

Management strategies for plant invasions: manipulating productivity, disturbance, and competition

Michael A. Huston

Department of Biology, Texas State University,
San Marcos, TX 78666, USA

ABSTRACT

The traditional approach to understanding invasions has focused on properties of the invasive species and of the communities that are invaded. A well-established concept is that communities with higher species diversity should be more resistant to invaders. However, most recently published field data contradict this theory, finding instead that areas with high native plant diversity also have high exotic plant diversity. An alternative environment-based approach to understanding patterns of invasions assumes that native and exotic species respond similarly to environmental conditions, and thus predicts that they should have similar patterns of abundance and diversity. Establishment and growth of native and exotic species are predicted to vary in response to the interaction of plant growth rates with the frequency and intensity of mortality-causing disturbances. This theory distinguishes between the probability of establishment and the probability of dominance, predicting that establishment should be highest under unproductive and undisturbed conditions and also disturbed productive conditions. However, the probability of dominance by exotic species, and thus of potential negative impacts on diversity, is highest under productive conditions. The theory predicts that a change in disturbance regime can have opposite effects in environments with contrasting levels of productivity. Manipulation of productivity and disturbance provides opportunities for resource managers to influence the interactions among species, offering the potential to reduce or eliminate some types of invasive species.

Keywords

Biological invasions, diversity, productivity, disturbance, competition, dominance, management.

Correspondence: Michael A. Huston,
Department of Biology, Texas State University,
San Marcos, TX 78666, USA. E-mail:
mh54@txstate.edu

INTRODUCTION

There is increasing recognition that the theories and experimental approaches of community ecology have the potential to make major contributions to understanding and managing plant invasions (Huston, 1994; Tilman, 1997; Davis *et al.*, 2000; Shea & Chesson, 2002). However, the various ecological theories, experiments, and observations have come to strikingly different conclusions. Well-established ecological theory makes the explicit prediction that communities with high species diversity should be more difficult to invade than communities with lower diversity (Elton, 1958; Tilman, 1997), yet experimental evidence is equivocal (D'Antonio & Levine, 1999) and nearly all observational data contradict this prediction (D'Antonio & Levine, 1999; Shea & Chesson, 2002).

Most of the theories about species invasions have focused on the properties of the species themselves, including both the invasive species and the native species that potentially resist the

invasion (Baker, 1965, 1974; Newsome & Noble, 1986; Binggeli, 1996; Rejmánek & Richardson, 1996; Roy, 1998; Daehler & Carino, 2000; Kolar & Lodge, 2001; Shea & Chesson, 2002). There is clearly variation in life-history attributes that affects invasive potential in different environments (Baker, 1965; Crawley, 1986; Rejmánek & Richardson, 1996; Rejmánek *et al.*, 2004). In addition, there may be genetic and evolutionary dynamics that alter the competitive ability of exotic species (Ellstrand & Schierenbeck, 2000; Siemann & Rogers, 2001).

Several recent invasion experiments in which species diversity was the treatment variable support the prediction that high diversity communities are more resistant to invasion (Tilman, 1993, 1997; Levine, 2000; Kennedy *et al.*, 2002). However, other experiments found no effect of species richness on invasibility (Lavorel *et al.*, 1999). Re-evaluation of the positive experimental results suggests that factors other than variation in species diversity, such as total biomass or plant density, may actually be causing the observed responses (Wardle, 2001; Weltzin *et al.*, 2003).

In addition, field surveys of invasive species richness in relation to native species richness have found a pattern opposite to that seen in the experiments. A survey of parks and preserves around the world found a positive correlation between the number of native species and the number of exotic species (Lonsdale, 1999). A higher-resolution study of vegetation in the Rocky Mountains, western deserts, and Great Plains of North America also found that native and exotic species richness were positively correlated across sample areas at several levels of sampling resolution (Stohlgren *et al.*, 1998; Stohlgren *et al.*, 2001). In riparian systems, the areas with the highest diversity of native plant species also had the greatest number of exotic species, in both California (Levine, 2000) and the southern Appalachians (Brown & Peet, 2003). The fact that almost all of the field data published to date contradict not only the primary theory of invasibility and diversity, but also the results of short-term experiments with randomly selected species assemblages, suggests that our understanding of this topic remains incomplete.

An environment-based theory of diversity and invasibility

While the traditional approach to understanding invasions has been to focus on the properties of the organisms themselves, e.g. a niche-based competition approach (Shea & Chesson, 2002), an alternative approach is to focus on the properties of the physical environment that affect species survival, growth, and interactions (Huston & DeAngelis, 1994; Huston, 1994; Stohlgren, 2002). The role of physical environmental conditions, such as soils and climate, is receiving increasing attention in discussions of invasive species (e.g. Crawley *et al.*, 1987; Hobbs & Atkins, 1988; Huenneke *et al.*, 1990; Vitousek, 1990; Stohlgren *et al.*, 1997, 1999a,b, 2001, 2002; Richardson & Bond, 1991; Higgins & Richardson, 1998; Alpert *et al.*, 2000; Larson *et al.*, 2001).

The basic premise of this approach is that invasive species are not qualitatively different from native species, and respond to environmental conditions in the same ways as native species respond (Huston, 1994). This premise is supported by the analysis of Sax (2001), who found that the latitudinal patterns of species richness and range size were similar between exotic and native species of birds, mammals and fish (this study did not examine plants). In a comparison of native and naturalized species richness of herbaceous plants in Mediterranean shrublands of Chile and California, Sax (2002) found positive correlations between native and naturalized species richness, as well as similar patterns of richness in relation to elevation.

Thus, the same processes that influence native species population dynamics and diversity also influence the establishment and survival of exotic species, and consequently allow prediction of patterns of exotic species diversity using the same theories and models used for native plant diversity (e.g. Huston, 1994; Williamson, 1996; D'Antonio & Levine, 1999; Davis *et al.*, 2000; Shea & Chesson, 2002). The approach presented here is derived from the dynamic equilibrium model of species diversity (Huston, 1979, 1994), and specifically addresses two distinct components of invasions: (1) the probability of successful establishment of

invaders, and (2) the probability that an established invader will have a significant (dominant) effect on the invaded community.

The dynamic equilibrium model is based on the interaction of two fundamental ecological processes that operate at the level of individual organisms: growth and mortality. Environmental properties that influence growth and mortality vary at all spatial scales, from topographic gradients on a hillside to continental or global gradients of temperature and precipitation (e.g. Franklin, 1995). Every landscape can be characterized on the basis of properties that affect plant growth, such as soil fertility and moisture, and properties that affect mortality, such as the frequency and intensity of natural or man-made disturbances. Across this range of interacting conditions, the relative importance of different ecological processes related to growth and survival varies consistently, allowing predictions about the availability of different types of resources, the dynamics of competitive exclusion, population stability and survival, species diversity, and the rates of many ecological and ecosystem processes (Huston, 1979, 1994).

Disturbances that cause sudden mortality can operate either to increase or to decrease the effect of two major causes of stress-related mortality, thus either increasing or decreasing population survival and species diversity (Paine, 1966; Connell, 1978; Huston, 1979, 1994; Sousa, 1979; Bakker, 1989). Such sudden mortality can result from biotic processes such as herbivory or predation, or from abiotic processes such as floods, lightning, extreme weather, etc.

The two primary non-disturbance processes that reduce population sizes are mortality due to abiotically generated stresses from extreme conditions or insufficient resources, and mortality caused by biotic stresses from competitive interactions that also reduce resources. These two types of stresses tend to occur in contrasting environments, which makes generalizations about the effect of stress or productivity on diversity and invasibility nearly impossible (e.g. Alpert *et al.*, 2000; Davis *et al.*, 2000).

Abiotically generated stresses typically occur in unproductive environments that are unfavourable because of climatic conditions (e.g. too hot, too cold, or too dry) or because of low resource availability caused by geological and soil conditions (e.g. infertile, toxic, or shallow soils). In these environments light availability for most plants is high because low levels of soil resources or a short growing season limit the accumulation of biomass that produces shade. Biotically generated stresses typically occur in more favourable environments, where most species can grow well, but the largest, most competitive species can reduce or eliminate populations of poorer competitors by reducing levels of resources such as light (i.e. causing stress due to low light levels). This shift of ecological processes, limiting resources, and types of stress along an environmental gradient from unfavourable to favourable growth conditions leads to the widely observed unimodal pattern of species diversity along productivity gradients (Grime, 1973a,b, 1979; Huston, 1979, 1980; Doyle, 1981; Tilman, 1987; Grace, 1999; Dodson *et al.*, 2000), as well as a shift from positive interspecific interactions (e.g. facilitation) to negative interactions (e.g. competition) (Callaway & Walker, 1997; Holmgren *et al.*, 1997).

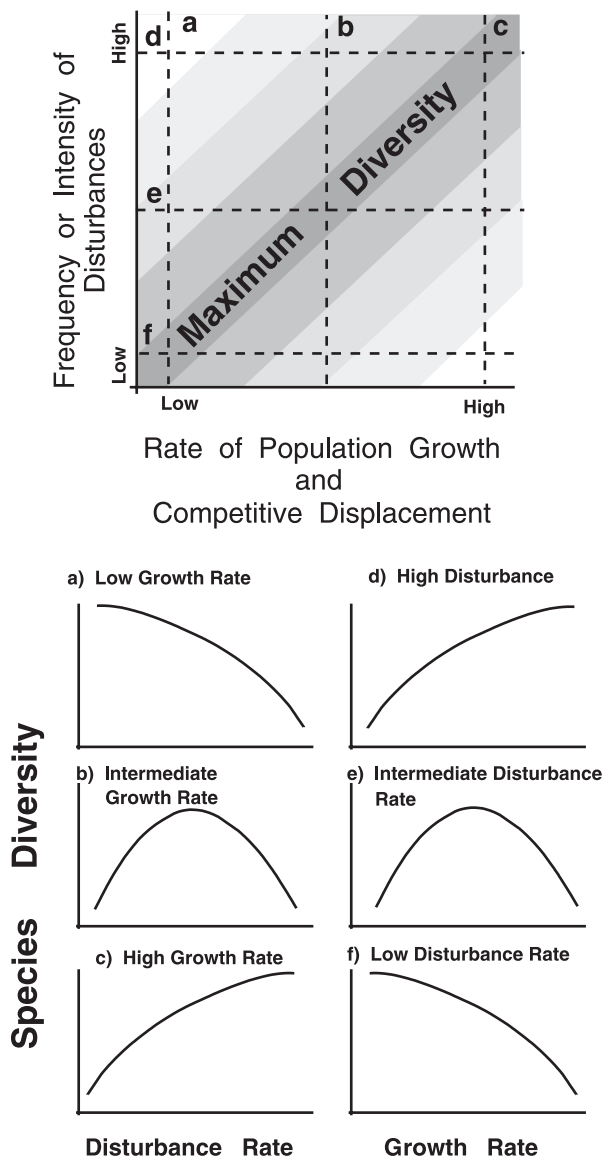


Figure 1 Predictions of the Dynamic Equilibrium Model of species diversity. Both disturbance type and frequency, and growth rates (plant productivity, population growth rates) vary across landscapes in response to geology, topography, and climate. Diversity is reduced by failure of populations to survive under conditions of high frequency of disturbances and low productivity (upper left corner), and also by competitive exclusion under high productivity conditions where mortality-causing disturbances are infrequent (lower right corner). Diversity is predicted to be highest where these two processes cancel each other, which is illustrated along the diagonal line from the lower left corner to the upper right (from Huston, 1994; based on Huston, 1979). The effect on species diversity of a change in disturbance frequency or intensity can be reversed from one environment to another, depending on local conditions of productivity and growth rates (e.g. (a) vs. (c)). Similarly, the effect on species diversity of the same change in productivity can completely reverse, depending on the disturbance regime (e.g. (d) vs. (f)). Intermediate conditions produce the classical unimodal response ((b) and (e)). Within a given disturbance regime, changing either frequency or intensity is predicted to have the effects shown. However, in situations where

The dynamic equilibrium model integrates the effect of disturbances with the changing resource levels and stresses that occur along a productivity gradient to predict population survival and species diversity. The unique prediction of this model is that the effect of mortality-causing disturbances on species diversity (i.e. on the survival of both native and exotic species) should *reverse* between productive and unproductive environments. That is, in unproductive environments, an increase in disturbance-caused mortality generally eliminates slowly growing species and leads to a *decrease* in species diversity (Fig. 1a), while in productive environments, an increase in disturbance-caused mortality causes an *increase* in diversity (Fig. 1c), by reducing the biomass of the dominant species and making critical resources, particularly light, available to smaller plants. An analogous reversal occurs for the effect of increased productivity in high (Fig. 2d) vs. low disturbance environments (Fig. 1f), because of the shift from stress tolerance to competitive exclusion as disturbance frequency decreases.

Tests of diversity predictions

The prediction about the reversal of disturbance effects on diversity (Huston, 1979) was recently tested using a meta-analysis of published studies of grazing effects in contrasting environments (Proulx & Mazumder, 1998). Grazing fits the definition of a mortality-causing disturbance because it results in the mortality of all (in the case of grazing of phytoplankton) or part (in the case of most terrestrial grazers) of a plant and thus affects both survival and competitive interactions. The relative ease of grazer manipulation in aquatic and terrestrial systems has led to a large number of published grazing experiments. These studies were reviewed by Proulx & Mazumder (1998) for their meta-analysis, which found numerous examples of the reversal of grazing effects on species diversity (plant species richness) between productive and unproductive environments predicted by the dynamic equilibrium model (Fig. 1). All of the studies conducted in nutrient-poor, unproductive systems showed that plant diversity *decreased* with increased intensity of grazing (Fig. 2a, compare with Fig. 1a). In contrast, most of the published experiments in systems that could be classified as productive (based on measured nutrient levels, precipitation, or qualitative assessments such as oligotrophic vs. mesotrophic) showed an *increase* in plant diversity in response to grazing (Fig. 2b, compare with Fig. 1c). Another meta-analysis (Worm *et al.*, 2002) confirmed the predicted reversals along productivity gradients (at different levels of disturbance) and also along disturbance gradients (at different levels of productivity). As with all ecological processes based on interactions among individual organisms, the effects of grazing on competitive interactions are likely to disappear at spatial scales larger than the scale at which organisms interact (see Huston,

frequency and intensity are inversely correlated, as most fire regimes, patterns can be more complex. In all cases, the properties of individual species must be considered in predicting species-specific or functional type responses. (from Huston, 1979, 1994).

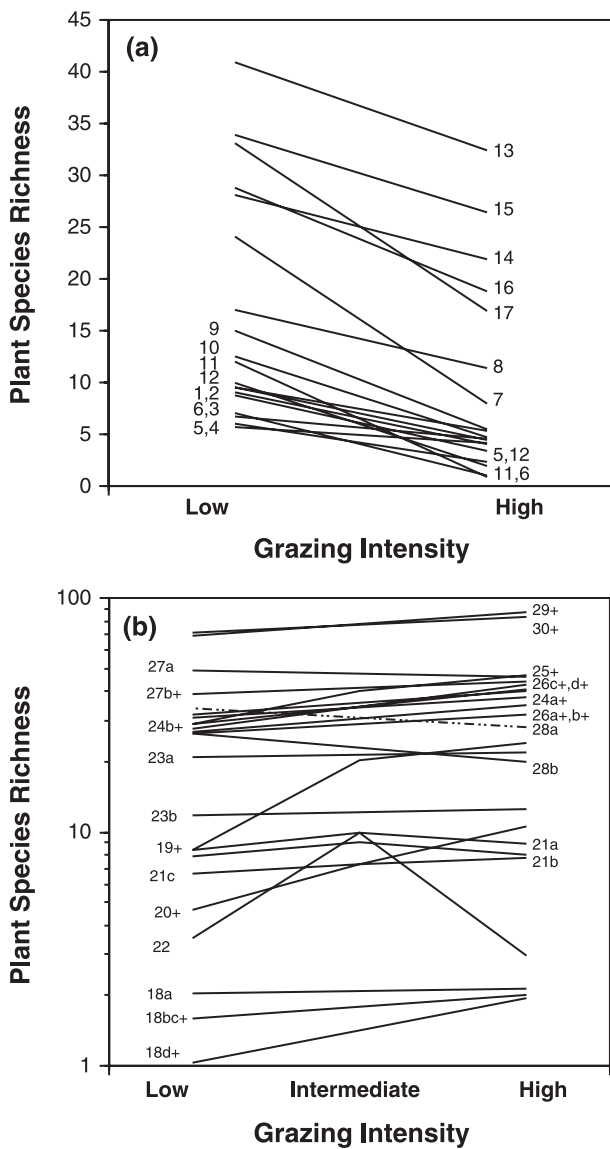


Figure 2 (a) Effect on plant species richness of mortality-causing disturbances in nutrient-poor ecosystems (aquatic and marine) in which mortality is caused by grazing (Proulx & Mazumder, 1998). All of the studies showed a *decrease* in species richness under unproductive conditions, as predicted by the dynamic equilibrium model (Figure 1a). (b) Effect on plant species richness of mortality caused by grazing or mowing in nutrient-rich (natural or fertilized) ecosystems (aquatic, marine, and terrestrial). Results are shown for 24 comparisons reported in 13 published studies examined in a literature review by Proulx & Mazumder (1998), most (21 of 24) showed the *increase* in species richness under productive (i.e. nutrient-rich) conditions predicted by the dynamic equilibrium model. These data are a test of the prediction illustrated in (Figure 1c, High Growth Rates). + indicates a significant positive response (14 out of 24 comparisons). - indicates a significant negative response (1 out of 24 comparisons). Numbers by lines refer to study numbers listed in Proulx & Mazumder (1998). Note that study 22, and to a lesser extent 21a and b, show the unimodal response of the 'intermediate disturbance hypothesis' (Figure 1b).

1999), where environmental heterogeneity obscures the effects of local interactions (e.g. Stohlgren *et al.*, 1999b).

As a consequence of these response reversals, it is often impossible to detect the effects of disturbance on diversity. Without an appropriate stratification of data based on environmental conditions (Huston, 2002), the patterns within the data are hidden, leading, for example, to the conclusion that grazing has no predictable effects on species diversity (Feminella & Hawkins, 1995; Steinman, 1996). Similarly, plant communities with different combinations of productivity and disturbance differ in invasibility, which can lead to the conclusion that productivity has no effect on invasibility (e.g. Davis *et al.*, 2000). This model helps explain many of the apparent inconsistencies and exceptions in the effects of stress, disturbance, nutrient addition, and other factors on both diversity and invasibility (e.g. Alpert *et al.*, 2000; Davis *et al.*, 2000; Shea & Chesson, 2002).

Environmental influences on invasibility

The predictions of the dynamic equilibrium model for the invasibility of different environments (Huston, 1994) are derived from its predictions for population survival and species diversity of plants in general, whether native or exotic, and address two distinct components of invasibility: (1) the probability of establishment; and (2) probability of dominance by established invaders.

With regard to establishment of exotic invaders, assuming equivalent propagule availability across all environments, the model predicts that the probability of successful establishment of plant species (native and exotic) is greatest under two contrasting sets of environmental conditions: unproductive and relatively undisturbed environments, and productive disturbed environments (Fig. 3a).

For the effect of invaders, the model predicts that the impact will generally be largest in the most productive environments, where plant growth rates are high, diversity is often low due to competitive exclusion, and dominant invaders can potentially replace dominant native species (Fig. 3b). Since successful establishment is required before a species can become dominant, the overall probability of dominance by an exotic species is greatest in the upper right quadrant of the environmental space (high disturbance, high productivity). This contrasts dramatically with the lower left quadrant (low disturbance, low productivity) where the probability of establishment is high, but the probability of dominance is low. Under these conditions, exotic species are predicted to have relatively little negative impact, and to assimilate into the native community, unless they change either productivity or the disturbance regime. Extremely unproductive and stressful environments have a low probability of successful invasion by any plant species, and typically have low diversity of native plants and few exotic species.

The resource-fluctuation theory of plant invasions (Davis *et al.*, 2000) also emphasizes that increases in resource availability, as a result of mortality-causing disturbances, natural climatic fluctuations, or eutrophication, tend to increase the invasibility of many environments. These predictions are generally consistent with the dynamic equilibrium model (Huston, 1979, 1994).

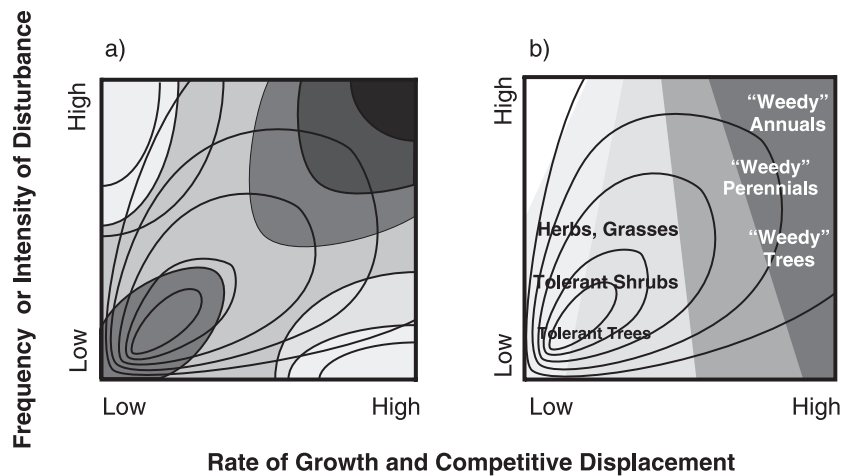


Figure 3 Predicted community susceptibility to invasions and degree of dominance of invading species in environments classified according to disturbance and productivity. The concentric ellipses represent contours of species diversity, with the high diversity represented by the small ellipse in the lower left corner and diversity decreasing away from the ellipse, analogous to Figure 1. (a) Predicted susceptibility of communities to invasion. Darker shading indicates higher probability of successful invasion. Note that communities with low diversity are least likely to be invaded successfully, and communities with high diversity are most likely have invaders establish successfully. (b) Predicted dominance and life histories of successful invaders under various combinations of productivity and disturbance. Darker shading indicates greater dominance of a community by a successful invader. Note that if invaders alter the disturbance regime by increasing frequency or intensity, the community will shift to lower diversity and higher dominance by the invader (from Huston, 1994).

Tests of invasibility predictions

Although the predictions of the dynamic equilibrium model for invasive species have never been explicitly tested, most of the recently published results are consistent with these predictions. The field surveys mentioned previously (Stohlgren *et al.*, 1998; Lonsdale, 1999; Levine, 2000) found a positive correlation between native and exotic species richness, as would be expected if both exotic and native species were responding similarly to environmental conditions over the full range from low diversity to high diversity.

An experimental study (Burke & Grime, 1996) produced results relevant to the dominance prediction of the dynamic equilibrium model, and found the highest percent cover of exotic species in the most productive and most disturbed experimental treatment (Fig. 4). These experimental results are consistent with the observation that riparian areas, which generally have fertile soils and a high disturbance frequency, plus effective long-distance transport of propagules, are among the most heavily invaded vegetation types (e.g. Stohlgren *et al.*, 1998, 2002; Brown & Peet, 2003).

The distinction between the conditions that allow plant establishment vs. those that promote dominance (Fig. 3) is clearly demonstrated in a detailed survey of alien plant distributions at Theodore Roosevelt National Park in North Dakota, USA (Larson *et al.*, 2001). Two contrasting vegetation types, riparian woodland and dry grassland, had numbers of alien species that were two to three times the mean of all 1300 transects sampled, indicating high rates of exotic establishment (cf. Figure 3a). Of these two types, the woody riparian vegetation (*Populus/Juniperus*) had a much higher frequency (~60%) of alien species per transect (an index of abundance or dominance) than did a drier grassland

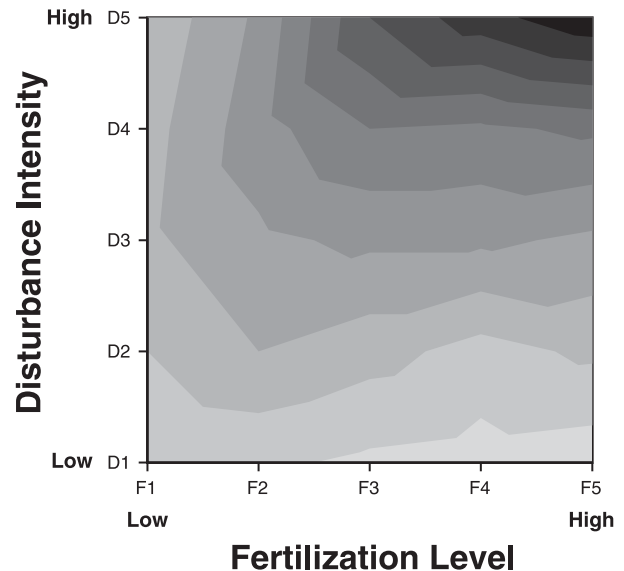


Figure 4 Dominance of invasive species in relation to the experimental interaction of productivity (fertilization) and disturbance regime. Darker shading indicates an increasing percentage of vegetative cover contributed by exotic species, in mixtures that include both native and exotic species. Note that this pattern results from both the increased probability of establishment under disturbed, productive conditions (Figure 3a) and the pattern of maximum dominance (Figure 3b) predicted by the dynamic equilibrium model. Based on data in Burke & Grime (1996).

type (*Agropyron smithii/Stipa viridula*), which had a frequency (~30%) that was less than the mean for all transects (Larson *et al.*, 2001; p. 135) (cf. Figure 3b). Overall, the riparian and mesic vegetation types had higher numbers or frequencies of

alien species, while the most xeric sites tended to have low numbers and frequencies, consistent with the expected decrease in total species richness under extremely unproductive conditions. Finally, the sites that showed the greatest increase in the number or frequency of alien species with disturbance were the more mesic sites, including the riparian vegetation types, as well as the *A. smithii*/*S. viridula* grasslands, consistent with the predictions of the dynamic equilibrium model (Fig. 1c).

Implications for management and control of exotic plants

The two primary options suggested by the dynamic equilibrium model for controlling or eliminating exotic species are: (1) manipulation of the disturbance regime; and (2) manipulation of productivity. The success of this approach depends on knowing enough about the productivity and disturbance regime of any location to estimate its relative location on the graph of productivity and disturbance (Fig. 1). In many situations, a qualitative estimate based on knowledge of the range of environmental conditions within the region should be sufficient to get started. All natural resource management should be carried out in the context of the adaptive management approach, in which management actions are treated as experiments, with careful monitoring of the results, and modification of future management as appropriate (Holling, 1978; Walters, 1986).

Disturbance management

Disturbed areas are more easily invaded (by native or exotic species) than undisturbed areas (Elton, 1958; Hobbs & Huenneke, 1992; Mack *et al.*, 2000), but this effect is found primarily under more productive conditions (Huston & DeAngelis, 1994; Huston, 1994). Environments that are both productive and disturbed, such as agricultural or riparian areas, often have serious exotic problems caused by dominance of the invading species.

The critical property of disturbances is that they kill part or all of some individual plants, thus affecting both survival and competitive ability, and making various types of resources available to surviving plants. Obviously any particular disturbance, such as a fire, flood or ice storm, will have different effects on individual plants that differ in species, size, and other properties. For example, a ground fire in a savanna is likely to cause mortality of tree seedlings, but have no effect on mature trees. Because of these differential effects, the consequences of many types of disturbances for species composition are fairly predictable (Huston, 1994, 2003), although the relative effects on native vs. exotic species will depend on the particular adaptations of the species involved. The imposition of species-specific mortality, such as grazing or forms of 'biocontrol', in a situation where growth of exotic plants is already reduced by competition or other causes of resource reduction, can have a strong negative effect on the population of the exotic species (McEvoy & Coombes, 1999; Scherber *et al.*, 2003).

Manipulation of disturbance often involves an effort to return to some approximation of the 'natural' disturbance regime. In

unproductive environments, increasing the frequency or the intensity of disturbances is likely to greatly reduce or even eliminate the populations of some species (hopefully including exotic species), and thus reduce overall diversity. In contrast, in productive environments, an intensified disturbance regime is more likely to decrease the biomass of dominant species and increase diversity, potentially allowing the successful establishment or expansion of both native and exotic species. Consequently, in productive environments the general management prescription for controlling most exotics will be a reduction in disturbance, which will often allow native species to out-compete exotics. In unproductive environments, the best management plan is likely to be an increase in disturbance mortality, at least to typical (or historic) levels to which native species are more likely to be adapted. The specific details of which native and which exotic species increase or decrease in response to the treatment will depend on the particular adaptations of each species in relation to the local environmental conditions, particularly productivity and disturbance.

In fire-adapted vegetation, such as Mediterranean climate shrublands, prevention of fire typically leads to a decrease in the abundance and diversity of small, fire-adapted species, and an increase in the abundance of species that are likely to be larger in size, and better competitors in the absence of fire (Barro & Conard, 1991; Sax, 2002; Keeley & Fotheringham, 2003). This change may be accompanied by a reduction in the relative abundance and species richness of herbaceous exotic species (Sax, 2002; Meiners *et al.*, 2002), which suggests that, at least in some cases, the invasive exotic species of disturbed sites may be less shade tolerant, or otherwise less able to withstand competition than are the native herbaceous species. Unfortunately, there are numerous examples of fire-adapted exotic species, generally grasses, that invade fire-sensitive vegetation and create a fire regime that severely impacts the native species (Mack, 1981, 1989; D'Antonio & Vitousek, 1992; Brooks *et al.*, 2004).

Control of exotics through manipulation of disturbance will inevitably reduce the abundance of some native species as well, which will require careful monitoring and adaptive management. In a study of five Italian cities (Grapow & Blasi, 1998), the urban exotic species increased in their absolute and relative contribution to the flora along a gradient of increasing disturbance impact. In other situations, such as the fire-adapted shrublands discussed above, increasing disturbance (fire frequency) would be expected to increase the abundance and proportion of native shrub species in the flora, but could also increase the abundance of exotic herbaceous species (e.g. Sax, 2002). When an extreme disturbance regime, such as cultivation, is terminated, and natural vegetation allowed to regenerate, there will generally be a 'succession' of invasive species that changes with disturbance frequency (and time since last disturbance). This scenario has occurred over much of eastern North America, where it is obvious that most of the invasive species of agriculture and old fields are no longer present in the forests that have regrown from the ploughed fields and pastures. Nonetheless, other exotic species may still be surviving in or newly invading the forests, representing 'later' stages of the succession of exotic species.

Resource and productivity management

Productivity is more difficult to manage than disturbance, because it is the continuous consequence of environmental conditions interacting with changing sizes and types of plants, rather than the result of episodic events. Plant productivity should not be confused with standing biomass, which may vary greatly in either productive or unproductive environments, depending on the length of time since the last mortality-causing disturbance. Productivity influences diversity by different mechanisms across the gradient from low to high potential productivity. In unproductive environments, any increase in plant growth rates can be critical for allowing plants to survive. In productive environments, high growth rates allow rapid accumulation of biomass, and (in the absence of imposed mortality such as grazing or fire) a high maximum level of biomass, which produces dense shade and competitive exclusion of smaller and/or less shade-tolerant plants (Keddy, 1989; Reader & Best, 1989; Berendse, 1994; Keddy *et al.*, 1997).

Management prescriptions for manipulation of productivity to control exotics in unproductive areas would include a reduction in nutrients or water, keeping in mind that this will affect some native species as well. In naturally productive areas, a further increase in productivity, particularly if there has been some degradation in productivity from human activities, may reduce exotics through competition from native species. A similar effect can be achieved even without fertilization, if plant succession and biomass accumulation are allowed to proceed. In this case, prevention of disturbance allows the natural processes of plant growth and competitive interactions to reduce water and nutrients through uptake, and light through shading. The shade intolerant exotic species of open or disturbed areas will be eliminated by succession over time, as will shade intolerant native species. This phenomenon can be observed during old-field succession anywhere in the world. In the eastern United States, exotic species such as Japanese honeysuckle (*Lonicera japonica*) and Japan grass (*Microstegium vimineum*) are greatly reduced in abundance, or completely eliminated by the development of a dense forest canopy (Huston, unpublished data).

Humans increase nutrients through eutrophication of terrestrial, aquatic, and marine systems, with dry deposition of nitrogen being the primary terrestrial impact (Vitousek *et al.*, 1997) and both nitrogen and phosphorus impacting waters. Humans also decrease soil nutrients through harvest and removal of nutrient-containing plant material, and through soil erosion (e.g. LaFon *et al.*, 2000). Areas with depleted nutrients can be at least partially replenished through fertilization, although changes in other soil properties, such as porosity, density, and organic matter content, are also necessary for restoration of productivity.

Short-term reductions in the nutrients available to plants can be achieved through addition of organic matter with low nutrient content, such as sawdust or sugar. This practice is potentially useful for the establishment of native species in eutrophied areas where competition from nutrient-demanding exotics is a problem (Wilson & Gerry, 1995; Kirkham & Kent, 1997) but may be less effective in extreme environments (Cione *et al.*, 2002).

Humans can impact resources indirectly through harvesting plants. Because harvests kill organisms, and thus make the resources that they contain or use available to other organisms, such disturbances generally increase the amount of resources (light, water, nutrients) for the organisms that survive. This may produce a response that differs from that expected from mortality alone. For example, in tall-grass prairies in North America, a high fire frequency (every one to two years) reduces, rather than increases, plant diversity because its primary effect is to increase productivity and the intensity of competition, rather than to kill plants (Briggs & Knapp, 1995). By burning dead plant litter, the fire releases nutrients that would otherwise be unavailable. The resulting increase in productivity leads to increased competition for light, which is the opposite of the effect of fire in some other situations. A similar reduction in diversity can result from increased productivity caused by invasion by nitrogen-fixing species (Vitousek & Walker, 1989; Maron & Connors, 1996).

Plants growing in productive environments (high nutrient and water availability) are likely to become larger and produce more seeds than plants growing in unproductive environments (Lang *et al.*, 1956; Meyer & Root, 1993; Greipsson & Davy, 1997; Loeppky *et al.*, 1999; Cheplick, 2001). Consequently, the actual number individual plants and of exotic species becoming established in a disturbed productive area is likely to be higher than in an equally invasible, unproductive area, where propagule production is much lower. The spatial arrangement of productive and unproductive areas on a landscape can have a strong influence on patterns of propagule availability (Shmida & Wilson, 1985), which can be further influenced by natural and anthropogenic disturbances patterns, and the input of propagules from outside the region (e.g. Brown & Peet, 2003). In contrast, in unproductive environments exotic species often 'fit in' with the natural community without becoming dominant and having a strong effect on the native species (Knops *et al.*, 1995; Kolb, 1999; cited in Alpert *et al.*, 2000; Meiners *et al.*, 2001).

In many cases of high-impact invasions, there is evidence that the 'natural' environmental conditions had been altered prior to the successful invasion. In general, such changes operate to reduce the stresses and low resource levels to which the native species have become adapted, and thus provide a competitive advantage to other species which do not have the restrictive adaptations (e.g. drought tolerance, slow growth, etc.) needed to survive the missing natural stresses. Examples include nitrogen deposition that has increased nutrient availability in European heathlands and in the mountains surrounding the Los Angeles Basin and may facilitate the replacement of native shrublands with either native or exotic grasses (Bakker & Berendse, 1999; Padgett & Allen, 1999; Edgerton-Warburton & Allen, 2000; Cione *et al.*, 2002); drying of the Everglades that reduced flooding stress and allowed *Melaleuca* to invade natural wetlands (Myers, 1983, 1984; Bodle *et al.*, 1994); and the overgrazing of western rangelands that may have facilitated the invasions of exotic species such as *Centaurea maculosa* and leafy spurge (*Euphorbia esula*), which now cover millions of acres (Asher, 1995; Westbrooks, 1998).

Climatic cycles, or directional climatic change, can have a similar effect on drought stresses and productivity. In particular,

prolonged wet periods are likely to facilitate invasions of exotics into arid systems or shallow-soil environments, such as barrens, in humid systems. Conversely, prolonged dry periods are likely to facilitate invasions into humid systems, by reducing the vigour and canopy density of native species and allowing the invasion of more drought-adapted species. However, in dry climates, extreme droughts are likely to reduce the distribution of exotic species (particularly perennials), and the distributions of some natives as well (Weaver & Albertson, 1939; Swetnam & Betancourt, 1998). Any shift to more favourable climatic conditions may favour species that evolved in less stressful environments (e.g. certain exotic species) that do not have the adaptations and associated reductions in competitive ability possessed by the native species, which are adapted to survive the extreme conditions periodically encountered over their evolutionary history.

Plant physiology and life history determine the environmental limitations of particular exotic (or native) species, and thus provide insights into their potential control, as well as their invasiveness (Rejmánek & Richardson, 1996). Shade tolerance is a fundamental plant property that is a consequence of plant adaptations (e.g. leaf structure, root:shoot allocation) and environmental conditions. Because plants lose water by transpiration when they are taking up carbon dioxide during photosynthesis, plants can use light more efficiently if they have abundant water (Smith & Huston, 1989). Shade has been observed to reduce drought tolerance in tree seedlings (Chapman, 1945; Kozłowski, 1949; Withers, 1979; Vance & Zaer, 1991; Veenendaal *et al.*, 1996). In low light conditions, such as forest understorey, this can be critical for survival.

The spatial coverage of shade-tolerant species such as *Microstegium* can be greatly reduced on landscapes where natural forest succession creates deeper shade and restricts them to the wettest portions of the landscape (Cole, 2002). In wetter years, or in wetter climates, the distribution of such moderately shade tolerant-species would be expected to expand over more of the landscape. Any management actions that increase the shade provided by the forest canopy, particularly if accompanied by drier conditions, should greatly reduce the abundance of such species.

In general, intact forests have very few successful invaders. However, few forests are free from disturbances that make them more susceptible to invasion. One suite of species in particular, those from Mediterranean climates that are drought tolerant and also relatively shade tolerant, are increasingly serious invaders of disturbed forests, particularly in urban areas where such species are used in horticulture. These species include English Ivy (*Hedera helix*), Oregon grape (*Mahonia* sp.), and *Vinca* sp. Fortunately, species with these adaptations are relatively slow growing, but unfortunately, they survive most natural stresses (Sack & Grubb, 2002).

The relative proportion of a landscape occupied by different combinations of productivity and disturbance differs from one climatic region to another. In arid regions, areas with high productivity are rare, and are likely to be heavily impacted by both native animals and human activities. In areas with higher precipitation, productive areas are more widespread, and unproductive areas are rare and potentially susceptible to invasion.

One critical consideration for management using either disturbance or productivity manipulation is the *RESPONSE reversal* that occurs between one extreme of a productivity or disturbance gradient and the other extreme. There are two fundamentally different types of response reversals (Huston, 2002), which must be distinguished for effective conservation and management. Single-factor response reversals occur in any situation with a unimodal response along an environmental gradient, such as a resource or temperature gradient. The biological response (e.g. species richness) increases from low to intermediate levels of the resource, and decreases from intermediate to high values, forming a unimodal or 'hump-backed' curve such as that described for species richness by Grime (1973a, 1979) and others. Thus, as has been observed, adding nutrients can increase diversity and invasibility, particularly on nutrient-poor soils (Hedde & Specht, 1975; Hobbs *et al.*, 1988; Huenneke *et al.*, 1990), but adding nutrients can also decrease diversity and invasibility on soils of intermediate to high fertility (Huston, 1980; Tilman, 1987; Huston & DeAngelis, 1994).

The second type of response reversal involves two interacting factors, such as growth rates and disturbance as described earlier (Fig. 1). In this situation, the biological response along an increasing gradient of one of two interacting factors (i.e. either increasing productivity or increasing disturbance frequency or intensity) will reverse along most or all of the gradient, depending on the level of the other factor (e.g. Figure 1a vs. 1c). The most important consequence of this process is that the same change in a factor (e.g. disturbance frequency) can have opposite effects on the same portion of the disturbance gradient, depending on the level of productivity.

CONCLUSIONS

Making *a priori* predictions about what portions of a landscape are most likely to be impacted by invasive plant species provides critical information for monitoring and managing plant invasions, and is likely to be much more accurate than predictions of which exotic species will be present. The predictions of the dynamic equilibrium model about the interactive effect of productivity and disturbance on both species diversity and invasibility differ from the predictions of classical ecological theory, and have been validated in studies over a wide range of environmental conditions.

Many properties of plant invasions can be predicted on the basis of environmental conditions that affect both native and exotic species. The probability of establishment (invasion) and the severity of impact (dominance) vary independently over environmental gradients, and have similar patterns in both native and exotic species. The critical environmental properties for predicting invasibility are productivity, which is influenced by climate and soils, and disturbance regimes, such as the frequency of fire, floods, ice storms, cultivation, grazing, etc. Both of these properties vary over landscapes at scales ranging from local to global, and both can be affected to some degree by human activities.

Low-productivity environments are relatively easily invaded, even in the absence of disturbance, but the cover of exotic invasive

species, and thus their potential negative impact, is generally low. In contrast, undisturbed productive environments are rarely invaded, as are extremely unproductive and stressful environments. Unproductive areas generally have fewer and less intense agricultural disturbances, and lower input of external propagules by humans and animals. Disturbed productive environments are most easily invaded, and the probability that the invaders become dominant and have a significant impact is high.

Understanding landscape variation in the probability and impact of invasion by exotic species should allow development of more efficient monitoring programs for exotic invasions, more effective control through management, and better prioritization of control activities.

ACKNOWLEDGEMENTS

This manuscript has benefited from the comments of Dave Richardson, Julie Rieder, and Tom Stohlgren, as well as from the insights and data of Scott Meiners, Dov Sax, and several anonymous reviewers. Although the research described in this article has been funded wholly or in part by the United States Environmental Protection Agency through grant agreement R-82889701-0 to Interdisciplinary Solutions for Environmental Sustainability, Inc. (ISESI), Oak Ridge, TN, it has not been subjected to the Agency's required peer and policy review and therefore does not necessarily reflect the views of the Agency and no official endorsement should be inferred.

REFERENCES

- Alpert, P., Bone, E. & Holzapfel, C. (2000) Invasiveness, invasibility and the role of environmental stress in the spread of non-native plants. *Perspectives in Plant Ecology, Evolution, and Systematics*, **3**, 52–66.
- Asher, J. (1995) Proliferation of invasive alien plants on Western Federal Lands. *Proceedings of the alien plant invasions symposium*, Society for Range Management, Annual Meeting, Phoenix, Arizona, January 17, 1995. Society for Range Management, Lakewood, CO, USA.
- Baker, H.G. (1965) Characteristics and modes of origin of weeds. *The genetics of colonizing species* (eds H.G. Baker and G.L. Stebbins), pp. 147–169. Academic Press, New York.
- Baker, H.G. (1974) The evolution of weeds. *Annual Review of Ecology and Systematics*, **5**, 1–24.
- Bakker, J.P. (1989) *Nature management by grazing and cutting. Geobotany 14*. Kluwer, Dordrecht, The Netherlands.
- Bakker, J.P. & Berendse, F. (1999) Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology and Evolution*, **14**, 63–68.
- Barro, S.C. & Conard, S.G. (1991) Fire effects on California chaparral systems — an overview. *Environment International*, **17**, 135–149.
- Berendse, F. (1994) Competition between plant populations at low and high nutrient supplies. *Oikos*, **71**, 253–260.
- Binggeli, P. (1996) A taxonomic, biogeographical, and ecological overview of invasive woody plants. *Journal of Vegetation Science*, **7**, 121–124.
- Bodley, M.J., Ferriter, A.P. & Thayer, D.D. (1994) The biology, distribution, and ecological consequences of *Melaleuca quinquenervia* in the Everglades. *Everglades, the ecosystem and its restoration* (eds S.M. Davis and J.C. Ogden), pp. 341–355. St. Lucie Press, Delray Beach, FL.
- Briggs, J.M. & Knapp, A.K. (1995) Interannual variability in primary production in tallgrass prairie — climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany*, **82**, 1024–1030.
- 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*, in press.
- Brown, R.L. & Peet, R.K. (2003) Diversity and invasibility of southern Appalachian plant communities. *Ecology*, **84**, 32–39.
- Burke, M.J.W. & Grime, J.P. (1996) An experimental study of plant community invasibility. *Ecology*, **77**, 796–790.
- Callaway, R.M. & Walker, L.R. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**, 1958–1965.
- Chapman, H.H. (1945) The effect of overhead shade on the survival of loblolly pine seedlings. *Ecology*, **26**, 274–283.
- Cheplick, G.P. (2001) Quantitative genetics of mass allocation and the allometry of reproduction in *Amaranthus albus*: relation to soil nutrients. *International Journal of Plant Sciences*, **162**, 807–816.
- Cione, N.K., Padgett, P.E. & Allen, E.B. (2002) Restoration of a native shrubland impacted by exotic grasses, frequent fire, and nitrogen deposition in southern California. *Restoration Ecology*, **10**, 376–384.
- Cole, P. (2002) Factors controlling the distribution of *Microstegium vimineum* on the Oak Ridge Reservation, Tennessee, Observations and Experiments. PhD Thesis, The University of Tennessee, Knoxville, TN.
- Connell, J.H. (1978) Diversity in tropical rain forests and coral reefs. *Science*, **199**, 1302–1309.
- Crawley, M.J. (1986) The population biology of invaders. *Philosophical Transactions of the Royal Society of London B*, **314**, 711–731.
- Crawley, M.J. (1987) What makes a community invulnerable? Colonization, succession, and stability (eds M.J. Crawley, P.J. Edwards and A.J. Gray), pp. 429–454. Blackwell Scientific, Oxford.
- D'Antonio, C.M. & Levine, J.M. (1999) Elton revisited: a review of evidence linking diversity and invasibility. *Oikos*, **87**, 15–26.
- D'Antonio, C.M. & Vitousek, P.M. (1992) Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics*, **23**, 63–87.
- Daehler, C.C. & Carino, D.A. (2000) Predicting invasive plants, prospects for a general screening system based on current regional models. *Biological Invasions*, **2**, 93–102.
- 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.
- Dodson, S.I., Arnott, S.E. & Cottingham, K.L. (2000) The relationship in lake communities between primary production and species richness. *Ecology*, **81**, 2662–2679.

- Doyle, T.W. (1981) The role of disturbance in the gap dynamics of a montane rain forest: an application of a tropical forest succession model. *Forest succession: concepts and applications* (eds D.C. West, H.H. Shugart and D.B. Botkin), pp. 56–73. Springer-Verlag, New York.
- Edgerton-Warburton, L.M. & Allen, E.B. (2000) Shifts in arbuscular mycorrhizal communities along an anthropogenic nitrogen deposition gradient. *Ecological Applications*, **10**, 484–496.
- Ellstrand, N.C. & Schierenbeck, K.A. (2000) Hybridization as a stimulus for the evolution of invasiveness in plants. *Proceedings of the National Academy of Science*, **97**, 7043–7050.
- Elton, C.S. (1958) *The ecology of invasions by animals and plants*. Methuen, London.
- Feminella, J.W. & Hawkins, C.P. (1995) Interactions between stream herbivores and periphyton, a quantitative analysis of past experiments. *Journal of the North American Benthological Society*, **14**, 465–509.
- Franklin, J. (1995) Predictive vegetation mapping, geographic modelling of biospatial patterns in relation to environmental gradients. *Progress in Physical Geography*, **19**, 474–499.
- Grace, J.B. (1999) The factors controlling species density in herbaceous plant communities, an assessment. *Perspectives in Plant Ecology, Evolution, and Systematics*, **2**, 1–28.
- Grapow, L.C. & Blasi, C. (1998) A comparison of the urban flora of different phytoclimatic regions in Italy. *Global Ecology and Biogeography*, **7**, 367–378.
- Greipsson, S. & Davy, A.J. (1997) Responses of *Leymus arenarius* to nutrients: improvement of seed production and seedling establishment for land reclamation. *Journal of Applied Ecology*, **34**, 1165–1176.
- Grime, J.P. (1973a) Competitive exclusion in herbaceous vegetation. *Nature*, **242**, 344–347.
- Grime, J.P. (1973b) Control of species density in herbaceous vegetation. *Journal of Environmental Management*, **1**, 151–167.
- Grime, J.P. (1979) *Plant strategies and vegetation processes*. Wiley, New York.
- Heddl, E.M. & Specht, R.L. (1975) Dark Island Heath (Ninety-Mile Plain, South Australia). VIII. The effects of fertilization on composition and growth. *Australian Journal of Botany*, **23**, 151–164.
- Higgins, S.I. & Richardson, D.M. (1998) Pine invasions in the southern hemisphere, modelling interactions between organism, environment, and disturbance. *Plant Ecology*, **135**, 79–93.
- 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., Gulmon, S.L., Hobbs, V.J. & Mooney, H.A. (1988) Effects of fertilizer addition and subsequent gopher disturbance on a serpentine annual grassland community. *Oecologia*, **75**, 291–295.
- Hobbs, R.J. & Huenneke, L.F. (1992) Disturbance, diversity, and invasion, implications for conservation. *Conservation Biology*, **6**, 324–337.
- Holling, C.S., ed. (1978) *Adaptive environmental assessment and management*. John Wiley & Sons, London.
- Holmgren, M., Scheffer, M. & Huston, M.A. (1997) The interplay of facilitation and competition in plant communities. *Ecology*, **78**, 1966–1975.
- Huenneke, L.F., Hamburg, S.P., Koide, R., Mooney, H.A. & Vitousek, P.M. (1990) Effects of soil resources on plant invasion and community structure in California serpentine grassland. *Ecology*, **71**, 478–491.
- Huston, M.A. (1979) A general hypothesis of species diversity. *American Naturalist*, **113**, 81–101.
- Huston, M.A. (1980) Soil nutrients and tree species richness in Costa Rican forests. *Journal of Biogeography*, **7**, 147–157.
- Huston, M.A. (1994) *Biology diversity: the coexistence of species on changing landscapes*. Cambridge University Press, Cambridge.
- Huston, M.A. (1999) Local processes and regional patterns, appropriate scales for understanding variation in the diversity of plants and animals. *Oikos*, **86**, 393–401.
- Huston, M.A. (2002) Critical issues for improving predictions. *Predicting species occurrences, issues of scale and accuracy* (eds J.M. Scott, P.J. Heglund, M.L. Morrison, et al.), pp. 7–21. Island Press, Washington, DC.
- Huston, M.A. (2003) Understanding the effect of fire and other mortality-causing disturbances on species diversity. *Fire in southwestern Australian ecosystems, impacts and management* (eds N.C. Burrows, et al.) Department of Conservation and Land Management, Perth, Western Australia, in press.
- Huston, M.A. & DeAngelis, D.L. (1994) Competition and coexistence, the effects of resource transport and supply rates. *American Naturalist*, **144**, 954–977.
- Keddy, P.A. (1989) *Competition*. Chapman & Hall, London.
- Keddy, P., Twolan-Strutt, L. & Shipley, B. (1997) Experimental evidence that interspecific competitive asymmetry increases with soil productivity. *Oikos*, **80**, 253–256.
- Keeley, J.E. & Fotheringham, C.J. (2003) Species-area relationships in Mediterranean-climate communities. *Journal of Biogeography*, **30**, 1629–1657.
- Kennedy, T.A., Naeem, S., Howe, K.M., Knops, J.M.H., Tilman, D. & Reich, P. (2002) Biodiversity as a barrier to ecological invasion. *Nature*, **417**, 636–638.
- Kirkham, F.W. & Kent, M. (1997) Soil seed bank composition in relation to the above-ground vegetation in fertilized and unfertilized hay meadows on a Somerset peat moor. *Journal of Applied Ecology*, **34**, 889–902.
- Knops, J.M.H., Griffin, J.R. & Royalty, A.C. (1995) Introduced and native plants of the Hastings Reservation, central coastal California — a comparison. *Biological Conservation*, **71**, 115–123.
- Kolar, C.S. & Lodge, D.M. (2001) Progress in invasion biology, predicting invaders. *Trends in Ecology and Evolution*, **16**, 199–204.
- Kolb, A. (1999) Patterns of biological invasions in a California coastal grassland — the role of environmental stress. MSc Thesis, University of Massachusetts, Amherst.
- Kozlowski, T.T. (1949) Light and water in relation to growth and competition of Piedmont forest tree species. *Ecological Monographs*, **19**, 207–231.
- LaFon, C.W., Huston, M.A. & Horn, S.P. (2000) Effects of agricultural soil loss on forest succession rates and tree diversity in East Tennessee. *Oikos*, **90**, 431–441.

- Lang, A.L., Pendleton, J.W. & Dungan, G.H. (1956) Influence of population and nitrogen level on yield and protein contents of nine corn hybrids. *Agronomy Journal*, **48**, 284–289.
- Larson, D.L., Anderson, P.J. & Newton, W. (2001) Alien plant invasion in mixed-grass prairie, effects of vegetation type and anthropogenic disturbance. *Ecological Applications*, **11**, 128–141.
- Lavelle, S., Prieur-Richard, A.-H. & Grigulis, K. (1999) Invasibility and diversity of plant communities, from patterns to processes. *Diversity and Distributions*, **5**, 41–49.
- Levine, J.M. (2000) Species diversity and biological invasions, relating local processes to community pattern. *Science*, **288**, 852–854.
- Loeppky, H.A., Horton, P.R., Bittman, S., Townley-Smith, L., Wright, T. & Nuttall, W.F. (1999) Forage seed yield response to N and P fertilizers and soil nutrients in north-eastern Saskatchewan. *Canadian Journal of Soil Science*, **79**, 265–271.
- Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. *Ecology*, **80**, 1522–1536.
- Mack, R.N. (1981) Invasion of *Bromus tectorum* into western North America, an ecological chronicle. *Agro-Ecosystems*, **7**, 145–165.
- Mack, R.N. (1989) Temperate grasslands vulnerable to plant invasions. characteristics and consequences. *Biological invasions: a global perspective*, SCOPE 37 (eds J. A. Drake, et al.), pp. 155–179. Wiley, Chichester.
- Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M. & Bazzaz, F.A. (2000) Biotic invasions, causes, epidemiology, global consequences, and control. *Ecological Applications*, **10**, 689–710.
- Maron, J.L. & Connors, P.G. (1996) A native nitrogen-fixing shrub facilitates weed invasion. *Oecologia*, **105**, 302–312.
- McEvoy, P.B. & Coombes, E.M. (1999) Biological control of plant invaders: regional patterns, field experiments, and structured population models. *Ecological Applications*, **9**, 387–401.
- Meiners, S.J., Pickett, S.T.A. & Cadenasso, M.L. (2001) Effects of plant invasions on the species richness of abandoned agricultural land. *Ecography*, **24**, 633–644.
- 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.
- Meyer, G.A. & Root, R.B. (1993) Effects of herbivorous insects and soil fertility on reproduction of goldenrod. *Ecology*, **74**, 1117–1128.
- Myers, R.L. (1983) Site susceptibility to invasion by the exotic tree *Melaleuca quinquenervia* in southern Florida. *Journal of Applied Ecology*, **20**, 645–658.
- Myers, R.L. (1984) Ecological compression of *Taxodium Distichum* var. *nutans* by *Melaleuca quinquenervia* in southern Florida. *Cypress swamps* (eds K.C. Ewel and H.T. Odum), pp. 358–364. University Presses of Florida, Gainesville, FL.
- Newsome, A.E. & Noble, I.R. (1986) Ecological and physiological attributes of invading species. *Ecology of biological invasions: an Australian perspective* (eds R.H. Groves and J.J. Burdon), pp. 1–20. Australian Academy of Science, Canberra, Australia.
- Padgett, P.E. & Allen, E.B. (1999) Differential responses to nitrogen fertilization in native shrubs and exotic annuals common to Mediterranean coastal sage scrub of California. *Plant Ecology*, **144**, 93–101.
- Paine, R.T. (1966) Food web complexity and species diversity. *American Naturalist*, **100**, 65–75.
- Proulx, M. & Mazumder, A. (1998) Reversal of grazing impact on plant species richness in nutrient poor versus nutrient rich ecosystems. *Ecology*, **79**, 2581–2592.
- Reader, R.J. & Best, B.J. (1989) Variation in competition along an environmental gradient, *Hieracium floribundum* in an abandoned pasture. *Journal of Ecology*, **77**, 673–684.
- Rejmánek, M. & Richardson, D.M. (1996) What attributes make some plant species more invasive? *Ecology*, **77**, 1655–1660.
- Rejmánek, M., Richardson, D.M., Higgins, S.I., Pitcairn, M. & Grotkopp, E. (2004) Plant invasion ecology, State of the art. *Invasive alien species, a new synthesis* (eds H.A. Mooney, R.N. Mack, J.A. McNeely, L. Neville, P.J. Schei and J.K. Waage) Island Press, Washington, DC. in press.
- Richardson, D.M. & Bond, W.J. (1991) Determinants of plant distribution, evidence from pine invasions. *American Naturalist*, **137**, 639–668.
- Roy, J. (1998) In search of the characteristics of plant invaders. *Biological invasions in Europe and the Mediterranean basin* (eds F. di Castri, A.J. Hansen and M. Debussche), pp. 335–352. Kluwer, Dordrecht, The Netherlands.
- Sack, L. & Grubb, P.J. (2002) The combined impacts of deep shade and drought on the growth and biomass allocation of shade-tolerant woody seedlings. *Oecologia*, **131**, 175–185.
- Sax, D.F. (2001) Latitudinal gradients and geographic ranges of exotic species, implications for biogeography. *Journal of Biogeography*, **28**, 139–150.
- Sax, D.F. (2002) Native and naturalized plant diversity are positively correlated in scrub communities of California and Chile. *Diversity and Distributions*, **8**, 193–210.
- Scherber, C., Crawley, M.J. & Porembski, S. (2003) The effects of herbivory and competition on the invasive alien plant *Senecio inaequidens* (Asteraceae). *Diversity and Distributions*, **9**, 415–426.
- Shea, K. & Chesson, P. (2002) Community ecology theory as a framework for biological invasions. *Trends in Ecology and Evolution*, **17**, 170–176.
- Shmida, A. & Wilson, M.F. (1985) Biological determinants of species diversity. *Journal of Biogeography*, **12**, 1–20.
- Siemann, E. & Rogers, W.E. (2001) Genetic differences in growth of an invasive tree species. *Ecology Letters*, **4**, 514–518.
- Smith, T.M. & Huston, M.A. (1989) A theory of the spatial and temporal dynamics of plant communities. *Vegetatio*, **83**, 49–69.
- Sousa, W.P. (1979) Disturbances in marine intertidal boulder fields, the non-equilibrium maintenance of species diversity. *Ecology*, **60**, 1225–1239.
- Steinman, A.D. (1996) Effects of grazers on freshwater benthic algae. *Ecology of freshwater benthic algae* (eds R.J. Stevenson, M.L. Bothwell and R.L. Lowe), pp. 341–374. Academic Press, New York.

- Stohlgren, T.J. (2002) Beyond theories of plant invasions, lessons from natural landscapes. *Comments on Theoretical Biology*, **7**, 1–25.
- Stohlgren, T.J., Binkley, D.A., Chong, G.W., Kalkhan, M.A., Schell, L.D., Bull, K.A., Otsuki, Y., Newman, G., Bashkin, M. & Son, Y. (1999a) Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs*, **69**, 25–46.
- Stohlgren, T.J., Bull, K.A., Otsuki, Y., Villa, C.A. & Lee, M. (1998) Riparian zones as havens for exotic plant species in the central grasslands. *Plant Ecology*, **138**, 113–125.
- Stohlgren, T.J., Chong, G.W., Kalkhan, M.A. & Schell, L.D. (1997) Rapid assessment of plant diversity patterns, a methodology for landscapes. *Environmental Monitoring and Assessment*, **48**, 25–43.
- Stohlgren, T.J., Chong, G.W., Schell, L.D., Rimar, K.A., Otsuki, Y., Lee, M., Kalkhan, M.A. & Villa, C.A. (2002) Assessing vulnerability to invasion by non-native plant species at multiple spatial scales. *Environmental Management*, **29**, 566–577.
- Stohlgren, T.J., Otsuki, Y., Villa, C.A., Lee, M. & Belnap, J. (2001) Patterns of plant invasions, a case example in native species hotspots and rare habitats. *Biological Invasions*, **3**, 37–50.
- Stohlgren, T.J., Schell, L.D. & Vanden Huevel, B. (1999b) How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. *Ecological Applications*, **9**, 45–64.
- Swetnam, T.W. & Betancourt, J.L. (1998) Mesoscale disturbance and ecological response to decadal climatic variability in the American Southwest. *Journal of Climate*, **11**, 3128–3147.
- Tilman, D. (1987) Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. *Ecological Monographs*, **57**, 189–214.
- Tilman, D. (1993) Species richness of experimental productivity gradients, how important is colonization limitation. *Ecology*, **74**, 2179–2191.
- Tilman, D. (1997) Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology*, **78**, 81–92.
- Vance, N.C. & Zaeer, J.B. (1991) The influence of drought stress and low irradiance on plant water relations and structural constituents in needs of *Pinus ponderosa* seedlings. *Tree Physiology*, **8**, 175–184.
- Veenendaal, E.M., Swaine, M.D., Agyeman, V.K., Blay, D., Abebrese, I.K. & Mullins, C.E. (1996) Differences in plant and soil water relations in and around a forest gap in West Africa during the dry season may influence seedling establishment and survival. *Journal of Ecology*, **84**, 83–90.
- Vitousek, P.M. (1990) Biological invasions and ecological process — towards an integration of population biology and ecosystem studies. *Oikos*, **57**, 7–13.
- Vitousek, P.M., Aber, J.D., Horwath, R.W., Likens, G.E., Matson, P.A., Schindler, D.W., Schlesinger, W.H. & Tilman, D. (1997) Human alteration of the global nitrogen cycle, sources and consequences. *Ecological Applications*, **7**, 737–750.
- Vitousek, P.M. & Walker, L.R. (1989) Biological invasion of *Myrica faya* in Hawaii, plant demography, nitrogen fixation, ecosystem effects. *Ecological Monographs*, **59**, 247–265.
- Walters, C.J. (1986) *Adaptive management of renewable resources*. McGraw-Hill, New York.
- Wardle, D. (2001) Experimental evidence that plant diversity reduces invasibility — evidence of a biological mechanism or a consequence of sampling effect. *Oikos*, **95**, 161–170.
- Weaver, J.E. & Albertson, F.W. (1939) Major changes in grassland as a result of continued drought. *Botanical Gazette*, **100**, 576–591.
- Weltzin, J.F., Muth, N.Z., Von Holle, B. & Cole, P.G. (2003) Genetic diversity and invasibility: a test using a model system with a novel experimental design. *Oikos*, **103**, 505–518.
- Westbrooks, R.G. (1998) *Invasive plants, changing the landscape of America, fact book*. Federal Interagency Committee for the Management of Noxious and Exotic Weeds, Washington, DC.
- Williamson, M. (1996) *Biological invasions*. Chapman & Hall, London, UK.
- Wilson, S.D. & Gerry, A.K. (1995) Strategies for mixed-grass prairie restoration, herbicide, tilling, and nitrogen manipulation. *Restoration Ecology*, **3**, 290–298.
- Withers, J.R. (1979) Studies on the status of unburnt *Eucalyptus* woodland at Ocean Grove, Victoria. V. The interactive effects of droughting and shading on seedlings under competition. *Australian Journal of Botany*, **27**, 285–300.
- Worm, B., Lotze, H.K., Hillebrand, H. & Sommer, U. (2002) Consumer versus resource control of species diversity and ecosystem functioning. *Nature*, **417**, 848–851.