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Research article

Environment and dispersal paths override life strategies and residence time in determining regional patterns of invasion by alien plants

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ABSTRACT

We describe a novel dissimilarity framework to analyze spatial patterns of species diversity and illustrate it with alien plant invasions in Northern Portugal. We used this framework to test the hypothesis that patterns of alien invasive plant species richness and composition are differently affected by differences in climate, land use and landscape connectivity (*i.e.* Geographic distance as a proxy and vectorial objects that facilitate dispersal such as roads and rivers) between pairs of localities at the regional scale. We further evaluated possible effects of plant life strategies (Grime's C-S-R) and residence time. Each locality consisted of a 1 km^2 landscape mosaic in which all alien invasive species were recorded by visiting all habitat types.

Multi-model inference revealed that dissimilarity in species richness is more influenced by environmental distance (particularly climate), whereas geographic distance (proxies for dispersal limitations) is more important to explain dissimilarity in species composition, with a prevailing role for ecotones and roads. However, only minor differences were found in the responses of the three C-S-R strategies. Some effect of residence time was found, but only for dissimilarity in species richness. Our results also indicated that environmental conditions (*e.g.* climate conditions) limit the number of alien species invading a given site, but that the presence of dispersal corridors determines the paths of invasion and therefore the pool of species reaching each site. As geographic distances (*e.g.* ecotones and roads) tend to explain invasion at our regional scale highlights the need to consider the management of alien invasions in the context of integrated landscape planning. Alien species management should include (but not be limited to) the mitigation of dispersal pathways along linear infrastructures. Our results therefore highlight potentially useful applications of the novel multimodel framework to the anticipation and management of plant invasions.

Introduction

Biological invasions constitute a major threat to native biodiversity in many regions of the world, right after habitat loss (Theoharides and Dukes, 2007), and are able to modify key processes within ecosystems and to cause economic damage (Leadley et al., 2010). Ecosystem invasion by alien species represents an important component of global environmental change, causing biotic homogenization and inducing changes in native biodiversity at the habitat and landscape levels (Theoharides and Dukes, 2007; Winter et al., 2010). Invasions often drive ecosystem processes to situations beyond the normal range of ecosystem resilience and are therefore difficult to reverse (Pereira et al., 2010). Much effort has been put into understanding the effects of habitat loss and fragmentation on biodiversity (Leadley et al., 2010), however the impacts of key geographic factors that shape biological invasions (and their effects on native biodiversity and the provision of valuable ecosystem services) are still poorly investigated (Le Maitre et al., 2004).

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Introduction pathways of alien species to new areas are linked to human activities at local, regional and continental scales (Thuiller et al., 2006). This is consistent with theories that relate urbanization and other human activities to higher levels of alien propagule pressure (Wilson et al., 2007). Understanding the mechanisms explaining how invasive species are spatially and ecologically distributed has become a central research issue in ecology and evolutionary biology, due to its close relation to the success of invasion (Alpert et al., 2000). Several studies have addressed the importance of environmental (Marco et al., 2011) or geographic distances (Minor et al., 2009) in species composition dissimilarities (Ferrier et al., 2007; Winter et al., 2010; Keil et al., 2012), but few comparing the relative effects of the two types of distances on patterns of (dis)similarity in alien species richness and composition (*e.g.* Lososová et al., 2011).

When evaluating the importance of distances to explain patterns of alien invaders (mainly in the case of neophytes, which may be far from occupying their full potential range in the invaded area), geographic distance between locations may play a more important role than environmental distance, unlike what could be expected for native biodiversity for some scales (Li et al., 2011). Indeed, time since introduction and species traits related to dispersal (*e.g.* seed or fruit size, seed or fruit resistance and longevity, dispersal mechanisms) can jointly constrain the ability of invaders to colonize their potential climatic range in the newly invaded area (Alpert et al., 2000). Moreover, it has been demonstrated that habitat connectivity and the presence of man-made connecting infrastructures (*e.g.* roads) or other corridors (*e.g.* river banks) offer preferential routes for the spread of alien species across the landscape or region (Proches et al., 2005; Christen and Matlack, 2006; Minor et al., 2009).

The anticipation of biological invasions can focus either on traits that favour species invasiveness or on features of the recipient environment that influence community or landscape invasibility (Vicente et al., 2010). One approach to assess the relative role of environment (related to invasibility), and dispersal (related to invasiveness) in controlling biological invasions is to fit distribution models relating alien species diversity to environmental predictors, and to account for potential dispersal vectors (*e.g.* Thuiller et al., 2006). Over the last two decades, the use of such empirical statistical models have increased in ecology to predict the geographic distribution of species and diversity measures, but they can also be used for testing hypotheses on the role of different environmental predictors (explanatory modelling sensu Shmueli, 2010; Broennimann and Guisan, 2008).

Invasibility and invasiveness, two key components of invasion, are thought to be primarily determined by habitat suitability and by propagule pressure and dispersal, respectively (Brooks, 2007). Consequently, invasiveness is expected to be mediated by life strategies (*e.g.* by intrinsic life-history or species traits; Pysek and Richardson, 2007), whereas invasibility is more related to local conditions at the site, habitat or landscape levels (Vicente et al., 2010). For vascular plants, a multitude of functional classifications have been proposed over recent decades, based on life strategies, growth forms and reproductive strategies, allowing many different groups to be tested in invasion biology (Grime, 2002). In the context of plant invasion, the integrative power of the "C-S-R functional signature" (*i.e.* the relative abundance of Competitors (C), Stress-tolerants (S) and Ruderals (R) in a given species pool; Grime, 1977) can be used to recognize community processes such as resistance, resilience, eutrophication and dereliction (Grime, 2002; Hunt et al., 2004).

Environmental conditions and dispersal limitations are known to shape the patterns of native biodiversity at the regional scale, with environmental heterogeneity influencing species richness and dispersal mainly constraining species composition (Ferrier et al., 2007; Theoharides and Dukes, 2007). This general pattern is a result of a long history of interactions among species and between these and their environment. However, the same could eventually not be true for the patterns of alien invasive species in a given region since: (i) alien species differ in the actual traits driving their invasiveness in the new territory, (ii) their residence time is quite heterogeneous and often very short (*i.e.* few years or decades), (iii) their whole residence time has coincided with human-driven environmental heterogeneity and changes, (iv) multiple introductions (in space and time) may produce complex patterns of expansion and distribution, and (v) multiple interaction with native species may further induce complex patterns of invasion (*e.g.* Van Kleunen et al., 2010).

Here we propose to evaluate the relative contribution of environmental and geographic distances in explaining spatial patterns of dissimilarities of alien plant species richness and composition, using Northwest Portugal, a heavily invaded region (see Vicente et al., 2010), as a test area. For this, we used an information-theoretic approach to test whether geographic distance between sites (as a proxy for dispersal constraints) is more important than environmental dissimilarity between those same sites in explaining patterns of (i) alien invasive species richness, and (ii) alien invasive species composition, both at the landscape level. We analyzed patterns for a total set of 86 species, and separately for two subsets of species based on the time since introduction *i.e.* species with long residence time (here defined as neophytes introduced between years 1500 and 1900) and species with short residence time (neophytes introduced after year 1900; Almeida and Freitas, 2006). We also analyzed patterns for the same set of 86 alien species classified according to Grime's (1977) C-S-R primary strategies, testing (iii) whether the relative importance of geographic distances and environmental dissimilarities on species richness and composition would differ among invasive plant strategies.

Methods

Analytical framework

Modelling the patterns of dissimilarity in species diversity among locations has been proposed in recent years as a complementary approach to direct correlation analysis (Ferrier et al., 2007). This approach has proven notably useful as the only robust way to take into account the effect of geographic distances in the study and modelling of dissimilarity patterns. In this study a dissimilarity approach (rather than direct correlation) was used, supported by multi-model inference, in order to assess patterns and drivers of both species richness and species composition dissimilarity under a common analytical framework. This allowed a direct comparison of results for the two components of alien species diversity and an assessment of their responses to a common set of environmental and geographic factors. Moreover, a multi-model inference approach allows a better assessment of the relative contribution of invaded landscapes (*i.e.* invasibility) and of the species' intrinsic properties (*i.e.* invasiveness).

Data analyses were organized according to the three major research questions. The first two addressed dissimilarities of alien species richness and composition for total, long residence time and short residence time species, and the third question addressed responses of species richness and composition for distinct alien plant strategies. For each of these three questions, we tested three groups of hypotheses using combinations of competing models (Table 1). These three groups of hypotheses ("General hypotheses" in Table 1) are related to: (i) the influence of geographic distances