Chapter 8

Linking Plant Invasions to Global Environmental Change

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8.1 Introduction

Biotic invasions have been recognized as an important element of global change (Vitousek 1994). Introductions of alien species into novel habitats have increased in tandem with travel and international trade (McNeely 2001). Many species have been introduced accidentally (e.g., in water ballast, in soil, or as crop seed "contaminants"), but some have been intentionally introduced as ornamentals, food, or fiber products.

The introduction of alien species can have many ecological impacts, and contribute to the homogenization of biological systems worldwide (Lockwood and McKinney 2001). Biotic invasions, along with alterations in land-use patterns and disturbance regimes, are among the major causes of biodiversity loss worldwide (Soulé 1991). In cases where alien species have quantitative or qualitative trait differences from native species, invasions can also alter ecosystem processes such as nutrient cycling dynamics and disturbance regimes (Vitousek et al. 1987; D'Antonio and Vitousek 1992; D'Antonio and Corbin 2003; Levine et al. 2003). There are some well known cases of devastating effects of invasive plants on ecosystems such as the invasion of annual grasses in western U.S. (Mack 1981) or the invasion of pines in South-African shrublands (Le Maitre et al. 1996). These dramatic invasions emphasize that invaders often parallel environmental changes that are taking place at the regional scale. Therefore, research on the links between invasions and environmental changes is urgent and timely.

Biotic invasions are capable of interacting with other anthropogenic changes in the environment to alter biodiversity and ecosystem processes in invaded habitats. For example, there is evidence from a variety of ecosystems that N inputs favor alien plant species (Huenneke et al. 1990; Vinton and Burke 1995; Maron and Connors 1996). Furthermore, land-use changes such as clearing for agriculture, road building (Gelbard and Belnap 2003), or alteration of disturbance regimes (Mack and D'Antonio 1998; D'Antonio et al. 1999) have been shown to facilitate plant invasions.

The aim of this chapter is to present evidence of the interactions between several components of global environmental change and plant invasions. We focus on the effects of increasing atmospheric CO_2 concentrations ($[CO_2]$), climate change, terrestrial eutrophication, and changes in land-use/cover on the distribution and performance of plant invasions. We focus on plant invasions because in terrestrial ecosystems plants interact most dramatically with environmental and landscape changes, often reverberating to higher tropic levels. We do not consider the interactions between changes in disturbance regimes "per se", such as wildfires and invasions, because they have been extensively reviewed elsewhere (Mack and D'Antonio 1998; D'Antonio et al. 1999).

8.2 Plant Invasions and Elevated CO_2

Atmospheric CO_2 concentration has increased ca. 35% since pre-industrial times, and is predicted to rise to double the preindustrial concentration by the end of this century. A great deal of research has shown that plant photosynthesis and growth are stimulated by elevated $[CO_2]$. Although invasive and native plant species responded similarly across a wide range of controlled-environment experiments, i.e., the average invasive species does not respond more strongly than the average native, several problematic invasive species are nonetheless strong responders (Dukes 2000). Indeed, recent research has highlighted several cases in which invasive species may be favored by the $[CO_2]$ increase (Moore 2004).

Results from several controlled-environment studies found growth of invasive species to be more strongly stimulated by elevated $[CO_2]$ than growth of native species that were either closely related or sympatric in the same habitat. The average E/A ratio (ratio of growth or final biomass at elevated/ambient $[CO_2]$) for an experimental doubling of $[CO_2]$ was 1.82 in non-native species vs. 1.28 in native species – 2.35 in the non-native vine *Lonicera japonica* vs. 1.40 in native sympatric vines (Sasek and Strain 1991); 1.56 in the non-native *Rhododendron ponticum* vs. 1.12 in native understory plants in a Swiss forest (Hättenschwiler and Körner 2003); and 1.54 in *Bromus tectorum* vs. 1.31 in native Great Basin grasses (Smith et al. 1987).

Most elevated [CO_2] research has examined responses of plants to projected future concentrations, but it is important to note that the present [CO_2] already represents a significant increase over pre-industrial times. Ziska (2003) found an average stimulation of biomass of six invasive species of 46% in response to a doubling of [CO_2]. However, the growth response among these species to the increase in [CO_2] during the 20th century (from ca. 280 to 370 μmol mol^{-1}, a 30% increase) was significantly higher, averaging 110%, and was much higher than in native species. This indicates that many plant invasions that have occurred in the 20th century have probably been stimulated by rising levels of [CO_2]. In addition to increased branching and leaf area, Ziska and colleagues also observed significantly higher pollen production in common ragweed (Ziska and Caulfied 2000) and higher spine production in Canada thistle (Ziska 2002), both in the past century and projected into the next century. This indicates that elevated [CO_2] may increase pollen counts from non-native weeds to the detriment of human health, and that weeds such as Canada thistle may become even more invasive at elevated [CO_2].

In a community context, Dukes (2002) found *Centaurea solstitialis* (yellow starthistle) to increase in biomass and seed production by ca. 70% in response to a doubling of [CO_2] in both monoculture and polyculture, whereas total biomass of the polyculture (made up primarily of native species) increased by less than 30%. This suggests a differential success of *Centaurea* in a community dominated by native species. Although the response of a species in a whole community is less straightforward than the response of individual pot-grown plants, the response of the monocultures and polycultures as a whole were similar in the Dukes (2002) experiment. In a similar vein, *Lonicera japonica* (Japanese honeysuckle, a C_3 vine) increased ANPP 2.9-fold and cover 2.2-fold at the Oak Ridge FACE site, whereas the total understory community did not show increased ANPP and only a 1.3-fold increase in cover (Belote et al. 2003).

At the Nevada Desert Free-air CO_2 Enrichment (FACE) Facility, an annual invasive grass (*Bromus madritensis* ssp. *rubens*; red brome) exhibited higher differential photosynthesis, productivity and seed production than native annuals at elevated CO_2 during an extremely wet (El Niño) year (Smith et al. 2000). *Bromus madritensis* is closely related to *B. tectorum* (cheatgrass), an annual Eurasian grass that has invaded most of the intermountain west of the U.S.A. (Mack 1981). *Bromus tectorum*, whose growth has also been shown to be differentially stimulated over native species at elevated [CO_2] (Smith et al. 1987), is well known to stimulate large grassland fires in this region (Knapp 1998), which in turn has converted large areas of diverse shrublands to annual grasslands (Young and Evans 1978). Similarly, the non-native *B. madritensis* has been shown to stimulate wildfires in the Mojave Desert (Brooks 1999), a region with no evolutionary history of wildfire on a recurring basis. This led Smith et al. (2000) to conclude that elevated [CO_2], through a differential stimulation of growth in *B. madritensis*, could potentially convert large areas of desert scrub to an alien-dominated annual grassland.

Why are invasive species more responsive to elevated [CO_2] than are natives in some of these recent studies? Three trends have been observed. First, there are potential plant architectural differences. Ziska (2003) examined the underpinnings of increased growth, namely the production of leaf area and net assimilation rate (NAR, a growth-related index of photosynthetic CO_2 assimilation) in six non-native species. Interestingly, increases in leaf area were consistently responsible for the stimulation of growth in these non-native species rather than increases in NAR. Similarly, Huxman and Smith (2001) found that elevated CO_2 stimulated growth of a Mojave Desert invasive grass much more than that of a native forb, even though both species had similar increases in photosynthesis. In a study of a non-native and native vines, Sasek and Strain (1991) observed that the differentially increased growth in the non-native vine at elevated [CO_2] was due to accelerated branching (up to 3-fold higher) that in turn resulted in a greater increase in leaf area. The precise mechanism for such a response is not presently known.

Second, there may be differences in plant construction cost between invasive and native plants. Several studies have shown invasive species to have lower construction costs than sympatric natives (Baruch and Goldstein 1999; Nagel and Griffin 2001), and elevated [CO_2] exacerbates this difference. In *Bromus madritensis*, plant construction cost is significantly lower at elevated [CO_2] than at ambient [CO_2], a response that was not observed in a native annual grass, *Vulpia octoflora* (Nagel et al. 2004). Lower construction cost allows *Bromus* seedlings to grow more quickly and assume larger size and greater seed rain than the native *Vulpia*, with *Bromus* exhibiting differentially greater growth than *Vulpia* at elevated [CO_2] (Table 8.1); this should give *Bromus* a strong competitive advantage during the short time window that soil resources are available in this desert ecosystem. Similar to *Bromus*, lower construction cost of the wetland macrophyte *Lythrum salicaria* (purple loosestrife) at elevated [CO_2] resulted in over a 200% increase in carbon fixation per unit of energy invested in leaf biomass, a much higher rate than in sympatric native species (Nagel and Griffin 2004). This dramatic increase in carbon assimilation efficiency occurred in *Lythrum* despite only modest increases in photosynthesis and no change in leaf respiration per unit leaf area.

Third, elevated [CO_2] may bring about changes in reproductive allocation, specifically investment of carbon and nitrogen in seeds. *Bromus madritensis* makes more seeds per unit carbon and nitrogen investment at elevated [CO_2] than in ambient [CO_2] (Huxman et al. 1998, 1999),

Table 8.1. Construction cost, relative growth rate (*RGR*), final plant biomass and total seed number in the native annual grass *Vulpia octoflora* and the invasive grass *Bromus madritensis* growing during a wet year at the Nevada Desert FACE Facility in the Mojave Desert. Elevated $[CO_2] = 550\ \mu mol\ mol^{-1}$. Also included is the ratio of the invasive-to-native species (*I*/*N*) for each parameter at each $[CO_2]$ (data are from Nagel et al. (2004))

Parameter	$[CO_2]$	*Vulpia octoflora*	*Bromus madritensis*	*I*/*N*
Construction cost ($g\ g^{-1}\ d^{-1}$)	Ambient	1.95	1.75	0.9
	Elevated	1.78	1.55	0.87
RGR ($g\ g^{-1}$ biomass d^{-1})	Ambient	0.054	0.068	1.26
	Elevated	0.062	0.108	1.74
Biomass (g)	Ambient	0.08	0.51	6.4
	Elevated	0.11	0.89	8.1
Seed number $plant^{-1}$	Ambient	128	231	1.8
	Elevated	226	533	2.36

thus significantly increasing their differential abundance in community seed rain (Smith et al. 2000).

Our current knowledge concerning the effects of elevated $[CO_2]$ on invasive plant species has mainly focused on plant performance and plant ecophysiology. However, we are still poorly prepared to predict the consequences for communities and ecosystems. This is because most studies that have examined the effects of elevated $[CO_2]$ on plants have been conducted on potted plants grown in glasshouses, a problem that has been alleviated in recent years by the advent of various technologies (e.g., FACE and Open-Top Chambers (OTC's)) that have allowed natural communities of plants to be continuously exposed to elevated $[CO_2]$. Additionally, relatively few studies have examined the CO_2 responses of invasive species grown in competition with the communities that they invade. Responses of individual species do not consistently predict the success of species grown in competition. Future research efforts need to prioritize (1) the mechanistic underpinnings for the differential success of invasive species to elevated $[CO_2]$, and (2) responses of invasive species grown under "realistic" circumstances.

8.3 Plant Invasions and Climatic Change

As fossil fuel burning and tropical forest clearing increasingly change the composition of the atmosphere, the Earth's climate is expected to change in tandem (IPCC 2001). Model predictions suggest that the future climate will be warmer, and that precipitation patterns will change. Although the rate and extent of these changes will depend largely on future human actions, even the mildest of expected changes would likely lead to range shifts among plant and animal species, along with changes in plant and animal phenology (IPCC 2001). Indeed, many species are already responding to changes in temperatures and growing season lengths (Peñuelas et al. 2002; Parmesan and Yohe 2003; Root et al. 2003). Will some invasive plant species be favored by these climate changes? If so, which ones?

Clearly, invasive species whose native ranges are warmer than their introduced ranges would be at an advantage. Two mechanisms would favor these species: first, the species should withstand the increasingly hot extreme temperatures better than natives, and second, they should experience less mortality due to extreme cold events. Examples of the first mechanism can be found among the C_4 species. The higher optimum temperature for photosynthesis found in C_4 species would provide an advantage over C_3 plants in a warmer environment (Ehleringer et al. 1997). Increases in warm extremes could help native C_4 grasses invade C_3 grasslands in New Zealand (White et al. 2000, 2001). Patterson (1995) provided examples of several tropical and warm-temperate agricultural weeds that are likely to become more problematic in the United States as temperatures increase. In an example of the second mechanism, warming may already have benefited cold-sensitive (i.e., frost-sensitive) invasive plants in Swiss forests. There, as the frequency of frost return intervals has declined over the past century, the abundance and diversity of alien evergreen broadleaved species have increased (Walther 2002).

Species interactions may be as sensitive to changes in precipitation patterns as to warming. In regions where precipitation increases, ornamental species that had been restricted to gardens by water limitation could become more problematic. In western North America, a wetter climate could cause several invasive grasses to become denser, with negative consequences for native plant and animal species (Dukes and Mooney 1999). On the other hand, a drier climate in this same general region could increase the prevalence and impacts of shrubby *Tamarix* species that invade riparian zones (Zavaleta and Royval 2002).

Certain properties are likely to confer advantages under any type of climate change. These properties include the ability to tolerate a wide range of climates, the ability to shift ranges rapidly, and the lack of dependence on other organisms for pollination and seed dispersal. Invasive species tend to have all of these favorable properties (Dukes and Mooney 1999).

Several studies of herbaceous plants have shown that the native ranges of invasive species span greater latitudinal distances or geographic ranges than the native ranges of non-invasive species (Rejmánek 2000). While debate continues about the cause for this pattern, a consequence is that many successful invaders tolerate a wide range of climates, and should be relatively insensitive to climate shifts over most of their ranges. Malcolm et al. (2002) presented evidence that the rate at which climatic zones shift under projected warming may, in some locations, exceed maximum rates of plant migration observed in post-glacial time periods, which suggests that the most mobile species will be favored by rapid warming. Indeed, several traits favoring long-distance dispersal are commonly found in invasive species (Rejmánek 1996), suggesting that these species will be among the fastest to migrate to newly suitable habitats. Finally, the ranges of invasive species are rarely limited to the range in which coevolved pollinators or seed dispersers exist. In fact, invasive species seem particularly adept at forming new mutualisms (Richardson et al. 2000a). Therefore, while some native species may be disadvantaged if mutualistic relationships are disrupted by climate change, most invasive species will not.

A handful of case studies have examined how climate change could alter the success of particular invasive species by combining climate model predictions with inferred environmental constraints. Based on two future climate scenarios, Beerling et al. (1995) predicted northward shifts of the European range of *Fallopia japonica*, which is native to Asia. In both scenarios, the new potential distribution moved from central Europe into Scandinavia, and into Iceland. This model was purely based on climate suitability, and did not limit ranges based on soil types or interactions with currently established species. In a climate envelope exercise carried out by Richardson et al. (2000b), potential ranges of five of South Africa's more noxious invasive plants decreased to 63–92% of their starting range under a ~2 °C warming. In this analysis, plant ranges were restricted to suitable soil types. Kritikos et al. (2003a,b) predicted potential ranges of a tropical woody vine, *Cryptostegia grandiflora*, and a woody legume, *Acacia nilotica*, under several future climate scenarios. Although the two invaders had not yet filled their current potential ranges in Australia, the studies suggest both species' ranges would expand under warming, and especially with decreased drought stress.

8.4 Plant Invasions and Land Eutrophication

Though N is the most abundant component of the Earth's atmosphere, it is unavailable for most vegetation unless it is "fixed", or converted from inert atmospheric N_2 into other forms of N, through such processes as lightning or biological fixation. As a result, it is frequently the nutrient most limiting primary productivity in the temperate region (Vitousek and Howarth 1991). Human alteration of the N cycle, however, has increased the rate of N fixation to such an extent that human-derived N now exceeds natural processes (Vitousek et al. 1997). Today, ecosystems in eastern North America, northern Europe, and localized habitats downwind of large sources of N such as urban areas receive orders of magnitude more N in wet and dry deposition than they would receive from natural sources (Aber et al. 1989, 1998; Galloway et al. 1995, 2003; Fenn et al. 1998).

Increasing N inputs have had important consequences for species composition and diversity of plant communities (e.g., Kellner 1993; Wedin and Tilman 1996). A number of European communities have changed dramatically as a result of increased N deposition. For example, the diversity of vascular plants, bryophytes, and lichens has declined in British acid grasslands (Stevens et al. 2004) and Dutch chalk grasslands (Bobbink 1991) as a result of decades of increased N inputs. Species composition has also shifted toward species characteristic of N-rich habitats in forests in France (Thimonier et al. 1992), the Netherlands (van Breemen and van Dijk 1988; DeVries et al. 1995), and Sweden, Norway and Finland (Falkengren-Grerup 1986; Hogbom and Hogberg 1991; Rosen et al. 1992).

Against the general background of changes in species composition and diversity following atmospheric N deposition, increased availability of N may facilitate the establishment and success of alien species (Jefferies and Maron 1997; Fenn et al. 2003b). Enhancement of N availability has been shown to favor establishment and success of fast-growing invasive species in a variety of habitats (e.g., Huenneke et al. 1990; Vinton and Burke 1995; Maron and Connors 1996). Therefore, the potential impact of N deposition would be expected to be greatest in relatively infertile habitats, by permitting the invasion of species characteristic of high-N conditions into formerly low- or moderate-N habitats.

The role of elevated N inputs in facilitating species invasions has been shown most clearly in infertile desert, grassland, and shrubland habitats of western and southwestern North America. Urban centers in the Southwest, including Phoenix and Tucson, AZ, Las Vegas, NV, and Los Angeles, CA have contributed to N deposition rates as high as 29 kg ha^{-1} yr^{-1} (Fenn et al. 2003a). Alien annual grasses, such as *Bromus madritensis* ssp. *rubens* and *Schismus* spp., and an alien forb, *Erodium cicutarium,* have invaded *Larrea tridentata* (Creosote bush) shrublands in the Mojave and Sonoran deserts. Brooks (2003) found that N and NPK fertilization (32 kg N ha^{-1} yr^{-1}) increased dominance of alien species in the Mojave Desert. While alien biomass increased in fertilized plots by 52–56% relative to controls, the density, biomass and diversity of native annual species decreased in fertilized plots. In contrast, fertilization (10 kg N ha^{-1} yr^{-1}) of a Mojave Desert annual plant community before the invasion of the alien grasses and forbs led to an increase in the biomass of native annual species (Romney et al. 1978). Brooks (2003) hypothesized that increased competition with alien species for soil water and other nutrients led to the decline in native species. Thus, native desert annuals are apparently able to take advantage of N inputs when aliens are scarce, but not when aliens are abundant (Brooks 2003).

Alien annual grasses have also invaded coastal sage scrub communities and serpentine grasslands in California. The increasing abundance of grass species such as *Avena* spp., *Bromus* spp., and *Vulpia* spp. in southern California coastal sage scrub ecosystems has coincided with increasing N deposition rates to >45 kg N ha^{-1} yr^{-1} (Allen 2003). In order to tie grass invasion to N inputs, Allen (2003) added N (60 kg N ha^{-1} yr^{-1} for 10 years) to a shrubland receiving low deposition rates. Annual grasses responded positively to N fertilization, though there was no effect on shrub growth or mortality, suggesting that changes in shrub cover requires many years to take place. The invasion of annual grasses such as *Lolium multiflorum*, *Avena* spp., and *Bromus mollis* into serpentine grasslands in the San Francisco Bay Area has also coincided with elevated N deposition (>10–15 kg N ha^{-1} yr^{-1}) (Huenneke et al. 1990; Weiss 1999). Serpentine soils in California have served as refuges for native grass and forb species because their low levels of N, P and K, coupled with high Mg/Ca ratios and high heavy metal content, have historically acted as barriers to alien species invasions (Murphy and Ehrlich 1989). Responses of serpentine vegetation to experimental N fertilization indicate that increasing N inputs are a driving factor in the invasion (Huenneke et al. 1990). Without active management to reduce the competitive effects of fast-growing alien species, native grasses and annual forbs, including rare serpentine endemics, may be lost from these communities with cascading effects to other trophic levels (Weiss 1999).

Elevated atmospheric N deposition may also increase the susceptibility and/or impacts of introduced pathogens or disease in forests (Brown 1995; Bobbink et al. 1998; Throop and Lerdau 2004). In eastern North America, introduced pests and pathogens such as the gypsy moth (*Lymantria dispar*), beech bark disease (*Cryptococcus fagisuga* and *Nectria* spp.) and the hemlock woolly adelgid (*Adelges tsugae*) have had substantial impacts on the community composition and ecosystem functioning of forests (Liebhold et al. 1995; Jenkins et al. 1999). The role that N inputs play in these invasions is not well-established, but there are indications that elevated foliar and bark N concentrations in trees experiencing N deposition have led to increased susceptibility to attack (Latty et al. 2003). Future research should consider the interactions between atmospheric N deposition, pathogen invasion and forest health.

8.5 Plant Invasions and Changes in Land Use/Cover

Man-induced transformation of natural systems is leading to a major biodiversity crisis in recent times (Vane-Wright et al. 1991; Reynolds et al. 2007, Chap. 8 of this volume). In the last century, land transformations have been extensive, rapid, and in most cases irreversible. Changes in land-use/cover (LUC hereafter) can be defined as land transformations from one ecosystem "state" to another in terms of ecosystem structure, composition and function (Hobbs 2000). Because plant invasions occur across landscapes, their dispersal and spread depends on landscape structure and dynamics (With 2002). For this reason, it is surprising that few studies have examined interactions between invasion patterns and changes in LUC.

There is a general presumption among ecologists and managers that changes in LUC directly increase biological invasions. Human population density has been used as a surrogate of LUC transformation, and it has been shown that there is a positive relationship between human population density and regional plant species density (Vilà and Pujadas 2001) or frequency distribution of species (Pysek et al. 1998). Moreover, observational analyses of the current relationship between invasions and LUC types almost always conclude that the most invaded habitats are the ones which directly or indirectly suffer major environmental fluctuations or changes and/or are "less natural" (e.g., urban, agricultural). Although these approaches support the notion that changes in LUC are drivers of invasion, we should emphasize that changes in LUC include a broad range of ecosystem degradation and ecosystem recovery changes (Hobbs 2000; Reynolds et al. 2007, Chap. 20 of this volume). Therefore, land transformation does not necessarily have a sole directional effect on plant invasions. Furthermore, differences in the distribution or abundance of an alien plant within a LUC type are not amenable to the static analysis of contemporary LUC if differences are due to differences in LUC history. For example, in Catalonia (NE Spain), shrublands and woodlands invaded by prickly-pear cacti, *Opuntia* spp., are the ones that were croplands 30 years ago (Vilà et al. 2003).

There are two main reasons why, in general, changes in LUC can influence invasions. First, LUC changes are frequently accompanied by disturbances. Disturbances are unanimously acknowledged to favor plant invasions because they provide "open windows" to the entrance of propagules and better conditions (i.e., more light, space and nutrients per capita) for seedling establishment and growth (Hobbs and Huenneke 1992). Regional surveys and flora screening for alien species often find higher alien species richness in altered ecosystems (e.g., ruderal and anthropogenic ecosystems) than in unaltered ones (e.g., forests, shrublands). For example, edges of highly used roads enhance dispersal and increase light levels and disturbance, which promote establishment of alien herbs (Parendes and Jones 2000).

Second, changes in LUC include modifications in landscape composition and structure, such as fragmentation, which increases the length of edges and the prevalence of corridors that can facilitate invasions. There is clear evidence that fragmentation creates more edge, which facilitates the spread of invasive species to habitat remnants within a man-modified land matrix. For example, in Quebec (Canada), forest fragments surrounded by agricultural fields that have been intensively farmed with the use of commercial fertilizers and herbicides contain a higher percentage of alien weeds than forests surrounded by low intensity farms (Boutin and Jobin 1998). In the same way, transportation corridors increase the spread and the opportunity of establishment of alien plants. In European countries, the density of alien plant species is positively correlated to the length of transport networks (Vilà and Pujadas 2001). The influence of transportation corridors on invasions is positively related to their improvement and frequency of use. For instance, in Utah there is higher cover and richness of alien plant species in semiarid grasslands and woodlands adjacent to paved roads than in graded or 4WD tracks (Gelbard and Belnap 2003). Likewise, in Glacier National Park (Montana-US), grasslands adjacent to primary and secondary roads have higher species richness than along back trails (Tyser and Worley 1992).

To properly test if changes in LUC directly increase invasions, we must relate spatially and temporally explicit knowledge of LUC changes to the presence, abundance and population performance of alien species. We propose the following LUC attributes as land transformation parameters for analysis: direction, intensity, number of stages and number of stage types (Table 8.2). Direction refers to the trajectory of the change, which can be to a more degraded or to a more recovered or restored state than the initial LUC; intensity means the magnitude of the change; number of stages means the number of steps analysed in the whole time series and; finally, the number of stage types refer to the identities of the LUC types that have characterized a given location through time. We expect invasions to be more frequent where the direction of LUC changes leads to greater degradation, where intensity is higher, and where more types of LUC changes have taken place. For example, we might expect higher abundance and diversity of alien species in oldfields than in mature woodland, in areas where the LUC changes have been large in extent or very extreme, and where repeated LUC changes have offered multiple openings for invasion to occur. To our knowledge, there are very few studies aimed to test this hypothesis. A positive relationship between intense habitat degradation over the last 50 years and high diversity of alien plants has been observed in several wetland and dune communities around the Mediterranean Basin (Pino et al. 2006).

Overall, despite the wide interest in biological invasions at a variety of scales, studies exploring invasion patterns and their main landscape correlates from a geographically explicit point of view are scarce. Moreover, interactions among plant invasions and the type, magnitude, trajectory, and direction of landscape changes remain to be explored.

8.6 Multiple Interactions

Most research on the effects of global environmental changes on biological invasions has examined effects of single environmental factors. Although different elements of global change act at different spatial scales, and their impacts are different depending on the biome considered, environmental changes interact in complex ways, complicating predictions of ecosystem responses (Norby et al. 2007, Chap. 3 of this volume). For example, the success of broad-leaved alien trees in Switzerland can be related to both recent climate shifts and elevated atmospheric [CO_2] (Hättenschwiler and Körner 2003).

Ongoing changes on land and in the atmosphere decrease our capacity to predict which introduced species are most likely to become invaders and which ecosystems are most vulnerable to invasion. To overcome this uncertainty, regional-scale studies from a geographically explicit point of view appear to be relevant to identify invasion hot spots and to compare the relative role of climatic, edaphic, landscape and socioeconomic factors on invasion patterns. Preliminary studies in Catalonia, a high diversity ecosystem region of 32 000 km^2 in NE Spain, point out that mean annual temperature influences plant invader diversity, which is also favoured by landscape diversity and regional disturbances (Pino et al. 2005). Ecological niche modeling, a technique in which georeferenced occurrences of alien species are linked to geographically explicit environmental datasets (Peterson

Table 8.2.
Proposed attributes of changes in land-use/cover (LUC) and their influence on plant invasions. S represents stages of LUC changing thought time from more (S_0) to less natural (S_n)

LUC attributes	Increasing invasion scenario		Decreasing invasion scenario	
Direction	Degradation:	$(S_0 \rightarrow S_n)$	Restoration:	$(S_n \rightarrow S_0)$
Intensity	More intense:	$(S_0 \rightarrow S_n)$	Less intense:	$(S_0 \rightarrow S_{n-1})$
Number of stages	3 stages:	$(S_0 \rightarrow S_{n-1} \rightarrow S_n)$	2 stages:	$(S_0 \rightarrow S_n)$
Number of stage types	3 stage types:	$(S_0 \rightarrow S_{n-1} \rightarrow S_n)$	2 stage types:	$(S_0 \rightarrow S_{n-1} \rightarrow S_0)$

et al. 2003), is another recent, reliable approach used to predict the potential distribution of invasions on a species-by-species basis. In essence, the ecological niches are modeled by combining occurrence points and environmental information of species in their native distribution area using a selected set of environmental datasets and diverse algorithms. These models are then projected onto potential receptor areas to identify geographic regions showing ecological conditions inside and outside of the species' niche. A number of recent examples including vertebrates, plants, and insects are available in the literature (Peterson and Vieglais 2001; Peterson et al. 2003; Roura-Pascual et al. 2004). Both approaches offer the hope that realistic predictions of future plant invasion patterns are possible.

Moreover, as changes in land-use cause vegetation changes and alter ecosystem biogeochemistry (Jackson et al. 2007, Chap. 19 of this volume; Reynolds et al. 2007, Chap. 20 of this volume), plant invasions transform vegetation structure, and can directly or indirectly affect ecosystem functioning (Ehrenfeld 2003; Levine et al. 2003), and consequently can exacerbate changes in land-use or environmental changes. Research on the feedbacks of plant invasions on environmental change has been scarce, and has mainly focused on how certain fire prone invasive plant species increase fire risk (D'Antonio et al. 1999), or whether invaders that expand their populations in tandem with land degradation limit restoration efforts back to former community composition (Corbin and D'Antonio 2004). There are many research areas which deserve greater attention. For example, it remains to be explored if plant invaders, responding with fast growth and high fitness to elevated [CO_2] and N deposition, increase soil respiration and N availability. Factorial field experiments comparing the responses of native and alien species to multiple environmental changes could provide answers to these questions.

8.7 Summary and Conclusions

Invasion by alien species is one of the most conspicuous human driven ecological changes, often with undesirable effects on biodiversity and ecosystem functioning. However, few studies have addressed how environmental change (i.e., elevated [CO_2], climate change, N deposition and changes in LUC) can influence the success of plant invaders, invasion impacts and feedbacks. Because global change components are interacting in multiple ways, increasing the uncertainty of species and ecosystem responses (Norby et al. 2007, Chap. 3 of this volume), there is an urgent need to increase research in this area.

While studies of invasive species' responses to elevated [CO_2] have mainly focused on ecophysiology and growth, studies examining responses to changes in climate, N deposition and land-use have examined patterns of plant distribution and abundance in the context of community structure. When comparing invasive with closely related or coexisting native species, the invasives often perform better than the natives or the alien but non-invasives. The mechanisms through which aspects of global change benefit invasive species and harm native species have begun to be explored. A particularly promising direction is to consider whether specific life-history traits, such as those that confer fast growth, broad ecological niches, high seed production or long-distance dispersal, offer hope in the development of predictions of future invasions (Grotkopp et al. 2002). We suggest that the exploration of plant invasions in the context of plant functional types (Lavorel et al. 2007, Chap. 13 of this volume) deserves further consideration. We also propose that exploring the multifactor effects of global change on plant invaders would increase our predictive power on habitat vulnerability to invasion.

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