

Plant invasions in the landscape

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Abstract Biological invasions and changes in land-use are two components of global change affecting biodiversity worldwide. There is overriding evidence that invasions can dramatically change the landscape and that particular land-use types facilitate invasions. Still, these issues have not formally percolated into risk analysis of biological invasions, and only recently has the influence of the surrounding landscape on invasive species spread started to be considered. In this paper we review the literature on the influence of the surrounding landscape on the local level of plant invasions (i.e., abundance and richness of alien plants in plant communities). Our review confirms that there are more alien plant species and they are more abundant at fragment edges than in the interior of fragments. The decline on the level of invasion towards the interior of fragments is

sharp. To a lesser extent, there is higher invasion in small isolated fragments than in large connected patches. However, despite their relevance, the influence of connectivity and shape of the fragments have been scarcely explored. Besides the fact that a site has more invaders if surrounded by a human-dominated landscape than by a natural one, the past history and the configuration of that landscape are also important. Invasion within land-uses is often associated with the historical legacy of changes in land-use, indicating that current land-uses might represent an invasion credit to future invasions. Accurate accounts of the invasion process and effective conservation programs will depend on such considerations.

Keywords Alien · Connectivity · Edge effects · Fragmentation · Global change · Invasion credit · Land-use change · Land-use legacy · Level of invasion

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Introduction

In some regions, biological invasions together with changes in land-use are considered two of the major drivers of biodiversity loss (Wilcove et al. 1998). Alien plant species that become invasive influence not only species richness and composition but also alter trophic interactions and ecosystem services (Levine et al. 2003; Vilà et al. 2010). Similarly, habitat loss and fragmentation are reducing species

diversity and population viability (Fischer and Lindenmayer 2007). Despite the two phenomena being closely associated (Didham et al. 2007), their impacts on biodiversity are usually considered separately (Hoffmeister et al. 2005).

Biological invasions and changes in land-use are two components of global change that can affect each other (Hobbs 2000). Invaders have the potential to dramatically alter land-uses and consequentially affect ecosystems functioning. For example, invasion by pine trees in South-Africa fynbos has transformed many low stature shrublands into woodlands, which has led to increases in ecosystem biomass and water demand, and the consequent decrease in water availability exerting a great strain on the local human population (Le Maitre et al. 1996; Richardson and van Wilgen 2004). In California, the introduction of Eurasian annual grasses during colonial times has increased a positive grass-fire feed-back in shrublands, leading to a transformation of shrublands into grasslands (D'Antonio and Vitousek 1992; Keeley et al. 2005). There is also an overwhelming body of empirical evidence showing that the occurrence and abundance of alien plant species is associated with the intensity of land-use (Chytrý et al. 2008; Pyšek et al. 2010). It is also clear that natural ecosystems embedded within human dominated landscapes are more invaded than large and continuous wilderness areas (Lindenmayer and McCarthy 2001; Guirado et al. 2006; Leyva et al. 2006; McKinney 2006). These last studies highlight the fact that at the local scale not only the land-use type influences invasion but, the characteristics of the surrounding landscape also play a role on the incidence of plant invasions.

Theoretical studies suggest that invasive species spread is tightly connected to factors operating at the landscape level (With 2002, 2004) and the number of empirical studies in this respect is rising (Ibáñez et al. 2009a; Minor et al. 2009). Additionally, ecologists are examining the role of landscape dynamics as a factor influencing invasion, demonstrating that extensive and repeated introductions, together with landscape level disturbances, have played a key role in the spread of some invasive species (Forseth and Innis 2004; DeGasperis and Motzkin 2007).

In this study, we review the empirical evidence that links the landscape context, including its dynamics, to the local level of plant invasion. We particularly emphasize two points that are usually ignored

while documenting the invasive process but that we believe play a key role in explaining invasions: (1) the vulnerability of a site to be invaded depends not only on the land-use type but on the composition and configuration of the surrounding landscape and, (2) the vulnerability of a site to be invaded depends on the historical land-uses that took place at that site. With the notion of landscape composition we refer to the types and relative abundance of land-uses on the landscape (e.g., proportion of agricultural land), whereas with landscape configuration we refer to the spatial arrangement of the land-uses such as edge length (Turner 2005).

The goal of this review is not to explore whether specific land-uses differ in their susceptibility to invasion, nor to study the influence of large-scale geographical variables on regional alien species pools. These two topics have been extensively covered in the invasion ecology literature (Chytrý et al. 2008; Gavier-Pizarro et al. 2010; Pyšek et al. 2010). In contrast, our aim is to point out the effects that the composition and configuration of the landscape, past and present, may exert on the incidence of invasive species at the local scales commonly considered in invasive species management programs. We first compare local versus landscape influences, emphasizing little explored landscape attributes. We then follow with a review of the historical legacies of past land-uses and the non-directional influences of changes in land-use, and conclude by suggesting future areas of invasive species research that would aid in our quest to disentangle the mechanisms behind the invasive process.

Local versus landscape influences

Factors affecting ecosystem vulnerability to invasions could be considered hierarchically, from the regional scale to the micro-site scale (Milbau et al. 2009). At a regional level, 100–1,000 km, climate still remains the major driver of species distributions, including alien species (Ibáñez et al. 2009b). At the local level, 10–1,000 m, it is the ecosystem type that mostly determines what grows at a site. In particular, resource availability tells us where introduced species may succeed (Saunders et al. 1991). But it is at the intermediate landscape level, 10–100 km, at which the invasive process—establishment, population

growth and further spread—takes place (Theoharides and Dukes 2007). Changes in land-cover and land-uses, such as clearings for pasture or agriculture, logging, forest plantations, field abandonment and urbanization, generate the conditions for new colonizations.

The landscape surrounding an area influences the incidence of invasive species in two ways (Fig. 1). First, certain landscapes, especially human-modified ones, will generate the “local” conditions in which many invasive species seem to thrive, such as disturbed habitats, edge habitats, nitrogen-rich soils, and habitats with high light levels (Saunders et al. 1991; Turner 2005). There is a large body of literature focusing on the influence of resource and environmental heterogeneity on alien plant species success (see Davis 2009 for a thorough review). These new habitats will differ from the original ones, and with the exception of early successional species and/or generalists, most native species will not be adapted to them. Such changes will generate a competitive imbalance that may favor the establishment of some introduced species in these ruderal habitats.

At a second level, landscape composition and configuration will have an indirect effect on the

invasion by affecting the availability of propagules, shaping the dispersal of the species, and by promoting the connectivity among populations that can positively feedback into each other (Fig. 1; Bartuszevige et al. 2006; Ohlemüller et al. 2006). Novel ecological conditions and dispersal opportunities arise and many local species may not be adapted to them. Under such circumstances, opportunistic alien species will have a chance to establish due to repeated propagule introductions and growing conditions favored by diminished competition from the local species.

Several studies have simultaneously tested the effect of local and landscape variables on the distribution and abundance of alien plants (see Supplementary material). A general pattern emerges: landscape configuration (e.g., presence of transport corridors, edges) is of primary importance to the presence and establishment of alien species, while local scale factors (e.g., vegetation structure, soil resources) are of key importance for population growth. For example, in New Zealand, the probability of forest patches to be invaded by the bird dispersed *Lonicera maackii* depends on the proximity to nearby towns, the forest edge extension and the area/perimeter relationship (Bartuszevige et al. 2006). However, once a forest has been invaded, *L. maackii*'s local abundance is associated with tree basal area possibly because large trees act as perches for birds (Borgmann and Rodewald 2005). These associations also occur when quantifying alien species richness. Also in New Zealand, the screening of 28 variables along coastal forests has found that stand variables explain little of the variation of alien species richness, while land-cover type and proximity to edges in small patches were the best predictors (Ohlemüller et al. 2006).

Connecting the influence of landscape composition and configuration to the local level of invasion is important for understanding the ecological mechanisms underlying the invasion process at different spatial scales (Milbau et al. 2009). But, it is also relevant because conservation efforts to prevent and control invasions mainly focus on the invader and to a lesser extent on the invaded community (Luken 1996). Our belief is that taking into consideration the landscape level, where the alien species is spreading, should also be part of the management plans developed to control invasive species.

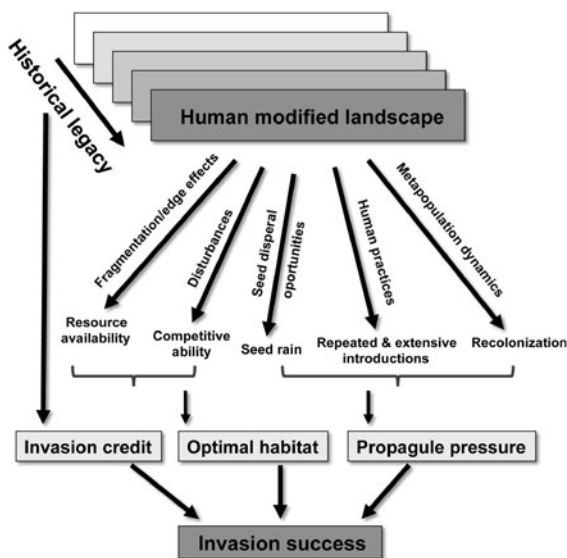


Fig. 1 Conceptual framework summarizing the influence of landscape composition, configuration and dynamics (historical legacy) on the success of plant invasions

The influence of the surrounding landscape

In January 2010 by accessing the ISI Web of Knowledge (www.isiwebofknowledge.com) with no restriction on publication year we retrieved a list of publications using the following search term combinations: (invasion OR alien) AND (land* structure OR fragmentation OR connectivity OR land-use OR land-cover). This resulted in 1,285 publications on genetics, cell biology and/or ecology. These ecology-related publications deal with all type of taxa. By reading the title and abstract, we performed a systematic search for empirical case studies on the influence of the surrounding landscape on the local level of plant invasion. From these selected publications we also screened the reference lists to identify other suitable publications. A total of 51 publications dealing with alien plants met our criteria (Supplementary material). Different metrics have been used as estimations of the level of invasion. In these

papers, richness and diversity of alien species, and occurrence and abundance of particular alien plant species were the most common estimators of plant invasion.

Most publications focus on landscape fragmentation as the driver of plant invasions (Fig. 2). Fragmentation is the process whereby ecosystem loss results in the isolation of small ecosystem patches that were formally continuous and large. Most current landscapes are composed of ecosystem patches of different types, sizes and spatial distributions. Natural or seminatural ecosystem fragments are usually surrounded by a matrix of agricultural or urbanized areas. A large body of literature demonstrates that changes in water, nutrient and energy fluxes from the interior to the edge of the patch can influence species establishment and persistence, especially at the habitats around the edges (Saunders et al. 1991). Landscape fragmentation, in association with human land-uses, generates ecological conditions that are

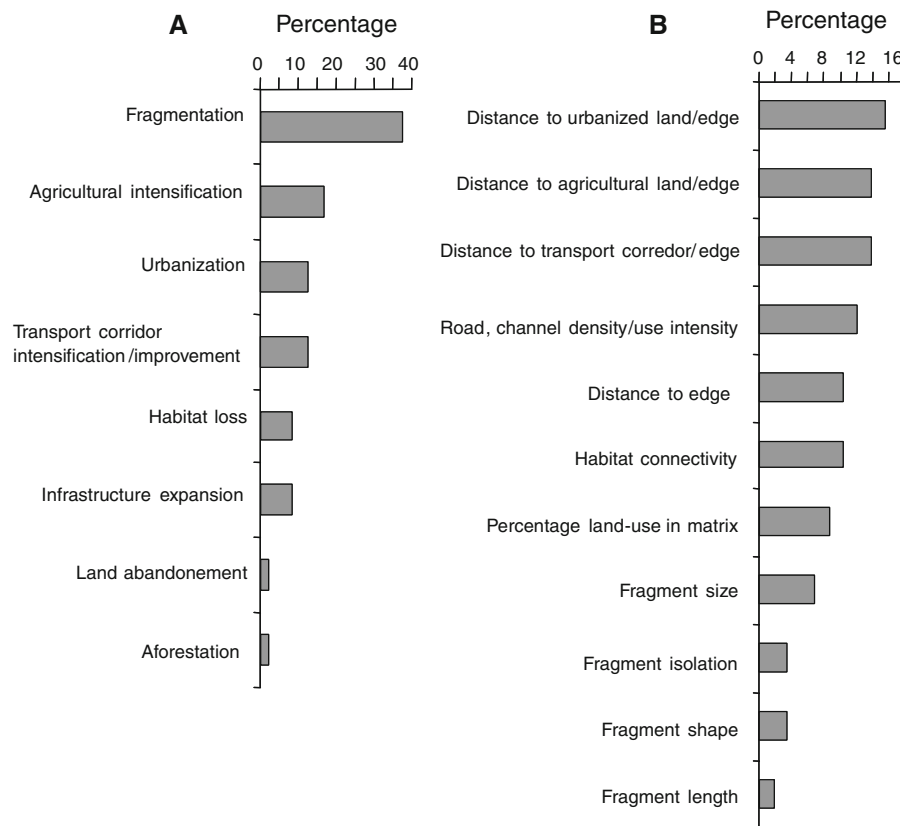


Fig. 2 Potential land-use drivers (a) and most studied landscape attributes (b) influencing the local level of invasion (i.e., occurrence, abundance, richness and diversity) on the

basis of 51 SCI papers published up to January 2010. See Supplementary material for more detailed information

highly susceptible to the incidence of invasive species (Fig. 2a).

Landscape composition matters

In addition to the effects of fragmentation, other land-use drivers, also affect the incidence of invasive species (Fig. 2). Agricultural intensification, urbanization and development of transport networks are among the most explored land-use drivers of invasion (Fig. 2a). Many empirical studies have conducted multivariate analysis to assess the influence of the proportion of different land-uses on the local level of plant invasion in natural or semi-natural areas (Supplementary material). Most studies have found a positive association between the percentage of urban land in the surrounding landscape and the level of invasion at a site (Borgmann and Rodewald 2005; Bartuszevige et al. 2006; Maheu-Giroux and de Blois 2007). Similarly, road density, frequency of road use and road improvement increases diversity of alien species in adjacent ecosystems (Tyser and Worley 1992; Parendes and Jones 2000; Gelbard and Belnap 2003). However, the influence of agricultural and grazing land on the level of plant invasion in adjacent natural areas is controversial (Pauchard and Alaback 2004; Borgmann and Rodewald 2005). This may be due to the fact that, as we describe in the following sections, the spatial variability on the local level of invasion is not only determined by landscape composition but also by landscape configuration.

High invasion at fragment edges and the effects of the surrounding landscape

Many empirical studies have compared the level of invasion along the patches' edge-interior gradient, especially in forests (Fig. 2b, Supplementary material). In general, these studies show a steep decrease of alien plant density, richness and cover with distance to the edge in natural or seminatural ecosystem fragments. In most cases, the decline from the edge to the interior of the fragment is exponential and sharp near the boundary (Watkins et al. 2003; Hansen and Clevenger 2005; Cilliers et al. 2008). Maximum distance of edge influence (i.e., the distance from the edge over which there is a statistically significant effect) ranges from 10 to

225 m, with a mean of 80.53 ± 20.53 m ($n = 17$ studies).

Nevertheless, not all edges are the same. The magnitude and distance of the edge effect depend on the identity and structure of the ecosystems at the boundary (Harper et al. 2005), that is, the surrounding landscape. Mediterranean grassland edges in Australia and in South Africa are more invaded when adjacent to urban areas than to agricultural land—perhaps because herbicides used in crops prevent establishment of alien plants in the surrounding edges—while urban areas act as propagule sources of alien plants (Cilliers et al. 2008). Still, proximity to urban areas does not always increase invasion frequency. In the Eastern USA, riparian forests are less invaded when close to highly developed commercial areas than when close to “greener” residential areas possibly because propagule pressure by ornamental plants is higher in the later (Vidra and Shear 2008).

Analogously, not all ecosystems close to roads are invaded to the same extent. In Canada, the frequency of unintentional introduced alien shrubs such as *Pyrus calleryana*, *Berberis thunbergii* and *Euonymus alata* in fragmented forests close to transport corridors is lower than in fragmented grasslands indicating that it is not only distance but also ecosystem suitability that determines invasion success (Hansen and Clevenger 2005).

Overall, alien species richness increases at the edge of natural ecosystems (Guirado et al. 2006; Ohlemüller et al. 2006; Joshi et al. 2009). The level of invasion depends on the intensity of anthropogenic development; whether it acts as a source of propagules (e.g., urbanized gardening areas, Cilliers et al. 2008; Sullivan et al. 2009) or as a barrier to propagules (e.g., largely impervious developments—Vidra and Shear 2008). The ability to ascertain which mechanisms underlie these differences requires a more profound fine-scale analysis of the heterogeneity within urban land-use categories and its impact on invasive success (Ehrenfeld 2008; Gavier-Pizarro et al. 2010).

Furthermore, the association between patterns of invasion at edges and the mechanisms underlying invasion success has scarcely been explored. Compared to the fair amount of literature on the processes explaining native species colonization of edges and how these change with distance (Ries et al. 2004;

Harper et al. 2005), the biological invasion literature has not explored the association between higher pools of alien plant species at edges and the differences in physical (i.e., microclimatic, soil resources) and biotic (i.e., interspecific interactions) factors between the edge and the interior.

Controversial influence of connectivity

Although natural corridors have been claimed as venues of alien species spread, especially for animals (Koch et al. 2006; Urban et al. 2008), the empirical evidence of ecosystem connectivity on plant invasion is scarce and controversial, with only 6 papers having been retrieved by our literature search (Fig. 2b). Some studies have found cover of alien species to increase when forest patches are connected (Hutchinson and Vankat 1998; Deckers et al. 2008; Thiele et al. 2008). However, other studies have found that corridors do not increase the abundance or the diversity of alien plant species (Bartuszevige et al. 2006; Damschen et al. 2006). Corridors might not increase the level of invasion when they are far from alien seed sources. Damschen et al. (2006) working on experimentally cleared forests found that there were no significant differences in alien species richness between isolated and connected cleared forests patches. In fact, the number of alien species richness was very low even 5 years after clearing. These clearings were surrounding by a matrix of mature forests, with a low alien species pool and forests possibly acting as a barrier of alien seed dispersal. In contrast, in most of the other studies, the connectivity tested is the converse: between natural land-use patches surrounded by a matrix of non-forested disturbed land.

The relationship of invasion success to connectivity depends on the corridor land-use type and the limitations of species dispersal through the landscape matrix. For example, in Argentinean grasslands 25% of the species are alien and their distribution across latitudinal gradients show a high dispersal capability in comparison to native species. Native species restricted distributions seem to be tightly associated with landscape heterogeneity (Perelman et al. 2001). In contrast, alien species may possibly spread more easily than native plant species through fragments due to direct or indirect human assistance, and also because wind seed dispersal is a prevalent dispersal

mechanism in alien species compared to other forms of dispersal (Thuiller et al. 2006; Gassó et al. 2009).

Little explored fragment attributes

Besides fragment edges and connectivity, landscape attributes such as patch size, patch shape and time since isolation have been less explored (Fig. 2b), and it is therefore difficult to draw conclusions. Fragments of small size usually have a higher density of alien species than large fragments (Ohlemüller et al. 2006, but see Cully et al. 2003) or continuous ecosystems (Harrison 1999; Guirado et al. 2006). This pattern is reversed for native species, for which habitat loss is driving populations and species extinctions (Shea and Chesson 2002). Alien abundance can also increase with time, since patch was isolated provided that propagule pressure of aliens is not interrupted (Lindenmayer and McCarthy 2001). This pattern can also be a consequence of the time lag needed for alien populations to build up (Kowarik 1995; Lockwood et al. 2005).

Few studies have explored the role of fragment shape in biodiversity compared to other landscape variables (Fahrig 2003), and this is also reflected in the invasion biology literature (Supplementary material). In many regions of the world, agricultural intensification has fragmented native forests. Alien species richness in these forest remnants increases with closeness to agricultural land especially in small patches but the lobation and area/perimeter of forest patches do not seem to have an effect (Bartuszevige et al. 2006; Damschen et al. 2006; Ohlemüller et al. 2006).

The historical legacy of past land-uses

It is well known that historical factors related to the introduction of alien species play a central role in invasion success (Lonsdale 1999). For example, an analysis of herbarium collections from Michigan and California found that minimum residence time is highly associated with landscape spread, explaining 39–44% of the variation in the number of counties invaded (Ahern et al. 2010). The land-uses at the time of the introduction may also influence invasions (Müllerová et al. 2005). Many alien species took advantage of “windows of opportunity” after

Table 1 Published studies addressing the influence of land-use history on plant invasions

Country/region	Alien species	Past land-use	Present land-use	Effect on invasion	Reference
Argentina/temperate	Many	Agricultural	Forest	↓ richness	Aragón and Morales (2003)
USA/temperate	<i>Alliaria petiolata</i>	Agricultural	Forest	= occurrence, abundance	Burls and McClaugherty (2008)
Puerto Rico/subtropical	<i>Leucaena leucocephala</i>	Agricultural, farmland	Forest	↑ basal area, density	Colón and Lugo (2006)
USA/temperate	<i>Berberis thunbergii</i>	Agricultural	Forest	↑ occurrence, abundance	DeGasperis and Motzkin (2007)
Catalonia/Mediterranean	<i>Cortaderia selloana</i>	Agricultural	Grassland	↑ occurrence	Domènech et al. (2005)
Australia/temperate	Many	Farmland	Forest	↑ richness, cover	Hill et al. (2005)
USA/Mediterranean	Many	Midden	Grassland	↑ cover	Karalius and Alpert (2010)
USA/temperate	Several	Agricultural	Forest roadsides	↓ richness	Kuhman et al. (2010)
Puerto Rico/tropical	Many	Agricultural	Forest	↑ occurrence	Martínez (2010)
USA/temperate	Many	Agricultural	Forest	↑ richness	Parker et al. (2010)
Catalonia/Mediterranean	Many	Agricultural	Marshland	↑ richness, cover	Pino et al. (2006)
Italy/Mediterranean	Several	Terracing	Forest	↓ richness	Pretto et al. (2010)
Australia/Mediterranean	<i>A. barbata</i>	Agricultural	Old-field	↑ persistence	Standish et al. (2008)
Germany/temperate	<i>Heracleum mantegazzianum</i>	Mining, agricultural	Grassland, forest	↑ occurrence, cover	Thiele and Otte (2006)
Catalonia/Mediterranean	<i>Opuntia maxima</i> <i>O. stricta</i>	Agricultural	Shrubland Woodland	↑ occurrence	Vilà et al. (2003)
USA/temperate	Many	Agricultural	Several	↑ richness	Von Holle and Motzkin (2007)

landscape scale disturbances facilitated their spread (DeGasperis and Motzkin 2007; Mosher et al. 2009).

At the landscape scale, there is usually a time lag between events such as disturbances and their ecological consequences (Lindemayer et al. 2008). The same is true for the extinction debt effect, which exists when there is a delayed extinction of native species after habitat loss (Helm et al. 2006). There is also a time lag between introduction of alien species and spread into the wild (Kowarik 1995; Lockwood et al. 2005). The eventual increase in the number of alien species after changes in land-use could be called an invasion credit (Fig. 1), a particular case of immigration credit experienced by a committed increase of species richness after a forcing event (Jackson and Sax 2010).

Some studies have focused on the extent to which landscape dynamics (i.e., changes in land-use through

time) influence biological invasions, especially after agricultural land abandonment (Table 1). Examination of time series changes in land-uses have shown that many invaders appear after crop abandonment. For example, some alien species are more abundant in secondary forests grown after crop abandonment, relative to undisturbed forests, despite their current similar forest structure (Aragón and Morales 2003; Vilà et al. 2003; DeGasperis and Motzkin 2007). In addition, time since abandonment also seems to increase alien plant population size. In Catalonia (NE Spain), the density of Pampas grass, *Cortaderia selloana*, in old-fields, is highly correlated with time since abandonment (Domènech et al. 2005). This phenomenon seems to be due to an increase in propagule pressure from nearby campground and residential areas where this perennial grass had been introduced as ornamental.

Particular human land-uses can also determine invasive events. In Costa Rica's subtropical dry forests, the alien tree *Leucaena leucocephala*, rare in undisturbed forests, achieves larger densities and basal area in previously forested areas cleared for housing compared to areas cleared for farmland and charcoal pits and then abandoned (Colón and Lugo 2006). And, in some cases, even the same history of land-use can have different invasion consequences, depending on the present vegetation type. Time series analysis in marshlands have found that old-fields restored back to reed-beds and dune communities host lower numbers of alien species than non-restored old fields or than old-fields restored back to halophilous shrubs or rush-beds (Pino et al. 2006).

However, despite the evidence pointing out the importance of the history of land-uses for plant invasions, few studies have investigated the ecological mechanisms triggering invasion credit besides those related to an increase in propagule pressure. Particular land-uses may change ecosystem invasibility (i.e., the intrinsic resistance of the ecosystem to invasion), and some will favor the establishment of aliens. That is the case with changes in soil quality, as has been reported for California grasslands where native-American mid-dens have higher N content and as a consequence higher alien plant cover than adjacent areas (Karalius and Alpert 2010). In Australia, the Eurasian grass *Avena barbata* is more persistent in previous agricultural lands with high soil P content than in old-fields that had not been cultivated (Standish et al. 2008).

The temporal sequence of land-use changes

Overall, there is a general presumption that changes in land-use directly increase biological invasions (see above). However, land-use changes may include either ecosystem degradation or restoration, which are usually associated with increases or decreases in invasion, respectively. Nevertheless, land degradation can be so drastic that colonization by alien plants might not occur in disturbed patches if they become isolated from propagule sources (Pretto et al. 2010). At the same time, the presence of alien plant species in some landscapes might be so pervasive and might have altered the composition and function of the local ecosystems to a degree that restoring the community back to a historical stage is not feasible (Didham et al. 2007). Therefore, the outcome of ecosystem

degradation or restoration for biological invasions is not unidirectional.

The consequences of the temporal sequence of land-use changes and their effects on invasions have scarcely been explored. We put forward the following framework to screen the importance of landscape dynamics in plant invasions. We propose that several related features such as direction, intensity and number of stages can modify the introduction, establishment, and spread of alien species at a site. Direction may indicate a trajectory towards more degraded or more restored land-use, intensity refers to the magnitude of the land-use change, and number of stages represents the number of land-use steps analyzed in the whole time series at a given site. Time series information is rarely available, making the exploration of these issues to be limited to a small number of studies (Domènech et al. 2005).

In Fig. 3, we draw a schematic representation of changes in land-use and their potential influence on the level of plant invasions at a site. We expect invasions to be more frequent in landscapes where the direction of land-use changes leads to greater degradation, where the intensity of the changes are high, and where more types of land-use changes have occurred. For example, we might expect higher abundance and diversity of alien species in old-fields than in mature woodland, in areas where land-use changes have been large in extent or very extreme, and where repeated land-use changes have offered multiple openings for invasion to occur.

In summary, current distributions of invasive species reflect the integration over time of both the invasibility of ecosystems and the availability of propagules across the landscape (Fig. 1). Therefore, understanding the dynamics of the invasion process at the time it took place and thereafter is critical for the implementation of any management practice targeting the control of invasive species (Svenning and Skov 2005). However, although these are general principles that frequently apply, we should always be aware that the outcomes may not be replicated from site to site or from one invasive event to another.

Conclusions and the way forward

Ecologists have traditionally matched the scale of resolution of the study to the analysis of the factors

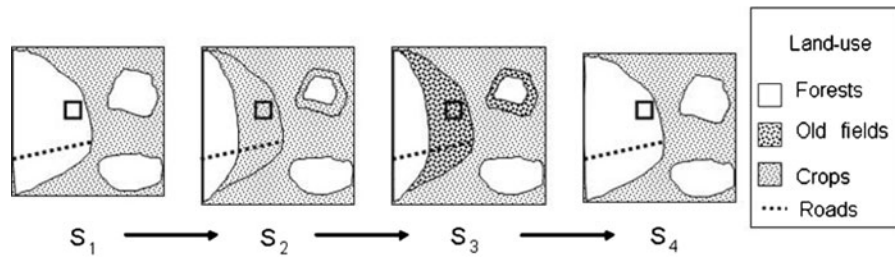


Fig. 3 Schematic representation of the dynamics in changes in land-use and their potential influence on the level of plant invasions at a site. The inserted *black square* indicates the site where the level of invasion is assessed. S_n represents a landscape stage with three different land-uses (forests, old fields and crops) changing through time to four stages (S_1 , S_2 , S_3 and S_4). During this period of time from S_1 to S_4 , the site goes through

acting at that scale. In the case of invasive species, the level of plant invasion at the local scale can be determined not only by the identity of the land-use, but also by the spatial distribution of these land-use types in the surrounding landscape. More importantly, differences in the level of invasion within land-use types is sometimes associated with the historical legacy of changes in land-use, indicating that current changes in the landscape can determine future invasions (i.e., invasion credit).

In this study, we have reviewed how taking the landscape context and its dynamics into account are crucial for understanding spatial patterns of plant invasions at a site. So far, most analyses are observational, have been conducted at one point in time, and have focused on describing the occurrence, abundance and/or diversity of invaders. As such, these studies do not offer information on the mechanisms through which the surrounding landscape influences the invasion process. They also do not indicate whether high levels of invasion depend upon high levels of propagule pressure, upon high ecosystem invasibility, or both (Lonsdale 1999). Besides observational analysis, other empirical approaches such as long term monitoring, including demographic studies, and field experiments are needed to disentangle the mechanisms determining the level of invasion at a site (Hierro et al. 2005).

In landscape ecology, studies are mainly comparative (McGarigal and Cushman 2002), thus, confounding factors might be driving the results. Large-scale manipulative experiments such as comparing pre- and post-treatment conditions are difficult to achieve. However, there are alternative ways of manipulating

four different land-uses (forest, crop, old field and forest again) but the level of invasion in stage S_4 will not be the same as in S_1 because the historical legacy of previous land-use changes would affect the incidence of invasive species. The direction of the changes in land-use from S_1 to S_2 is towards degradation, while from S_3 to S_4 is towards restoration. Invasion would be more pronounced in S_3 and even in S_4 than in S_1

the organisms under study rather than the landscape. For example, seeds and seedlings can be transplanted as phytometers in different landscape settings (e.g., edge types) and plant performance can be studied to investigate whether key plant–animal interactions (e.g., pollination, herbivory) or resource availability (e.g. shading, soil nutrients) differ between landscape settings. But only long-term monitoring of alien species populations would be able to provide information on whether there are differences in demographic constraints among different landscapes.

Moreover, the role of the landscape in biological invasions has not yet been formally incorporated into risk analysis and management of biological invasions. The understanding of the influence of landscape composition, configuration, and dynamics on ecosystem invasibility remains speculative and rests on broad generalizations (e.g., ecological corridors increase invasions, anthropogenic ecosystems are highly invaded). Certainly, anthropogenic landscapes are highly invaded. However, there are differences in the level of invasion even within a particular land-use type, as invasion can be fine-tuned by small-grain landscape differences such as housing variables (e.g., wildland-urban interface areas, density of residential areas (Gavier-Pizarro et al. 2010).

From a conservation point of view, there is an increasing emphasis on the importance of managing the landscape to cope with the loss of biodiversity and to sustain natural resources (Lindemayer et al. 2008). There have been calls to design landscapes that could reduce the pervasive effects of intensive land-use changes such as large-scale plantations (Koh et al. 2009), but there has been little focus on whether

these changes promote invasions. Most efforts related to preventing and controlling invasions are conducted at the local scale, where the influence of the dynamics of land-uses on invasion is seldom explored. This review suggests that successful strategies for reducing alien species abundance and richness should be coupled with landscape management approaches that deter alien plant propagule pressure and reduce ecosystem invasibility.

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