INTERACTIONS BETWEEN ENVIRONMENT, SPECIES TRAITS, AND HUMAN USES DESCRIBE PATTERNS OF PLANT INVASIONS

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Abstract. Although invasive alien species (IAS) are a major threat to biodiversity, human health, and economy, our understanding of the factors controlling their distribution and abundance is limited. Here, we determine how environmental factors, land use, life-history traits of the invaders, residence time, origin, and human usage interact to shape the spatial pattern of invasive alien plant species in South Africa. Relationships between the environmental factors and the extrinsic and intrinsic attributes of species were investigated using RLQ analysis, a multivariate method for relating a species-attribute table to an environmental table by way of a species presence/absence table. We then clustered species according to their position on the RLQ axes, and tested these groups for phylogenetic independence. The first three axes of the RLQ explained 99% of the variation and were strongly related to the species attributes. The clustering showed that, after accounting for environmental factors, the spatial pattern of IAS in South Africa was driven by human uses, life forms, and reproductive traits. The seven clusters of species strongly reflected geographical distribution, but also intrinsic species attributes and patterns of human use. Two of the clusters, centered on the genera *Acacia* and *Opuntia*, were phylogenetically non-independent. The remaining clusters comprised species of diverse taxonomic affinities, but sharing traits facilitating invasion in particular habitats. This information is useful for assessing the extent to which the potential spread of recent introductions can be predicted by considering the interaction of their biological attributes, region of origin, and human use.

Key words: biological invasions; co-inertia analysis; environment; exotic species; human uses; invasive alien plants; life-history traits; plant invasions; RLQ analysis; South Africa.

INTRODUCTION

The intentional or accidental movement of species by humans to regions far removed from their natural ranges has accelerated dramatically in frequency and extent in recent decades as human movements have become more global, and international trade has increased (Levine and D'Antonio 2003). Because of the ecological and economic impacts of invasive species (Pimentel et al. 2001), there is an urgent need to understand the factors that determine the arrival, initial dispersal, and establishment of self-sustaining populations, and the spread of invasive species.

To date, most research on invasive alien species (IAS, sensu Richardson et al. 2000*b*) has focused on species-specific (or intrinsic) traits, assuming that a species has particular attributes that can explain its abundance, its geographical extent, and hence its invasive status (Kolar and Lodge 2001, Hamilton et al. 2005). For instance, the invasiveness of different plant groups is often explained by differences in growth rates, reproduction, and dispersal ability, but factors relating to the original distribution range of species have also been useful in explaining degrees of invasiveness (Rejmánek et al. 2005). However, with a few exceptions (e.g., Rejmánek and Richardson 1996), the conclusion has been that few or no factors allow consistent prediction of invasiveness, let alone of the extent of adventive distribution.

Factors extrinsic to a particular species are also clearly implicated in defining the course of an invasion. These include the biological diversity of the invaded community (Kennedy et al. 2002, Stohlgren et al. 2003, Richardson et al. 2005), attributes of the native biota that interacts with the exotics (Richardson et al. 2000*a*, Zavaleta et al. 2001), and patterns of landscape disturbance (Higgins and Richardson 1998, Pauchard et al. 2004). While intrinsic and extrinsic factors may be mutually related, some authors have argued that the abundance or geographical extent of an introduced organism may be more influenced by the initial circumstances of colonization than by specific morphofunctional traits (Lonsdale 1999, Lockwood et al. 2005). For example, an analysis of the geographic extent of alien plants in Chile found that mean residence time was a

better explanatory variable for the extent of invasion than inherent biological factors (Castro et al. 2005; see also Pyšek et al. 2005).

Surprisingly few studies of the determinants of invasiveness have quantified the role of the initial reason for introduction. Most of the world's most widespread invasive alien plant species were introduced intentionally and are used for specific purposes (Ewel et al. 1999, Pyšek et al. 2002, Kowarik 2005). Taylor and Irwin (2004) demonstrated the strong influence of economics on the distribution of alien species, by linking economic activities to the distribution of IAS. Economics is a crucial driver of biological invasions because the underlying causes (and some of the solutions) may lie in socioeconomic behaviors (Thuiller et al. 2005).

Also, few studies have sought an integrated understanding of all the potential factors (intrinsic and extrinsic) that determine the spatial pattern of a set of IAS. For such an analysis, alien plant invasions in South Africa provide an ideal natural experiment. The region (1 219 090 km^2) has a long history of exposure to alien plant species (>350 yr)—enough time for many species to have sampled a wide range of environmental conditions—and many plant species are naturalized or invasive (Nel et al. 2004). The region has a wide range of major habitat types, including desert, semiarid shrublands, mediterranean-type ecosystems, grasslands, savannas, and temperate forest (Cowling et al. 1997a), providing potential habitat for a high diversity of alien plants. Taking advantage of an extensive database of distribution records for IAS and the good knowledge of biology of the invasive plants, this paper examines the factors (intrinsic and extrinsic) that determine the geographic extent and distribution pattern of major invaders in South Africa. In particular, we assess how environmental features, land transformation, life-history traits, residence time, region of origin, and reason for introduction interact to shape the spatial pattern of IAS in South Africa.

MATERIALS AND METHODS

Species distribution

The Southern African Plant Invaders Atlas (SAPIA) is the best source of data on the distribution of invasive plant species in South Africa, Lesotho, and Swaziland. The SAPIA database has records for over 500 species, with information on their distribution, abundance, habitat preferences, and dates of introduction (Henderson 1998, 1999, 2001). Records are geo-referenced at a quarter-degree square resolution (QDS, ~25 × 25 km at this latitude). Only alien species invading natural or seminatural habitats are listed in SAPIA (weeds of agricultural lands and human-dominated systems are not included); we considered all species in SAPIA to be naturalized or invasive (sensu Richardson et al. 2000b). SAPIA is biased in favor of woody species, and invasive alien grasses and other herbaceous taxa are underrepresented (Nel et al. 2004).

In order to have reliable information on the spatial distribution of the IAS, we excluded species recorded in less than 20 QDSs, and taxa which are notoriously difficult to identify to species level in the field (e.g., *Casuarina* and some *Eucalyptus* species; see Nel et al. 2004 for discussion on the taxa that were excluded from the analysis). As our aim was to explore the determinants of distribution for aggressively invasive species that are well established in South Africa, we also limited our analysis to taxa that have been in the country for at least 100 years and are classified as "major invaders" ("invasive alien species that are well established, and which already have a substantial impact on natural and seminatural ecosystems" [Nel et al. 2004]). Sixty-two IAS were finally selected for the analysis (See Appendix A for species names and abbreviations).

Species attributes

We collated information on a wide range of intrinsic and extrinsic attributes considered potentially important mediators of the success of IAS (Rejmánek 1995, Rejmánek and Richardson 1996, Castro et al. 2005; Table 1).

Intrinsic.—We examined life-history traits related to dispersal (seed size, dispersal mode), ability to fix atmospheric nitrogen, vegetative reproduction capacity, origin (biogeographic region, latitudinal band); and the type of habitat that the species is currently invading in South Africa: landscape (species that invade large tracts of land with no obvious association with water courses), riparian (species that typically invade along water courses), or both (Nel et al. 2004).

Extrinsic.—We considered the minimum residence time (years since the earliest reliable record of the species being present in South Africa, either from a herbarium specimen or an authoritative publication); the reason for introduction; the main current use of the species by humans in South Africa; and the number of different uses (see Table 1 for details).

Environmental variables

We considered three types of environmental variables (climatic, topographic, and land transformation) that are known to influence species distribution and diversity.

Climatic variables.—The climatic data set used for this study contained eight variables that are considered to be critical to the physiological functioning and survival of plants (Woodward 1987). These variables are representative of mean energy availability (mean annual precipitation, mean annual temperature, potential evapotranspiration); potential limits to growth (minimum temperatures of the coldest and warmest months, growing degree days above 10°C); amount of water available (ratio of actual to potential evapotranspiration); and seasonality (plant productivity index, PPI). These simple climatic variables have been derived from Schulze (1997) at a resolution of 1 × 1 km, and were scaled up to QDS by averaging (Schulze 1997). Potential

TABLE 1. List of the species attributes analyzed in the study.

Type and attributes	Abbreviation	Levels
Intrinsic		
Life-history traits		
Life form	form	tree (TR), shrub (SH), succulent (SC), herb (HE)
Seed size†	seed	no seed (NO), very small (VS), small (SM), medium (M)
Seed dispersal mode‡		
Wind	wind	0/1
Water	water	0/1
Bird	bird	0/1
Mammal	mam	0/1
Vegetative reproduction‡		
Coppice	coppice	0/1
Sucker or runner	sucker	0/1
Vegetative division (e.g., *Opuntia*)	division	0/1
Nitrogen fixer	Nfix	0/1
Origin		
Region	region	Africa, Australia (Aust), Australasia (Aust_asia), Mediterranean (Med), Eurasia (Euras), North America (N_Amer), South America (S_Amer), tropical America (Trop_Amer)
Latitudinal band	lat_band	tropical (T), southern temperate (ST), northern temperate (NT)
Extrinsic		
Habitat	habitat	landscape (LA), riparian (RI), both (LR)
Introduction date	date	1700, 1750, 1800, 1850, 1900
Primary use	use	agriculture (AG), barrier (BA), cover/binder (CO), ornament (OR), silviculture (SI), none (accidental introduction) (NO)
Type of use		
Ornamental	ornam	0/1
Agricultural crop	agric	0/1
Cover/blinder	cover	0/1
Silviculture crop	silvic	0/1
Barrier	barrier	0/1
Number of uses	useno	from 0 to 5

Notes: Data are principally from Richardson et al. (1997), Henderson (1998, 1999, 2001), and L. Henderson (*unpublished data*), unless otherwise specified. In the Levels column, "0/1" indicates absence/presence of particular modes or uses.

† Sources: Dean et al. (1986), Henderson (2001).

‡ Sources: Richardson et al. (1997); Pacific Islands Ecosystems at Risk project ⟨http://www.hear.org/pier/index.html⟩

evapotranspiration estimates were calculated using the FAO 56 Penman Monteith combination equation (Allen et al. 1998), while actual evapotranspiration estimates were derived using the LPJ dynamic global vegetation model (Hickler et al. 2004). The plant productivity index corresponds to the number of months per year receiving more rainfall (mm) than twice the mean annual temperature (°C) for that site. This provides a surrogate for rainfall seasonality and length of growing season (le Houérou 1984). We also added a measure of available energy (the mean net primary productivity by QDS) that was derived using the Sheffield dynamic global vegetation model (SDGVM; Woodward and Lomas 2004).

Topography.—We included two variables related to topography: mean altitude and the standard deviation of altitude in a QDS from a digital elevation model at a resolution of 200 × 200 m.

Land transformation.—Data on land transformation were resampled from the 0.5' resolution "human footprint" data set (Sanderson et al. 2002). This is the most consistent source of land transformation globally. The

human footprint data set is similar to the ecological footprint, a set of techniques for estimating the amount of land or sea necessary to support the consumption habits of one individual, population, product, activity, or service (Wackernagel and Rees 1996). The human footprint represents to some extent the sum of ecological footprints of the human population. The human footprint uses four types of data as proxies for human influence: population density, land transformation, accessibility, and electrical power infrastructure. It ranges from 0 to 1 (natural to completely transformed and unsuitable for wildlife).

Three-way ordinations

The purpose of this analysis was to relate three tables (species-sites, environment-sites, species-attributes) to extract the joint structure between them. We used a multivariate method that provides a general solution to this problem: RLQ analysis (Dolédec et al. 1996). RLQ analysis aims to investigate the relationships between two tables, R (environmental characteristics) and Q

(species attributes in our case), using a third table, L (a species distribution matrix). Here, R represents a matrix whose rows are QDSs (sites) and columns the environmental characteristics for each QDS; Q represents a matrix whose rows are alien plant invaders and columns the attributes for each species; L represents a matrix whose rows are QDSs, and whose columns are alien plant species.

The RLQ analysis facilitates the study of the joint structure of these three data tables, irrespective of whether the data are quantitative or qualitative. As far as we know, few published studies have carried out such three-table joint analyses (but see Dolédec et al. 1996, Legendre et al. 1997, Ribera et al. 2001, Dray et al. 2003). The general mathematical model of RLQ analysis, which basically consists of an eigen analysis of the matrix R^TLQ, is fully explained in Dolédec et al. (1996). Here, we describe only some of its basic properties. In RLQ analysis, the eigenvalue decomposition of the cross-matrix provides ordination axes (environmental and species trait axes) onto which sites and species are projected. This results in new sets of scores for sites and species, respectively. As we used a version of RLQ analysis based on correspondence analysis of the species distribution table, these new scores for sites and species had maximal covariance (see Dolédec et al. 1996 for a demonstration). Because the structure of the individual tables can only be partially optimized (owing to constraints imposed by a joint analysis), RLQ takes into account only a fraction of the total variance. Furthermore, the highest possible correlation (canonical correlation) between rows and columns in a contingency table is given by the square root of the first eigenvalue of its correspondence analysis (Williams 1952). Consequently, the correlation computed from the first RLQ axis cannot be higher than the canonical correlation obtained from the first CA axis of the species distribution table. This means that the structure of the species distribution table can only be partially optimized, since only the variability associated with environmental characteristics of sites and species attributes is accounted for. In summary, the maximization of covariance results in the best joint combination of the ordination of sites by their environmental characteristics (optimization of the site score variability), the ordination of species by their attributes (optimization of the species score variability), and the simultaneous ordination of species and sites (optimization of the correlation between the sites scores and the species scores; Dolédec et al. 1996, Ribera et al. 2001).

All calculations and graphs were made using the ADE4 library in the open-source R-CRAN software (R Development Core Team 2004).

Clustering

We used a Hartigan's K-Means clustering method (Hartigan and Wong 1979) to group species into seven clusters according to the positions of the species on the RLQ axes. This means that species were grouped based on their particular attributes (intrinsic and extrinsic) and on the environmental variables (climate, topography, and land transformation). The choice of the number of clusters was subjective, but there was the clear aim of producing ecologically interpretable patterns. This required a compromise between lumping together distinct groups of species and producing very small groups that would lack generality and possibly be phylogenetically non-independent. We ran the clustering method with different numbers of cluster (five to 15) and found that seven clusters was the most manageable and interpretable number, given the available information.

Of the 62 species analyzed in this study, some belong to the same genus and family, so the clusters obtained might not be phylogenetically independent. We constructed a phylogenetic tree from Davies et al. (2004) (with additional information from Murphy et al. 2003, Grotkopp et al. 2004, Sytsma et al. 2004, Wojciechowski et al. 2004, Bohs 2005, Edwards et al. 2005). Then we ran a Moran's I randomization tests (10 000 permutations) for spatial and phylogenetic autocorrelation to assess whether the clustering was independent of phylogenetic associations. The randomization test (implemented in the ADE4 library) assesses whether the clustering is phylogenetically autocorrelated (Cliff and Ord 1973, Thioulouse et al. 1995). The phylogenetic tree replaced the geographic information in the usual spatial autocorrelation test. Should some clusters be phylogenetically non-independent, it could be argued that those clusters reflect phylogeny more than invasive potential.

Mapping

We took the spatial distribution of every species in a cluster, and, for each pixel, summed the number of presence records for that cluster. This resulted in a species-richness by cluster map that could be used to compare the geographic distributions of the clusters.

RESULTS

Joint structure between the R, L, and Q tables

Only three axes were required to explain 99% of the total variation (total inertia) (57.7%, 30.8%, and 10.5%, respectively).

The correlations between the environmental variables and the RLQ axes showed that the first axis was strongly correlated with temperature: the first axis separated areas that were warm throughout the year from those that were seasonally cool (Table 2). The second axis showed a more complex gradient, related to the intuitive (if somewhat anthropocentric) concept of "favorableness" that combined annual temperature, minimum temperature of the coldest month (MTC), and humidity. The third axis was related to an energy–altitude gradient, from low to high altitude and energy.

The correlation ratios between species attributes and the first three RLQ axes showed that both extrinsic and intrinsic attributes played a major role in separating the

TABLE 2. Correlation between the environmental variables and the RLQ axes.

Environmental variable	Abbreviation	RLQ axis1	RLQ axis 2	RLQ axis 3
Mean annual evapotranspiration	Evtr0112	−0.34	0.19	0.26
Mean growing degree days above 10°C	Gdd10	**−0.44**	**−0.33**	0.15
Mean temperature of the coldest month	MTC	−0.21	**−0.39**	**−0.40**
Mean temperature of the warmest month	MTW	**−0.41**	0.14	0.21
Mean annual precipitation	Prec0112	0.21	**−0.38**	0.21
Mean annual temperature	Tmean	**−0.44**	**−0.34**	0.10
Net primary productivity	NPP	0.05	**−0.36**	**0.46**
Ratio actual/potential evapotranspiration	Aetpet	0.28	**−0.34**	0.19
Mean elevation	Elemean	0.21	0.23	**0.57**
Spatial heterogeneity index	Elestd	0.17	−0.10	−0.27
Plant productivity index	PPI	0.24	−0.21	0.04
Human footprint	Hfoot	0.14	−0.27	−0.03

Note: Boldface type highlights the highest correlation values. For this RLQ analysis, the R table comprises environmental characteristics, the Q table comprises species attributes, and the L table comprises a species distribution matrix.

IAS (Table 3). Of all species attributes considered, the main human use of a species was the most correlated with the RLQ axis 1, i.e., use was the factor most correlated to the spatial pattern of IAS in South Africa (Table 3). However, the life form of the species was also strongly correlated with RLQ Axis 1. The only attribute substantially correlated with the RLQ Axis 2 was an intrinsic factor: seed size (Table 3, $R^2 = 0.28$). Region of origin and latitudinal band, both extrinsic factors, seemed to explain the spatial pattern of IAS in South Africa after accounting for environment (RLQ axis 3, Table 3).

The results of the RLQ analysis were best summarized by representing the scores of the environment and species variables on the RLQ axes (Figs. 1 and 2).

Axis 1.—Region of origin, number of uses and primary use, seed size, and life form were the most powerful explanatory attributes for this RLQ axis (explained by both the length and the angle between the axes and the vectors); they seemed strongly related to the environment (Fig. 3). Species with negative positions on this axis (warmer areas), tended to come from Africa, South and tropical America; to have small seeds; to be succulent plants or herbs; and to have a limited number of uses (mostly no use or agricultural use) (Figs. 1 and 3). Species with positive positions on axis 1 (cooler and seasonal areas) tended to be trees from northern temperate regions, with many different uses, but used mostly in silviculture, for barriers and cover (Figs. 1 and 3).

Axis 2.—Life-history traits (seed size and vegetative reproduction), origin, main habitat, number and type of uses, and date of introduction were the main attributes related to RLQ axis 2 (Figs. 1 and 3). Species with negative positions on this axis (warm and humid areas where winter temperatures were cool) tended to have been imported for ornamental reasons, and were originally from Africa, Asia, Australia, and tropical America. These species also tended to have riparian distributions. On the positive side of axis 2 (cooler, drier areas with colder winters), species tended to have no seeds (reproduction being entirely vegetative) or very small seeds (in which case they also reproduce by

vegetative division). They did not seem to have been imported for ornamental purposes but mostly accidentally (no use) or for cover, around the eighteenth century. These species (with positive values on axis 2) originated mainly in temperate regions and invaded landscapes, rather than riparian zones.

Axis 3.—This axis did not separate species on the basis of life-history traits, but mostly by region of origin and type of human use (Figs. 2 and 3). On the negative side of axis 3 (areas at low elevation and with low energy), species came mainly from Australia and the Mediterranean, and had a high number of uses (but mostly cover and silvicultural). On the positive side of axis 3 (areas at higher elevation and with higher energy), species tended to have fewer uses (mainly ornamental or agricultural). Species with a positive value on axis 3 had been imported mainly from northern temperate or tropical regions (Fig. 3).

TABLE 3. Correlation ratios between the qualitative morphological and life traits of the species and the RLQ axes.

Attributes	RLQ axis 1	RLQ axis 2	RLQ axis 3
form	**0.38**	0.14	0.05
date	0.08	0.01	0.08
habitat	0.11	0.14	0.04
use	**0.48**	0.07	0.06
ornam	0.07	0.09	0.01
agric	0.01	0.07	0.00
cover	0.20	0.03	0.02
silvic	0.23	0.00	0.02
barrier	0.08	0.02	0.05
useno	**0.38**	0.07	0.12
seed	0.34	**0.28**	0.07
wind	0.07	0.05	0.11
water	0.15	0.00	0.00
bird	0.09	0.02	0.00
mam	0.04	0.01	0.00
coppice	0.00	0.06	0.00
sucker	0.10	0.01	0.13
division	0.01	0.13	0.10
nfix	0.12	0.09	0.03
region	**0.36**	0.12	**0.39**
lat_band	0.29	0.09	**0.27**

Notes: See Table 1 for the meaning of the attribute codes. Boldface type highlights the highest correlation values.
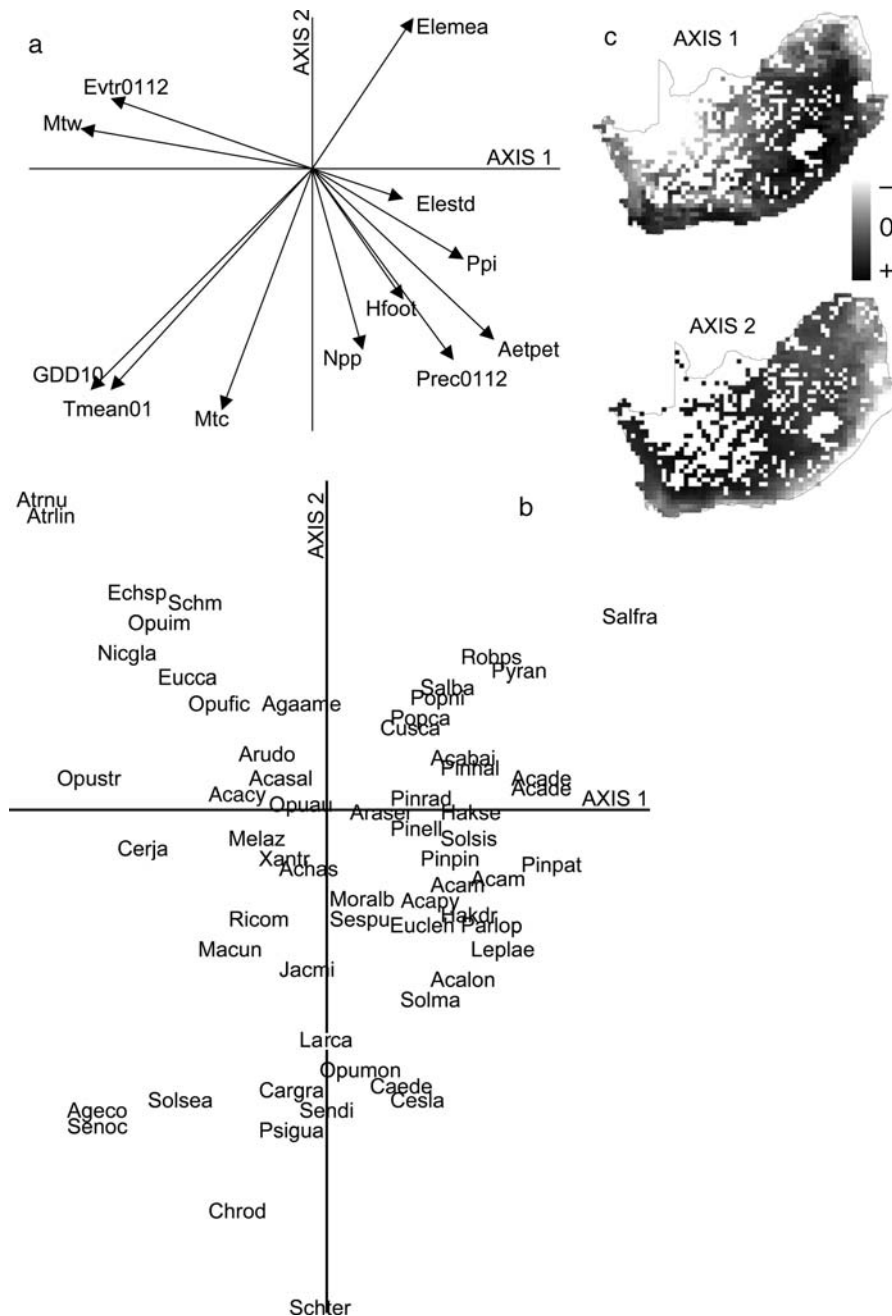
FIG. 1. Multiple representation of the three-way ordination on axis 1 vs. axis 2: (a) environmental variables, (b) mean position of species in the RLQ plan, (c) geographical distribution of the RLQ axis scores. For this RLQ analysis, R comprises environmental characteristics, Q comprises species attributes, and L comprises a species distribution matrix.

Classification of species based on environmental variables and species attributes

The K-means analysis separated seven clusters based on the mean position of every species on the three RLQ axes (Fig. 4; see Appendix B for a three-dimensional plot). Each cluster was then described based on the mean position of the species on the RLQ axis (Table 4). The randomization test showed that only clusters 4 and 7 were phylogenetically non-independent ($P > 0.05$, Fig. 4).

Cluster 1.—Tropical species with small to medium seeds used for ornamental and agricultural purposes (Table 4 and Fig. 4). These species reproduce vegetatively by coppicing. They are mostly found in the extreme northeastern part of South Africa in warm and humid climates (Fig. 5).
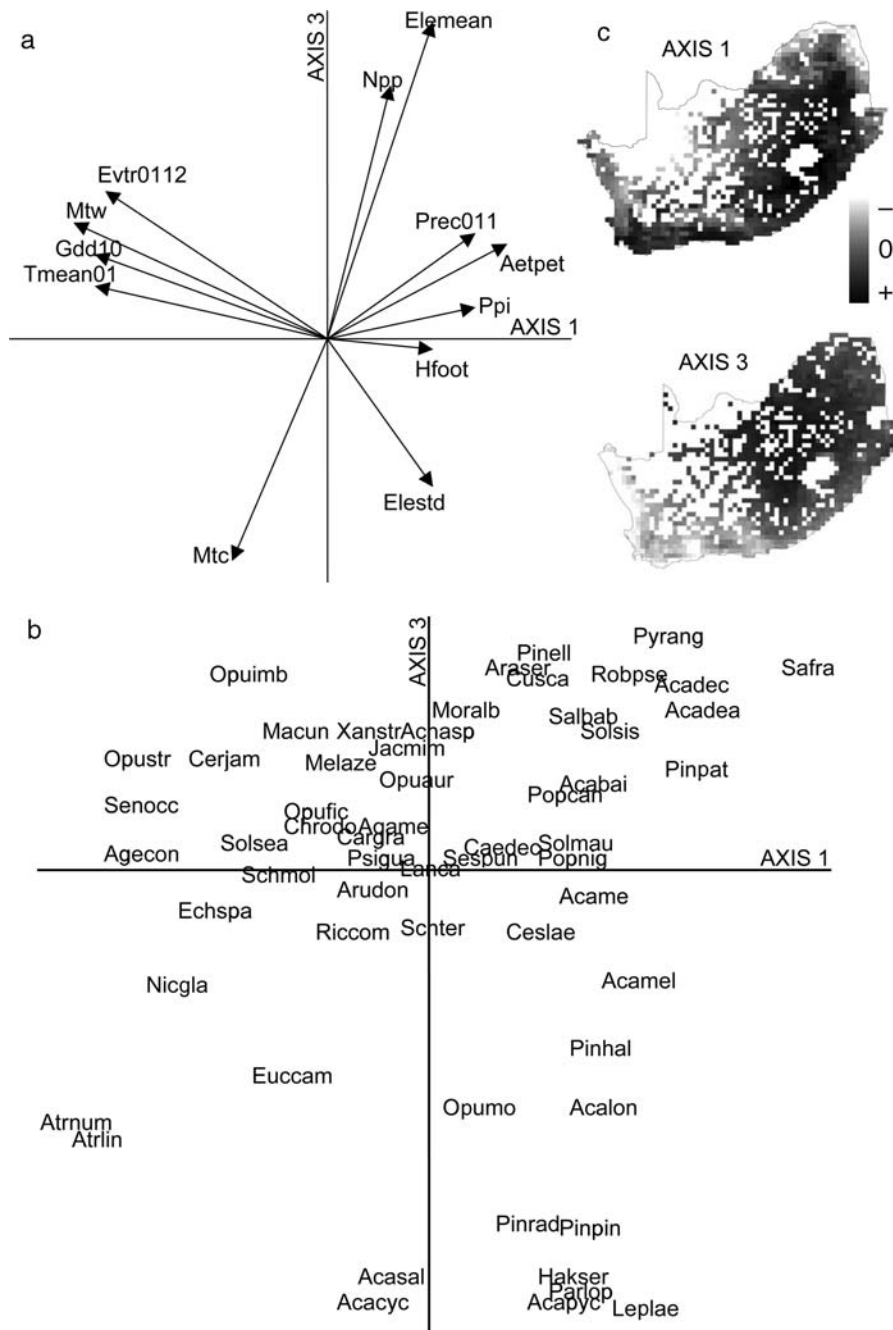
FIG. 2. Multiple representation of the three-way ordination on axis 1 vs. axis 3: (a) environmental variables, (b) mean position of species in the RLQ plan, (c) geographical distribution of the RLQ axis scores. For this RLQ analysis, R comprises environmental characteristics, Q comprises species attributes, and L comprises a species distribution matrix.

Cluster 2.—Species found at medium to high elevation that do not share any particular life-history traits (Table 4, Fig. 4). They were imported from temperate regions for ornamental and barrier purposes and are landscape or landscape/riparian invaders (Fig. 5).

Cluster 3.—Succulent and herbaceous species that have invaded the mountains of the Cape Floristic Region and the Succulent Karoo (Fig. 5), where winters

are cold and rainy, and summers are hot and dry. The species in this group have small to very small seeds and were imported from Australia for all listed purposes (Table 4 and Fig. 4).

Cluster 4.—Typical Mediterranean species that have invaded landscapes in the Cape Floristic Region (Fig. 5) that have cool and humid winters, and warm and dry summers. These species were imported from Europe and
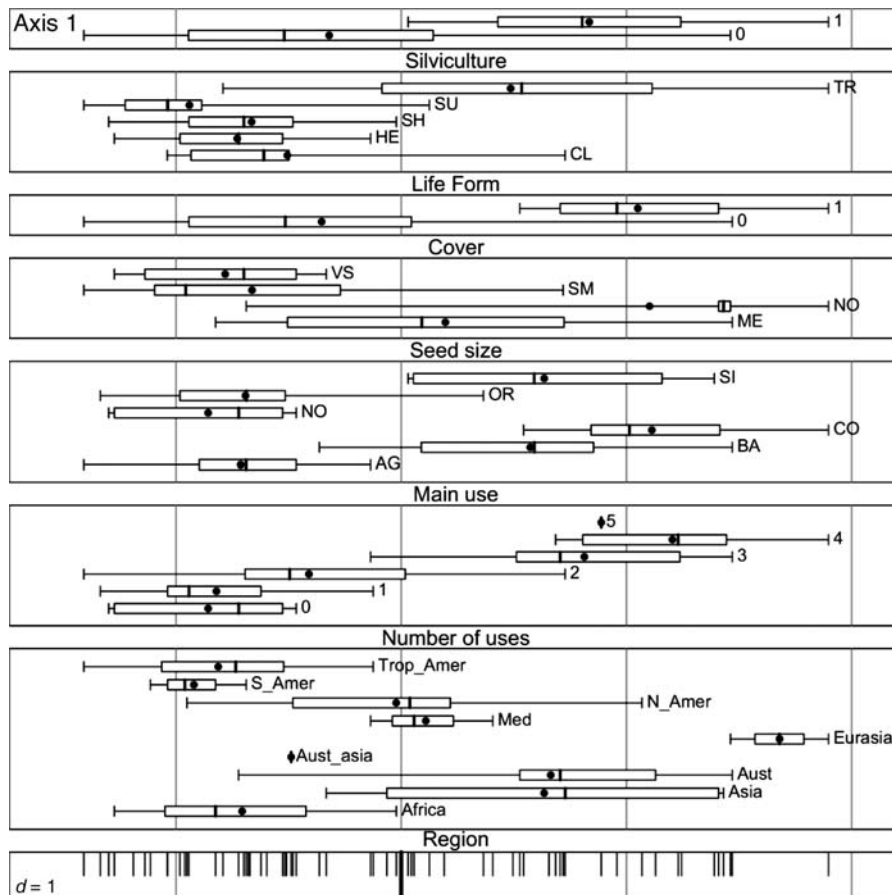
Fig. 3. Representation of the species attributes on the RLQ axes. The horizontal lines for every attribute show minimum and maximum, while the ends of boxes show the second and fourth quartiles of the values. Vertical lines inside boxes represent medians, while the dots represent means. The species attributes most correlated with the RLQ axes are shown, with the factor most strongly correlated shown at the bottom. Small vertical lines at the bottom of each panel correspond to the position of species along the axes. See Table 1 for identification of regional codes.

Australia and were used extensively for all the listed purposes (Table 4 and Fig. 4).

Cluster 5.—Shown to be phylogenetically non-independent (containing several *Opuntia* species). This cluster grouped species occurring everywhere in South Africa at high elevations (Fig. 5). Compared to species in cluster 2, species from this cluster have small seeds dispersed by birds and wind, and are mostly used for ornamental purposes (Table 4 and Fig. 4). The species in this cluster originated from west temperate and tropical regions and have mostly invaded landscapes.

Cluster 6.—Species which have not been imported for specific purposes (Table 4 and Fig. 4). They have invaded landscapes and riparian areas of the eastern part of South Africa and warm areas providing optimal growing days (Fig. 5). They typically come from tropical or warm temperate areas.

Cluster 7.—Phylogenetically non-independent cluster that contained several *Acacia* species. Species from mid-range altitudes close to the sea where the climate is

humid and warm. These species have medium-sized seeds and fix atmospheric nitrogen (Table 4 and Fig. 4). These trees were imported from temperate areas (mostly Australia) for ornamental, silvicultural, and barriers purposes, and are currently invading landscapes and riparian areas (Fig. 5).

DISCUSSION

Joint structure between invasive alien species distribution, environment, and species attributes

The RLQ analysis applied here provides a powerful framework for analyzing the joint structure between species distribution, environmental factors, and species attributes (Dray et al. 2003).

We found strong relationships between the attributes of a species (as measured by a set of intrinsic and extrinsic characters) and the environmental characteristics of the habitats a species invades (as measured by the main underlying environmental gradients). The principal interest in this result resides in its generality:
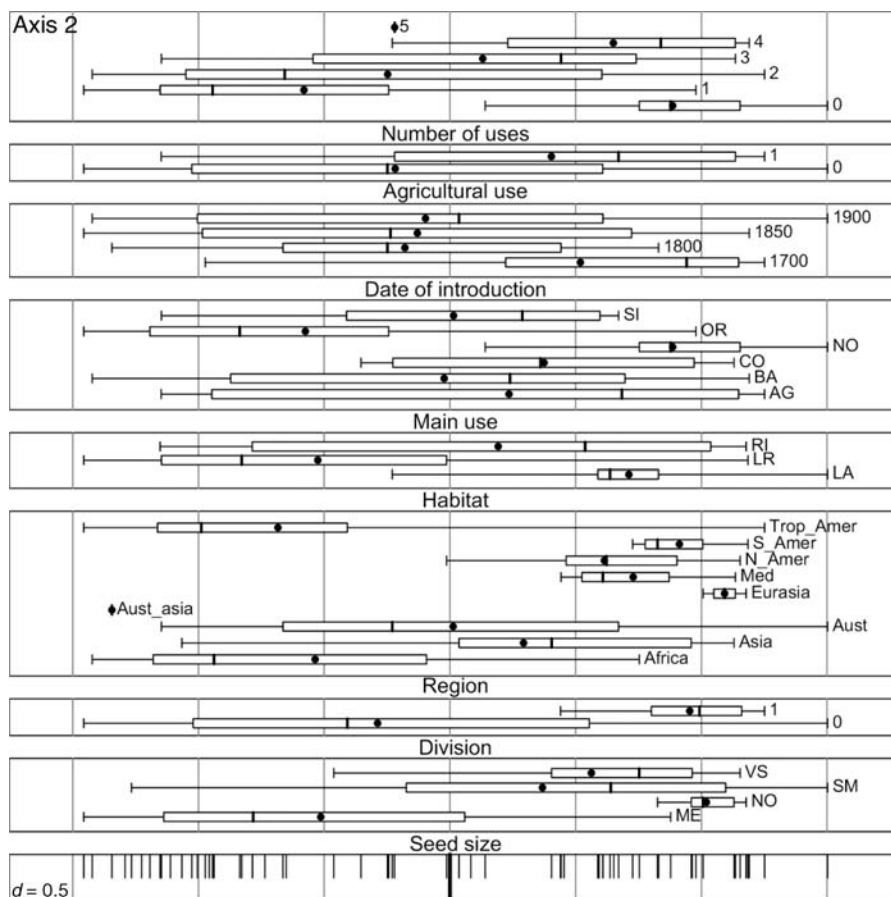
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it demonstrates the direct relationship, reflected in common axes, between an optimized compound measure of environmental variability and an optimized compound measure of intrinsic and extrinsic attribute diversity. The RLQ analysis is, however, mainly descriptive and does not test specific hypotheses. A possible concern relates to the proportion of the results that are explained by the spatial structure of the data. In other words, does spatial autocorrelation inflate the explained deviance? Spatial autocorrelation is inherent to this study, as we used species distribution and environmental variables which are, by their nature, autocorrelated. However, we do not see spatial autocorrelation as a problem in this case. Spatial autocorrelation is problematic when statistical tests are invoked to test hypotheses, because it tends to inflate the actual number of degrees of freedom, and thus leads to the acceptance of some hypotheses which should be rejected. The RLQ analysis provides no such test of hypotheses.

In the RLQ analysis, the first ordination axis explained a large proportion of the total variance in the environmental and species attributes data sets. This suggests a strong underlying environmental gradient

structuring the characteristic of the QDSs and the species invading them. The ordination of the QDSs along this axis closely followed a temperature gradient that drives species diversity and endemicity in South Africa (Cowling et al. 1997b, Thuiller et al. 2004). This main temperature gradient was strongly related to extrinsic attributes of the species and, to a lesser extent, to the life form of the species. In the cooler areas of South Africa the invasive plants are mostly trees that have been imported from Eurasia for specific purposes, such as silviculture. They have been extensively used and planted, many of them in the Cape Floristic Region (Richardson and Cowling 1992, Richardson et al. 1994). Such findings corroborate recent studies demonstrating the importance of the economic context and associated human-mediated vectors in enhancing propagule pressure (Taylor and Irwin 2004, Lockwood et al. 2005).

The second environmental gradient highlighted by the RLQ analysis consisted of humidity and two measures of temperature. It differentiated areas with pronounced extreme temperatures and humidities from areas with less extreme climatic conditions. Not surprisingly, areas with lower mean temperature of the coldest month were
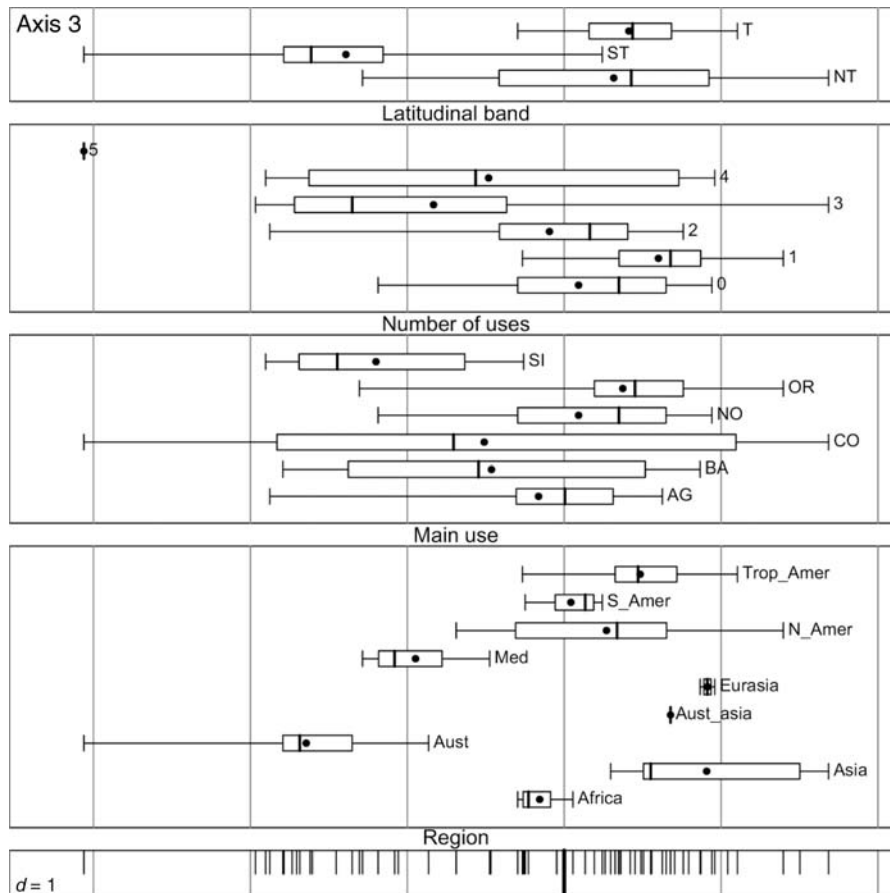
Fig. 3. Continued.

invaded by opportunistic ruderal species or those used for agricultural purposes. The fact that the species invading these areas were introduced recently shows that the increase of transportation networks favors the spread of invasive species, even in remote and extreme areas (Lonsdale 1999).

Finally, the third environmental gradient extracted by the RLQ analysis explained a relatively low fraction of the explained variance for the environmental and the attributes data sets. This energy-altitude gradient was only related to extrinsic characteristics of the species like biogeographical origin and human uses. This gradient separated species that invade at low altitudes and were introduced from Australia for specific commercial and economic reasons (wood production, cover, or barriers) from species that invade more productive areas at higher altitudes, and which were mostly imported as ornamentals. Again, after the integration of environment, this emphasizes that human activity is strongly implicated in shaping the distribution of invasive plant species in South Africa. For example, nonindigenous trees have been imported to South Africa for more than two centuries because of the paucity of native tree species useful in forestry (Richardson 1998).

What explains the spatial pattern of invasive alien species in South Africa?

It is widely recognized that biological invasions are highly idiosyncratic and that predicting the outcome of specific introductions with the precision and accuracy required to have value for management is probably an unrealistic aim (Mack 1996). Although some authors argue that the only generalizations that can be made have very limited value for management, considerable progress has been made in formulating generalizations that explain general patterns and trends (Rejmánek 2000). What is becoming clearly evident is that an understanding of invasion success, expressed for example as the geographic extent of distribution of an introduced species, demands the consideration of numerous intrinsic and extrinsic factors (Rejmánek et al. 2005).

As far as we know, this study is the first detailed assessment of the role of a large number of intrinsic and extrinsic factors in shaping the structure of the geographical ranges of a large number of invasive alien plant species at the scale of a large region (Timmins and Williams 1991). As pointed out by Rejmánek et al. (2005), the main factor preventing the formulation of
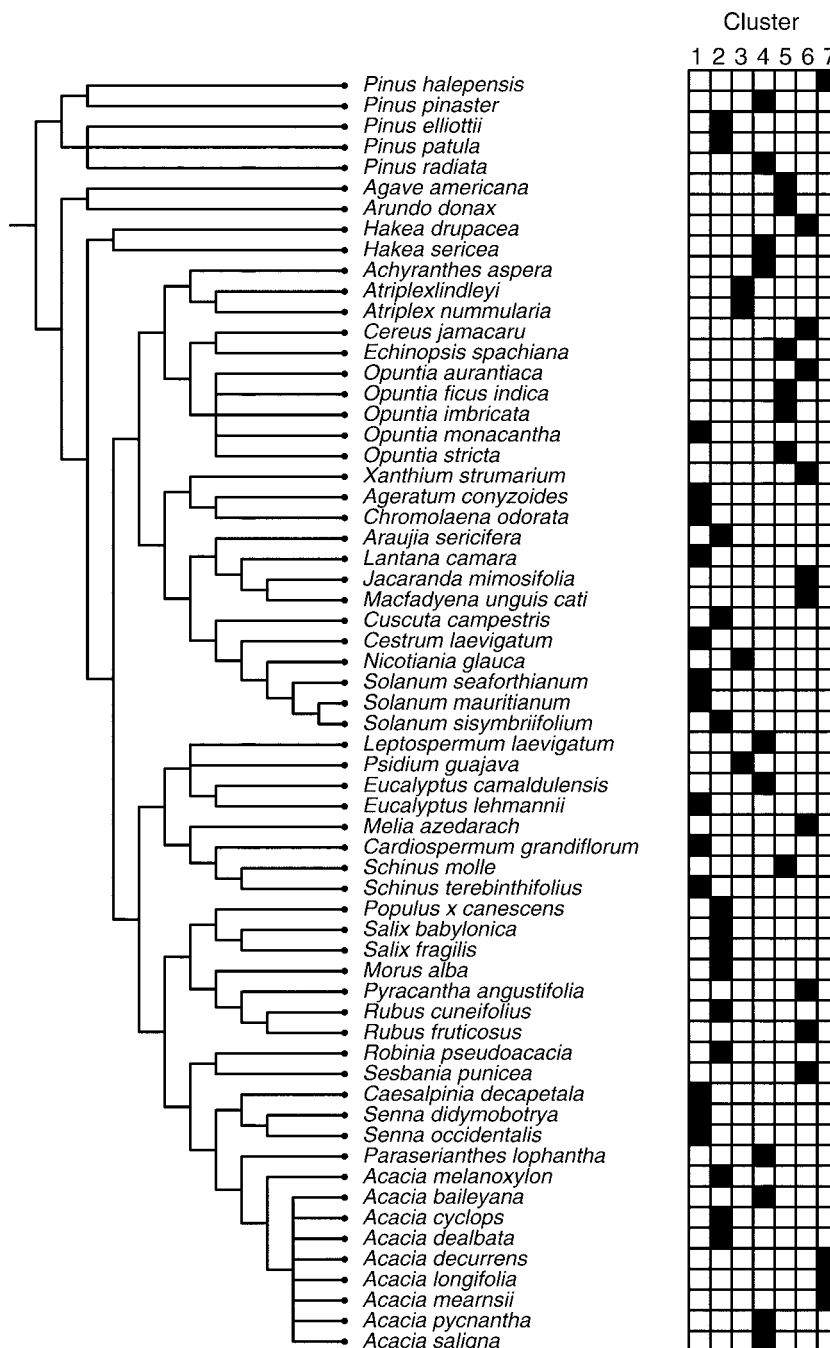
FIG. 4. The seven species clusters, mapped onto a phylogeny of the 62 species.

generalizations at a scale useful to managers is the effect of the environment. In this analysis, by incorporating environmental effects (the R table), we were able to identify the different extrinsic and intrinsic factors which could explain IAS distribution.

By taking environmental factors into account, we showed that the use of species by humans is one of the most important factors explaining the spatial patterns of IAS in South Africa. For instance, in the Cape Floristic

Region most of the major invaders considered in this study were initially grown in large plantations. Similar results have also been observed in southeastern Australia, where Mulvaney (2001) found a strong correlation between the extent of planting and the probability that a woody taxon had become naturalized. In the Southern Hemisphere, the extent of eucalypt planting (propagule pressure) is much more correlated with invasive success than any biological factors used to separate invasive

TABLE 4. Main geographic, environmental, and species attributes characteristics of each cluster.

				Attributes
Cluster	Geography	Environment	Date	Life-history traits
1	Indian Ocean coast, Kruger National Park	warm, humid	1832	small to medium seed, vegetative reproduction by coppice
2	Cape Mountains, high central plateau, Drakensberg Mountains	humid, medium-high elevation	1864	all
3	Cape Mountain succulent karoo	cold in winter, warm in summer, dry; medium elevation	1850	very small, small seed
4	Cape Floristic region	cool and humid in winter; warm and dry in summer	1810	medium seed
5	all South Africa except coastal region	high to medium-high elevation	1829	small seed, wind and bird dispersal
6	eastern South Africa, mostly north	warm, optimal growth	1810	mostly medium seed
7	South African mid-elevation mountains	humid, warm	1812	medium seed, nitrogen fixer

Notes: A prominent example of species is given for each cluster. Date is the mean date of introduction of the species in each cluster.

from less-invasive taxa (Rejmánek et al. 2005). Our findings also corroborate several recent analyses that demonstrate that the underlying causes of biological invasions, and potentially the solution, often lies in the realm of human economic behavior (Taylor and Irwin 2004). In the Cape Floristic Region, this is clearly the case as most major invaders spread from forestry plantations or widespread plantings used to stabilize sand dunes (Richardson 1998).

Although residence time is often identified as a very good correlate of the extent of occurrence of invasive plant species (Rejmánek 2000, Castro et al. 2005), it did not explain the distribution patterns of invaders in South Africa, even after removing the confounding effect of the environment. Although there are obvious reasons to believe that residence time is positively correlated with the extent of occurrence (see Rejmánek

2000, Castro et al. 2005 for discussion), our results show that it is of limited value when considering distribution patterns at the regional scale after a century of residence.

Some life-history traits invoked to explain the invasive potential of species, like seed size, dispersal vectors or vegetative reproduction (Rejmánek and Richardson 1996), are correlated with regional-scale distribution patterns of invasive alien plants in South Africa. For instance, cluster 1 species, invaders in the wet tropical and disturbed environments of South Africa, have very small seed masses and/or are capable of vegetative reproduction. Vegetative reproduction is indeed often responsible for an increase of habitat compatibility and therefore for successful establishment and spread of many species in terrestrial environments and even more so for dispersal in aquatic and wetland habitats (Henderson 1991, Aptekar and Rejmánek 2000). It has
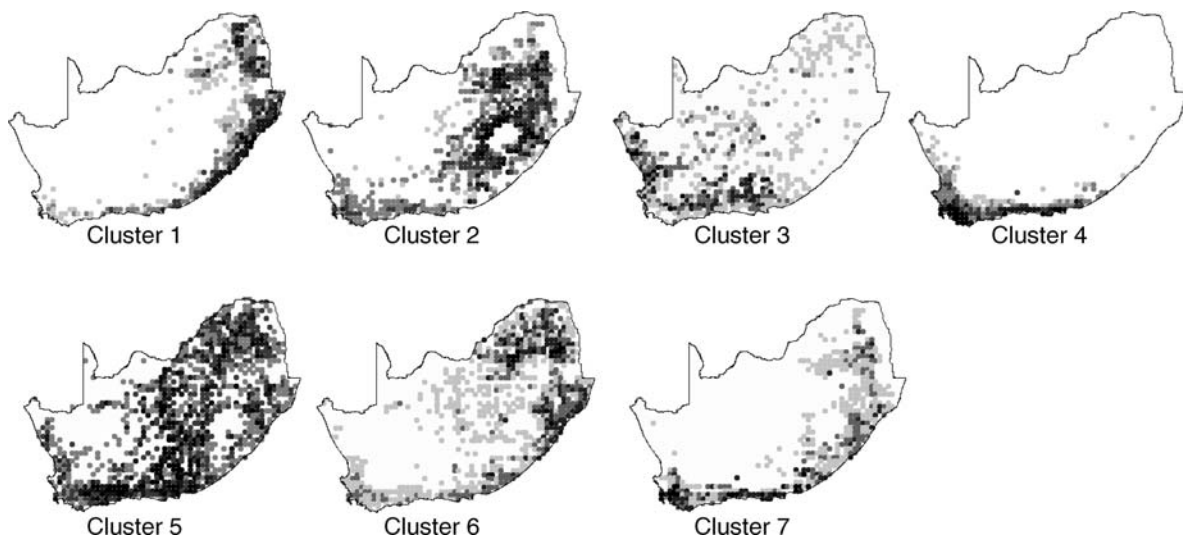

FIG. 5. Geographic representation of the species clusters. The gray scale corresponds to the number of species from each cluster present in each QDS, varying from zero (white) to all species in the cluster present (black).

TABLE 4.   Extended

Attributes			
Use	Origin	Habitat	Species example
ornamental agriculture	tropical	landscape, riparian	*Chromolaena odorata*
ornamental Barrier	temperate	landscape, riparian	*Populus nigra*
all	Australia	landscape, riparian	*Eucalyptus camaldulensis*
all uses extensively	temperate (Australia, Europe)	landscape	*Acacia cyclops*
ornamental	west, temperate and tropical	landscape	*Opuntia stricta*
low no. uses, mostly ornamental	tropical or warm temperate	landscape, riparian	*Jacaranda mimosifolia*
ornamental, silviculture and barrier trees	temperate (Australia)	landscape, riparian	*Acacia mearnsii*

also been observed that invasions of woody species with very small seeds are limited to wet and preferably mineral substrates (Rejmánek and Richardson 1996).

It is also remarkable that only two of the seven clusters were determined by phylogenetic relatedness, and in both of these cases this had to do with en masse introductions of species belonging to recent radiations within genera (in *Acacia* and *Opuntia*; Murphy et al. 2003, Edwards et al. 2005). At higher taxonomic level, the remarkable phenotypic plasticity of higher plants erases all connections with environmental factors, intrinsic species attributes, or human use. Thus, species of similar affinities assemble across South Africa irrespective of their phylogenetic origin.

CONCLUSION

Only after introduced species have been present in an area for long enough to have sampled enough potentially invasible sites and to spread to the full range of such sites, can we assess the relative (and interacting) roles of the many factors that potentially shape the adventive distributions of invasive species (Castro et al. 2005). This study demonstrates that, although biological invasions are species specific, the distribution and spread of major plant invaders can be explained by a combination of environmental factors, life-history traits, and human uses. At large spatial scales (subcontinental in this case) we found that the geographic ranges of invasive species tend to converge on a few relatively distinct clusters. Interestingly, the membership of these clusters can be explained by a small number of intrinsic and extrinsic factors related to the biology and ecology of the taxa and their interaction with the environment and humans. Such information is very useful for improving our ability to screen species and identify which ones might spread in different regions, and to predict the geographic area most likely to be impacted by a given species. It is also crucial to recognize that human-aided dissemination is critically important for dispersal within the adventive range—and is often much more important than the intrinsic dispersal capacity of the IAS (Lonsdale 1999, Lockwood et al. 2005).

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APPENDIX A

A list of names and abbreviations of the species entered in the analysis (*Ecological Archives* E087-103-A1).

APPENDIX B

A three-dimensional representation of the K-means cluster analysis based on the mean position of the species along the three RLQ axes (*Ecological Archives* E087-103-A2).