species by increasing genetic variation (Ellstrand & Schierenbeck 2000; Rieseberg et al. 2007), and increasing vigour through increasing heterozygosity (Ellstrand & Schierenbeck 2000; Rieseberg et al. 2007). Hybrids can also express novel traits and extreme phenotypes not observed in either parent species (Ellstrand & Schierenbeck 2000; Prentis et al. 2008), and hybridization can facilitate the transfer of adaptive alleles between species (Prentis et al. 2008). Clearly, hybridization is an important, yet often-underappreciated (Ellstrand & Schierenbeck 2000) pathway for the evolution of introduced species.

We are at a very early stage in understanding the genetics of invasions. Future research is required to identify the cir-cumstances where invasive populations can overcome the depletion of additive genetic variance experienced after bottlenecks, and to identify the key factors contributing to maintaining genetic variance in populations of invasive species. Further research is also required to understand how hybridization has contributed to evolution in introduced species. In particular, increased epigenetic variation is associated with hybridization (Bossdorf, Richards & Pigliucci 2008), and epigenetic variation promotes adaptation in newly formed hybrid species (Hegarty et al. 2011). The relationship between hybridization and epigenetic variation may be important in understanding adaptation and evolution in many introduced species.

Evolution in introduced species

One of the most recent fields to emerge in invasion biology is the study of rapid evolution in introduced species. Several aspects of species introductions can stimulate evolutionary change (Vellend et al. 2007). A small fraction of the source population is sampled (whether intentionally or unintentionally), often generating founder effects and genetic bottlenecks (Dlugosch & Parker 2008). The introduced population is exposed to a range of new biotic conditions, including a new suite of pollinators, pathogens, seed dispersers, seed predators, herbivores, coexisting plants and changes in the invader's population density. Both theory (e.g. the enemy release hypothesis and the evolution of increased competitive ability hypothesis) and data suggest that these changed biotic conditions can result in evolutionary change (Blossey & Nötzold 1995; Keane & Crawley 2002; Bossdorf et al. 2005; Zangerl & Berenbaum 2005; Barrett, Colautti & Eckert 2008). Abiotic conditions, such as rainfall, temperature, soil fertility and disturbance regimes in the new range may also differ from those with which the species evolved, which can result in selection and adaptation (Maron, Elmendorf & Vila 2007). Finally, the colonization of a new landscape can be associated with the selection for altered dispersal (Cody & Overton 1996; Phillips et al. 2006; Cheptou et al. 2008). The prevalence of all these factors and their combined effects makes rapid evolution likely in introduced species. Buswell, Moles & Hartley (2011) found that 70% of 23 plant species introduced to Australia had undergone significant morphological change within c. 100 years. The magnitude of these changes was substantial, with several species doubling or halving crucial traits like plant height and leaf area.

We have reached the point where additional case studies demonstrating rapid evolutionary change in introduced species are unlikely to have a major impact on our understanding of invasions. However, there is a lot of scope for progress in understanding the general principles underlying rapid evolutionary change. For instance, we can ask whether introduced species tend to evolve greater similarity to resident native species (as might be expected if residents are adapted for success under local environmental conditions), or whether limiting similarity might result in introduced species evolving different suites of traits to those of resident native species. We can also ask whether observed trait changes in introduced species

coincide with predictions based on the differences between the climatic conditions in the species' introduced vs. native ranges.

It will also be interesting to determine whether evolutionary changes in introduced species tend to level off after a few generations, or whether the changes are ongoing. If the latter, we should ask whether introduced populations might eventually become sufficiently different to their source populations that they qualify as new species. If so, this raises interesting management questions. For example, at what point do we stop trying to eradicate these taxa as unwelcome invaders, and begin trying to protect them as unique endemic species? To what extent might evolutionary diversification in introduced species offset biodiversity losses in native taxa (Vellend *et al.* 2007)?

Factors that determine community and habitat susceptibility to invasion

One of the most intensively investigated ideas regarding community susceptibility to invasion is that high diversity makes communities more resistant to invasion, through mechanisms such as biotic resistance, limiting similarity and competitive exclusion (Elton 1958; Fridley *et al.* 2007). In line with these ideas, meta-analysis has shown that competition from resident plants and pressure from resident herbivores (but not the soil fungal community) have significant negative effects on the establishment and performance of introduced species (Levine, Adler & Yelenik 2004). However, positive, negative and null relationships between native species richness and the number of introduced species in a community are all commonly reported at a diversity of spatial scales (Levine & D'Antonio 1999; Meiners, Pickett & Cadenasso 2002; Herben *et al.* 2004; Howard *et al.* 2004; Richardson & Pyšek 2006; Fridley *et al.* 2007). Approaches that include information about the taxonomic (Rejmanek 1996; Daehler 2001; Strauss, Webb & Salamin 2006; Diez *et al.* 2009) and functional (Hooper & Dukes 2010) similarity between native and introduced species have had similarly mixed results. A range of factors (including spatial heterogeneity, neutral processes, disturbance and productivity) likely underlie the complex relationships between the recipient community and the invaders (Levine & D'Antonio 1999; Herben *et al.* 2004; Davies *et al.* 2005; Fridley *et al.* 2007; Hooper & Dukes 2010), and a simple unifying theory relating the suite of resident species to invasibility seems unlikely to emerge.

Several characteristics of habitats affect the success of invasions. There is generally a higher rate of invasion in small habitat fragments and at fragment edges (Lonsdale 1999; Vilà & Ibáñez 2011), and a higher rate of invasion in temperate than tropical mainlands (but not on islands, and the latitudinal gradient within the temperate zone runs in the opposite direction; Lonsdale 1999; Pyšek & Richardson 2006). The rate of invasion tends to be higher on islands (Lonsdale 1999; Pyšek & Richardson 2006), although the impacts of invasions are not significantly different between islands and mainland sites (Vilà *et al.* 2011). It has also been suggested that habitats that are already invaded are more susceptible to further invasion, as the presence of introduced species can facilitate future invad-

ers, for instance, by changing the disturbance regime (Mack & D'Antonio 1998; Simberloff & Von Holle 1999; Brooks *et al.* 2004). The effects of connectivity between habitat patches are equivocal (Vilà & Ibáñez 2011), as are the effects of environmental heterogeneity, which sometimes increases invasion success (e.g. in response to resource pulses), and sometimes decreases invasion success (Melbourne *et al.* 2007). Despite some areas of agreement in the literature about factors that affect a habitat's susceptibility to invasion, we are still some way from practical outcomes such as being able to predict the likely effects changes in basic factors like temperature and rainfall under global change might have, either on specific introduced species (Bradley *et al.* 2010) or on habitat susceptibility to invasion. This is an area that merits further attention.

Impacts of invasive species on native communities

Many papers on invasions begin with statements about the negative effects of introduced species on native communities (Lonsdale 1999; Levine *et al.* 2003; Morales & Traveset 2009). However, the evidence for the impacts of invasive plant species is actually quite weak. For example, it is widely accepted that introduced species are one of the major causes of native species extinction (Gurevitch & Padilla 2004). However, although introduced predators and pathogens have caused many extinctions, there are astonishingly few documented cases of native plants being driven to extinction by competition from introduced plants (Sax *et al.* 2007). There is no evidence for any native species in the United States being driven to extinction, even within a state, by competition from an introduced plant species (Davis 2003). Gurevitch & Padilla (2004) conclude a review on the impacts of invaders on native species by stating that "the assumed importance of the invaders in causing widespread extinctions is to date unproven, and is based upon limited observation and inference". Further research is urgently needed to quantify the impact of introduced species on the extinction of native species.

The evidence for effects of introduced species on factors other than extinction is stronger. Meta-analyses have shown that introduced species can decrease the fitness, diversity, abundance and growth of resident plant species while increasing community level plant production (Vilà *et al.* 2011). Meta-analyses also show that introduced plants can impact animals, decreasing fitness and abundance (Vilà *et al.* 2011) and decreasing pollinator visitation (which was associated with a decrease in the reproductive success of co-flowering plants; Morales & Traveset 2009). The effects of introduced species are thought to arise through a range of mechanisms, including competition, changes in the availability of resources such as nitrogen and water, changed disturbance regimes and altered food webs, but these effects are usually not well quantified (Levine *et al.* 2003; Ehrenfeld 2010). Further, studies of different sites often give contradictory results about the effects of introduced species on native species (Levine *et al.* 2003; Ehrenfeld 2010; Vilà *et al.* 2011). Instances where the same introduced species has different impacts on different recipient

communities, and cases where community responses to invasive species do not differ to responses to native species are common (Ehrenfeld 2010). Establishing generalizations about the magnitude and type of impacts associated with introduced species, and the mechanisms that underlie the impacts is a top priority for this field. Sampling bias may complicate this effort – if ecologists are more likely to study highly invasive species than low-density, low-impact introduced species, then meta-analyses will overestimate the effects of introduced species.

Conclusions from literature review

Many lines of investigation, including the search for species' traits that are associated with high invasiveness, the search for features of communities that make them susceptible to invasions and the search for generalities about the effects of introduced species, are yielding idiosyncratic results. This idiosyncrasy highlights the need to gather detailed information to understand the biology of particular introduced species. However, since we cannot study every introduced species separately, we need to continue the search for generalizations. We join a growing chorus, suggesting that our approach to invasion biology has been too simplistic. Despite wide recognition that there will be no one explanation that fits all biological invasions (Davis, Grime & Thompson 2000; Gurevitch et al. 2011), relatively few studies actually consider a range of factors/theories simultaneously. Rather than focussing on one factor at a time, we need to find ways (including multivariate analyses) to synthesize information about the recipient habitats/communities, the characteristics of both resident species and the invaders, demographic processes, propagule pressure, the differences between current conditions and those with which the resident species evolved, evolutionary change in both native and introduced species, plasticity, and feedbacks and interactions between different species and processes (Lockwood, Cassey & Blackburn 2005; Moles, Gruber & Bonser 2008; Ordonez, Wright & Olff 2010; Gurevitch et al. 2011). By incorporating a range of different types of information, we hope that it will be possible to cut through the apparent idiosyncrasies and predict the circumstances under which species and ecosystems will respond in different ways. This will not be simple, but even combining information about three or four processes (e.g. differences between climatic conditions in home and introduced ranges, evolutionary change in the new range and demographic processes) would represent a major advance.

It is common for researchers to specialize in one branch of ecology (e.g. invasion ecology, tropical biology, molecular ecology), and to feel that the literature and ecological community is so huge even within each sub-discipline that there is no way we could keep up with developments in ecology as a whole. To bring together widely, divergent lines of evidence about invasions will therefore require researchers with different types of expertise to work together. This has a strong parallel with calls for invasion ecologists to stop treating invasion as a process separate from the rest of ecology (e.g. Davis et al. 2005) and (i) use introduced species to help us understand fundamental processes in ecology (e.g. community assembly, succession, species' distributions and evolution), and (ii) use knowledge and techniques from other parts of biology (e.g. demography) to improve our understanding of invasion biology (Sax et al. 2007). Thus, we see large multiauthor collaborations and big data syntheses as an important part of the future of invasion biology.

Since eradicating all introduced species is an unachievable or impractical goal in many ecosystems (Hobbs et al. 2006; Davis et al. 2011), we also need to consider the consequences of the long-term presence of some introduced species. After a few hundred years in an ecosystem, both introduced species and resident natives will have had time to adapt to the new conditions. Local herbivores, pollinators, seed dispersers, seed predators and pathogens are likely to be interacting with the introduced species, making them part of food webs and other ecological networks (e.g. Pyšek et al. 2011). Does there come a point where we should stop fighting introduced species and simply accept them as plants that provide a range of ecosystem services, or is this opening the door to disaster? Debate on this topic is fierce (Davis et al. 2011; Simberloff 2011). We might gain some insight about the future trajectories of invasions by looking at long-invaded places such as Europe, and by studying the long-term effects of previous biotic interchanges (e.g. the joining of North and South America).

Many of the ideas presented in the literature have become reified without ever being subjected to formal testing (see Slobodkin 2001). Other ideas have been subjected only to weak tests that were the best available at the time, but which have been superseded in recent decades as a result of the increasing availability of large datasets and sophisticated analytical methods. Yet other ideas have been accepted as truths despite contradictory empirical evidence. Thus, one of the most important goals for the future is searching for any untested or inadequately tested assumptions underlying our understanding of invasion biology (the same applies to many other fields in ecology). For the researcher, providing the first test of a broadly accepted idea is a win/win situation. If the dogma is right, the first empirical test will likely go on to be a citation classic. If the dogma is wrong, then the first empirical test will overturn our traditional understanding of the field, thus stimulating the development of new theoretical ideas and many other empirical tests.

Following this goal of testing dogma, we tackle one idea that has become widely accepted despite equivocal evidence in empirical tests: the idea that disturbance facilitates invasion.

Testing ideas about the role of disturbance in facilitating invasion

Many introduced species seem to be most dominant at highly modified sites. Moreover, the idea that disturbance facilitates invasion has been called 'one of the most commonly accepted truisms in the field of invasion ecology' (Lockwood, Hoopes & Marchetti 2007). Disturbance is thought to facilitate invasion by simultaneously opening new ground for colonization, decreasing the competition from

resident native plants and releasing pulses of resources (Davis, Grime & Thompson 2000). A positive relationship between disturbance and invasion has been found for terrestrial plants (Hobbs & Atkins 1988; Burke & Grime 1996; Belote *et al*. 2008; Eschtruth & Battles 2009), terrestrial animals (Corlett 2010; Rickart *et al*. 2011) and marine organisms (Bando 2006; Altman & Whitlatch 2007). However, not all studies show positive relationships between disturbance and invasion. Some find no relationship (Hester & Hobbs 1992), some show negative relationships (Smart, Hatton & Spence 1985; Smith & Knapp 1999) and some show hump-shaped relationships (Tiegs *et al*. 2005). Theory is also mixed on the topic, with one model suggesting that disturbance should only promote invasion when disturbance of sites unoccupied by invaders is greater than disturbance of occupied sites (Buckley, Bolker & Rees 2007). Even when disturbances do facilitate the establishment of introduced species, modelling suggests that disturbance frequency will have little long-term effect (Spence *et al*. 2011).

Sometimes researchers use the term 'disturbed' to mean that humans have recently disrupted natural conditions (including the natural disturbance regime), while others take disturbance as "the partial or total destruction of the plant biomass and arises from the activities of herbivores, pathogens, man (trampling, mowing, and plowing), and from phenomena such as wind damage, frosts, desiccation, soil erosion, and fire" (Grime 1977). Because both situations are common and important in invasion biology, researchers need to be careful in their use of the term. Here, we use 'disturbance' in the classic sense (*sensu* Grime 1977).

Closer consideration of the role of disturbance in plant communities casts doubt on the idea that high rates of disturbance should be a strong predictor of invasion. Disturbance is a natural feature of all ecological communities, and the resident native species in a community have had many generations of selection for traits that allow them to flourish under the natural disturbance regime. Dramatically increasing the rate of disturbance in an ecosystem (e.g. introducing frequent fires to a region that seldom burned) might disfavour native species and favour introduced species that are pre-adapted for more frequent disturbances. However, decreasing the rate of disturbance in an ecosystem (e.g. fire suppression) might also disadvantage natives and favour introduced species that are pre-adapted for longer disturbance intervals. Thus, it may not be disturbance *per se* that disadvantages native species and allows introduced species to establish, but rather a change in the disturbance regime.

Previous studies have raised the idea that changes in disturbance regime are important in facilitating invasion (Hobbs & Huenneke 1992; D'Antonio, Dudley & Mack 1999; Sher, Marshall & Gilbert 2000), and the importance of the natural disturbance regime in community resistance to invasion is well known in many ecosystems (Scholes & Archer 1997; Sher, Marshall & Gilbert 2000). However, the statement that 'disturbance increases community susceptibility to invasion' and tests of this idea are often made without consideration of the natural disturbance regime.

Our aim was to test two hypotheses: (i) That the percentage of species richness and cover contributed by introduced species will be more closely related to the difference between the present and natural disturbance regime than with disturbance *per se*, and (ii) That disturbance will only explain a small proportion of the variation in the % cover or species richness of introduced species. To test these hypotheses, we collected data from 200 sites from eight countries; Argentina, Australia, Costa Rica, Japan, Mexico, New Zealand, Uganda and the United States of America (Appendices S1 and S2 in Supporting Information).

We only included sites for which the historic disturbance regime was known. The historic disturbance regime was defined as the regime under which the community assembled and/or which was important in the evolution of the species (in many cases, this was the pre-European disturbance regime). We included sites with a wide range of historic disturbance frequencies and intensities, thus diminishing the importance of exact quantification of the historic regime, the finer details of which can be controversial.

Current disturbance frequency/intensity data were taken from scientific studies, local knowledge and/or records from the last few decades (details in Appendix S1). We avoided sites that had experienced alterations in addition to changes in disturbance regime (for example, sites that now experience nutrient or water addition as well as having a modified fire/grazing regime were excluded) – although changes in resource availability that result from change in disturbance regime are unavoidable. We included only sites that currently experience the same type of disturbance as they historically experienced (e.g. sites with a change in fire frequency or grazing intensity were included, sites that had changed from fire to grazing disturbance were excluded). Where possible, sites were surveyed when the time since disturbance was between half and 1.5 times the current disturbance interval (to quantify the typical community of the area, rather than just the very first colonists or those few species persisting in a highly senescent site). Where the current disturbance frequency was greater than or equal to the historic disturbance frequency, the current regime had to have been in place for at least three cycles for the site to be included. Our analyses compared the predictive power of the change in the disturbance regime with the current disturbance regime rather than with the historic disturbance regime, as in most cases few if any introduced species will have been present while the historic disturbance regime was still in place.

Site locations were chosen without regard for the proportion of introduced species present. We excluded sites in Europe, where the history of introduction is long enough that the definition and identity of 'native' species has become arguable. Replicate quadrats in a 'site' share a common vegetation type and disturbance regime and are located close enough in space that other variables (such as soil fertility, altitude, aspect and climate) do not/are unlikely to differ between quadrats. Replicate sites in a 'study' share a common vegetation type, geographic region and disturbance type (e.g. fire, grazing or treefalls), but differ in disturbance intensity and/or frequency.

The average number of quadrats sampled per site was 36.5 (a total of 7298 quadrats), with a minimum sample size of 5 quadrats (Appendix S1). An exception was made for five sites in Uganda, where data were from one *c.* 2 Ha quadrat per site. Quadrat size ranged from 0.5 to 21 200 m^2, with an average of 560 m^2 (Appendix S1). In each quadrat, we recorded the number of native and introduced species (to calculate the % of species richness at each site contributed by introduced species), and the % of projected cover contributed by introduced species. The quadrats are subsamples in our analyses; the replicates are the 200 study sites.

Disturbance data were divided into those that showed changes in the frequency of disturbances (including frequency of fires, floods and tree falls), and those that showed changes in intensity of grazing. All frequency data were converted to units of disturbances per year. All grazing data were standardized to units of dry (non-reproductive) sheep equivalents (DSE; McLaren 1997) to enable direct comparisons between sites with different grazers.

We calculated change in disturbance regime as the absolute difference between $\log_{10}$ current disturbance and $\log_{10}$ historic disturbance. The log transformation makes this a proportional metric. That is, a change from a 1 to 2 year interval between

disturbances appropriately receives the same score as a change from a 10 to 20 year interval between disturbances, and a higher score than a change from a 10 to 11 year interval. We recorded whether each change was an increase or a decrease in disturbance frequency or intensity.

We ran two levels of analyses: global and local. The local analyses provide a controlled test of the hypotheses where factors such as vegetation type, substrate, climate and biological history are held constant, while the global analysis enables us to determine whether our results have general applicability. Local analyses were run on all contributed datasets that contained at least 10 sites from the same study.

A single global analysis was undertaken across all studies using a generalized linear mixed model. As a test statistic, we used the decrease in deviance when using change in disturbance regime as the fixed effect in the model instead of current disturbance rate. A normal random intercept was included in the model for study, to account for variation in response due to study that was not explained by disturbance. When modelling the % of species richness contributed by introduced species, the response was treated as binomial and analysed using logistic regression, with an additional normal random intercept for each observation to account for overdispersion
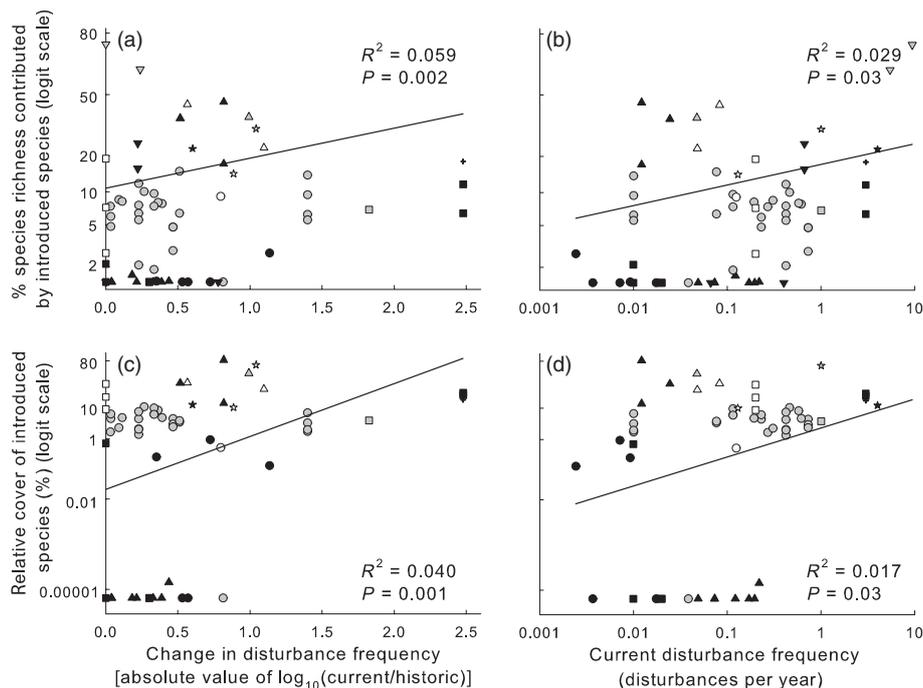

Fig. 1. Relationships between % of species richness contributed by introduced species and (a) change in disturbance frequency and (b) disturbance frequency; and between % of projected cover contributed by introduced species and (c) change in disturbance frequency and (d) disturbance frequency. Disturbance frequency is the number of disturbances per year. Change in disturbance frequency is the proportional change between current and historic disturbance frequency, calculated as the absolute value of ($\log_{10}$ current disturbance frequency – $\log_{10}$ historic disturbance frequency). A change of 0.3 corresponds to a doubling or halving in disturbance frequency, and a change of 1 corresponds to a 10-fold increase or decrease in disturbance frequency. Each site is represented by a single point, coded for study; white up triangle = Japan forest (treefall); grey up triangle = Japan savanna (treefall); black triangle = Sydney sclerophyll woodland (fire); black circle = Uganda rainforest (treefall); grey circle = USA oak savanna/woodland (fire); white circle = Mexico forest (fire); black star = Mexico grassland (mowing); grey star = Mexico grassland (flood); white star = Mexico wetland (salt water inundation); black square = Costa Rica rainforest (treefall); plus sign = Costa Rica cloud forest (treefall); grey square = Mexico riparian (river drying); white square = Costa Rica rainforest (flood); down triangle black = Australia savanna (fire); down triangle grey = New Zealand riparian (flood).

relative to the binomial (Warton & Hui 2011). When modelling relative cover of introduced species, a linear mixed model was fitted to logit-transformed cover $[\ln(p/(1-p))]$. To handle sites with zero % cover for introduced species, for which the logit transform is undefined, a small positive constant (equal to the smallest non-zero observation) was added to the numerator and denominator in logit transformation (Warton & Hui 2011). The same procedure was applied to allow us to graph the results (Figs 1 and 2).

Testing whether change in disturbance better explains the richness and/or cover of introduced species than does current disturbance involves two non-nested hypotheses. This means that classical approaches to hypothesis testing cannot be used, so we used a simulation approach (Lewis, Butler & Gilbert 2011). The significance of our log-likelihood ratio (LR) test statistic was evaluated by parametric simulation (Davison & Hinkley 1997), recalculating the test statistic using each of 1000 datasets simulated under the null hypothesis that there was a linear effect of current disturbance. We used R^2 as a summary of goodness-of-fit of different models, where R^2 was calculated as the proportion of deviance in a mixed model with an intercept term only that is explained by adding a linear disturbance term.

Change in disturbance frequency was a significantly better predictor (LR statistic $= 5.53$; $P = 0.003$) of the % of species richness that was contributed by introduced species (Fig. 1a;

$R^2 = 0.059$; $P = 0.002$) than was the current disturbance frequency (Fig. 1b; $R^2 = 0.029$; $P = 0.03$). Similarly, change in grazing intensity was a significantly better predictor (LR $= 5.04$; $P = 0.02$) of the % of species richness that was contributed by introduced species (Fig. 2a; $R^2 = 0.036$; $P = 0.01$) than was the current grazing intensity (Fig. 2b; $R^2 = 0.015$; $P = 0.11$). The % of cover contributed by introduced species was significantly (LR $= 7.82$; $P < 0.001$) better predicted by change in disturbance frequency (Fig. 1c; $R^2 = 0.038$; $P = 0.001$) than by current disturbance frequency (Fig. 1d; $R^2 = 0.018$; $P = 0.029$). Change in grazing intensity explained 0.9% of the variation in the % of cover contributed by introduced species (Fig. 2c; $P = 0.09$), while current grazing intensity explained 0.46% (Fig. 2d; $P = 0.10$). This difference was not statistically significant (LR $= 1.92$; $P = 0.16$). Overall, the % of species richness and cover contributed by introduced species is better explained by change in disturbance than by disturbance *per se*. Change in disturbance regime explained around twice as much variation as did current disturbance regime in all four cases. However, the predictive power of both disturbance and change in disturbance was low, with no R^2s above 7%.

To check how sensitive our results were to choice of method of measuring relative change in disturbance, we also consider using a quadratic model for relative change in disturbance, i.e. using as the linear predictor $[\log(\text{current}/\text{historic})]^2$. Results
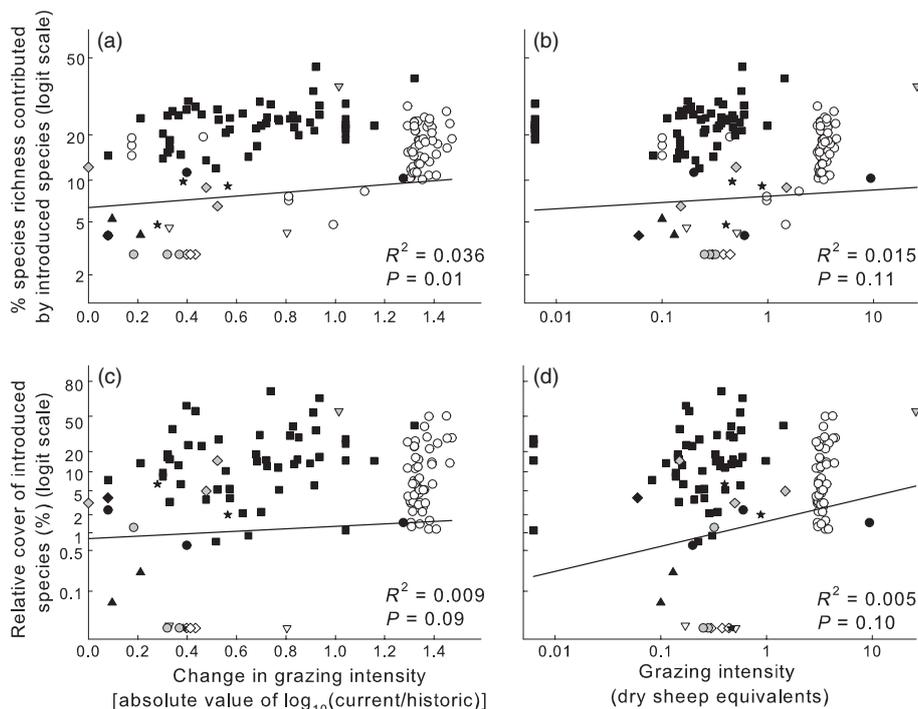

Fig. 2. Relationships between % of species richness contributed by introduced species and (a) change in grazing intensity and (b) grazing intensity; and between % of projected cover contributed by introduced species and (c) change in grazing intensity and (d) grazing intensity. Grazing intensity is measured in units of dry sheep equivalents, to allow comparisons between sites with different grazer communities. Each site is represented by a single point, coded for study; up triangle black = Patagonia grassland; down triangle white = Patagonia shrubland; down triangle grey = Japan savanna; white circle = Australia Eucalypt woodland; black square = Australia chenopod shrubland; white diamond = Mexico grassland; black diamond = Australia *Acacia* woodland; black star = Mexico thornscrub; grey circle = Mexico dry forest/shrubland/grassland; black circle = Argentina grassland; grey diamond = Argentina forest.

were very similar to those presented earlier (R^2s within 0.006), and *P*-values yielded the same significance, except that the change in grazing intensity became a significantly (LR = 3.21; *P* = 0.05) better predictor of the % cover contributed by introduced species than was current grazing intensity.

We also considered an alternative measure of grazing intensity; the number of dry sheep equivalents per unit net primary productivity (NPP), to account for the fact that a given stocking density will have different impacts on ecosystems with different levels of productivity. NPP data were taken from Imhoff *et al.* (2004). This correction affects the current grazing intensity calculations, but not those for change in grazing intensity (a doubling in grazing intensity remains a doubling, regardless of the NPP). Including NPP improved the R^2 for the relationship between current grazing intensity and the % of species richness contributed by introduced species from 0.015 to 0.025. This is still a lower R^2 than found with change in disturbance intensity (0.036), but the difference between models for current grazing and change in grazing dropped to marginal significance (LR = 2.58; *P* = 0.068). Including NPP improved the R^2 for the relationship between current grazing intensity and the % cover contributed by introduced species from 0.0046 to 0.038, with the NPP-corrected R^2 exceeding the R^2 for change in disturbance regime (0.009). However, as in the uncorrected analysis, the difference between models remains non-significant (LR = −12.34; *P* = 0.46). Thus, while including NPP in the models for current disturbance regime did improve the fits, it did not alter our overall conclusions.

Finally, we ran local analyses for the four studies (Sydney sclerophyll woodland, Australia; Cedar Creek oak woodland/savanna, USA; New South Wales eucalypt woodland, Australia; New South Wales chenopod shrubland, Australia) that included at least ten sites. These analyses repeated the method from the global analyses, except there was no longer a need for a random effect for study in the model. Change in disturbance regime was a significantly (*P* = 0.01) or marginally significantly (*P* = 0.06) better predictor of the % of species richness contributed by introduced species in three of four regions, and a significantly better predictor of the % cover contributed by introduced species in one of four regions (Table 1). In three of the eight local analyses, the slope of the relationship between the % cover or richness of introduced species and current disturbance regime was negative rather than positive as predicted by the theory that disturbance facilitates introduced species by increasing recruitment opportunities. That is, increasing disturbance was associated with *fewer* introduced species, not more. In these cases, even if the statistical fit for change in disturbance regime is not significantly better, the prediction from the theory that change in disturbance regime facilitates introduced species fits the data better than does the prediction from the classic idea that increasing disturbance facilitates introduced species. Thus, six of eight local analyses provide support for the idea that it is change in disturbance rather than disturbance *per se* that facilitates introduced species.

Our finding that the richness and cover of introduced species at a site are better predicted by changes in the disturbance regime than by disturbance *per se* is in line with the recent trend towards a more holistic approach to predicting the traits of introduced species. That is, simple measures of current ecosystem properties yield only weak and/or idiosyncratic patterns,

Table 1. Results of local analyses on studies with at least 10 sites. Parameter estimates are for logit transformed y variables. Positive LR indicate that the change in disturbance is a better predictor of the y variable than is current disturbance regime. In the x variable column, change refers to changes in disturbance frequency (the absolute value of $\log_{10}$(current disturbance/historic disturbance)), while current refers to $\log_{10}$(current disturbance)

Study region/system	No of sites	y variable	x variable	Slope	R^2	LR	P
Sydney woodland, Australia	10	% introduced species	Change	8.77	0.34	0.41	0.06*
			Current	−4.60	0.32		
		Relative cover of introduced species	Change	25.19	0.68	−53.6	1.00*
			Current	−15.39	0.76		
Cedar Creek oak savanna/ woodland, USA	26	% introduced species	Change	0.21	0.02	−0.32	0.63*
			Current	−0.19	0.03		
		Relative cover of introduced species	Change	−1.20	0.04	−2.11	0.94
			Current	0.97	0.05		
New South Wales, *Eucalyptus* woodland, Australia	58	% introduced species	Change	0.21	0.012	0.45	0.06
			Current	0.13	0.007		
		Relative cover of introduced species	Change	8.25	0.09	2×10^{-8}	0.05
			Current	8.25	0.09		
New South Wales, chenopod shrubland, Australia	54	% introduced species	Change	0.38	0.08	4.94	0.01
			Current	0.09	0.02		
		Relative cover of introduced species	Change	0.99	0.04	0.87	0.46
			Current	0.46	0.03		

LR, likelihood ratio.
P-values marked with asterisks denote cases where the fit for current disturbance regime is a negative relationship, rather than the positive relationship predicted.

while measures that incorporate information about factors that have shaped both ecosystem development and the evolutionary trajectory of the resident species provide a more robust understanding. Our results also support the idea that capturing information about the differences between the conditions under which native species evolved/assembled, and current conditions are likely to be particularly informative (Moles, Gruber & Bonser 2008).

On one hand, our finding that disturbance has low power to explain global patterns in the species richness and cover of introduced species is unsurprising. Many factors are thought to affect an ecosystem's susceptibility to invasion (including disturbance, species composition, species richness, resource availability and propagule pressure, Hooper *et al*. 2005; Eschtruth & Battles 2009), and the sites included in our analyses span a wide range of disturbance types, geographical locations and vegetation types. On the other hand, our results show that, although disturbance has some explanatory power and can have clear effects in carefully controlled experiments, it is not likely to be the primary determinant of a site's invasibility. Nonetheless, as many of the determinants of a site's invasibility are likely factors external to the site (e.g. propagule availability or management and use of the land surrounding the site), disturbance likely explains a larger, and perhaps much larger, fraction of the intrinsic invasibility of a site than a statistical test that includes all sources of variation (intrinsic and extrinsic signals as well as noise) might suggest. Quantifying the relative importance of different explanatory variables, and partitioning them in to internal and external drivers, is an important direction for future research.

Overall conclusions

The field of invasion biology shares a few characteristics with the species it seeks to understand. The number of both papers and introduced plants in the field has been increasing exponentially through time, and the impact of both the plants and the research on them can be (but is not always) very high. Invasions are complex processes, and simple approaches that focus on one factor at a time (such as the traits of invaders or recipient communities) have had limited success. We believe that the best way to further our understanding of invasions will be to adopt more holistic approaches that incorporate several different types of information simultaneously, especially information about the ways conditions have changed. This will not be simple to achieve, but we have an army of enthusiastic ecologists who want to understand invasions, so it seems likely that we will make substantial progress relatively quickly. Finally, invasion biologists (like other ecologists; Cooper 1926) need to take a good hard look at the fundamental tenets of the discipline and ensure that our understanding is built on hard evidence rather than assumptions, or on theories that have equivocal empirical support. Invasion biology is a big field, but there are still plenty of opportunities for new, exciting and urgently needed science.

References

Altman, S. & Whitlatch, R.B. (2007) Effects of small-scale disturbance on invasion success in marine communities. *Journal of Experimental Marine Biology and Ecology*, **342**, 15–29.

Baker, H.G. (1965) Characteristics and modes of origin of weeds. *The Genetics of Colonizing Species* (eds H.G. Baker & G.L. Stebbins), pp. 147–168. Academic Press, New York.

Baker, H.G. (1974) The evolution of weeds. *Annual Review of Ecology and Systematics*, **5**, 1–24.

Bando, K.J. (2006) The roles of competition and disturbance in a marine invasion. *Biological Invasions*, **8**, 755–763.

Barrett, S.C.H., Colautti, R.I. & Eckert, C.G. (2008) Plant reproductive systems and evolution during biological invasion. *Molecular Ecology*, **17**, 373–383.

Belote, R.T., Jones, R.H., Hood, S.M. & Wender, B.W. (2008) Diversity-invasibility across an experimental disturbance gradient in Appalachian forests. *Ecology*, **89**, 183–192.

Blossey, B. & Nötzold, R. (1995) Evolution of increased competitive ability in invasive nonindigenous plants: a hypothesis. *Journal of Ecology*, **83**, 887–889.

Bossdorf, O., Richards, C.L. & Pigliucci, M. (2008) Epigenetics for ecologists. *Ecology Letters*, **11**, 106–115.

Bossdorf, O., Auge, H., Lafuma, L., Rogers, W.E., Siemann, E. & Prati, D. (2005) Phenotypic and genetic differentiation between native and introduced plant populations. *Oecologia*, **144**, 1–11.

Bradley, B.A., Blumenthal, D.M., Wilcove, D.S. & Ziska, L.H. (2010) Predicting plant invasions in an era of global change. *Trends in Ecology & Evolution*, **25**, 310–318.

Brooks, M.L., D'Antonio, C.M., Richardson, D.M., Grace, J.B., Keeley, J.E., DiTomaso, J.M., Hobbs, R.J., Pellant, M. & Pyke, D. (2004) Effects of invasive alien plants on fire regimes. *BioScience*, **54**, 677–688.

Buckley, Y.M., Bolker, B.M. & Rees, M. (2007) Disturbance, invasion and reinvasion: managing the weed-shaped hole in disturbed ecosystems. *Ecology Letters*, **10**, 809–817.

Burke, M.J.W. & Grime, J.P. (1996) An experimental study of plant community invasibility. *Ecology*, **77**, 776–790.

Buswell, J.M., Moles, A.T. & Hartley, S. (2011) Rapid evolution is common in introduced plant species. *Journal of Ecology*, **99**, 214–224.

Cheptou, P.-O., Carrue, O., Rouifed, S. & Cantarel, A. (2008) Rapid evolution of seed dispersal in an urban environment in the weed *Crepis sancta*. *Proceedings of the National Adademy of Sciences of the United States of America*, **105**, 3796–3799.

Cheverud, J.M., Vaughn, T.T., Pletscher, L.S., King-Ellison, K., Bailiff, J., Adams, E., Erickson, C. & Bonislawski, A. (1999) Epistasis and the evolution of additive genetic variance in populations that pass through a bottleneck. *Evolution*, **53**, 1009–1018.

Cody, M.L. & Overton, J.M. (1996) Short-term evolution of reduced dispersal in island plant populations. *Journal of Ecology*, **84**, 53–61.

Cooper, W.S. (1926) The fundamentals of vegetational change. *Ecology*, **7**, 391–413.

Corlett, R.T. (2010) Invasive aliens on tropical East Asian islands. *Biodiversity and Conservation*, **19**, 411–423.

Cowan, P.E. (1992) The eradication of introduced Australian brushtail possums, *Trichosurus vulpecula*, from Kapiti Island, a New Zealand nature reserve. *Biological Conservation*, **61**, 217–226.

CRC Weed Management (2003) *Weeds of National Significance. Weed Management Guide – Lantana (*Lantana camara*).* CRC for Australian Weed Management, and Commonwealth Department of Environment and Heritage, Canberra.

Daehler, C.C. (2001) Darwin's naturalization hypothesis revisited. *The American Naturalist*, **158**, 324–330.

Daehler, C.C. (2003) Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. *Annual Review of Ecology and Systematics*, **34**, 183–211.

D'Antonio, C.M., Dudley, T.L. & Mack, M. (1999) Disturbance and biological invasions: direct effects and feedbacks. *Ecosystems of Disturbed Ground* (ed. L.R. Walker), pp. 413–452. Elsevier, New York, USA.

Davidson, A.M., Jennions, M. & Nicotra, A.B. (2011) Do invasive species show higher phenotypic plasticity than native species and, if so, is it adaptive? A meta-analysis. *Ecology Letters*, **14**, 419–431.

Davies, K.F., Chesson, P., Harrison, S., Inouye, B.D., Melbourne, B.A. & Rice, K.J. (2005) Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. *Ecology*, **86**, 1602–1610.

Davis, M.A. (2003) Biotic globalization: does competition from introduced species threaten biodiversity? *BioScience*, **53**, 481–489.

Davis, M.A., Grime, J.P. & Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology*, **88**, 528–534.

Davis, M.A., Pergl, J., Truscott, A.M., Kollmann, J., Bakker, J.P., Domenech, R. *et al.* (2005) Vegetation change: a reunifying concept in plant ecology. *Perspectives in Plant Ecology Evolution and Systematics*, **7**, 69–76.

Davis, M., Chew, M.K., Hobbs, R.J., Lugo, A.E., Ewel, J.J., Vermeij, G.J. *et al.* (2011) Don't judge species on their origins. *Nature*, **474**, 153–154.

Davison, A.C. & Hinkley, D.V. (1997) *Bootstrap Methods and Their Application.* Cambridge University Press, Cambridge, UK.

Diez, J.M., Williams, P.A., Randall, R.P., Sullivan, J.J., Hulme, P.E. & Duncan, R.P. (2009) Learning from failures: testing broad taxonomic hypotheses about plant naturalization. *Ecology Letters*, **12**, 1174–1183.

Dlugosch, K.M. & Parker, I.M. (2008) Founding events in species invasions: genetic variation, adaptive evolution, and the role of multiple introductions. *Molecular Ecology*, **17**, 431–449.

Ehrenfeld, J.G. (2010) Ecosystem consequences of biological invasions. *Annual Review of Ecology, Evolution, and Systematics*, **41**, 59–80.

Ellstrand, N.C. & Schierenbeck, K.A. (2000) Hybridization as a stimulus for the evolution of invasiveness in plants? *Proceedings of the National Academy of Sciences of the United States of America*, **97**, 7043–7050.

Elton, C. (1958) *The Ecology of Invasions by Animals and Plants.* Methuen, London, UK.

Eschtruth, A.K. & Battles, J.J. (2009) Assessing the relative importance of disturbance, herbivory, diversity, and propagule pressure in exotic plant invasion. *Ecological Monographs*, **79**, 265–280.

Firn, J., Moore, J.L., MacDougall, A.S., Borer, E.T., Seabloom, E.W., HilleRisLambers, J. *et al.* (2011) Abundance of introduced species at home predicts abundance away in herbaceous communities. *Ecology Letters*, **14**, 274–281.

Fridley, J.D., Stachowicz, J.J., Naeem, S., Sax, D.F., Seabloom, E.W., Smith, M.D., Stohlgren, T.J., Tilman, D. & Von Holle, B. (2007) The invasion paradox: reconciling pattern and process in species invasions. *Ecology*, **88**, 3–17.

Grime, J.P. (1977) Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169–1194.

Gurevitch, J. & Padilla, D.K. (2004) Are invasive species a major cause of extinctions? *Trends in Ecology & Evolution*, **19**, 470–474.

Gurevitch, J., Fox, G.A., Wardle, G.M., Inderjit & Taub, D. (2011) Emergent insights from the synthesis of conceptual frameworks for biological invasions. *Ecology Letters*, **14**, 407–418.

Hawkes, C.V. (2007) Are invaders moving targets? The generality and persistence of advantages in size, reproduction, and enemy release in invasive plant species with time since introduction. *The American Naturalist*, **170**, 832–843.

Hegarty, M.J., Batstone, T., Barker, G.L., Edwards, K.J., Abbott, R.J. & S.J., H. (2011) Nonadditive changes to cytosine methylation as a consequence of hybridization and genome duplication in *Senecio* (Asteraceae). *Molecular Ecology*, **20**, 105–113.

Herben, T., Mandak, B., Bimova, K. & Munzbergova, Z. (2004) Invasibility and species richness of a community: a neutral model and a survey of published data. *Ecology*, **85**, 3223–3233.

Hester, A.J. & Hobbs, R.J. (1992) Influence of fire and soil nutrients on native and non-native annuals at remnant vegetation edges in the Western Australian wheatbelt. *Journal of Vegetation Science*, **3**, 101–108.

Hobbs, R.J. & Atkins, L. (1988) Effect of disturbance and nutrient addition on native and introduced annuals in plant communities in the Western Australian wheatbelt. *Australian Journal of Ecology*, **13**, 171–179.

Hobbs, R.J. & Huenneke, L.F. (1992) Disturbance, diversity, and invasion: implications for conservation. *Conservation Biology*, **6**, 324–337.

Hobbs, R.J., Arico, S., Aronson, J., Baron, J.S., Bridgewater, P., Cramer, V.A. *et al.* (2006) Novel ecosystems: theoretical and management aspects of the new ecological world order. *Global Ecology and Biogeography*, **15**, 1–7.

Hooper, D.A. & Dukes, J.S. (2010) Functional composition controls invasion success in a California serpentine grassland. *Journal of Ecology*, **98**, 764–777.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S. *et al.* (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*, **75**, 3–35.

Howard, T.G., Gurevitch, J., Hyatt, L. & Carreiro, M. (2004) Forest invasibility in communities in southeastern New York. *Biological Invasions*, **6**, 393–410.

Imhoff, M.L., Bounoua, L., Ricketts, T., Loucks, C., Harriss, R. & Lawrence, W.T. (2004) Global patterns in human consumption of net primary production. *Nature*, **429**, 870–873.

Keane, R.M. & Crawley, M.J. (2002) Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, **17**, 164–170.

van Kleunen, M., Weber, E. & Fischer, M. (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters*, **13**, 235–245.

Lee, C.E. (2002) Evolutionary genetics of invasive species. *Trends in Ecology & Evolution*, **17**, 386–391.

Levine, J.M., Adler, P.B. & Yelenik, S.G. (2004) A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, **7**, 975–989.

Levine, J.M. & D'Antonio, C.M. (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, **87**, 15–26.

Levine, J.M., Vila, M., D'Antonio, C.M., Dukes, J.S., Grigulis, K. & Lavorel, S. (2003) Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **270**, 775–781.

Lewis, F., Butler, A. & Gilbert, L. (2011) A unified approach to model selection using the likelihood ratio test. *Methods in Ecology and Evolution*, **2**, 155–162.

Lockwood, J.L., Cassey, P. & Blackburn, T. (2005) The role of propagule pressure in explaining species invasions. *Trends in Ecology & Evolution*, **20**, 223–228.

Lockwood, J.L., Hoopes, M.F. & Marchetti, M.P. (2007) *Invasion Ecology.* Blackwell Publishing, Oxford, UK.

Lodge, D.M. (1993) Biological invasions: lessons for ecology. *Trends in Ecology & Evolution*, **8**, 133–137.

Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.

Mack, M.C. & D'Antonio, C.M. (1998) Impacts of biological invasions on disturbance regimes. *Trends in Ecology & Evolution*, **13**, 195–198.

Maron, J.L., Elmendorf, S.C. & Vila, M. (2007) Contrasting plant physiological adaptation to climate in the native and introduced range of *Hypericum perforatum*. *Evolution*, **61**, 1912–1924.

Marzluff, J.M., Shulenberger, E., Bradley, G., Alberti, M., Ryan, C., ZumBrunnen, C., Endlicher, W. & Simon, U. (2008) *Urban Ecology: An International Perspective on the Interaction of Humans and Nature*. Springer, New York, pp. 807.

Mason, R., Cooke, J., Moles, A.T. & Leishman, M.R. (2008) Reproductive output of native and exotic plants: a global comparison. *Global Ecology and Biogeography*, **17**, 633–640.

McLaren, C. (1997) *Dry Sheep Equivalents for Comparing Different Classes of Livestock*. Department of Primary Industries, Melbourne, Vic., Australia.

Meiners, S.J., Pickett, S.T.A. & Cadenasso, M.L. (2002) Exotic plant invasions over 40 years of old field succession: community patterns and associations. *Ecography*, **25**, 215–223.

Melbourne, B.A., Cornell, H.V., Davies, K.F., Dugaw, C.J., Elmendorf, S., Freestone, A.L. *et al.* (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecology Letters*, **10**, 77–94.

Meyer, J.-Y. (1996) Status of *Miconia calvescens* (Melastomataceae), a dominant invasive tree in the Society Islands (French Polynesia). *Pacific Science*, **50**, 66–76.

Moles, A.T., Gruber, M.A.M. & Bonser, S.P. (2008) A new framework for predicting invasive plant species. *Journal of Ecology*, **96**, 13–17.

Morales, C.L. & Traveset, A. (2009) A meta-analysis of impacts of alien vs. native plants on pollinator visitation and reproductive success of co-flowering native plants. *Ecology Letters*, **12**, 716–728.

Ordonez, A., Wright, I.J. & Olff, H. (2010) Functional differences between native and alien species: a global-scale comparison. *Functional Ecology*, **24**, 1353–1361.

Phillips, B.L., Brown, G.P., Webb, J.K. & Shine, R. (2006) Invasion and the evolution of speed in toads. *Nature*, **439**, 803.

Pimentel, D., McNair, S., Janecka, J., Wightman, J., Simmonds, C., O'Connell, C., Wong, E., Russel, L., Zern, J., Aquino, T. & Tsomondo, T. (2001) Economic and environmental threats of alien plant, animal, and microbe invasions. *Agriculture, Ecosystems and Environment*, **84**, 1–20.

Prentis, P.J., Wilson, J.R.U., Dormontt, E.E., Richardson, D.M. & Lowe, A.J. (2008) Adaptive evolution in invasive species. *Trends in Plant Science*, **13**, 288–294.

Puillandre, N., Dupas, S., Dangles, O., Zeddam, J.L., Capdevielle-Dulac, C., Barbin, K., Torres-Leguizamon, M. & Silvain, J.F. (2008) Genetic bottleneck in invasive species: the potato tuber moth adds to the list. *Biological Invasions*, **10**, 319–333.

Pyšek, P. & Richardson, D.M. (2006) The biogeography of naturalization in alien plants. *Journal of Biogeography*, **33**, 2040–2050.

Pyšek, P. & Richardson, D.M. (2007) Traits associated with invasiveness in alien plants: where do we stand? *Biological Invasions, Ecological Studies* (ed. W. Nentwig), pp. 97–126. Springer-Verlag, Berlin & Heidelberg.

Pyšek, P., Jarošík, V., Hulme, P.E., Kühn, I., Wild, J., Arianoutsou, M. *et al.* (2010) Disentangling the role of environmental and human pressures on biological invasions. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 12157–12162.

Pyšek, P., Jarosik, V., Chytry, M., Danihelka, J., Kuhn, I., Jergl, J., Tichy, L., Biesmeijer, J.C., Ellis, W.N., Kunin, W.E. & Settele, J. (2011) Successful invaders co-opt pollinators of native flora and accumulate insect pollinators with increasing residence time. *Ecological Monographs*, **81**, 277–293.

Ramula, S., Knight, T.M., Burns, J.H. & Buckley, Y.M. (2008) General guidelines for invasive plant management based on comparative demography of invasive and native plant populations. *Journal of Applied Ecology*, **45**, 1124–1133.

Rejmanek, M. (1996) A theory of seed plant invasiveness – the first sketch. *Biological Conservation*, **78**, 171–181.

Richardson, D.M. & Pyšek, P. (2006) Plant invasions: merging the concepts of species invasiveness and community invasibility. *Progress in Physical Geography*, **30**, 409–431.

Rickart, E.A., Balete, D.S., Rowe, R.J. & Heaney, L.R. (2011) Mammals of the northern Philippines: tolerance for habitat disturbance and resistance to invasive species in an endemic insular fauna. *Diversity and distributions*, **17**, 530–541.

Rieseberg, L.H., Kim, S.C., Randell, R.A., Whitney, K.D., Gross, B.L., Lexer, C. & Clay, K. (2007) Hybridization and the colonization of novel habitats by annual sunflowers. *Genetica*, **129**, 149–165.

Roman, J. & Darling, J.A. (2007) Paradox lost: genetic diversity and the success of aquatic invasions. *Trends in Ecology & Evolution*, **22**, 454–464.

Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A. *et al.* (2001) The population biology of invasive species. *Annual Review of Ecology and Systematics*, **32**, 305–332.

Sax, D.F., Stachowicz, J.J., Brown, J.H., Bruno, J.F., Dawson, M.N., Gaines, S.D., Grosberg, R.K., Hastings, A., Holt, R.D., Mayfield, M.M., O'Connor, M.I. & Rice, W.R. (2007) Ecological and evolutionary insights from species invasions. *Trends in Ecology & Evolution*, **22**, 465–471.

Scholes, R.J. & Archer, S.R. (1997) Tree-grass interaction in savannas. *Annual Review of Ecology and Systematics*, **28**, 517–544.

Sher, A.A., Marshall, D.L. & Gilbert, S.A. (2000) Competition between native *Populus deltoids* and invasive *Tamarix ramosissima* and the implications for reestablishing flooding disturbance. *Conservation Biology*, **14**, 1744–1754.

Simberloff, D. (2009) The role of propagule pressure in biological invasions. *Annual Review of Ecology Evolution and Systematics*, **40**, 81–102.

Simberloff, D. (2011) Non natives: 141 scientists object. *Nature*, **475**, 36.

Simberloff, D. & Von Holle, B. (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions*, **1**, 21–32.

Slobodkin, L.B. (2001) The good, the bad and the reified. *Evolutionary Ecology Research*, **3**, 1–13.

Smart, N.O.E., Hatton, J.C. & Spence, D.H.N. (1985) The effect of long-term exclusion of large herbivores on vegetation in Murchison Falls National Park, Uganda. *Biological Conservation*, **33**, 229–245.

Smith, M.D. & Knapp, A.K. (1999) Exotic plant species in a C4-dominated grassland: invasibility, disturbance, and community structure. *Oecologia*, **120**, 605–612.

Spence, L.A., Ross, J.V., Wiser, S.K., Allen, R.B. & Coomes, D.A. (2011) Disturbance affects short-term facilitation, but not long-term saturation, of exotic plant invasion in New Zealand forest. *Proceedings of the Royal Society B-Biological Sciences*, **278**, 1457–1466.

Strauss, S.Y., Webb, C.O. & Salamin, N. (2006) Exotic taxa less related to native species are more invasive. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 5841–5845.

Tiegs, S.D., O'Leary, J.F., Pohl, M.M. & Munill, C.L. (2005) Flood disturbance and riparian species diversity on the Colorado River Delta. *Biodiversity and Conservation*, **14**, 1175–1194.

Turelli, M. & Barton, N.H. (2006) Will population bottlenecks and multilocus epistasis increase additive genetic variance? *Evolution*, **60**, 1763–1776.

Vellend, M., Harmon, L.J., Lockwood, J.L., Mayfield, M.M., Hughes, A.R., Wares, J.P. & Sax, D.F. (2007) Effects of exotic species on evolutionary diversification. *Trends in Ecology & Evolution*, **22**, 481–488.

Vilà, M. & Ibáñez, I. (2011) Plant invasions in the landscape. *Landscape Ecology*, **26**, 461–472.

Vilà, M., Espinar, J.L., Hejda, M., Hulme, P.E., Jarosik, 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. *Ecology Letters*, **14**, 702–708.

Vitousek, P.M., D'Antonio, C.M., Loope, L.L. & Westbrooks, R. (1996) Biological invasions as global environmental change. *American Scientist*, **84**, 468–478.

Von Holle, B. & Simberloff, D. (2005) Ecological resistance to biological invasion overwhelmed by propagule pressure. *Ecology*, **86**, 3212–3218.

Warton, D.I. & Hui, F.K.C. (2011) The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, **92**, 3–10.

Wilcove, D.S., Rothstein, D., Diubow, J., Phillips, A. & Losos, E. (1998) Quantifying threats to imperiled species in the United States. *BioScience*, **48**, 607–615.

Williamson, M.H. & Fitter, A. (1996) The characters of successful invaders. *Biological Conservation*, **78**, 163–170.

Zangerl, A.R. & Berenbaum, M.R. (2005) Increase in toxicity of an invasive weed after reassociation with its coevolved herbivore. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 15529–15532.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. List of study sites.

Appendix S2. World map showing site locations.

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