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Species richness of alien plants in South Africa: Environmental correlates and the relationship with indigenous plant species richness[1]

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Abstract: This study explores the correlates of alien plant species richness in South Africa at the scale of quarter-degree squares (QDS; ≈ 25 × 27 km; 675 km^2). We considered all alien plant species for which we had records and a subset of these – those that invade natural and semi-natural vegetation. The main source of data for species richness of indigenous and alien plant species was a national database based on herbarium specimens. For invasive alien species, data were from a national atlassing project. First, we explored the importance of energy availability and habitat heterogeneity as correlates of indigenous, alien, and invasive alien plant species richness. Linear regression models showed that species richness in the three groups of plants was explained by the same variables: a principal component of climatic factors and topographic roughness were the top-ranking variables for all groups. Next, we examined the role of indigenous species richness together with a range of environmental and human-activity variables in explaining species richness of alien and invasive alien plants. Results reveal an interplay of natural features and variables that quantify the dimension of human activities. If indigenous species richness is ignored, human-activity variables are more strongly correlated with alien species richness than with invasive alien species richness. Numbers of alien and invasive species in QDSs are significantly correlated with indigenous plant species richness in the 1,597 QDSs selected for analysis, a pattern consistent with findings from other parts of the world. Analysis of residuals between observed and predicted values showed that patterns differed between biomes. The results are useful for planning long-term intervention policy at the national scale; they suggest that areas with rich native biodiversity will face a sustained onslaught from invasive alien species and that ongoing management actions will be required to reduce and mitigate impacts from biological invasions in these areas.

Keywords: biological invasions, determinants of species richness, exotic species, plant invasions.

Résumé : Cette étude explore les patrons géographiques de la richesse en espèces chez les plantes exotiques de l'Afrique du Sud au sein de zones ayant une superficie approximative de 675 km^2 (25 × 27 km). Nous avons tenu compte de toutes les espèces exotiques pour lesquelles nous avions une mention et d'un sous-ensemble de celles-ci, soit les espèces qui envahissent la végétation naturelle et semi-naturelle. Nous avons utilisé comme principale source d'informations une banque de données nationale constituée à l'aide de spécimens d'herbier. Les données spécifiques aux espèces exotiques envahissantes proviennent d'un projet d'atlas national. Nous avons d'abord évalué l'importance de la disponibilité en énergie et l'hétérogénéité de l'habitat en tant qu'indicateurs de la richesse des espèces indigènes, exotiques et envahissantes. Les modèles de régression linéaire montrent que la richesse en espèces des trois groupes de plantes est expliquée par les mêmes variables. Les deux groupes de variables les plus importants sont les facteurs climatiques et le relief. Nous avons également examiné le role des espèces indigènes, de plusieurs variables environnementales et d'autres variables associées aux activités humaines pour expliquer la richesse des espèces exotiques et envahissantes. Les résultats révèlent une interaction entre les caractéristiques naturelles et les variables qui quantifient l'importance des activités humaines. Lorsque la richesse des espèces indigènes est ignorée, les variables associées aux activités humaines sont plus fortement corrélées à la richesse des espèces exotiques qu'avec celle des espèces envahissantes. Le nombre d'espèces exotiques et d'espèces envahissantes au sein de chaque zone de 675 km^2 est corrélé de façon significative avec la richesse des espèces indigènes, un phénomène qui a été observé ailleurs dans le monde. L'analyse des résidus des valeurs observées et des valeurs prédites montre que les patrons diffèrent toutefois selon les biomes. Les résultats peuvent servir à planifier des politiques d'intervention à long terme, à l'échelle nationale. Ils suggèrent que les secteurs riches en espèces indigènes seront plus susceptibles d'être colonisés de façon soutenue par des plantes exotiques envahissantes et que des mesures d'atténuation devront être prises pour en diminuer les impacts.

Mots-clés : determinants de la richesse des espèces, espèces exotiques, invasions biologiques, plantes envahissantes.

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Introduction

Many factors interact to determine whether an organism can gain entry to and then maintain membership of a community. Questions relating to these issues are at the core of biogeography, community ecology, and associated disciplines. Research in this area has been given new impetus in recent decades with the dramatic increase in the human-mediated movement of organisms around the world. Major biogeographic barriers are now readily breached and a bewildering number of organisms are being exposed to new environments. The increasing pervasiveness of biological invasions and the escalating magnitude of impacts caused by alien species have added urgency to the quest for a robust understanding of the determinants of invasibility. Practical insights are required to inform management, but biological invasions also provide superb opportunities for testing key assumptions underpinning theory in biogeography and ecology.

Global and regional-scale studies, starting with Elton (1958), have found that diverse communities better resist invasion by exotic species than do communities comprising fewer species, implying some kind of "biotic resistance", a notion supported by MacArthur's species-packing and diversity-stability models (Levine, Adler & Yelenik, 2004). On the other hand, Lonsdale's (1999) influential global assessment of patterns of plant invasion revealed that "communities" (actually regions of varying size and complexity) richer in indigenous species had more, not fewer, alien species. Many recent studies across the globe have confirmed this pattern. At scales of landscapes and above, there is a strong positive relationship between indigenous and alien species richness (reviewed by Stohlgren, Barnett & Kartesz, 2003). The recent explosion of empirical studies, mostly in small plots, shows the opposite: a negative relationship between indigenous and alien species richness.

It appears that biotic resistance generally applies at small spatial scales, although there is little evidence that this can ever completely repel invasions (review in Levine, Adler & Yelenik, 2004). As one moves to larger spatial scales, the increased area simply translates to increased habitat heterogeneity (or "habitat diversity") which is well known to be positively correlated with species richness for many taxa (Rosenzweig, 1995; Ricklefs & Lovette, 1999; Qian & Rickleffs, 2000; Kerr, Southwood & Cihlar, 2001; Pyšek, Jarošík & Kucera, 2002; Pino *et al.,* 2005). At such (large) spatial scales, there is thus support for the notion that "the rich get richer" (Stohlgren, Barnett & Kartesz, 2003). The implication is that the threat of invasion by alien plants is greatest in hotspots of biodiversity.

South Africa has one of the biggest problems with invasive alien plants in the world, and the region has a long history of research on plant invasions. Most insights are from studies at small spatial scales (reviews in Richardson *et al.,* 1997; Richardson & van Wilgen, 2004), and there is uneven coverage of information across the region; by far the most work has been in the fynbos biome. The substantial problems caused by alien plant invasions are being addressed in a major national program (Working for Water; van Wilgen, Le Maitre & Cowling, 1998; Hobbs, 2004). This program, one of the largest ecosystem restoration initiatives in the world, has made significant progress in combating the spread and impacts of invasive alien species across South Africa. Sustained success in such a program demands national-scale planning to optimize the allocation of resources with regard to regions and species (Nel *et al.,* 2004; Rouget *et al.,* 2004). This paper contributes to informing national-scale planning to guide strategic management interventions through an improved understanding of invasion dynamics and the susceptibility of different biotic entities (communities, biomes) to invasion.

The South African region is ideal for testing key assumptions relating to the relationship between indigenous richness of ecosystems and their susceptibility to invasion by introduced plants. Firstly, the region has a spectacularly rich native flora (*ca* 23,000 species) that is well documented, with relatively good data on the distribution of individual taxa. Secondly, South Africa (1,219,090 km^2) has a wide range of major habitats, including deserts, semi-arid shrublands, mediterranean-type ecosystems, grasslands, savannas, and temperate forests (eight major terrestrial biomes; Rutherford, 1997). This provides the opportunity of exploring whether relationships between species richness and invasibility differ between biomes. Thirdly, the region has a long history of exposure to alien plant species (> 350 y) — enough time for many species to be exposed to a wide range of environmental conditions. Many plant species are naturalized or invasive (Richardson *et al.,* 1997; Henderson, 2001; Nel *et al.,* 2004; Rouget *et al.,* 2004), and good distribution data are available at the same scale as for indigenous species (Henderson 1998; 1999; 2001). Importantly, we have a reasonable understanding of the determinants of indigenous plant species richness throughout the region (Linder, 1991; Cowling *et al.,* 1997; O'Brien, Field & Whittaker, 2000; Cowling & Lombard, 2002). Considerable effort has been devoted to planning conservation strategies to ensure the long-term persistence of the region's rich biodiversity (see Balmford, 2003; Cowling *et al.,* 2003). Knowing whether parts of the region are predisposed to invasions would be useful for planning effective conservation strategies.

This paper examines the broad-scale distribution and richness patterns of alien plant species in South Africa. In particular, we examine whether the richness of alien species is correlated with the same suite of variables as indigenous species. For alien and invasive alien species we then explore how environmental factors (metrics of energy availability and habitat heterogeneity) and human-activity factors interact with indigenous plant species richness to determine richness patterns.

Methods

DATABASES

PRECIS

The National Herbarium Pretoria (PRE) Computerized Information Service ("PRECIS") comprises over 800,000 herbarium specimens collated from all major South African herbaria (Germishuizen & Meyer, 2003). It is the largest plant specimen collection in Africa, with records for over 24,000 taxa. PRECIS specimens cover mostly southern Africa, and most of them were collected after 1960. For each record, the specimen locality is indicated using a grid reference system of 0.25 degrees latitude by 0.25 degrees longitude (roughly 25 × 27 km; 675 km^2). Despite the large number of records, some geographic areas have clearly been under-sampled and others over-sampled (see later for discussion on dealing with sampling biases). We used PRECIS to compile a list of all species occurring in each of the 2,014 quarter-degree squares (QDS) covering South Africa. A species was considered as a binomial taxon (genus and species name); we did not consider sub-species or varieties. 1,294 taxa in PRECIS were classified as alien, including cultivated species.

CATALOGUE OF PROBLEM PLANTS (WELLS)

The "Catalogue of problem plants in southern Africa" (Wells *et al.,* 1986) (hereafter "Wells") lists 1,653 plant taxa that cause a wide range of problems (environmental and a range of human health problems). A filtered list of taxa from Wells including 711 species alien to South Africa (see Richardson *et al.,* 2003, p. 295 for details) was used in this study.

SAPIA

The Southern African Plant Invaders Atlas (SAPIA) is the best source of data on the distribution of invasive alien plants in South Africa, Lesotho, and Swaziland. The SAPIA database contains records for over 500 species, with information on their distribution, abundance, habitat preferences, and date of introduction (Henderson, 1998; 1999; 2001). Only alien species invading natural or semi-natural 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.,* 2000). It is important to note that SAPIA is biased in favour of woody species. Invasive alien grasses and other herbaceous taxa are under-represented. Records are geo-referenced by QDS. A problem we confronted was how to deal with records that gave only a genus name (*ca* 10% of taxa in SAPIA). Our approach was to include genus-level records only where the record was the only one in the database for that genus. All other genus-level records were ignored, since such records overlap with taxa already included in the dataset and inclusion of such taxa would inflate species richness (see further discussion in Nel *et al.,* 2004).

DATA PREPARATION

SPECIES DATABASES

We compiled three species lists (alien, invasive alien, and indigenous species) from the PRECIS, Wells, and SAPIA databases described above.

ALIEN SPECIES LIST

We combined all species classified as alien from PRECIS, Wells, and SAPIA. Considerable effort was made to align taxon names in the three datasets; this involved mainly combining synonyms. All species were also checked to verify their distribution status (alien *versus* indigenous; see discussion in Pyšek *et al.,* 2004). Special attention was required for taxa classified as of "unknown" origin in PRECIS. If these were recorded as alien in Wells or SAPIA, they were taken to be alien; otherwise they were classified as indigenous. We only added cultivated alien species if they were also recorded in SAPIA (*i.e.,* naturalized or invasive alien). The final list of "alien" taxa includes 1,226 taxa that are not native to South Africa. Distribution records for each taxon were sourced from PRECIS and SAPIA. An important difference between this list and that of invasive alien species is that the "alien" list includes many weeds of agriculture and other human-modified habitats.

INVASIVE SPECIES LIST

Our list of "invasive alien" species includes only those species listed in SAPIA, *i.e.,* those taxa that are naturalized or invasive *sensu* Richardson *et al.* (2000) and Pyšek *et al.* (2004) in natural or semi-natural vegetation. "Natural or semi-natural vegetation" includes all vegetation that has not been markedly transformed through human activity. Distribution records for these species were drawn only from SAPIA. The list contained 497 species. All of these species are also included in the "alien" list.

INDIGENOUS SPECIES LIST

All species listed in PRECIS but not included in the alien species list (see above) were deemed indigenous. This includes 21,962 species listed as indigenous or unknown in PRECIS. Distribution records were sourced only from PRECIS.

We computed the number of indigenous, alien, and invasive alien plant species for each of the 2,014 QDSs in South Africa. These data were plotted on maps using ArcView GIS software, version 3.2, ESRI, Redlands, California, USA.

DATA ON ENVIRONMENTAL FEATURES AND HUMAN ACTIVITIES

For each QDS we identified and computed various explanatory variables relating to environmental features and human activities. Our set of environmental variables was compiled to capture (as best we could, given the crude spatial scale) factors relating to energy availability and habitat heterogeneity (see Table I). We chose these two variable groups since research on the determinants of plant richness in southern Africa at the regional scale has consistently shown that patterns are explained by energy availability (*sensu* Evans, Warren & Gaston, 2004) and habitat heterogeneity (O'Brien, 1993; Cowling *et al.,* 1997; O'Brien, 1998; O'Brien, Field & Whittaker, 2000; Cowling & Lombard, 2002). For energy availability, we used three components from a Principal Components Analysis conducted by Rouget *et al.* (2004) to derive a small number of variables with interpretable influence on plant distribution (see Table I and Figure 1 in Rouget *et al.,* 2004). PCA1, which was most strongly correlated with number of growth days per year, minimum soil water stress, and mean annual precipitation, appears to be a particularly useful variable for summarizing "productive energy metrics" as defined by Evans, Warren, and Gaston (2004), whereas PCA2, associated mainly with frost duration and mean temperature of the coldest month, integrates important "solar energy metrics" (*sensu* Evans, Warren & Gaston, 2004). Species richness and abundance

TABLE I. List of variables related to environmental and human-activities factors used in the analysis.

Factors (codes)	Description	Source
ENVIRONMENTAL – ENERGY AVAILABILITY		
3 PCA components (PCA1; PCA2; PCA3)	First three components of a Principal Components Analysis based on eight climatic factors. Factors contributing most to the components are: 1) growth days per year (+), minimum soil water stress (-), mean annual precipitation (+), and mean temperature of the hottest month (-); 2) frost duration (-) and mean temperature of the coldest month (+); 3) growth temperature (+) and mean annual precipitation (+).	Rouget *et al.*, 2004
ENVIRONMENTAL – HABITAT DIVERSITY		
Topographic roughness (TOPO)	Ratio between planimetric and real surface	South African National Biodiversity Institute, unpubl. data
Number of vegetation types (VEG TYPE)	Vegetation type diversity as a surrogate of environmental heterogeneity	Mucina & Rutherford, in press
Ecotones (ECOTONE)	Presence of two or more biomes in a QDS	Mucina & Rutherford, in press
Biomes (BIOME)	Predominant biome in each QDS	Mucina & Rutherford, in press
HUMAN-ACTIVITY FACTORS		
Human population density (POP96)	Population density based on 1996 survey, summarized to QDS	Statistics South Africa, unpubl. data
Road density (ROADS)	Road density (excluding gravel roads) (km) per QDS	Department of Survey and Mapping, unpubl. data
(Major roads)	Major road density (km) per QDS	Department of Survey and Mapping, unpubl. data
% of urban area (URBAN)	Urban area expressed as a percentage of QDS area	Fairbanks *et al.*, 2000
% of natural vegetation (NATURAL)	Natural vegetation area expressed as a percentage of QDS area	Fairbanks *et al.*, 2000

of alien species is, by definition, highly dependent on human activities. We selected a suite of human-activity factors (appropriate and feasible to compute at the scale of QDSs; Table I) that are known to affect the presence and abundance of alien and invasive alien plant species in South Africa (for a review, see Le Maitre, Richardson & Chapman, 2004).

DEALING WITH SAMPLING BIAS IN THE DATASETS

Neither PRECIS nor SAPIA is an ideal source of distribution data for our study. Both suffer from being based on *ad hoc* specimen collections and atlas records rather than a systematic sampling of taxa. To reduce spurious results due to collection bias to some extent (the arid interior of the country has clearly been under-sampled for indigenous, alien, and invasive alien species) (Gibbs Russell, Retief & Smook, 1984), we excluded from our analysis those QDSs where fewer than 10 indigenous species and/or where no alien species had been recorded. This cut-off excludes most areas known to be poorly collected. Over-sampling bias could not be controlled systematically since concentrations of plant species richness are known to coincide with concentrations of human activity at the scale of our study, and because alien density is likely to be influenced by human activity.

DEFINING SPATIAL EXTENT OF BIOMES AND MAJOR HABITAT TYPES

To facilitate separate analyses of the relationship between alien and indigenous species richness in different major habitat types, we classified QDSs by overlaying the grid of cells with the South African biomes defined by Mucina and Rutherford (in press). Biomes in South Africa, and their constituent vegetation types, are regularly used as a framework for generalizations concerning the ecology and biogeography of the region's biota, and as a foundation for conservation assessments and actions (Huntley, 1989; Low & Rebelo, 1996; Barnes, 1998; Van Rensburg *et al.,* 2004). There are reasonably sharp transitions between biomes (Rutherford & Westfall, 1994; Low & Rebelo, 1996). The biomes are defined based on five explicit criteria: *i*) they are the largest land community unit recognized at a continental or subcontinental level; *ii*) they are mappable at a scale of no larger than about 1:10 million; *iii*) they are distinguished from other biomes primarily on the basis of Raunkiaer's life-form classes; *iv*) they are distinguished from other biomes secondarily on the basis of major climatic features that most affect the biota; and *v*) they are not unnatural or major anthropogenic systems. Characteristics of the biomes are described by Rutherford and Westfall (1994) and Rutherford (1997). Where > 75% of the area of a QDS was covered by any one of the major biomes of South Africa (*i.e.,* forest, fynbos, grassland, Nama-karoo, savanna, succulent karoo, thicket, and wetlands), the QDS was assigned to that biome. Because of the small size of patches comprising the forest biome and the wetlands, no QDSs were classified as forest or wetland. Only 22 QDSs were assigned to thicket, and this biome was not considered in the analysis. We were also interested to flag those QDSs covered by large sections of more than one biome, since such areas presumably have greater habitat heterogeneity (and thus, potentially, species richness). QDSs where no single biome/habitat type covered > 75% of the cell were classified as "ecotones". From here on, reference to "biomes" includes the category "ecotones".

ANALYSES

Linear least-squares regression models were used to explore the relative importance of a range of variables associated with energy and habitat heterogeneity (Table I) in explaining species richness of indigenous, alien, and invasive plants in QDSs. Regression tree analysis was then used to show how indigenous species richness and the full suite of metrics of energy availability, habitat heterogeneity, and human activities affected species richness of alien and invasive alien plants. This non-parametric technique is appropriate because it detects interactions between factors and accommodates both categorical and continuous factors. Regression tree analysis successively splits the data into smaller subsets, based on the values of the predictor variables (Breinam *et al.*, 1994). Each split is designed to separate the cases in the node being split into a set of successor nodes that are maximally homogeneous. The output is a dendrogram, or tree diagram, which provides an intuitive pictorial interface for understanding the structuring of the problem and an effective way for making further predictions. Regression tree analysis has been successfully used in similar studies (De'ath & Fabricius, 2000; Foxcroft *et al.,* 2004; Thuiller *et al.,* 2003). We used S-Plus 2000 Professional Release 3 (MathSoft Inc., 2000) for the linear regression models and for fitting and examining regression trees. The number of nodes in the regression trees was limited to 10 as our primary interest was to identify the main factors controlling species richness.

For exploring the relationship between indigenous and alien and invasive alien species richness, data were log transformed (log [x + 1]) to ensure normality: (x + 1) to deal with zero values. We fitted linear regression models to predict alien and invasive alien species richness using indigenous species richness as the independent variable. We plotted indigenous *versus* predicted alien and indigenous *versus* predicted invasive alien species richness for the whole of South Africa and separately for each of six biomes to compare patterns and slopes. We then calculated the average residual value for all QDSs assigned to different biomes.

We mapped the residuals of the national model for alien and invasive alien plant species richness. We further explored factors influencing residuals in the national model using the variables in Table I in a regression tree analysis (see above).

Results

National-scale patterns

417 QDSs (out of 2,014; 21%), mainly concentrated in the arid interior of the country, were excluded from the analysis because of low sampling effort (Figure 1a). Areas of high species richness coincide in the maps for

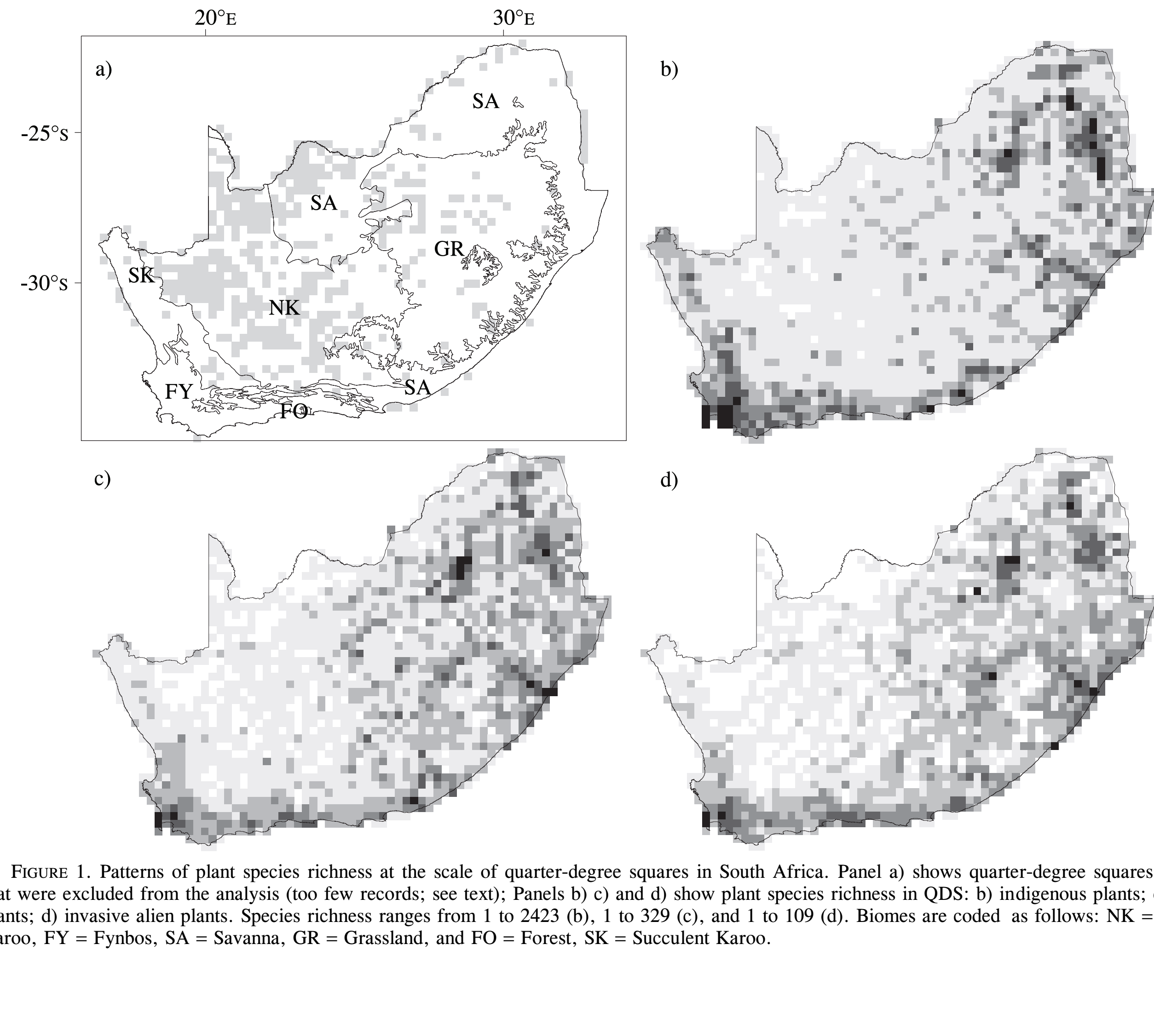

FIGURE 1. Patterns of plant species richness at the scale of quarter-degree squares in South Africa. Panel a) shows quarter-degree squares (QDS) that were excluded from the analysis (too few records; see text); Panels b) c) and d) show plant species richness in QDS: b) indigenous plants; c) alien plants; d) invasive alien plants. Species richness ranges from 1 to 2423 (b), 1 to 329 (c), and 1 to 109 (d). Biomes are coded as follows: NK = Nama-Karoo, FY = Fynbos, SA = Savanna, GR = Grassland, and FO = Forest, SK = Succulent Karoo.

indigenous, alien, and invasive alien plants; all show highest richness at the southwest tip of the region, extending eastwards along the coast and into the northeastern interior (Figure 1b-d). Linear regression showed that species richness in the three groups of species is determined by the same set of factors, with PCA1 and TOPO emerging as the most important contributors to deviance in the models for all groups (Table II). These two variables accounted for 27% of deviance explained for the three groups in stepwise linear regression.

When indigenous plant richness is added to models for alien and invasive alien species, it emerges as the pivotal factor for explaining species richness, with human-activity and environmental factors emerging as secondary determinants (Figures 2 and 3). Alien species richness is highest in areas of high indigenous richness that are also highly urbanized with dense networks of roads and/or dense concentrations of humans (Figure 2). In this group, environmental correlates of richness seem to be adequately captured by the richness of indigenous species, and metrics of energy availability and habitat heterogeneity add little additional explanatory power. The pattern for invasive alien species seems to be explained by factors that define where species-rich natural vegetation occurs in close proximity to areas with high levels of human activity (Figure 3).

Strong positive relationships are evident between indigenous and alien/invasive alien species richness (Figure 4a and b). There is a stronger correlation between indigenous and alien species than between indigenous and invasive alien species richness (Spearman's rho = 0.75 and 0.54, respectively).

The spatial pattern of residuals (QDSs where species richness is over- or under-predicted) is not random (Moran's I randomization test [1,000 permutations] using Ade4 library in R; Cliff & Ord, 1973; Thioulouse, Chessel & Champely, 1995; $P < 0.001$ for both alien and invasive alien species) (Figure 5). The pattern of QDSs with good fit (*i.e.,* good match between observed and predicted richness) closely matches the pattern of highest species richness for all taxa (Figure 1b-d). Under-prediction (fewer alien and invasive alien species predicted than observed) is concentrated in the eastern interior of the country, whereas over-prediction is concentrated in the west. The key factor explaining residuals is biome, followed by a variety of human-activity and environmental factors (Figure 6).

BIOME-SCALE PATTERNS

Species richness of alien and invasive alien species is over-predicted in two biomes (Nama-karoo and succulent karoo) and under-predicted in one biome (grassland) (Figure 7). The fit is reasonable in fynbos, savanna, and ecotone. Interestingly, the trend (over- or under-prediction) was the same for alien and invasive alien species in all biomes except for fynbos, where alien species were slightly over-predicted whereas invasive aliens were slightly under-predicted.

Figures 8 and 9 show the relationships between indigenous and alien species richness (Figure 8) and between indigenous and invasive alien species richness (Figure 9) for the six biomes. Alien species richness was more strongly correlated with indigenous species richness than was richness of invasive alien species with indigenous species. There are marked differences (with fairly similar patterns in Figures 8 and 9) between biomes. For alien species, there are significant differences between biome and average models for the grassland and savanna biomes (slopes and intercepts significantly different; $P < 0.05$). For invasive alien species, significant differences were evident for the fynbos and ecotone (slopes significantly different; $P < 0.05$) and for the grassland biome (intercepts significantly different; $P < 0.05$).

Discussion

The main finding of this study is that species richness for the three groups of plant species studied (indigenous, alien, and invasive alien) at the scale of quarter-degree squares (QDSs) in South Africa is strongly inter-correlated, and that richness in all three groups can be explained by the same set of variables related to energy and habitat heterogeneity. For both alien and invasive alien species, the best single predictor of species richness at the scale of QDSs is the richness of indigenous plant species. Richness in all groups is highest in areas of high productivity (where moisture and thermal conditions are favourable for plant growth) that are also environmentally heterogeneous. These factors explain plant richness at this (regional) scale in many other situations (Richerson & Lum, 1980; Rosenzweig, 1995; Qian & Ricklefs, 2000). The finding that species richness of alien plant species is highly correlated with richness of native plant species corroborates results from other studies at the scale of landscapes and regions from other parts of the world (Lonsdale, 1999; Stohlgren, Barnett & Kartesz, 2003). The relationship between indigenous and alien (and invasive alien) species richness at the scale of QDSs also holds when different biomes are analyzed separately, although the strength of the relationship differs between

TABLE II. The contribution of metrics of energy availability and habitat diversity to deviance in species richness in indigenous, alien, and invasive alien plant species in quarter-degree squares in South Africa. Results are from Generalized Linear Models (see text). Variables (see Table I for explanation) are ranked in descending order of deviance. The cumulative deviance (Cum Dev) is shown.

	Indigenous plants		Alien plants		Invasive alien plants	
Rank	Variable	Cum Dev	Variable	Cum Dev	Variable	Cum Dev
1	TOPO	17.4	PCA1	18.8	PCA1	16.0
2	PCA1	27.7	TOPO	27.3	TOPO	26.6
3	VEG TYPE	35.3	VEG TYPE	31.1	VEG TYPE	36.3
4	PCA2	40.4	PCA2	33.6	PCA2	37.9
5	PCA3	40.7	PCA3	34.5	ECOTONE	39.0
6	ECOTONE	40.8	ECOTONE	34.6	PCA3	39.8

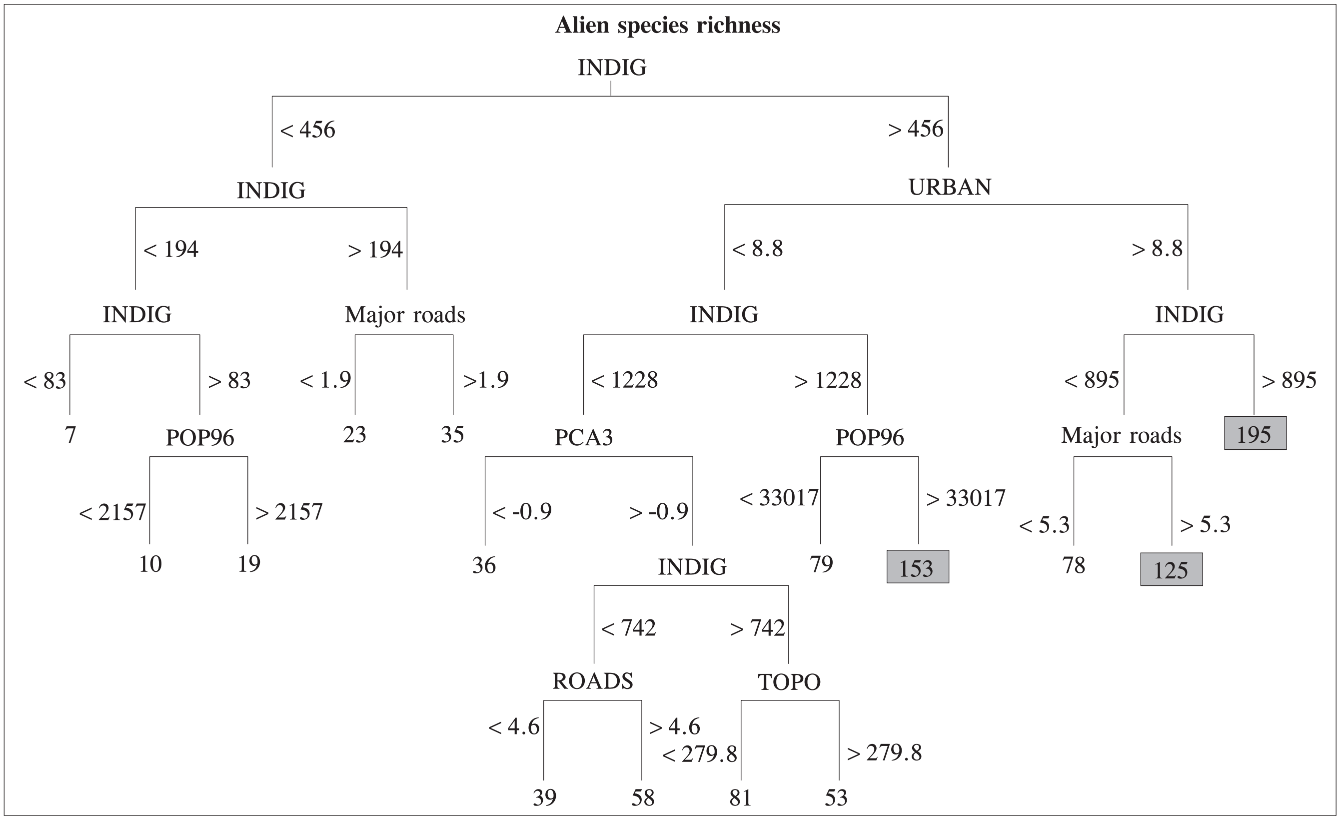

FIGURE 2. Regression tree showing the determinants of species richness for alien plants at the scale of quarter-degree squares in South Africa. Significant variables are mentioned at the top of the branch, conditional values are shown on both sides of each branch, and predicted alien species richness is indicated for each terminal node (*e.g.*, predicted alien species richness = 7 for QDS with < 83 indigenous plant species). Codes of significant variables are listed in Table I. Terminal nodes where highest species richness is predicted are highlighted.

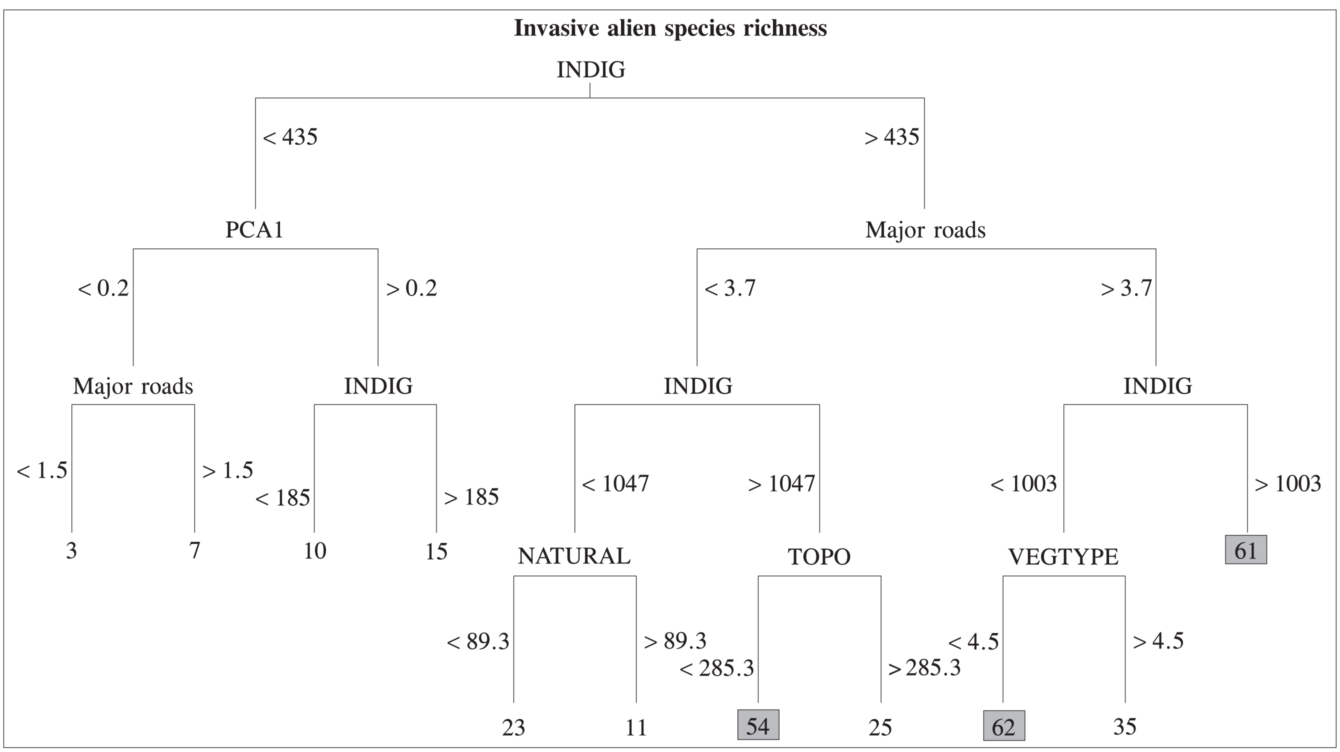

FIGURE 3. Regression tree showing the determinants of species richness for invasive alien plants at the scale of quarter-degree squares in South Africa. Significant variables are mentioned at the top of the branch, conditional values are shown on both sides of each branch, and predicted invasive alien species richness is indicated for each terminal node. Codes of significant variables are listed in Table I. Terminal nodes where highest species richness is predicted are highlighted.

these units. Differences in the relationships between biomes are probably at least partly due to sampling biases. Although we attempted to reduce the influence of sampling bias by excluding from the analysis areas known to be under-sampled, further work is required to understand fully the influence of this bias. However, since the data sets from PRECIS (for indigenous and alien species) and SAPIA (for invasive alien species) have similar biases (under-collection in remote regions), we believe that such biases do not alter the major patterns that emerge. Certainly, there is considerable scope for further work to produce enhanced surfaces of species richness for the different plant groups. We believe that the broad-scale patterns of species-richness of alien and invasive alien species, and therefore the observed set of correlates, are robust. Support for this notion comes from the results of the modelling study of Rouget *et al.* (2004), which derived a map of potential species richness of invasive species based on combined bioclimatic envelopes of 71 of the most important invasive species. Their derived map of potential species richness is very similar to Figure 1d. Given that most of the emerging invaders in South Africa are spreading in the same areas currently affected by those invaders that are already well established (Nel *et al.,* 2004), this gives us further confidence that the patterns captured in Figure 1 are real and not artefacts of sampling. We should stress that patterns of species richness do not necessarily equate to species cover or biomass of alien species and therefore impact (for discussion see Rouget *et al.,* 2004).

The findings of our study provide further support for the notion that "the rich get richer", *i.e.,* that alien species richness is highest in regions with the most diverse assemblages of indigenous species, or that what is good for native species is good for alien species (Stohlgren, Barnett & Kartesz, 2003 and references therein). The similarity in patterns of species richness for indigenous and alien species is remarkable, since the processes that produce the patterns are very different. For indigenous species, richness patterns are the product of ecological processes including speciation, migration, and extinction over evolutionary timescales. For alien plant species in South Africa, species richness patterns are largely the result of introduction patterns: alien species are concentrated in regions where humans have formed hubs of settlement over the past three centuries (Le Maitre, Richardson & Chapman, 2004). Previous studies have documented the strong correlation between species richness and human density in South Africa: both respond

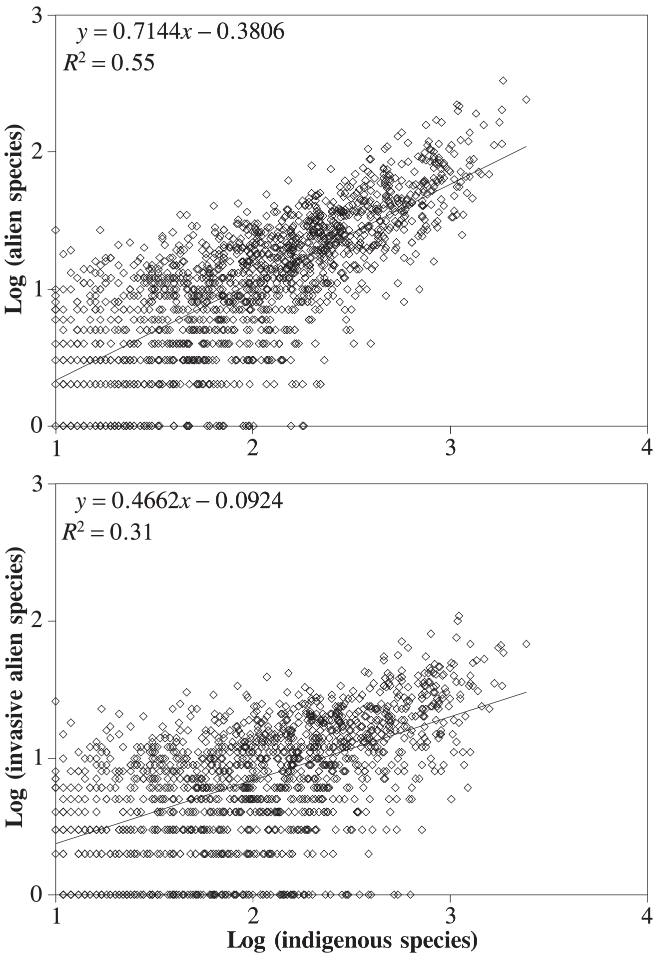

FIGURE 4. Relationships between species richness of indigenous and alien (a) and indigenous and invasive alien plant species (b) ($P < 0.0001$ for both).

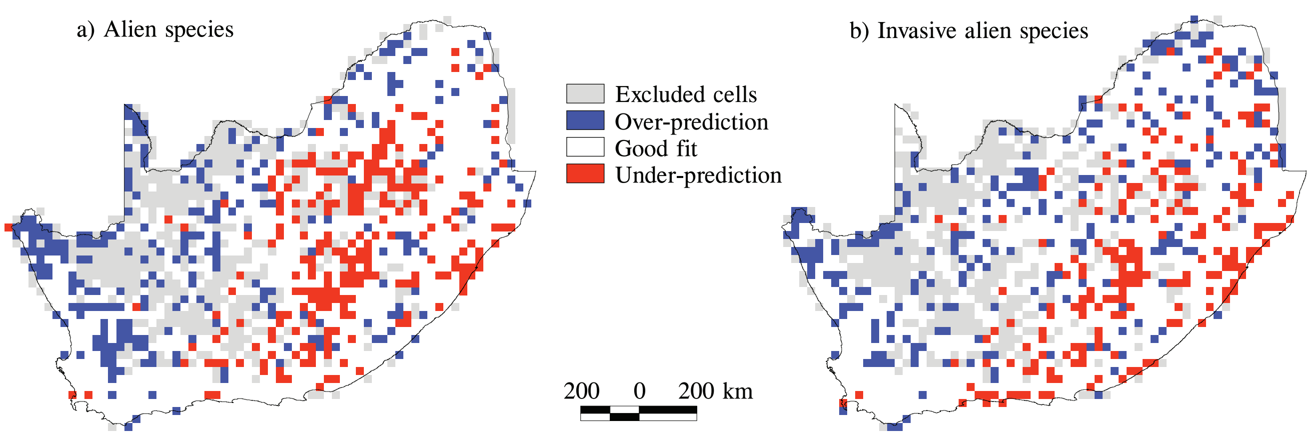

FIGURE 5. Map of residuals between actual (from atlas data) and predicted species richness for a) alien plant species and b) invasive alien plant species richness predicted from indigenous species richness at the scale of quarter-degree squares.

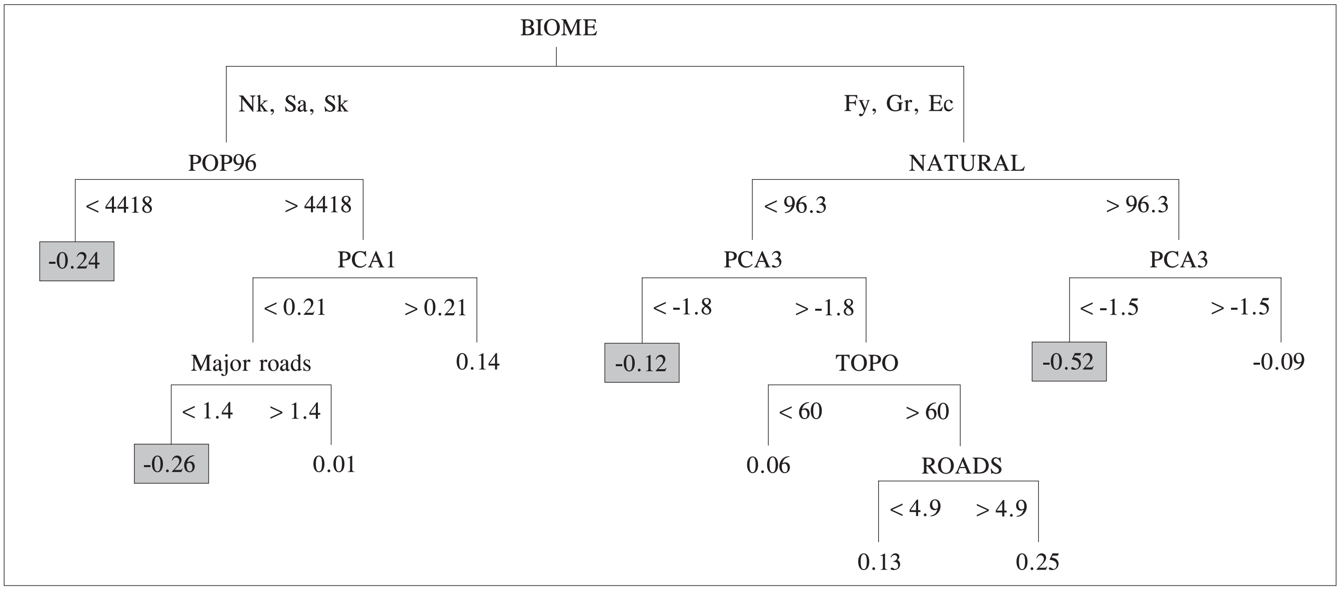

FIGURE 6. Regression tree showing the determinants of residuals between actual (from atlas data) and predicted invasive alien plant species richness based on richness of indigenous species. Significant variables are mentioned at the top of the branch, conditional values are shown on the side of each branch, and predicted invasive alien species richness is indicated for each terminal node. Codes of significant variables are listed in Table I. Biomes are coded as follows: Sk = Succulent Karoo, Nk = Nama-Karoo, Fy = Fynbos, Sa = Savanna, Gr = Grassland, and Ec = Ecotone.

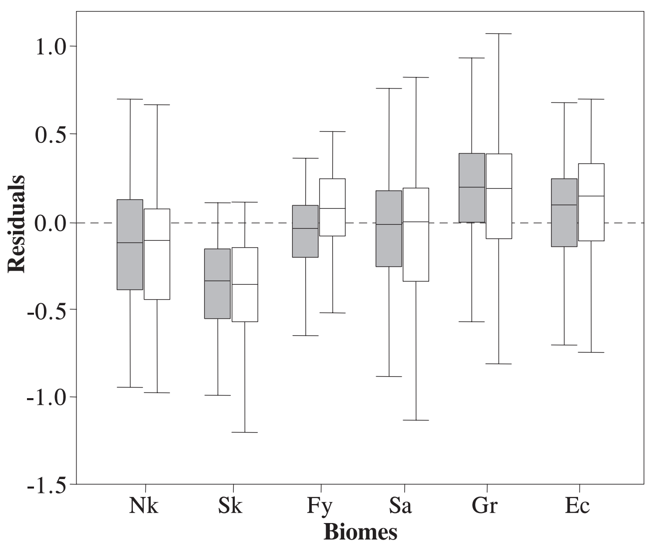

FIGURE 7. Mean residual values for predicted alien and invasive alien species richness based on indigenous species richness. Residual values were summarized per biome (Sk = Succulent Karoo, Nk = Nama-Karoo, Fy = Fynbos, Sa = Savanna, Gr = Grassland, and Ec = Ecotone). Average residuals below 0 indicate over-prediction of species richness; average residuals above 0 indicate under-prediction. Grey bars indicate alien species; open bars indicate invasive alien species.

positively to increasing levels of primary productivity (Chown *et al.,* 2003 for birds). Since alien species are, by definition, concentrated in areas of high human activity, the positive relationship between these two metrics is to be expected. The spatial scale of this study (quarter-degree squares) is appropriate for demonstrating this relationship. Given that the "invasive alien species" used in this study are, by definition (since these occur in natural and semi-natural vegetation), less closely associated with hubs of human settlement, we would expect a difference in the correlates of richness. Differences between the regression trees in Figures 2 and 3 suggest some differences in the correlates besides native species richness. For instance, areas with low topographic roughness in naturally species-rich areas and areas with high road densities have the highest predicted richness of invasive alien species (Figure 3). The differences revealed by analyses at the spatial scale of our study are, however, fairly subtle. This is, we suggest, because the scale is not appropriate to show the marked influence of human-mediated disturbance and other factors such as propagule pressure that become increasingly important as determinants of invasibility at finer spatial scales (Rouget *et al.,* 2002; Rouget & Richardson, 2003a,b; Foxcroft *et al.,* 2004; Huston, 2004). The spatial scale of the study, therefore, offers some unique insights to the broad-scale distribution patterns of alien plant invasions in South Africa, but is not appropriate for considering the important roles of factors that drive invasions at the scale of landscapes and smaller units. Unravelling differences in scale dependence in plant biodiversity (*sensu* Crawley & Harral, 2001) between native and alien species is a major challenge.

Of what practical use is our finding that alien and invasive alien species are most numerous in those parts of South Africa that are home to the most native plant species? It comes as no surprise that the region's most biodiverse regions are most at threat from human-related factors such as biological invasions. Worldwide, regions with the most biodiversity are most highly threatened (Myers *et al.,* 2000). Even within global hotspots of biodiversity, nodes of above-average biodiversity appear to be disproportionably susceptible to invasion (Higgins *et al.,* 1999). The clear implication is that South Africa's most important regions for biodiversity will continue to face an onslaught from invasive alien species and the many other threats that are inseparably linked with human activity.

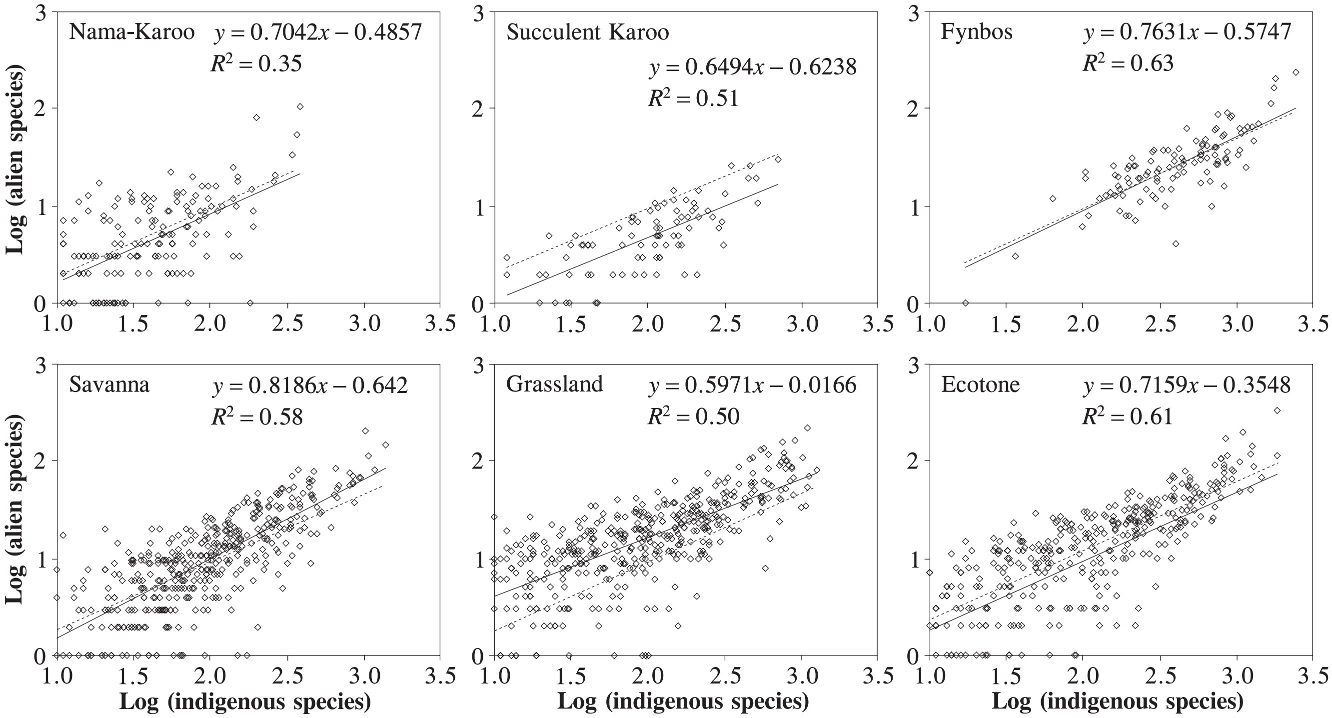

FIGURE 8. Relationships between the number of indigenous and alien plant species in quarter-degree square per biome. Solid lines show the fitted linear regression for each biome; the dotted lines show the linear regression based on average values for all biomes except the biome in that panel. All regressions are significant ($P < 0.0001$).

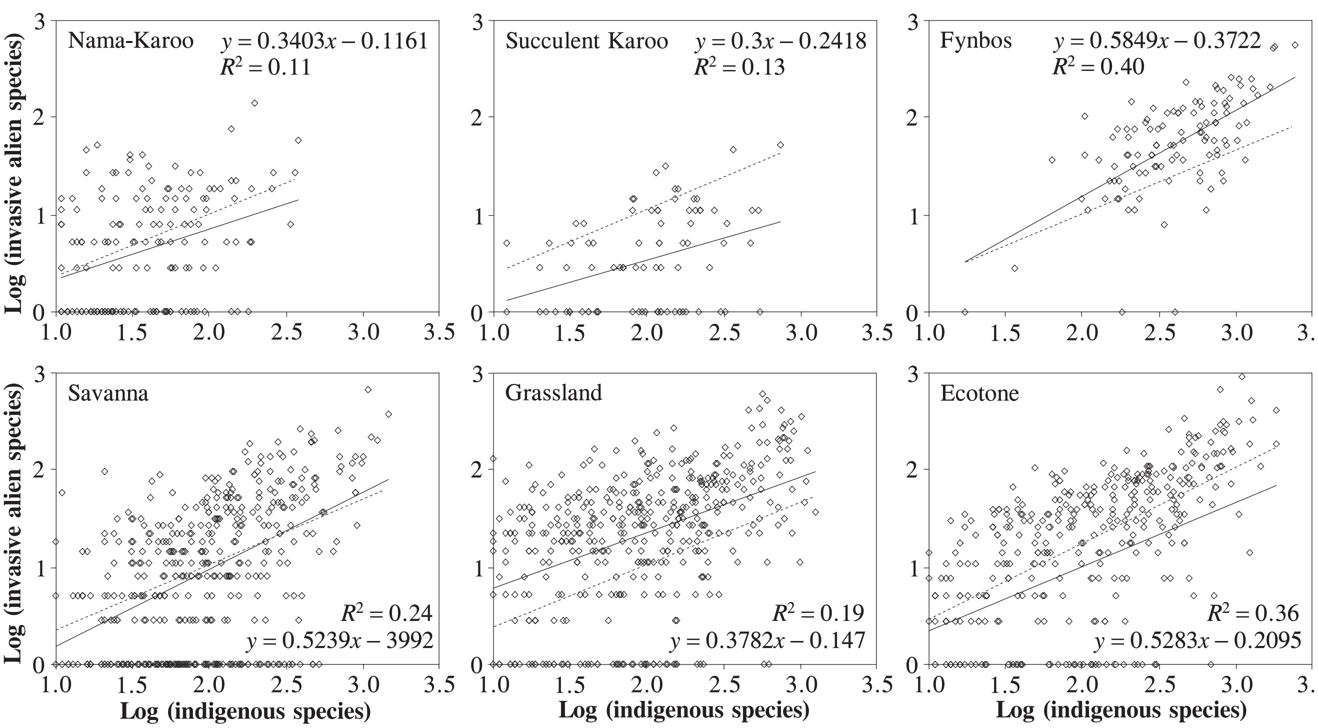

FIGURE 9. Relationships between the number of indigenous and invasive alien plant species in quarter-degree square per biome. Solid lines show the fitted linear regression for each biome; dotted lines show the linear regression based on average values for all biomes except the biome in that panel. All regressions are significant ($P < 0.0001$ except for Nama-karoo and Succulent karoo, where $P < 0.005$).

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