How do introduction characteristics influence the invasion success of Mediterranean alien plants?

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Abstract

Invasive plant species are becoming increasingly widespread following accelerated anthropogenic activity in the Mediterranean region. Humans have played a central role in the expansion process, and it is important to incorporate such considerations into management plans. Using generalized linear models, our first aim was to describe how the invasion success of 862 prominent alien plant species on Mediterranean islands is related to characteristics of the introduction process: introduction frequency, date and region of origin, range size and purpose of import. The importance of each was measured by the numbers of species present and their average invasiveness. The main findings were: (a) accidental imports and ornamentals accounted for a high proportion of all aliens, although neither group had particularly high average invasiveness; (b) introduction frequency had a comparatively modest influence, with the most commonly-introduced species naturalized only three times more widely than those rarely-introduced; (c) rates of species introduction appear to have increased dramatically in the last century, although aliens which have been present in the region for more than 200 years were most widespread, indicating that it may be centuries before some species fill their potential range; (d) there were small tendencies for successful invaders to originate in the Neotropics or in regions with Mediterranean climate biomes and to have large range sizes. Our second aim was to determine whether the number or average invasiveness of species introduced via a given pathway had the most influence on the overall probability of invasion on a given island. An elasticity analysis suggested that the number of species was substantially the best predictor of the two. This finding arises largely because invasion events are rare and remain unpredictable, and has significant implications for assessing invasion risk. We discuss how substantial sources of error and intrinsic variability in invasiveness within species groups limit the potential for developing accurate risk models.
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Introduction

The complex interactions which determine the ecological success or failure of species in different environments

are still poorly understood. A stark reminder is provided by current attempts to predict the invasiveness of plants introduced to new ranges, which remains one of the most pressing yet intractable problems facing ecology (Lodge, 1993; McNeely et al., 2001). Unavoidably a major issue, the economic cost of alien (non-native) plant species has been estimated to be far in excess of $158 million in the USA alone (Pimentel et al., 2005), and the environmental threat posed is undoubtedly far more severe (Manchester and Bullock, 2000).

Biological invasions were identified by Sala et al. (2000) as one of the most important threats to biodiversity in Mediterranean climate areas and second only to land-use change, although much interest to date has focused on ecosystems in Australia, California and South Africa. Similar concern has recently increased dramatically in the Mediterranean basin, where a combination of factors renders the region particularly susceptible (Hulme, 2004). Massive tourist pressures together with a long history of trade ensure a high rate of plant introductions, whilst many islands are already densely populated and extensively urbanized and agriculturalized (le Floc'h, 1991; Blondel and Aronson, 1999). This provides much habitat suitable for weedy species (Baker, 1965), together with well-developed road networks which act as invasion corridors, facilitating rapid spread of new colonists. The problems are likely to intensify due to further economic growth (especially in the leisure sector which creates a demand for ornamental and amenity species), escalating the necessity to develop workable control strategies.

From this brief description, it is clear that the developing risk is heavily exacerbated by anthropogenic factors (Mack and Erneberg, 2002). Human activities play a critical role which affects the origin, duration and dispersal patterns of alien plants. Fig. 1 shows a schematic pathway of five steps which ultimately determine the success or failure of species to become widely established. Currently, much research into management strategy is focused on trait analysis, which in turn is focused heavily on the ecological character of the species (e.g. Pyšek et al., 1995; Crawley et al., 1996; Lloret et al., 2003, 2005; Lake and Leishman, 2004). However, species ecology only has a direct bearing on Steps 4 and 5 of the pathway. In Step 1, trade and tourism determine the number of species infiltrating the region, purposefully or otherwise. Steps 2 and 3 are related to the distribution and intensity of introduction events in space and time, which influence the dynamics of establishment and spread (Kareiva, 1990; Hodkinson and Thompson, 1997; Hulme, 2003; Mack, 2003), and are therefore central not only to risk prediction, but also their manipulation offers other possibilities for managing the advance of invasive plants.

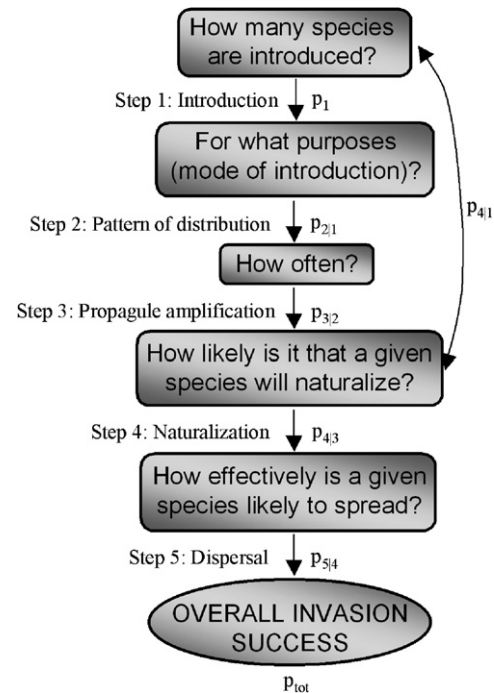In this paper, we aim firstly to describe how anthropogenic factors have influenced Mediterranean

Fig. 1. Schematic diagram identifying five measurable components of invasion success. Each step is conditional on the previous one, and thus, the product of probabilities p_1–$p_{5|4}$ gives p_{tot}, the overall probability of invasion. In the pathways analysis, Steps 2 and 3 were omitted and therefore p_4 was conditional on Step 1.

plant invasions by examining the introduction characteristics of alien species present on islands of the Mediterranean basin. Such information is potentially useful not only for extending the predictive value of models but also in directing policy decisions to target funding, available to control plant introductions, at key vulnerable points. We compare these characteristics both numerically (in terms of the number of species introduced), and in terms of the average risk per species (average "invasiveness", based on the number of islands invaded). But this presents a further question relevant to both prediction and management policy: if we consider a group of species sharing a given trait, should we be more concerned with "how many" or with "what type"? Is the number of species introduced or their average invasiveness more important in determining the overall risk of invasion? Species number (controlled during Step 1 of the invasion scheme in Fig. 1) indicates the frequency with which new genotypes, adapted ecologically to various habitats and climatic conditions, arrive in the region: the greater the diversity, the more likely it is that a few will possess the necessary characters to succeed. Average invasiveness is principally determined by the nature of the species introduced, and therefore reflects the introductory and biological characteristics central to Steps 2–5 of the invasion scheme.

As a second aim, we therefore attempt to resolve an answer to the above question. The relative influence of numbers vs. average invasiveness is seldom assessed because both factors are normally used as measures of invasion risk rather than drivers of it, and are not directly comparable because they have different properties and qualities. However, a comparison can be facilitated by expressing the relevant variables in such a way that they are all measured as conditional probabilities, based on the likelihood of success at the appropriate step of the invasion pathway (in Fig. 1, p_1 is concerned with "how many?" and $p_{2|1}$–$p_{5|4}$ are concerned with "what type?"). By conducting an elasticity analysis to measure the leverage of the variables on overall invasion success, we can obtain a basic evaluation of their relative contribution to risk.

Methods

Database

The study was based on over 100 published floras. We selected only the 79 islands for which full species lists were available, differing widely in size and longitude but including only European territories. We omitted species which were considered to be native in some parts of the Mediterranean region, since their status is open to controversy on many islands and their inclusion would have created inbalances when measuring invasion success.

The data set comprised all alien higher plant records, totalling 854 species. This does not represent the entire source pool of alien plants in the Mediterranean but covers the more common introductions, many which are not yet found outside cultivation. The inclusion of the latter element is essential to gain an accurate comparison between failed and successful invasions. The status of a species on each island was determined from the flora as "Planted", "Casual" or "Naturalized" (for definitions see Richardson et al., 2000), although where any ambiguity arose in the classification the status was generally recorded as "Casual". For the purposes of this paper, only naturalized records (established and reproducing in the wild) were considered to have invaded successfully.

The database was supplemented with descriptive information on the plant species, which was organized into a series of binary descriptive parameters, each denoting presence or absence of a given feature. These fell into several main classes, mostly describing features of the introduction process, although two further parameter classes describing biological characteristics were also included (Table 1). Where appropriate, species were assigned to multiple parameters within a class.

Information was extracted primarily from the source floras and from a questionnaire completed by ecologists with expert knowledge of certain key islands (the Balearics, Porquerolles, Corsica, Sardinia, Lesvos and Crete). Taxonomic designations at the levels of family, order and subclass were obtained from Mabberley (1997). Where data were still lacking, other botanical literature was used (over 300 sources in total), including official websites from professional institutions, such as the USDA Plants Database (http://plants.usda.gov/index.html) and the Hawaiian Ecosystems at Risk website (http://www.hear.org/gcw). Native ranges were determined primarily from Flora Europaea (Tutin et al., 1964–1980), but a variety of alternative literature was also required. Dates of introduction were generally very approximate, often given as a date range (perhaps only to the nearest century), or as first records, which may not be reliable indicators of the true date of introduction. We therefore adopted a categorical system, dividing the species into five broad date of introduction categories, since this was the highest level of precision which could be analysed with confidence. If characterizations were still not available then the species were omitted from relevant analyses, although these omissions were not considered to impose an excessive bias on the composition of the source pool.

An index, F, was also created to reflect the extent of deliberate human introduction of the species. This was derived from questionnaires and descriptive data in the Flora of Malta (Haslam et al., 1977). The respondents were asked to rank the species on an ascending seven-point scale, depending on the frequency of introduction to their island. For species not introduced deliberately, the assessments were not considered to be reliable. The scores were weighted by island area and averaged over all islands.

Analysis of species numbers and average invasiveness

For each parameter class, differences in species numbers between the various parameter categories were analysed using a χ^2 test. The expected values were equal for each category and based on the overall mean number of species for the class.

Our measure of average invasiveness was $p_{nat(i)}$, defined as the probability of an alien species being naturalized on a randomly selected island. Generalized linear models were used to determine the relationship between $p_{nat(i)}$ and various explanatory variables, based on a binomial regression (the GENMOD procedure of SAS/STAT 9.1; SAS Institute Inc., 2002). Thus, the dependent variable denoted presence or absence of the species on each island (1 or 0, respectively), and we aimed to model the probability of obtaining a value of 1. The error term was assumed to be binomially

Table 1. Summary of traits examined

Introduction parameter classes		Biological parameter classes	
(1) *Mode of introduction*–Questionnaires and literature were used to identify one or more of the principal routes via which the species entered the Mediterranean region		(7) *Growth form*–Based on the Raunkiaer classification (Raunkiaer, 1934), with additional categories defined to distinguish distinctive growth forms	
Crop	Crop species (field-scale)	Geophyte	Perennates below-ground during dry season
Forestry	Forestry species	Therophyte	Annual
Horticultural	Horticultural uses (small-scale, often a few plants in garden or village)	Cha/hemi	Chamephyte or hemicryptophyte, herbs with growth shoots above ground during dry season
Amenity	Grown in public places for practical purposes (e.g. landscaping, stabilization)	Phanaerophyte	Tree or shrub
Ornamental	Grown for ornament (in gardens or indoors)	Suffrutescent	Semi-woody chamephytes ("subshrubs")
Agcont	Introduced accidentally with seeds or soil	Hydrophyte	Submersed or floating for most of the year
Accidental	Other accidental introductions	Vine	Growing with support from other plants, cliffs or walls
(2) *Utility breadth*–The no. of modes of introduction		Succulent	Succulents
(3) *Frequency of introduction*–See Methods for description (F)		(8) *Reproductive strategy*–Identified from the source literature. Pollination types and vegetative traits (clonal growth) were determined separately, with clonal "vigour" attributed to any species where the description remarked on rapid vegetative spread	
(4) *Date of introduction*–Identified from the oldest literature record available		Water	Water-pollinated
Archaeophyte	Introduced pre 1500	Wind	Wind-pollinated
D1500–1800	Introduced 1500–1800	Insect (rad)	Insect-pollinated with radial symmetry (available to most insects)
D1800–1900	Introduced 1800–1900	Insect (zyg)	Insect-pollinated with zygomorphic symmetry or tubular corolla (available to many insects adapted to access corolla)
D1900–1950	Introduced 1900–1950	Self	Self-pollinated
D1950+	Introduced since 1950	Vertebrate	Pollinated by birds or mammals
(5) *Region of origin*–Identified source floras and some global literature sources. Initially classified on as fine a scale as possible, and later amalgamated. A region was only included where good evidence exists that the species is native		Clonal (all)	Capable of clonal (vegetative) growth
Europe	Europe (see Fig. 3)	Clonal (vigorous)	Can spread rapidly by vegetative growth
ME/NA	Middle East and North Africa (see Fig. 3)		
NCAs	N. and C. Asia (see Fig. 3)		
EAsia	East Asia (see Fig. 3)		
SAsia	South and South-East Asia (see Fig. 3)		
CAfrica	C. Africa (see Fig. 3)		
SAfrica	Southern Africa (see Fig. 3)		
Austr	Australia (see Fig. 3)		
Mx/Clf	Mexico–California (see Fig. 3)		
NAmer	Northern America (see Fig. 3)		
Arg/Chi	Argentina, Chile and Uruguay (see Fig. 3)		
Neotrp	Neotropics (see Fig. 3)		
Oceanic	Oceanic islands (see Fig. 3)		
Uncert	Uncertain (usually arising in cultivation)		
(6) *Range size*–The no. of regions of origin (R)			

Most variables are binary (presence or absence).

Table 2. Deviance explained by the parameter classes

Parameter class	No. of species	No. of categories	Deviance explained	Percentage of species term	Numerator d.f.	Denominator d.f.	F	p
Mode of introduction (all species)	846	7	1238.3	32.4	6	839	28.96	<0.0001
Mode of introduction (naturalized species)[a]	846	7	437.1	26.9	6	839	11.40	<0.0001
No. of modes of introduction[a]	265	4	367.9	22.6	3	735	2.87	0.0002
Frequency of introduction	834	4	294.3	7.8	3	830	11.83	<0.0001
Date of introduction	374	5	155.8	6.3	4	369	2.82	0.0252
Region of origin	786	14	298.0	8.3	13	772	2.72	0.0009
Range size	854	3	103.5	2.9	2	851	6.18	0.0022
Mode of reproduction	596	8	554.7	16.9	7	588	8.57	<0.0001
Growth form	837	8	300.3	7.9	7	829	5.15	<0.0001
Subclass	856	4	257.7	6.7	3	735	9.05	<0.0001
Order within Subclass	856	55	325.4	8.5	54	735	0.67	0.9690
Family within order	856	120	535.4	14.0	64	735	1.00	0.4800

Continuous variables were broken-down into 3–5 range categories due to non-linearity. In each case, a significance test is given based on approximate F-statistics.

[a]For the mode of introduction parameter class, the analysis was also conducted only for the subset of species which have been naturalized somewhere in the region, since non-deliberate introductions are rarely recorded until they are established.

distributed, and solutions were obtained by maximum likelihood iteration using a logit link function (Agresti, 1996). The island effect was controlled before estimating other parameters, allowing the overall variance to be partitioned more efficiently. The simplest model was as follows:

$$\text{logit}(p_{\text{nat(i)}}) = \text{intercept} + \text{island} + \text{species}. \quad (1)$$

To convert the results to invasion probabilities, we evaluated the model using an average island effect and back-transformed the logit outcomes. To avoid distortion caused by inter-correlations, we entered each variable individually, thus obtaining a reflection of the overall parameter effect in isolation. In Eq. (1), "island" explained 22% of the total deviance and "species" 41%. Subsequently, the species term was modelled further, by substituting with various explanatory terms. We compared the deviance explained by these models to estimate the explanatory power of each variable. We also calculated the overall explanatory power of each parameter class by entering all its sub-categories into the model simultaneously (i.e. for region of origin, species was replaced by Europe + ME/NA + ⋯ + Oceanic + Uncert). Since the species term represents the maximum deviance which could be explained by such effects, all estimates of explanatory power were expressed as a percent of this total. Approximate F-tests were used to evaluate significance, with the degrees of freedom based on the number of species rather than the full number of degrees of freedom in the binomial data set.

We encountered two specific problems with this methodology, which require further comment:

(1) For mode of introduction, the two categories of non-deliberate introductions (Agcont and Accidental) suffered from an observer bias. Since accidentals are usually imported as seed and are often only briefly casual, they tend to be particularly inconspicuous, and we suspected that the non-naturalized component of the introduction pool was substantially under-represented. In order to test for this possibility, we repeated the analysis only on species which have been recorded as naturalized at least once. The overall geometric mean $p_{\text{nat(i)}}$ was 3.22 times higher for the restricted subset than for the entire data set, but the order of the categories did not change and the parameter estimates were correlated strongly ($r^2 = 0.88$). Therefore, no subsequent amendments are presented (except in Table 2, which compares the percent of deviance explained).

(2) For date of introduction, recent imports are likely to display more restricted ranges than older ones (Pyšek and Jarošik, 2005), which is a purely mechanistic and reveals little about the intrinsic naturalization ability of the species. We therefore also examined the regional naturalization rate, $p_{\text{nat(r)}}$, (the proportion of species found naturalized at least once across the entire region) as an additional measure of invasion success. Although $p_{\text{nat(r)}}$ remains

time-dependent, an initial naturalization event is likely to occur much more rapidly than dispersal, so it is less confounded than $p_{\text{nat(i)}}$. The relationship between $p_{\text{nat(r)}}$ and date of introduction was estimated using the binomial regression technique described above.

For all analyses, when examining the parameter estimates it was inevitable that some significant results would be obtained by chance due to the large number of tests conducted, and Bonferroni experiment-wise error rates were adopted.

Analysis of the invasion scheme

Although the following approach could be used to analyse the relative influence of all steps presented in Fig. 1, this was not practically possible due to an insufficient sample size. Steps 2 and 3 are particularly complicated because they each have several possible outcomes rather than a single successful (binary) outcome. However, we were able to include the number of species introduced (Step 1), and to break down our measure of "average invasibility" into the ability to naturalize (Step 4) and the ability, once naturalized, to spread between islands (Step 5). Theoretically, all binary probability measures can be combined by multiplication provided they are conditional on the outcome of the previous step. Where n is the number of species in a group, conditional probabilities were estimated using the following measures:

(1) The probability that a species with a given trait has been introduced to the region.

$$p_1 = \frac{n}{\text{total no. of valid species}}. \qquad (2)$$

(2) The probability that a species with the given trait has become naturalized somewhere in the region, given that it has been introduced (Step 4 given Step 1):

$$p_{4|1} = \frac{\text{no. of naturalized species in group}}{n}. \qquad (3)$$

(3) The probability that a naturalized species with the trait has spread to a given island, given that it has naturalized (Step 5 given Step 4):

$$p_{5|4} = \frac{\sum_j^n [(\text{no. of islands on which species } j \text{ is naturalized})/(\text{total no. of islands})]}{n}. \qquad (4)$$

The overall measure of invasion success, p_{tot}, was calculated from their product, $p_1 \times p_{4|1} \times p_{5|4}$.

An elasticity analysis was then conducted to examine the influence of p_1, $p_{4|1}$ and $p_{5|4}$ on p_{tot}. To evaluate as

many data cases as possible, we tested all parameter classes, P. Comparisons pooling different classes are not valid because some parameters may have been related to each other leading to potential biases, so P was included as a model effect. Within classes, category membership was usually approximately independent and all species were represented with more or less equal frequency. The probabilities were normalized by converting to logit scores, L. These were standardized to range between 0 and 1 for each probability estimate, and the constants, k, obtained by solving Eq. (5), were thus equivalent to elasticity coefficients (Kotz and Johnson, 1983):

$$L_{\text{tot}} = k_P + k_1 \times L_1 + k_{4|1} \times L_{4|1} + k_{5|4} \times L_{5|4} + k_{1,P} \times L_1$$
$$+ k_{4|1,P} \times L_{4|1} + k_{5|4,P} \times L_{5|4}. \qquad (5)$$

As before, this model was solved using the GENMOD procedure of SAS/STAT 9.1. Univariate correlation coefficients (r) were also obtained between L_{tot} and the other scores.

Results

Numbers of species

(1) *Mode of introduction*: There were clear significant differences between categories ($\chi^2_6 = 805.88$, $p < 0.0001$), with considerably more species arriving in the Mediterranean as ornamentals than by any other means (Fig. 2a). A high proportion of the remainder is introduced accidentally (in either the Accidental or Agcont categories), with approximately 20% of these associated with agriculture (Agcont). Furthermore, the importance of Ornamental and Accidental species may still be substantially underestimated. The data set comprised only particularly visible or apparent introductions, and is unlikely to have omitted Crop, Forestry or Amenity species which tend to be propagated on a large-scale, at least locally. Ornamentals contained the highest proportion of species which are reported only as planted (i.e. never casual or naturalized). The difference was significantly more than expected by chance ($\chi^2_1 = 14.11$, $p < 0.0002$), and this was the only parameter from any class where such a test was significant at $p < 0.05$. The true number of cultivated ornamentals is therefore undoubtedly much higher, whereas for most other modes of introduction, a substantial proportion of the true pool may be represented within our sample.

(2) *Date of introduction*: Numbers of species in the five date ranges did not differ significantly ($\chi^2_4 = 8.91$,
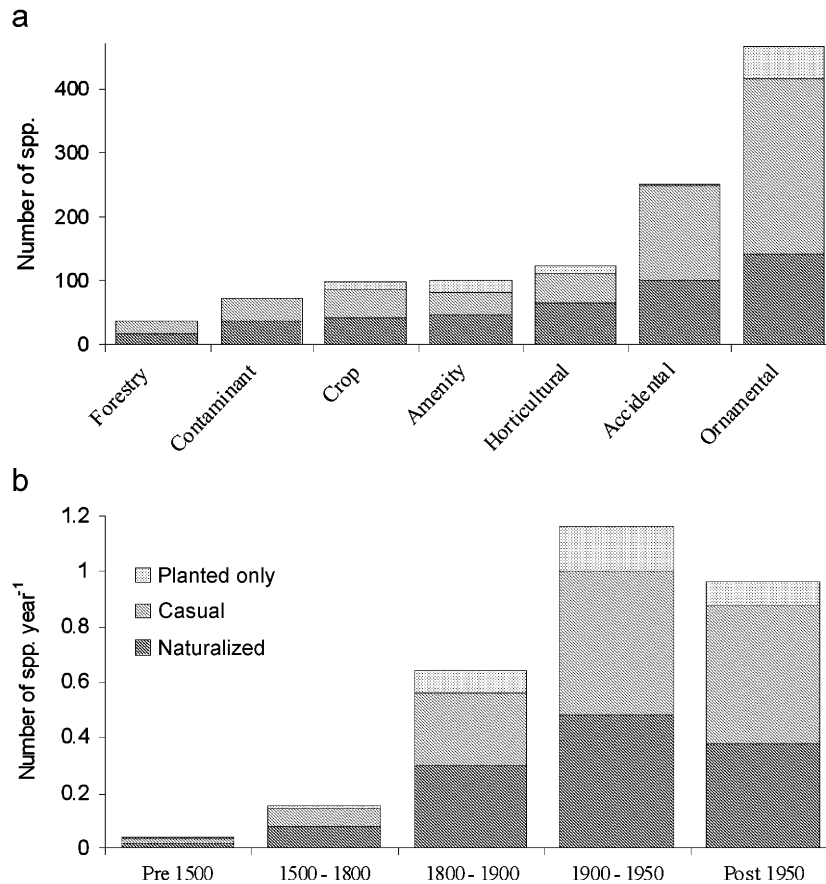
Fig. 2. (a) Numbers of species attributed to each of seven modes of introduction. (b) Relative rates of introduction of new species across five date classes. Estimates are average numbers of known introductions per year. The rate for archaeophytes is based on an approximated time-span of 1000 years. Shading indicates the status category.

$p = 0.0632$). Since the date ranges cover a shorter time period with each successive class (a millennium down to 50 years), this indicates a dramatic increase in the rate at which new plant species are introduced (Fig. 2b). The trend appears to be particularly strong for accidental imports: 49% of species introduced entirely unintentionally (i.e. those categories only scoring as Agcont or Accidental) arrived during the last century, compared with 30% of species introduced deliberately. Thus, there is no evidence that import interception and management strategies are succeeding in halting the arrival of new aliens.

(3) *Region of origin*: Mediterranean aliens display a fairly even spread of geographical origins (Fig. 3), although they differed significantly ($\chi^2_{13} = 220.90$, $p < 0.0001$). Five regions contributed significantly more species than would have been expected if their chance of donation was equal ($p < 0.05$). Two of these regions are exceptionally biodiverse with a large indigenous species pool (the Neotropics and southern Asia), whilst two have strong trade links with the Mediterranean (the Middle East/North Africa and northern America). The fifth region, Mexico and California, may be important for both

reasons (sharing species with both the Neotropics and northern America).

Average invasiveness

The relative explanatory powers of each parameter class are described in Table 2.

(1) *Mode of introduction*: This parameter class explained the largest proportion of model deviance, which remained at 26% even when limited to naturalizing species only. The horticultural, soil or seed contaminant (Agcont), crop and amenity categories all contained high proportions of strong naturalizers (Fig. 4a). Since these categories tend to exhibit mass importation, the trend may be related partly to propagule pressure, although the effect was not replicated amongst forestry species. Notably, the categories with the greatest numbers of introductions (Ornamentals and Accidentals) did not display high levels of naturalization.

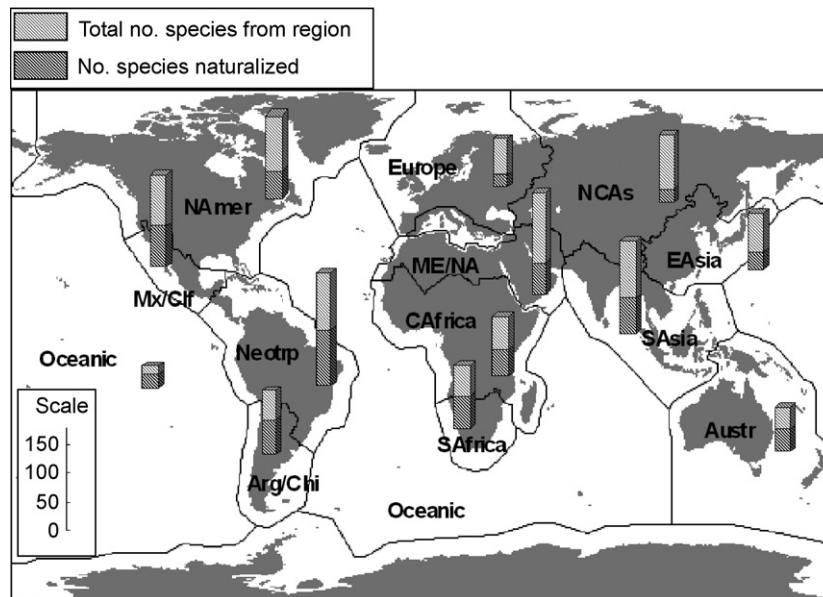(2) *Utility breadth* (Fig. 4b): A high proportion of the deviance attributed to mode of introduction appears

Fig. 3. Regions of origin: the bars represent the number of species introduced to the Mediterranean, and the proportion naturalized is indicated by darker shading.

to be due to utility breadth (ranging from 1 to 4 mode categories). This factor accounted for $>22\%$ of model deviance, only slightly less than the identity of the categories.

(3) *Frequency of introduction*: Since very little information is available to assess the true introduction frequencies of accidental species (some of which are highly invasive), our scoring system can only be considered a useful reflection of deliberate introductions. When these alone were included, a trend was revealed, although only very frequently introduced species showed an increased level of naturalization, and this was, on average, just three times higher than for other species (Fig. 4c).

(4) *Date of introduction*: One might expect a positive relationship between time since introduction and the extent of naturalization, simply due to mechanistic bias resulting from the duration of presence. According to the regression analysis, older introductions (those introduced between 1500 and 1900) were indeed more widespread than recent ones, although the most ancient (Archaeophytes) were less likely to be naturalized than those appearing after 1500 (Fig. 5a). However, the potential threat posed by recent introductions may well be increasing. The probability of becoming naturalized in the region, $p_{nat(r)}$, is extremely high for species introduced within the last century, being three to four times greater than that observed for introductions predating 1800 (Fig. 5b). If these species go on to achieve the same average range sizes as their more established counterparts, then the number of aliens attaining pest status will rise dramatically. However, some will

undoubtedly be eradicated purposefully and others will fail to adapt to changes in land management. Furthermore, most of the botanical records date from the last century, making it more likely that temporary naturalization events will be detected in imports which are currently fashionable.

(5) *Region of origin*: The probability of successful invasion was significantly higher in five regions, although differences between parameters were small (Fig. 6a). The highest levels of naturalization were found in species from southern Africa, several of which are very invasive in the study area (e.g. *Oxalis pes-caprae* L., *Carpobrotus* L. spp., *Senecio mikanioides* Otto). It may be important that these tend to originate from the Fynbos—a zone which is climatically very similar to the Mediterranean basin. Two of the other three regions containing Mediterranean climate zones (in California and Chile) were ranked highly, these also being part of a New World predominance including the Neotropics. Species from temperate regions, particularly Asia, generally displayed low levels of naturalization.

(6) *Range size*: According to the regression analysis, species with large ranges were significantly more likely to be naturalized than species native to three regions or less. However, this trend explained only 3% of the deviance accounted for by the species term in the model.

Biological parameters

(1) *Growth form*: This parameter class was a moderate explanator of naturalization patterns (7.9% of the species term). Geophytes and succulents tended to be
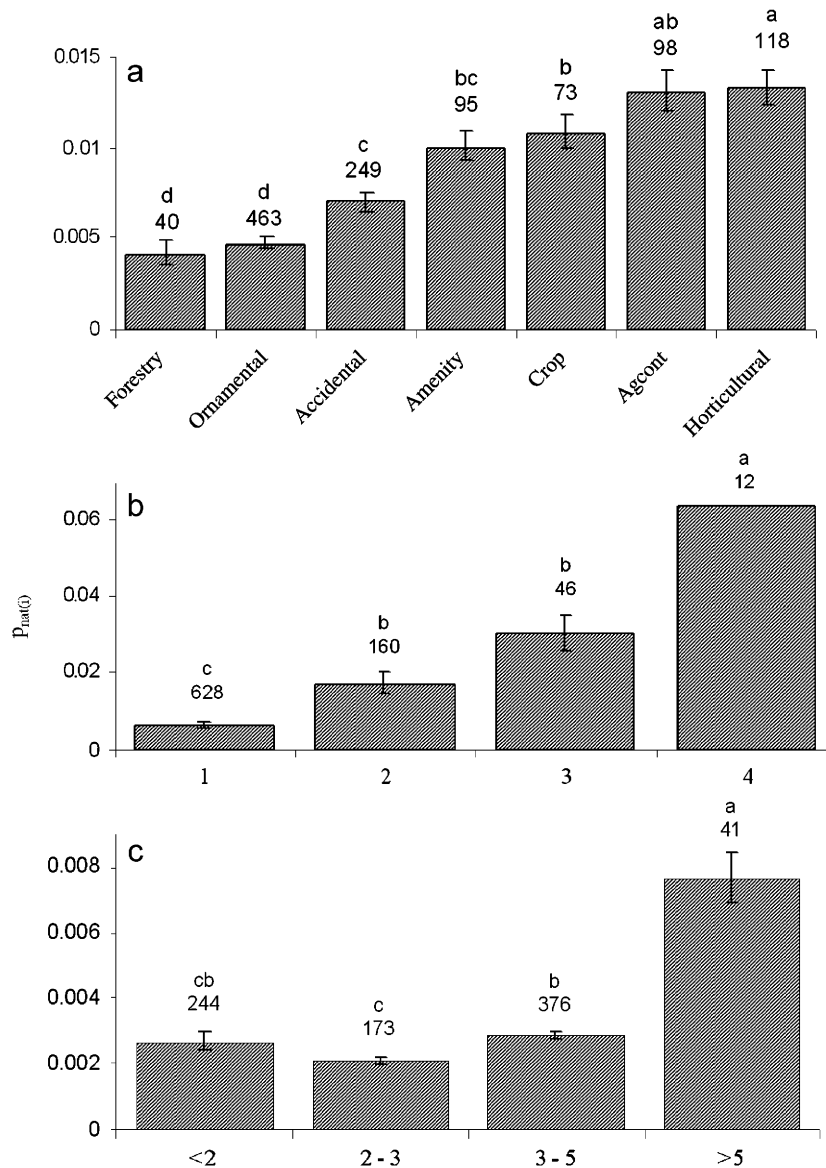
Fig. 4. Relationship between $p_{nat(i)}$ and three parameter classes related to introduction rates and patterns: (a) mode of introduction, (b) utility breadth, (c) frequency of introduction. Error bars indicate $\pm$S.E. Letters a–d denote groups of parameters which did not differ significantly from each other (experiment-wise error rate of $p < 0.05$ for 50 tests), and the number of species is given.

good naturalizers, followed by therophytes, but the large number of phanaerophytes (trees and shrubs) were generally poor (Fig. 6b). Vines, a predominantly tropical group favouring forest habitats, were the least successful, which may reflect the paucity of suitable environments on the islands.

(2) *Reproductive strategy*: Parameter estimates from this class accounted for a relatively high proportion of the deviance attributed to the species term. They provide some support for the contention that pollinator limitations can have an effect on the extent of naturalization (Fig. 6c). The highest values were observed in the categories denoting species independent of cross-pollination: those which are self-fertile or which propagate vegetatively ($p_{nat(i)}$ for

merged categories $= 0.0158 \pm 0.0014$ S.E., $n = 84$). The least successful species tended to utilize animal vectors for pollination, especially those which relied exclusively on such means ($p_{nat(i)}$ for species only occurring in animal-pollinated categories $= 0.0043 \pm 0.0003$ S.E., $n = 214$). These two parameter groupings differed significantly ($p < 0.05$, based on a comparison of 95% experiment-wise confidence limits). Despite the paucity of mammalian pollinators in the Mediterranean, the vertebrate-pollinated species compared favourably with those which utilized insects, although in many cases, insects may be an adequate substitute.

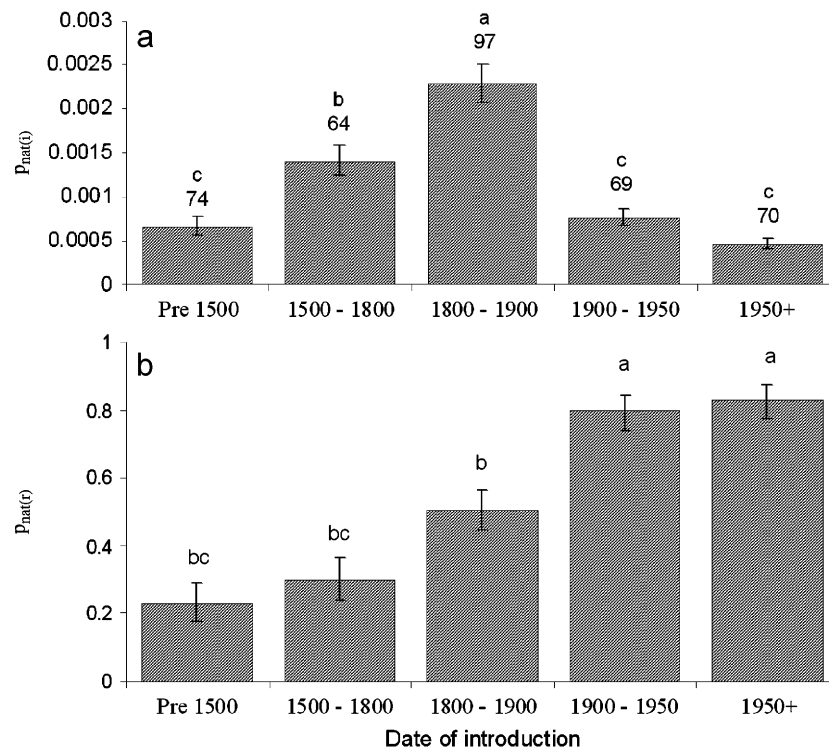(3) *Taxonomy*: Variation in $p_{nat(i)}$ was examined at the taxonomic ranks of family, order and subclass. In a

Fig. 5. Relationship between the likelihood of invasion and date of introduction: (a) the probability of a species being naturalized on an "average" island ($p_{nat(i)}$), (b) the probability of a species being naturalized anywhere in the region ($p_{nat(r)}$). Error bars indicate $\pm$S.E. Letters a–c denote groups of parameters which did not differ significantly from each other (experiment-wise error rate of $p < 0.05$ for 50 tests), and the number of species is given.

hierarchical model, subclass was the weakest explanator (Table 2), although neither order nor family was significant due to the large number of parameters necessary. No subclasses differed significantly from each other ($p > 0.05$), and only one order showed a significantly lower level of naturalization than the data set average—the Asparagales, comprising the families Agavaceae and Amaryllidaceae. Even within this group, one member, *Agave americana* L., is a very widespread alien, and other species (e.g. *Agave sisalana* Perrine, *Amaryllis belladonna* L.) which are not widely reported as naturalized on the islands are known to be moderately successful elsewhere in the Mediterranean (Tutin et al., 1964–1980).

Analysis of the invasion scheme

The three steps of the invasion pathway differed widely in their influence on the overall probability of invasion (Table 3). Pair-wise correlations revealed that p_1 correlated most strongly, explaining 75% of the variance in p_{tot}, followed by $p_{5|4}$ which explained 46%. The remaining variable, $p_{4|1}$, displayed a weak negative correlation with p_{tot}, and it is assumed that the real influence is negligible since this is contrary to expectation (a high ability to naturalize can only increase the overall probability of naturalization). These differences in explanatory power were mirrored by the elasticity coefficients, with that of p_1 being more than twice that of $p_{5|4}$ and four times higher than $p_{4|1}$, although by a small margin the latter two terms did not differ significantly from each other ($p = 0.07$). The result was remarkably consistent between parameter classes, with very similar r values and only two elasticity coefficients for the class $\times$ step interaction differing significantly from zero ($p < 0.05$, two-way ANOVA). Even in these cases, the order of the coefficients remained unchanged.

In summary, this pattern suggests that Step 1 (the number of species being introduced via a given pathway) accounts for a large part of the measurable component of invasion success. Steps 4 and 5 are much poorer predictors, but Step 5 (the ability to spread widely) is the major explanator of the two, since $p_{4|1}$ (reflecting the ability to naturalize) varied little between categories. The same pattern was observed in all parameter classes, which suggests that the trend may be generally applicable and more than a mere feature of the categories chosen.
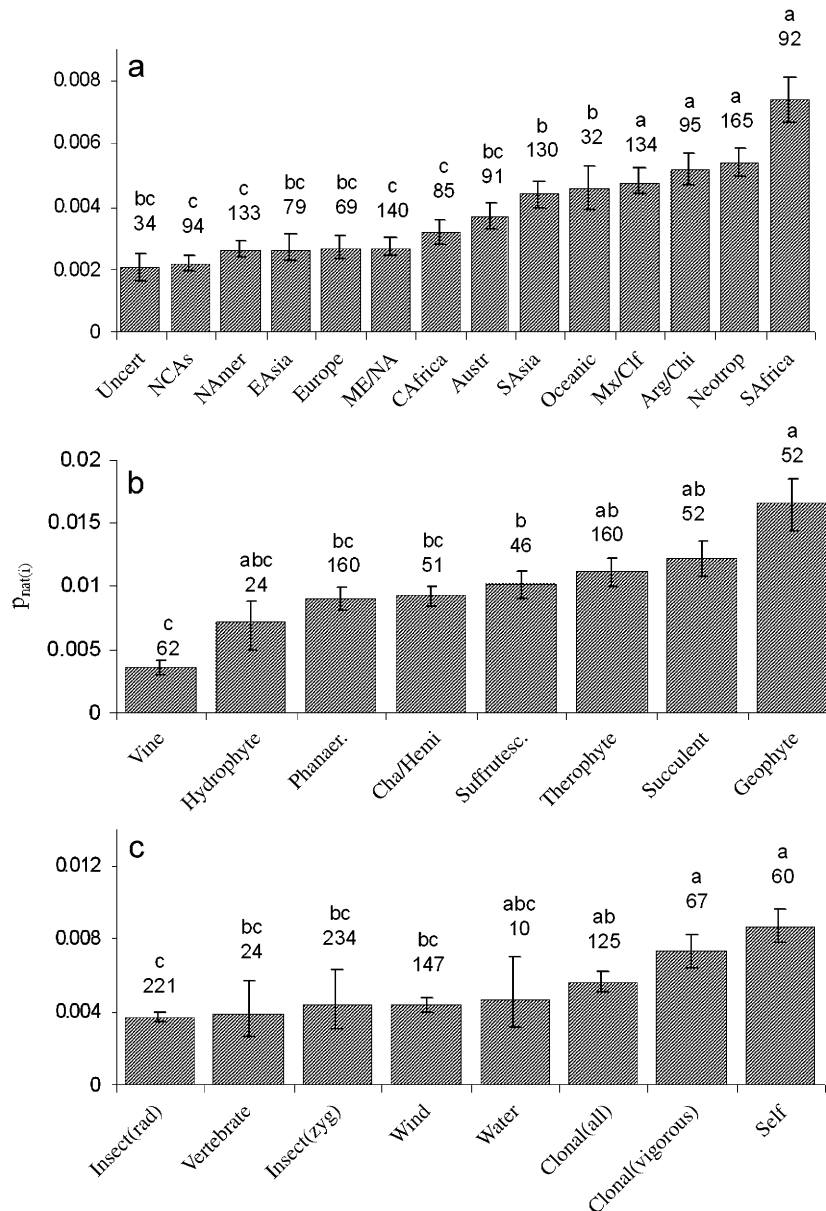
Fig. 6. Relationship between $p_{nat(i)}$ and three parameter classes describing bioglogical and biogeographic characteristics: (a) region of origin, (b) growth form, (c) reproductive strategy. Error bars indicate $\pm$ S.E. Letters a–c denote groups of parameters which did not differ significantly from each other (experiment-wise error rate of $p < 0.05$ for 50 tests), and the number of species is given.

Discussion

Current and future threats

Our findings are sufficient to draw some conclusions regarding the current state of Mediterranean plant introductions. Over time, both the number of species introduced and their levels of naturalization appear to be increasing dramatically, paralleling recent observations from the United Kingdom (Walker, 2007, see also Ruiz and Fofonoff, 2000 for similar trends in North American marine aliens). Although such trends may be accentuated by increases in recording effort, experiences elsewhere have shown that there is often a prolonged lag phase in establishment which could lead to a further explosion in the future (Crooks and Soulé, 1999). Maximal $p_{nat(i)}$ was observed in neophytes from the 16th–18th century, which suggests that some species may take hundreds of years to reach their full range, but this is not always true and some (e.g. *O. pes-caprae* and certain *Solanum* L. spp.) can spread very quickly (Economidou and Yannitsaros, 1975; Hantz, 1986).

The number of recognized archaeophytes (pre-Columbian introductions) is low in the Mediterranean, possibly due to a number of factors. There is little information to assess whether many candidates are

Table 3. Results of elasticity analysis on invasion scheme (see Eq. (5))

	Parameter class		
	L_1	$L_{4\|1}$	$L_{5\|4}$
Elasticity coefficient, k			
Main effect			
All	1.06^a	0.25^b	0.42^b
Interactions with parameter class			
Mode of introduction	-0.14	ns	ns
Region of origin	ns	ns	ns
Growth form	ns	ns	ns
Mode of reproduction	ns	ns	-0.08
Correlation with L_{tot} (r)			
All	0.87	-0.08^{ns}	0.66
Mode of introduction	0.85	-0.23^{ns}	0.75
Region of origin	0.84	0.33^{ns}	0.65
Growth form	0.89	-0.37^{ns}	0.63
Mode of reproduction	0.93	-0.85	0.63
Proportion of variance explained (r^2)			
All	0.76	0	0.43
Mode of introduction	0.72	0	0.57
Region of origin	0.71	0.11	0.42
Growth form	0.79	0	0.40
Mode of reproduction	0.85	0	0.39

All significances are evaluated at $p < 0.05$, ns: non-significant. The main effect terms separated into two significantly different groups, a and b. All k_P terms were non-significant and have been omitted, and interactions are only included where they significantly differed from zero.

native or introduced by humans, and the former designation is often politically and aesthetically favourable (Kühn and Klotz, 2003; Preston et al., 2004). This may result in some archaeophytes, particularly the more successful ones, being overlooked. At the mechanistic level, the considerable time since introduction leads to a greater chance of extinction, further exacerbated by the fact that some of the habitats in which the species originally thrived have declined with modern land-use changes (Pyšek et al., 2005). Also, there is a greater chance that the fashion for import will have diminished. Archaeophytes are often singled-out from more recent introductions for possessing distinctive distribution patterns and ecologies (Preston et al., 2004; Pyšek et al., 2005), although ultimately they may simply represent the most clearly defined of several introduction phases. Imports have been subject to waves of changing trends throughout history: the post-Columbian era being characterized by a period of great global exploration and the return of exotic curiosities from distant regions, whereas the industrial era was characterized by a proliferation of new food, commodity and forestry crops intended to enhance rates of production. This phase is now probably also in decline, but is being superseded by an increase in the import of exotic ornamental species to satisfy the garden industry, boosted by rising wealth and time available for leisure.

Most of the hypotheses regarding invasiveness traits advanced in studies elsewhere concern biological and biogeographically based characters:

(1) *Climate*: In certain regions, climatic matching is suggested in both the composition and patterns of success of alien floras (e.g. Pyšek et al., 1995; Crawley et al., 1996; Rouget et al., 2004). Our findings indicate that species from Mediterranean biomes were slightly more invasive, but in common with some other previous studies (e.g. Pyšek et al., 1995; Reichard and Hamilton, 1997), introductions were distributed relatively evenly amongst global regions.

(2) *Range size*: A number of studies have found that species with broad native ranges are more likely to be found as invaders elsewhere (e.g. Rejmánek, 1996; Goodwin et al., 1999). There may be an ecological basis to this argument (Kelly, 1996), although Pyšek et al. (2004b) suggested that it may also be associated with an increased chance of being exported. We find limited evidence for an influence of range size, but the effect is small and likely to be overestimated. The origin of many of the most widespread weeds is now obscure, and these species are often erroneously considered to be native in many parts of their range.

(3) *Clonality*: The ability to reproduce vegetatively is often associated with invasiveness (Reichard and Hamilton, 1997), and several alien species which possess this trait are very prominent in the Mediterranean (e.g. *A. americana*, *Ailanthus altissima* (Miller) Swingle, *Carpobrotus* spp., *Opuntia ficus-indica* (L.) Miller, *O. pes-caprae*). However, clonality was not as strong an influence as these high profile examples may suggest, and many other clonal aliens remain rare. A further distinction which may be necessary is that most of the abundant members of the group display rapid growth rates (cf. Burns, 2004). These are difficult to assess objectively and few records exist. We attempted to define a subset of the most vigorous species, and the analysis suggests that they do have higher naturalization levels, although there remain members which are not renowned for invasiveness (e.g. various horticultural mints, *Mentha* L. spp.). Others which are vigorous invaders elsewhere have failed to establish widely on Mediterranean islands, possibly because they either have not yet been introduced to the region in great numbers, or are not adapted to the dry summers (e.g. *Fallopia japonica* (Houtt.) Ronse, *Myriophyllum aquaticum* (Vellozo) Verdcourt, *Eichornia crassipes* (C.F.P. Mart) Solms-Laub, *Solidago canadensis* L.).

Yet others may be in the early stages of invasion but are not yet widespread enough to obtain high $p_{5|4}$ scores (*Lantana camara* L., *Parthenocissus quinque-folia* (L.) Planch, *Ipomoea* L. spp.). Prach and Pyšek (1994) suggest that successful clonal species tend to be dominant in wet, mid-successional habitats, which are more scarce, especially in the eastern Mediterranean, than in temperate or tropical regions.

Such biological parameters displayed modest predictive power. In general, introduction characteristics proved to be comparable or better as explanators. Specifically, the mode of introduction appeared to be particularly important, and species introduced for a number of different reasons (i.e. those with high utility breadths) carried a substantially increased risk. The latter suggests that wide and varied dispersal patterns are critical in bringing potentially invasive species into repeated contact with their habitable niches. However, the high proportion of variance explained might be influenced substantially by biases. Utility breadth may be confounded with introduction frequency to some extent, and affected by a strong artefact; widespread and familiar species present in many different places are more likely to be exploited, and minor uses to be recorded, than rare species. Therefore, high utility breadth may be a consequence rather than a driver of invasiveness. Such a complication underlines the difficulty in evaluating the true mechanisms behind invasion patterns (cf. Lambdon, 2008).

Of the individual introduction modes, ornamentals have a low average invasibility but comprise a large and diverse source pool. If even a few species have serious consequences then the garden trade may merit attention as a potential management problem. Its importance in initiating invasive plant problems has been highlighted previously (Bell et al., 2003), although is still often overlooked. Accidental species also have only modest naturalization levels (which may even be overestimated), but again they represent a large source pool. One subgroup, soil or seed contaminants, appear to be less important than suggested by previous studies (e.g. Pyšek, 1998), but by definition, they tend to be associated with high economic costs. Numerical proportions for these categories appear to be comparable in the USA and Australia (Reichard and White, 2001; Mack and Erneberg, 2002), where risk evaluations treat the problems very seriously.

How useful are broad-scale analyses of invasion patterns?

The motivation behind our study is to improve knowledge of invasion prediction and to inform management strategies. But to what extent do such broad-scale approaches genuinely advance such aims, and are they achievable anyway? It is inevitable that all broad-scale studies are biased in the species included, and limited by the extent of available information. To accurately catalogue all introductions to an area would be a huge undertaking, and our data set comprises only a sample of the highest profile elements. Five general shortcomings are particularly common, from which we are not excepted:

(1) *Traits are rarely independent*. For example, in our data set, recent introductions (which have had limited time to become widely-distributed) are more likely to be non-deliberate imports, to come from the New World and, at least initially, to have low frequencies of introduction. Several categories may be confounded with non-deliberate imports and thereby be subject to the recording bias outlined for the Agcont and Accidental groups (but in all cases this affected <18% of species).

(2) *Statistical tests rarely achieve suitable data distributions*. Since records of naturalized species remain relatively rare in most regions, model solutions are based on data comprising a moderate proportion of zero cells, and statistical tests assuming normality are strongly flawed. We used a much better Poisson approach, but even this fails to satisfy the recommendation of Cochran (Cochran, 1954), that χ^2 tests of independence with more than one degree of freedom should have a frequency of at least 5 in 80% of cells, and our errors were somewhat under-dispersed.

(3) The analyses are based on patterns of plant invasion currently documented in the Mediterranean, which is generally an under-recorded region (e.g. compared to parts of northern Europe). Literature discrepancies may contribute substantially to random error in the data set (Pyšek, 2003; Pauchard et al., 2004; Pyšek et al., 2004a). Also, the isolation of island populations results in generally slow rates of spread. Many range expansions are incomplete, and a number of species which are very invasive locally remain restricted. As an example, forestry species (e.g. *Pinus*) currently have very low mean naturalization levels, but have been less benign in other parts of the world (Rejmánek and Richardson, 1996). Trends in 50 years, when many extant invaders have come to occupy a greater part of their potential range, may therefore present very different patterns.

(4) For screening purposes, it is essential to consider species which are not threats as well as those which are potentially damaging, although the necessary information is hard to obtain. Despite much effort, our data set still omits many of the rarer introductions. In general, species overlooked are likely to

originate from more exotic sources and have a low probability of naturalization. However, many which have not naturalized may be only very rarely imported, and could still present a potential threat. This will not bias the analysis if the species excluded are balanced evenly between categories; and in most cases, we have little reason to suspect problems. The underestimated number of ornamental species introduced appears to be the most serious, but imports of accidental species are particularly difficult to catalogue, and only those which become at least temporarily established are likely to be detected. Accidentals may therefore be underestimated numerically, but their levels of naturalization overestimated.

(5) One essential requirement for improving predictive models is an accurate and objective means of assessing invasiveness. Our estimate relied on the number of islands on which the species was naturalized. However, this does not reflect the negative ecological and economic impacts caused, and is not necessarily a true reflection of the potential to become invasive at small spatial scales, although it correlates reasonably well with mean abundance within islands (Lloret et al., 2004).

This combination of limitations has serious consequences for the value of predictive modelling. A number of major, and numerous minor factors, determine invasiveness. The strength of any explanatory effect must be viewed in relation to these potential sources of error, the large number of species included in the analyses, and their widely varying natures. As a rule-of-thumb, if there are 10 important determinants of invasiveness, then it would be unrealistic to expect any single parameter class to explain as much as 10% of model deviance. Since few similar studies report explanatory powers directly, it is difficult to make comparisons, but there is little evidence to suspect that our findings are atypical. The individual, unadjusted significance tests suggest similar probabilities to significant trends uncovered in other studies, and in general, multi-parameter invasion models (which may incorporate several parameter classes) tend to explain 20–35% of model deviance overall (Lambdon and Hulme, 2006). We therefore suggest that regular reporting of model explanatory powers is essential to form more realistic perceptions of the complexity of invasion systems. Faced with such facts, the aim of very accurate prediction seems a long way off.

Influence of steps in the invasion pathway

A further barrier to the goal of prediction is highlighted by the invasion scheme analysis, where we examined which of three aspects of invasiveness were most influential to overall invasion risk. The findings suggest that considerably the most important effect is the number of species imported, which was dominant over measures of average invasiveness. This result raises questions over standard approaches, since most risk models are based on forms of the latter. It arises because the probability of an invasive species being encountered is generally very low (Mack and Erneberg, 2002), so that most grouping systems display a Poisson-distribution. Under these circumstances, simple statistical theory predicts that frequency may be a more reliable indicator than the mean, and the likelihood of releasing at least one harmful species will therefore be related directly to the number present. Indeed, a better measure of overall invasion "risk" may produce an even stronger effect since even fewer of the most invasive species are disproportionately important in terms of impact, which is not reflected by our measure describing only the number of islands invaded.

The ability to naturalize ($p_{4|1}$) had very little influence in the elasticity analysis. Initially, this implies that screening species by whether or not they can sustain themselves in the wild, though a quick and comparatively easy criterion to assess, would be ineffective. The weak response reflects low variation between categories and clearly the mechanism is not irrelevant, so such an inference need not always be true. It would be interesting to discover whether similar patterns apply in other alien floras.

Although more influential, dispersal ability ($p_{5|4}$) also had a modest influence. This is consistent with the fact that frequently introduced species were found to be only three to four times more invasive than rare species, even though high propagule pressures should greatly facilitate increased rates of spread (Rouget et al., 2004; Lockwood et al., 2005). Because our frequency scores were subjective, they may be prone to inaccuracies which dampen their effect. However, weak patterns have also been observed elsewhere (Pyšek et al., 1995), and it seems that propagule pressure interacts in complex ways with intrinsic naturalization and dispersal abilities. Many widespread amenity and ornamental species have remained benign for long periods. Since some (e.g. various Eucalyptus L'Hér. or Bougainvillea Comm. spp.) bring substantial economic benefits, it is important to distinguish these from their more hazardous counterparts (Smith et al., 1999).

To develop efficient screening protocols, one would wish to identify an optimal "search procedure". Our ability to predict invasiveness depends ultimately on how species are partitioned into groups: prediction will be poor if the measure of invasiveness exhibits more variation between groups than within them. At present, this appears to be the case.

Implications for policy

Complacency over the threat posed by plant invasions in the Mediterranean is unjustified. The region faces rampant increases in introduction and rising probabilities of naturalization. However, despite compelling incentives and many scientific studies, our ability to identify potentially invasive species remains disappointing (Daehler and Carino, 2000; Mack, 2003; Lambdon and Hulme, 2006). Here, all parameter classes proved to be weak explanators, and we have argued that this is unlikely to be unusual. A large part of the difficulty is that in any natural grouping of species, the frequency of proven aggressive invaders is generally very low, typically leading to weak statistical resolution in tests (Williamson and Fitter, 1996). We suggest that, in some respects, predicting invasion success from traits is effectively "worse than nothing"; basing predictions on an entirely non-descriptive measure, the number of species present, is a more reliable indicator. Since comparable assessments are seldom if ever conducted, there is an overdue need to recognize and explore more critically the current limitations on risk model methodology.

Risk prediction still has a role in screening and intercepting potentially invasive species, but we suggest that it may be most effective as an initial filter to focus attention. Additional policies are necessary to develop effective management of the problems *in situ*, and data describing how risk is influenced by introduction patterns remain highly relevant to this task. Since the threat posed by a pathway is in some respect strongly linked to the number of species involved, broad-scale analyses remain relevant to such risk assessments, and the need for accuracy is less limiting. For example, mode of introduction clearly has a particularly important influence on naturalization patterns. The key aspect appears to be associated with the diversity of imports, so perhaps more focus is required on limiting the breadth of introductions and on promoting the utilization of fewer alternatives which are, from the best knowledge available, considered to be benign. The garden industry merits particular attention from this point of view. In some cases, the threat posed may also be mitigated by controlling the situations in which species are planted. Amenity species are widely cultivated in semi-wild locations, and therefore, individually, are at higher risk of establishing than those in gardens. Selection of suitable options requires special care, although currently, those most often utilized include some of the region's worst invaders (e.g. species of *Carpobrotus*, *Agave* and *Acacia*).

Processes which determine invasibility are clearly very complex, but introduction dynamics currently represent a significant knowledge gap and require more focused attention in the future. Detailed information on how the distribution and density of propagules relate to naturalization events will be essential to combat the problems effectively.

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