Habitat selection by invasive alien plants: a bootstrap approach

Výběr stanovišť invazními rostlinami: přístup na základě statistického bootstrapingu

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Even though there is no doubt that an invasion of a landscape by plants is a function of the abundance and spatial arrangement of different types of habitat, to the best of our knowledge, there has been no analysis of the relation between the patterns of plant invasion and the availability of specific habitats within landscapes invaded. The application of habitat selection functions (HSFs) provides a quantitative measure for determining if specific habitats are more likely to be invaded by a given species. The remarkable dynamics of spread of invasive alien plants makes them an ideal species pool for applying HSFs. This paper discusses the possible application of a bootstrap test of significance for identifying habitat types where the incidence of alien species is higher (preferred) or lower (avoided) than would be expected from a random null model for which all habitat types are invaded in proportion to their availability. In order to demonstrate the usefulness of the proposed approach we explored the habitat selection of a coastal alien plant, *Carpobrotus* aff. *acinaciformis,* in the Tyrrhenian coastal dunes of central Italy. According to this bootstrap test of significance, some important habitats of European conservation interest were more readily invaded by *Carpobrotus* than expected. From an applied research perspective, the use of an HSF approach can help identify the most invasion-prone habitats and, therefore, may facilitate the development of a clear and targeted prevention policy to control the introduction and spread of alien species in a landscape, for example, coastal dune habitats.

K e y w o r d s: *Carpobrotus* aff. *acinaciformis*, central Italy, coastal dune, habitat selection function, resampling methods

Introduction

Although invasion by alien plants is a major threat to the integrity of natural habitats and causes an annual economic loss of billions of euros (Hulme et al. 2009), distinct habitats vary considerably in their vulnerability to invasion. Therefore, any action aimed at reducing the effect of such invasions requires reliable information on the extent to which different habitats are susceptible to invasion (Chytrý et al. 2008a, Essl et al. 2009). The application of habitat selection functions (HSFs) provides a quantitative measure that indicates whether specific habitats are positively or negatively selected by a given species, i.e. occupied more or less than expected based on the level of habitat availability (Manly et al. 2002). While the analysis of habitat selection is widely used in wildlife science, the remarkable dynamics of spread that allows invasive alien plants to colonize large areas in regions where they are introduced (Pyšek et al. 2004) make them an ideal species pool for applying this kind of function.

Following the HSF approach, alien species can be considered to be "settlers", which preferentially select particular habitats in a new landscape they invade. If the habitats are all equally prone to invasion then alien species would occur randomly in the landscape with the proportion of habitats invaded equal to their availability. On the contrary, not all habitats are equally likely to be invaded; that is, they act as a selective resource for invasive species. Accordingly, measures aimed at preventing the spread of alien species should concentrate on such invasion-prone habitats.

In this paper, we propose to apply a bootstrap test of significance in order to identify habitat types where the incidence of alien species is higher (preferred) or lower (avoided) than would be expected from a random null model in which all the habitats are invaded in proportion to their availability. In order to demonstrate the usefulness of HSFs in this context, habitat invasion by the alien plant *Carpobrotus* aff. *acinaciformis* in the Tyrrhenian coastal dunes of central Italy was explored.

Materials and methods

Study site

Invasion by the alien *Carpobrotus* (*Carpobrotus edulis/acinaciformis*, *Aizoaceae*) is considered a serious threat to numerous terrestrial plant communities in coastal habitats (D'Antonio 1993, Vilà et al. 2006). *Carpobrotus* species are widely distributed outside their native range (Vilà et al. 2006) and establish almost monospecific patches of cover in invaded habitats, obstructing the occurrence of the natural spontaneous vegetation (Traveset et al. 2008). For this reason, *Carpobrotus* is included in the list of the most invasive alien plants of the world (Weber 2003) and among the worst invasive alien species threatening biodiversity in Europe (Council of Europe 2005, Sheppard et al. 2005).

A test area including 10 km of Tyrrhenian coast located approximately 30 km north of Rome (central Italy) was selected for this study (Fig. 1). Climate there is typically Mediterranean with hot and dry summers and cool wet winters; most of the study area is made up of sandy beaches with an extensive ridge of Holocenic dunes. According to a complex sea-to-inland environmental gradient the study site hosts many structurally and floristically different types of vegetation invaded by *Carpobrotus* (Acosta et al. 2008, Carboni et al. 2010).

Although Pignatti (1982) identified two different species of *Carpobrotus, C. acinaciformis* and *C. edulis*, on the Tyrrhenian coast of central Italy, we studied only the most abundant, *C.* aff. *acinaciformis* (termed *Carpobrotus* throughout this manuscript).

Data

Based on high-resolution panchromatic aerial photographs (dated 2002) and an extensive field survey (spring-summer 2007), we produced a detailed map at a scale of 1 : 5000 of the coastal dune habitats in the study area. For details see Carranza et al. (2010). The map legend is composed of six types of habitat and contains most of the sand dunes and sandy

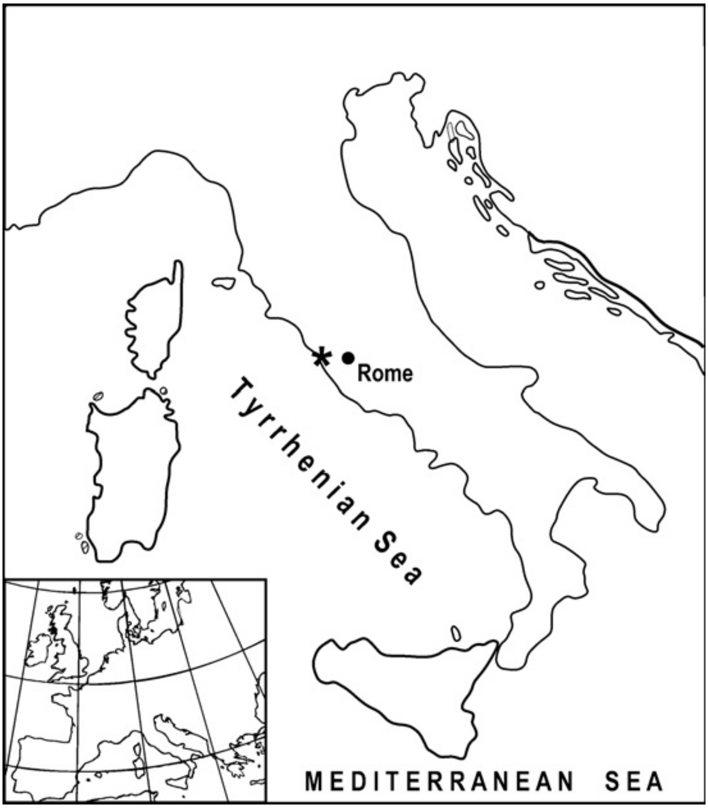

Fig. 1. – Location of the coastal area selected for studying habitat invasion by *Carpobrotus*.

beach habitats of European conservation interest according to the Annex I of the European Council Directive 92/43/EEC (1992, see Carranza et al. 2008) (Table 1). We also produced a vector database of *Carpobrotus* distribution that includes all *Carpobrotus* patches larger than 100 m^2. These *Carpobrotus* patches were detected in high resolution panchromatic digital aerial photographs (dated 2002), while the polygon perimeters were mapped in the field with GPS. The size of invaded polygons ranges from 100 to 6504 m^2 while the total area invaded by *Carpobrotus* is 26,752 m^2.

Testing the habitat selectivity of Carpobrotus

To calculate the area of each type of habitat invaded by *Carpobrotus* we overlaid the *Carpobrotus* polygons on the habitat map and obtained a 6-dimensional compositional vector of invaded habitats for each *Carpobrotus* polygon. Then, we summed the compositional vectors of all invaded polygons to obtain a vector of invaded habitats for the whole landscape. Finally, we tested the habitat selectivity of *Carpobrotus* using a bootstrap procedure (Efron 1979).

Bootstrapping methods are applicable in situations where the usual statistical methods are inappropriate for hypothesis testing. In the absence of any other piece of information about a population, the method consists in resampling the original sample with replacement with the objective of achieving approximately what would happen if the population was resampled (Manly 2007). In order to establish whether habitats were invaded differentially a bootstrap test was carried out to establish whether the proportional area of a given habitat *i* that has been invaded by *Carpobrotus* p_{iC} is significantly different from the proportional area of that habitat in the entire landscape p_{iL}, where the value of p_{iC} is obtained from the compositional vector of invaded habitats for the whole landscape.

For an appropriate test statistic *S*, the test involves comparing the value of *S* for the observed data to the bootstrap distribution of *S*. If the actual value of *S* is sufficiently extreme in comparison to the bootstrap distribution, the null hypothesis of random habitat colonization by *Carpobrotus* is rejected. Given the test statistic:

$$S = \left| p_{iC} - p_{iL} \right| \tag{1}$$

The actual value of S can then be compared with the bootstrap distribution of $S_B = \left| p_{iB} - p_{iL} \right|$, where p_{iB} is the bootstrapped proportional extent of a given habitat invaded by *Carpobrotus* that is obtained by resampling with replacement the 6-dimensional compositional vectors of single *Carpobrotus* polygons. In Eq. (1), absolute values are used because invasion selectivity can be either positive or negative (i.e. a given habitat type can be invaded more or less than expected from a random null model). Therefore, a two-sided test is needed.

Nonetheless, for large values of $\left| p_{iC} - p_{iL} \right|$, all bootstrapped values of S_B also tend to be large, so that their distribution will reflect the distribution of the statistic when the null hypothesis is rejected. Therefore, the test was adjusted to reflect the distribution of the statistic when the null hypothesis is accepted. As proposed by Manly (2007), a simple approach is to compare the actual values of $\left| p_{iC} - p_{iL} \right|$ with the bootstrapped values

$$S'_B = \left| p_{iB} - p_{iC} \right| \tag{2}$$

This is equivalent to using the distribution of absolute differences between the bootstrapped invaded areas and the actual invaded areas in order to mimic the distribution of the differences between the original sample statistics and the population statistics (see Manly 2007).

We tested the significance of the invasion selectivity of the mapped habitats using 999 bootstrap samples generated by resampling the compositional vectors of single *Carpobrotus* polygons. P-values were computed as the proportion of bootstrapped values S'_B that were as extreme as or more extreme than the actual values of *S*. After identifying a habitat for which the null hypothesis is rejected, we used the ratio p_{iC} / p_{iL} to identify whether that habitat is selected positively or negatively by *Carpobrotus*. Values of $p_{iC} / p_{iL} > 1$ signify that the habitat is invaded more than would be expected by chance alone, whereas if $p_{iC} / p_{iL} < 1$, the habitat is negatively selected by *Carpobrotus*.

Results

According to the bootstrap test of significance most habitats are invaded differently by *Carpobrotus* (Table 1). Two habitats, the shifting dunes with *Ammophila arenaria* and the fixed beach dunes with *Crucianella maritima* are positively selected by *Carpobrotus* ($P < 0.05$). By contrast, the embryonic shifting dunes are invaded in proportion to their availability, while the *Cakile maritima* vegetation, the inter-dune annual grasslands with *Vulpia fasciculata* and the continuous grasslands are negatively selected by *Carpobrotus*. The negative selection ratios obtained for these three habitats suggest that they are only marginally threatened by *Carpobrotus* invasion. In contrast, the marked preference of *Carpobrotus* for two coastal dune habitats of European interest underlines the need to produce a targeted prevention policy to control the introduction and spread of *Carpobrotus* in these specific environments.

Table 1. – Habitats within the study area on the Tyrrhenian coast of central Italy and their degree of invasion by *Carpobrotus*. p_{iC} = proportional area of habitat i invaded by *Carpobrotus*; p_{iL} = proportional area of habitat i in the study area; p_{iB} = bootstrapped proportional area of habitat i invaded by *Carpobrotus* (i.e. the bootstrapped analogue of p_{iC}). The codes of habitats of European conservation interest according to the Annex I of the European Council Directive 92/43/EEC (1992) are given in brackets following the habitat names. Bold characters denote the habitats that are positively selected by *Carpobrotus*, NS = not significant at P = 0.05. Values of p_{iC}/p_{iL} > 1 show that the habitat is positively selected by *Carpobrotus*; values of p_{iC}/p_{iL}< 1 show that the habitat is negatively selected by *Carpobrotus*.

Habitat	Habitat surface			Invaded surface			Observed values	Mean bootstrap values	Selection ratio
	Number of polygons	Total area [m^2]	p_{iL}	Number of polygons	Total area [m^2]	p_{iC}	$\lvert p_{iC} - p_{iL}\rvert$	$\lvert p_{iB} - p_{iC}\rvert$	p_{iC} / p_{iL}
Annual vegetation on drift lines with *Cakile maritima* (EC 1210)	13	443,532	0.305	4	1258	0.047	0.258	0.026	0.154
Embryonic shifting dunes with *Elymus farctus* (EC 2110)	59	55,941	0.038	5	1776	0.066	0.027^{NS}	0.030	1.737
Shifting dunes along the shoreline with *Ammophila arenaria* (EC 2120)	62	156,906	0.108	33	18,935	0.708	**0.600**	0.062	6.556
Camephitic vegetation of fixed beach dunes with *Crucianella maritima* (EC 2210)	9	2912	0.002	5	820	0.031	**0.029**	0.012	15.500
Interdune annual grasslands with *Vulpia fasciculata* (EC 2230)	97	257,983	0.177	4	549	0.021	0.156	0.009	0.119
Continuous grasslands	78	537,607	0.370	11	3414	0.127	0.243	0.063	0.343

Discussion and further perspectives

The ability of alien invasive species to spread and become locally dominant represents a threat to the integrity of the invaded habitats (Richardson et al. 2000, Kolar & Lodge 2001, Chytrý et al. 2009a, b, Moravcová et al. 2010). Even though there is no doubt that the spread of an invasive species across a landscape is a function of the abundance and spatial arrangement of different habitats (Higgins et al. 1999, Pauchard & Alaback 2004), the relationship between the patterns of plant invasion and the availability of specific habitats within the invaded landscape is poorly understood.

Although studies on resource selection are commonly used to determine the relationship between habitat and wildlife populations (for a review see Alldredge & Griswold 2006, Thomas & Taylor 2006), their application to plants has received far less attention. In the current study some habitats were more invasion-prone than others and these habitats could be considered as selective resources for specific invaders. In this view, a detailed description of how alien species "use" the landscape (i.e. which habitats are more or less likely to be invaded) will improve our understanding of their role in coastal dune processes.

From an applied perspective, the use of HSFs to analyze the selectivity of alien species for specific habitats constitutes essential knowledge when dealing with land management and invasion-prevention issues (Collingham et al. 2000, Marvier et al. 2004), as it could reduce the economic costs associated with the natural, mechanical and chemical control of high-impact invaders (Sheppard et al. 2005, Scalera 2010). In this framework, this analysis complements that of habitat invasibility proposed by Chytrý et al. (2008a, b, 2009a, b); while their approach is aimed at identifying strongly invaded habitats in general, irrespective of the specific invaders, the method proposed here identifies habitats specifically threatened by particular invasive plant species. Further, this method approaches the issue from a landscape perspective by relying on synthetic maps of habitat distributions rather than on detailed vegetation relevés for identifying habitat types.

Also, while habitat selection by animals is usually assessed by radio-tracking or visual observation at a set of specific points in time, in this study the potentially available habitat and the habitat actually invaded by *Carpobrotus* are both represented by polygons in GIS, which is the operational tool used by most plant and landscape ecologists. Since many alien species can be detected and mapped through remotely-sensed imagery (e.g. Everitt et al. 1995, Müllerová et al. 2005, Bradley & Mustard 2006) or field GPS surveys (Kollmann et al. 2009), while maps of ecosystems of conservation interest are available at different scales around the world (e.g. Convention on Biological Diversity 1992, European Council Directive 92/43/EEC 1992), our approach can be used to analyze invasion patterns of numerous alien plants taking into consideration the most important habitats for biodiversity conservation in different contexts and regions. From a statistical viewpoint, bootstrap is a well-established technique for assessing the accuracy of models of habitat selection (Manly et al. 2002) that is easy to perform on any spatial scale and with any meaningful habitat classification scheme, providing valuable information for the development of strategies for invasion prevention and control.

Finally, as a cautionary remark, it is worth noting that, while there may be some degree of spatial autocorrelation in the alien species distribution among invaded habitats, the proposed method does not explicitly incorporate this aspect in the statistical analysis, possibly resulting in inflated type I error rates (i.e. the rate of false positives; Thomas & Taylor 2006). However, as our major aim was to determine the likelihood of particular habitats being invaded, the overestimation of invasion susceptibility obtained by excluding spatial aspects from the analysis is a less serious error than type II errors. For instance, a type II error means that the model has a limited capacity of detecting a significant invasion of particular habitats by specific aliens, which is the more important error. Therefore, due to the conceptual simplicity of our proposal, we hope it will be widely used for assessing the risk of invasion by alien plants.

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Souhrn

Invaze rostlin v krajinném měřítku závisí na početnosti a prostorovém uspořádání stanovišť, vztah mezi invazemi a nabídkou stanovišt v krajině však dosud nebyl důkladně analyzován. Funkce výběru stanovišť (habitat selection function, HSF) umožňují kvantitativně vyjádřit pravděpodobnost, že určité stanoviště bude invadováno; invazní druhy jsou vzhledem k dynamickému šíření ideální skupinou druhů pro využití HSF. V práci jsou rozebírány možnosti využití přístupu na základě statistického bootstrapingu k identifikaci stanovišť, u nichž lze ve srovnání s nulovým modelem, v němž jsou všechna stanoviště invadována v poměrech odpovídajících jejich dostupnosti, očekávat častější nebo naopak méně častý výskyt invazních druhů. Užitečnost přístupu je ilustrována na příkladu druhu *Carpobrotus* aff. *acinaciformis*, nepůvodní rostliny pobřežních dun střední Itálie. Popsanou metodou bylo zjištěno, že druh přednostně invaduje některá v evropském měřítku ochranářsky významná stanoviště. Metoda HSF má potenciální praktické využití, neboť umožňuje identifikovat stanoviště náchylná k invazím a využít tuto znalost k navržení jasně zacílených kontrolních opatření.

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