

Are environmental transitions more prone to biological invasions?

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Abstract

Aim

To examine whether at a subcontinental-scale ecotonal areas of transition between vegetation communities are at higher risk of plant invasion.

Location

South Africa and Lesotho.

Methods

Using plant data on native and established alien species in South Africa, we examined the relationship between plant richness (native and alien) in each grid cell (quarter-degree resolution) in the study area and the distance of the grid cell to the nearest ecotone between vegetation communities. We used a residual analysis to estimate each grid cell's relative invasibility (i.e. susceptibility to invasion) relative to its ecotone distance. We further explored the relative importance of ecotones in relation to large-scale environmental variation, and the importance of ecotonal spatial heterogeneity, in structuring alien species richness patterns.

Results

Both alien and native richness patterns become higher with declining distance to ecotones, suggesting that transitional environments are more susceptible to invasion than areas located farther away; however, levels of invasibility vary across South Africa. The negative relationship between ecotone distance and alien species richness remained negative and significant for the whole of South Africa, grassland and Nama-Karoo, after controlling for environmental variables.

Several sources of environmental heterogeneity, which were shown here to be associated with ecotones, were also found to be important determinants of alien species richness.

Main conclusions

While most of the current conservation efforts at the regional and global scales are currently directed to distinct ecosystems, our results suggest that much more effort should be directed to the transitions between them, which are small in size and have high native richness, but are also under greater threat from invasive alien species. Understanding how alien species richness and invasibility change across transitions and sharp gradients, where environmental heterogeneity is high, is important for ongoing conservation planning in a biogeographical context.

Keywords : Alien plants, biological invasions, ecotones, invasibility, native biodiversity, subcontinental scale.

Introduction

Fifty years ago, Elton (1958) discussed the relationship between environmental conditions and native and alien species richness, suggesting that species-rich communities are more resistant to invasion. Since then, this classical ecological theory has been tested at various spatial scales and it was revealed that biotic resistance to invasion is mainly observed at local spatial scales, whereas larger regional-scale studies revealed mainly positive native–alien species richness spatial relationships (Stohlgren *et al.*, 1999, 2003; Levine, 2000; Kennedy *et al.*, 2002; Ricciardi & Maclsaac, 2008). However, currently, it remains unknown how ecotones, that is, areas of sharp environmental transition between different ecological communities (reviewed in Kark & van Rensburg, 2006), influence alien species richness patterns and the susceptibility of the environment to invasion by alien species (hereby termed invasibility; Davis *et al.*, 2000).

Studies spanning a range of taxonomic groups and spatial scales, representing both terrestrial and aquatic systems, often document complex ecological and historical mechanisms in ecotones (Gosz, 1993; Kolasa & Zalewski, 1995). These important, and often unique, ecosystem characteristics and functions relate to the fact that ecotones (1) tend to show high spatial and temporal variability due to greater fluctuations in environmental variables, (2) are small in area, (3) experience high edge or mass effects and (4) act as geographical barriers to dispersal (Gosz, 1993; Kolasa & Zalewski, 1995; Risser, 1995). Because these are all important features responsible for much of Earth's diversity patterns, transitional environments often show elevated (1) levels of rare species (Kark *et al.*, 2007; Ribalet *et al.*, 2010), (2) speciation rates (Schilthuizen, 2000), (3) evolutionary novelty (Smith *et al.*, 1997) and (4) overall biodiversity (e.g. genetic diversity Fjeldså *et al.*, 2007; morphological divergence, Smith *et al.*, 1997; species diversity, Spector, 2002).

The positive native–alien spatial relationship would imply that both native and alien species richness would be relatively higher at ecotones at large spatial scales. High temporal and spatial heterogeneity of environmental variables at ecotones would further promote invasion by alien species (e.g. Gosz, 1993; Risser, 1995; Davis *et al.*, 2000; Pino *et al.*, 2005; Thuiller *et al.*, 2006). In addition, ecotones often have large edge-to-area ratios and may show high speciation rates (Smith *et al.*, 1997; Schilthuizen, 2000); therefore, a larger portion of their species will be

rare and will have small range sizes (Kark *et al.*, 2007; van Rensburg *et al.*, 2009). Consequently, it may be hypothesized that areas of sharp environmental transition that harbour ecotonal communities will be more sensitive to invasions by alien species.

In this framework, our goal in this study was to examine whether ecotones harbour high numbers of alien species. More specifically, we here ask whether ecological processes occurring within ecotones promote biological invasions. A better understanding of the above hypothesis will contribute towards understanding the complex relationships between environments, native and invasive alien richness. This is also important for determining future policies on where to invest our limited conservation and management resources aimed to maximize native biodiversity and to reduce and mitigate the impacts from biological invasions in areas known for their important ecological and historical processes.

Using data on established invasive alien species in South Africa (Nel *et al.*, 2004; Rouget *et al.*, 2004), we here examine at a broad-scale whether areas of transition between native vegetation communities are at higher risk of plant invasion. We also investigate possible sources of environmental heterogeneity likely to be associated with ecotones and promote invasibility (Gosz, 1993; Davis *et al.*, 2000; Thuiller *et al.*, 2006). We take into account the effect of variables that are known for their role in generating spatial variation in species richness patterns, such as environmental energy, remotely sensed surrogates of productivity (NDVI), spatial scale and human-related land transformation (Currie, 1991; O'Brien, 1998; Richardson *et al.*, 2005). We are unaware of studies to date that were designed to specifically examine plant invasions in ecotones versus core areas at the broad regional scale (see e.g. Stohlgren *et al.*, 2000, for a local-scale approach).

Methods

Data

South Africa spans from subtropical to Mediterranean and arid climatic regions over several latitudinal belts (see Fig. S1 in Supporting Information) and is rich in biological diversity (Huntley, 1989; Myers *et al.*, 2000), ranked in the top 25 most biodiversity-rich nations worldwide (WCMC, 1992; Conservation International, 1998). The country hosts high levels of native plant richness (*c.* 20,000 species) and plant endemism (*c.* 11,700 species) (Germishuizen *et al.*, 2006). Distribution records for native plant species were obtained from the Pretoria National Herbarium Computerized Information Service (PRECIS; Germishuizen & Meyer, 2003). The dataset includes *c.* 21,962 species listed as native, and the distribution of each species is indicated using a grid reference system at a quarter-degree resolution (*c.* $15' \times 15' \approx 676 \text{ km}^2$). Based on this dataset, we computed the number of native plant species for quarter-degree grid cells ($n = 1818$) spanning South Africa and Lesotho (hereafter referred to as South Africa) except for those cells that included both land and ocean surfaces.

South Africa has been exposed to alien plant invasion for more than 350 years, allowing many species to become naturalized or invasive across a wide range of environmental conditions (Richardson *et al.*, 1996). Indeed, compared to other countries globally, South Africa has one of the biggest problems with invasive alien plant species causing loss of natural biodiversity, water

shortages, loss of crop and forest production and increased soil erosion (Le Maitre *et al.*, 2011); see also van Rensburg *et al.* (2011) for a perspective on invasive vertebrates. Based on the South African Plant Invaders Atlas (SAPIA; Henderson, 1999, 2001), Nel *et al.* (2004) used species distribution and abundance data to identify 126 invasive alien plant species across South Africa that need to be prioritized as far as management action is concerned. In order to map the potential ranges of invasive plants from these 126 species, Rouget *et al.* (2004) made use of only those alien plants with at least 50 records in SAPIA, resulting in 71 important plant invaders known to have spread successfully in South Africa. We computed how many of these 71 species were found in each of the 1818 quarter-degree grid cells spanning South Africa.

Characteristic of atlas data, both PRECIS and SAPIA are based on ad hoc specimen collections and atlas records. Thus, some areas have been under-sampled (e.g. the arid interior of the country) (Gibbs Russell *et al.*, 1984), while others have been over-sampled due to a lack of a systematic sampling approach. Due to such sampling bias, these datasets are therefore not ideal sources. Nevertheless, they currently represent the best available plant distribution data on established invasive alien and native species in South Africa, and there are options to reduce, at least to some extent, spurious results that may arise from such sampling bias. For example, in a study by Richardson *et al.* (2005), PRECIS and SAPIA were used to investigate the correlates of alien plant species richness in South Africa. To reduce the effects of sampling bias in their analysis, at least that of under-sampling, they excluded all those grid cells where fewer than 10 native species and where no invasive alien species had been recorded. Following a similar approach, analysis was conducted based on a total of 1575 quarter-degree grid cells for native plant species and 1335 cells for invasive alien plant species (see Fig. S2). Although it was not possible to control for over-sampling in our analyses (see also Richardson *et al.*, 2005), it is expected that the potential effects of such bias leading to artificially high richness values should have less of an effect on altering the major species richness patterns of well-established invasive alien species, as examined in our study.

In order to locate and map the ecotones, we followed the methods applied in our earlier work (van Rensburg *et al.*, 2009), where we made use of Low & Rebelo's (1996) classification system of 68 vegetation types for the region to identify the spatial position of the margins of each vegetation type. The marginal areas where the ecotones are located (Kark & van Rensburg, 2006) are transitional area between vegetation communities (see Fig. S1, and van Rensburg *et al.*, 2009; for a map of the vegetation communities). Although more comprehensive and updated than the Low & Rebelo's (1996) vegetation map, we opted not to use the Mucina & Rutherford (2006) classification system of 435 vegetation types for the region due to the spatial resolution of this classification being too fine relative to the coarse quarter-degree grid cell resolution of the biological data (i.e. the native and invasive alien plant richness data). Consequently, a coarser vegetation classification, even though somewhat less accurate, is more appropriate in order to address the broader regional-scale questions in this study. Using an Albers equal area map projection, calculations of the distance from the mid-point of each grid cell to the nearest ecotone between vegetation communities (hereafter referred to as 'ecotone distance') were performed using an extension for arcview gis 3.X named Nearest Features, with Distance and Bearings (v. 3.5) (Jenness, 2001).

The environmental variables that were used to further examine the spatial relationship between ecotones and alien species can be classified as (1) those that are known to influence spatial patterns in species richness, regardless of the presence of ecotones (see e.g. Currie, 1991; O'Brien, 1998; Richardson *et al.*, 2005), and (2) those that indicate the higher environmental heterogeneity that is reputedly associated with the ecotones themselves. In the first class, we investigated mean January normalized difference vegetation index (NDVI) as a surrogate of productive energy availability (Hurlbert & Haskell, 2003) and minimum mean annual temperature (°C) as a surrogate for solar energy (see van Rensburg *et al.*, 2009; for more information on these datasets). In the second class, we investigated topographical heterogeneity (the maximum elevation above sea level minus minimum elevation above sea level, in metres, see van Rensburg *et al.*, 2009), geological heterogeneity (the number of geological zones in each cell) and degree of variation in total rainfall (the maximum annual precipitation minus the minimum precipitation in millimetres). See an explanation of how we selected these heterogeneity variables in the 'Analysis' section. The geology dataset was derived from the Council for Geoscience's Geological Data Set. Unlike the other datasets, the Geological map did not include Lesotho. The rainfall dataset was based on interpolated climate surfaces averaged over the long term at an 8-km resolution as published by the Agricultural Research Council's (ARC) Institute for Soil, Climate and Water (ISCW). Geographical Information System (GIS) maps of precipitation and geological zones (simplified 1:1 million) were downloaded from the ARC's GIS website at <http://www.agis.agric.za/agisweb/agis.html>.

Table 1 Characteristics of each biome investigated. (Mean invasibility, i.e. the susceptibility to invasion, was calculated based on the residuals of a linear regression between native and invasive alien plant richness ($y = 0.0141x + 4.9504$; $r = 0.61$; $P < 0.001$; d.f. = 1, 1249); positive values reflect high levels of invasibility, while negative values reflect low levels of invasibility)

Biome	Number of quarter-degree grid cells	Number of ecotones	Number (and percentage) of grid cells with invasive alien species (%)	Mean number of invasive alien plant species	Mean invasibility (SD = 4.85)
Savanna	625	1836	433 (69)	8.51	+0.42
Grassland	483	2198	421 (87)	9.18	+1.50
Nama-Karoo	457	378	232 (51)	5.04	-1.03
Succulent Karoo	131	296	96 (73)	6.32	-2.09
Fynbos	116	1108	110 (95)	10.47	-0.13
Forest	46	5015	43 (93)	12.17	+2.39

SD, standard deviation. 'Number of ecotones' refers to the total number of instances where two or more different vegetation types abut within each biome type.

The relative importance of ecotones and their characteristic environmental heterogeneity are likely to vary depending on the region and spatial scale considered. Therefore, we analysed the data at two spatial extents. These included the whole of South Africa and the biome scale based on South Africa's seven major plant biomes as defined by Rutherford & Westfall (1986), varying in their climate and ecosystem structure. Using the same subset of grid cells as for the South African scale, each grid cell was assigned to a specific biome according to the dominant biome type in the particular cell (see van Rensburg *et al.*, 2009; for more information on the biome classification procedure). For the biome-scale analyses, the savanna, grassland, Nama-Karoo, succulent Karoo, fynbos and forest (including the thicket biome) biomes were included (Figs 1 & S1; Table 1).

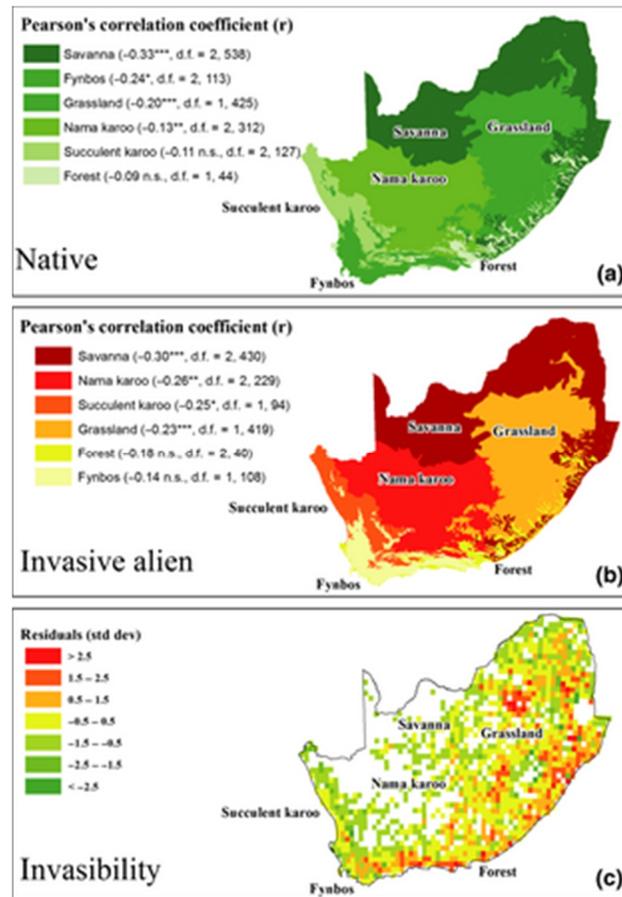


Figure 1. Pearson's correlation coefficients between distance to the nearest ecotone (boundary between vegetation communities) and (a) native plant richness, and (b) invasive alien plant richness. The results are shown for each of the major plant biomes of South Africa and Lesotho. Significance levels show levels after a sequential Bonferroni correction; d.f., degrees of freedom; n.s., not significant; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Finally, (c) indicates the level of invasibility, that is, the susceptibility to invasion, calculated based on the residuals of a linear relationship between native and invasive alien plant richness (positive values reflect high levels of invasibility, while negative values reflect low levels of invasibility). All calculations were made at the quarter-degree grid cell resolution.

To examine the effects of human-related land transformation, a major factor shaping native and invasive alien species richness patterns (Richardson *et al.*, 2005), on the extent to which plant species richness is related to ecotone distance, we conducted our analyses using (1) all grid cells and (2) only those cells with 50% or less land transformation (see van Rensburg *et al.*, 2009). The extent of land transformation was obtained by calculating and summing up the percentage of each land cover class in each grid cell, based on the six transformed land cover classes identified by Fairbanks & Thompson (1996) and Fairbanks *et al.* (2000). These classes were based on seasonally standardized Landsat TM satellite imagery captured primarily during 1994–1995 and included anthropogenic effects such as forest plantations, artificial water bodies, urban/built-up areas, cultivated lands, degraded land as well as mines or quarries. The results using these two

datasets (with and without some level of land transformation) were qualitatively similar (see e.g. Tables S1–S3), and therefore, we only present those from analyses that used the entire dataset.

Analyses

Examining the contrasting ecotone-invasion hypotheses in a biome that is not well represented by the invasive alien plants considered here could lead to spurious results. Consequently, the spatial aggregation of the invasive alien plant species present in each of the six biomes was calculated. For each biome, the number of grid cells with one or more invasive species present, expressed as a percentage relative to the total number of grid cells representing a given biome, was calculated. To ensure that the relationship between ecotone distance and invasive alien plant richness is not a simple outcome of more humans living closer to ecotones, we calculated the relationship between distance to nearest ecotone and human population density supplied by South African census data (Anonymous, 2001). In addition, we used a residual analysis to estimate the relative invasibility of each quarter-degree cell, that is, the susceptibility of the environment in each cell to invasion by alien species. For this analysis, we calculated the residuals of a linear regression between native richness and invasive alien richness ($y = 0.0141x + 4.9504$; $r = 0.61$; $P < 0.001$; d.f. = 1, 1249). In this estimate, positive residual values show relatively high levels of invasibility, while negative values show relatively low levels of invasibility (see Fig. 1c). These residuals were then used to evaluate the relationship between distance to nearest ecotone and invasibility. This was carried out for the whole of South Africa and for each of the biomes separately.

Linear and curvilinear regressions were used to assess how well distance to the nearest ecotone explained variation in native and invasive alien plant richness and the form this relationship takes (significance was tested after a sequential Bonferroni correction). We also used multiple regression procedures to examine ecotone distance together with minimum temperature and NDVI as predictors of species richness, to indicate the relative importance of ecotone distance in relation to energy availability in structuring alien species richness patterns.

Following, we investigated environmental heterogeneity as a possible driver of alien species richness at ecotones, by first selecting variables best representing increased environmental heterogeneity at biomes (with significant negative correlations with ecotone distance) and then investigating these variables as predictors of alien species richness. We first examined a variety of topographical heterogeneity, geological heterogeneity and climatic (e.g. monthly rainfall and temperature) heterogeneity variables as predictors of ecotone distance, and we selected topographical, geological and total rainfall heterogeneity as those best representing overall ecotonal heterogeneity. The best predictors of these three within each region (i.e. the combination with the best model fit, see the next paragraph) were then examined as predictors of alien species richness for that region, to indicate possible environmental determinants of alien species richness at ecotones.

The multiple regression models were constructed using the sas v. 9.1 (SAS Institute Inc., Cary, USA) procedures PROC GLM, which provides coefficients of determination with which to indicate and compare the explanatory power of different models, and PROC MIXED, which supplies Akaike's Information Criterion values which indicate model fit (AIC; Burnham &

Anderson, 1998; the model with the best fit is the model with the lowest value). In addition, we re-examined all models with PROC MIXED to determine the effect of spatial autocorrelation (see Littell *et al.*, 1996, for more information on how this procedure fits a spatial covariance matrix to the data). Unfortunately, to date, there are no statistical procedures available that provide coefficients of determination for spatial models. Although the AIC values were used to compare models with the same response variable (the same dataset) to indicate the best combinations of predictor variables, they were not reported as they do not have any inherent meaning, cannot be compared between different analyses and therefore do not supply any additional information.

To reduce heteroscedasticity in our response variables, species richness values for both native and invasive alien plants were logarithmically transformed to base 10 for all the above-mentioned analyses. Further, in some models, a predictor's log transformation, or the addition of a predictor's squared term (to determine nonlinearity), improved a model. No significant collinearity was found between the predictors in any of the described models.

Results

In all six biomes, over 50% of the grid cells representing a given biome were represented by invasive alien species, with exceptionally high representation for the fynbos (95% of its cells had records of invasive species), forest (93%) and grassland biomes (87%) (Table 1; Fig. S2b). These three biomes (fynbos, forest and grassland) also showed higher mean invasive alien plant richness values compared to the other biomes examined (Table 1). The total number of ecotones (i.e. number of instances where two or more different vegetation types abut) in each of the six biomes varied between 296 and 5015 with forest showing the highest number of ecotones (Table 1). We therefore consider the spatial extent of the different biomes examined to be well represented with alien plants and that the invasive alien plant data that we used here are suitable for testing our hypotheses related to ecotone resistance and susceptibility to invasions. Testing the relationship between ecotone distance and invasive alien plant richness was not affected by human population density given the weak relationship between human density and ecotone distance ($r = -0.07$; $P < 0.05$; d.f. = 1, 1816).

In all cases, we found a negative relationship between invasive alien richness and distance to the nearest ecotone (Fig. 1b). This relationship was significant within all the biomes except for the forest and fynbos, where sample size (i.e. number of grid cells) was smaller, for example forest ($r = -0.18$; $P > 0.05$; d.f. = 2, 40). The strongest relationship was found when calculated for the savanna biome (-0.30 ; $P < 0.001$) followed by the Nama-Karoo (-0.26 ; $P < 0.01$). When analysed at the whole of South Africa scale, the relationship was also negative and was significant ($r = -0.29$; $P < 0.001$; d.f. = 1, 1333; see Fig. S3b). Native species showed similar negative relationship between plant richness and ecotone distance within biomes (Fig. 1a) and for the whole of South Africa ($r = -0.31$; $P < 0.001$; d.f. = 2, 1572; see Fig. S3a). Thus, cells located closer to ecotones had higher native and invasive alien plant species richness both across the whole of South Africa and within all its biomes. This relationship, for both invasive alien and native plants, was strongest when examined for the whole of South Africa combined, and for the savanna biome, which is also the largest biome in South Africa (Fig. 1). This relationship was mostly linear, with weak curvilinear patterns found in four (considering native species) and three

(considering invasive species) of the biomes, respectively, that did not substantially change the fit of the models. As expected, the level of invasibility in the different quarter-degree cells was not homogenous across South Africa (Table 1; Fig. 1c).

When accounting for additional environmental variables, the form of the relationship between invasive alien plant richness and ecotone distance remained mostly negative, although in most cases non-significant (Table 2). Ecotone distance remained significant for the whole of South Africa, the grassland biome and the Nama-Karoo; however, the explanatory power of ecotone distance was strongest for the whole of South Africa and the savanna biome (partial r^2 in Table 2). The full model (all variables, including ecotone distance and environment) explained between 19% and 55% of the total variation in invasive alien plant richness (Table 2). No indication of a unimodal relationship was evident for any of the biomes (Table 2). Spatial autocorrelation had an effect on the whole of South Africa, the fynbos, the grassland and the succulent Karoo, although most variables remained significant in spatial models (Table S4).

Table 2 Distance to the nearest ecotone (boundary between vegetation communities), variation in energy (minimum temperature) and productivity (NDVI) were analysed as predictors of invasive alien species richness. We represent here, for each multiple regression model, the coefficient of determination indicating the explanatory power of all relevant predictors in that model (full model r^2), a partial coefficient of determination indicating the explanatory power of only the ecotone distance variable, and the F ratio, significance level and the sign of the slope (positive or negative relationship) of each predictor variable. The response variable, alien plant species richness, was logarithmically transformed prior to analysis to improve heteroscedasticity. Similarly, a log transformation of a predictor variable, or the addition of its squared term, is used if it substantially improved model fit, and this is indicated for each relevant predictor

Region	d.f.	Ecotone distance	Temp (min)	NDVI	Full model r^2 (%)	r^2 for Ecotone distance term (%)
South Africa	1, 1326	$F = 53.57\ddagger\ddagger\ddagger\ddagger$	$F = 51.65****$; sq	$F = 422.26****$	31.3	8.2
Savanna	1, 424	$F = 0.28\ddagger$ n.s.	$F = 30.97\ddagger\ddagger\ddagger\ddagger$; L	$F = 313.12****$	47.4	7.9
Grassland	1, 412	$F = 16.82\ddagger\ddagger\ddagger\ddagger$	$F = 43.20****$; L	$F = 29.70****$; L	20.3	5.1
Nama-Karoo	1, 223	$F = 4.85\ddagger$; L	n.i.	$F = 43.74****$; L	19.9	4.6
Succulent Karoo	1, 87	$F = 0.35\ddagger$ n.s.	n.i.	$F = 39.20****$	34.2	6.5
Fynbos	1, 101	$F = 1.01\ddagger$ n.s.; L	$F = 6.38\ddagger$; L	$F = 116.91\ddagger\ddagger\ddagger\ddagger$; L	55.3	2.3
Forest	1, 34	$F = 1.61*$ n.s.; L	n.i.	$F = 9.37**$	19.5	3.4

d.f., degrees of freedom; temp (min), minimum temperatures ($^{\circ}$ C); NDVI, normalized difference vegetation index; n.i., not included in the model; n.s., not significant; L, log of predictor used; sq, squared term of predictor included in model.

Levels of significance: positive slope: *n.s. $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, **** $P < 0.0001$; negative slope: \ddagger n.s. $P > 0.05$, $\ddagger P < 0.05$, $\ddagger\ddagger\ddagger\ddagger P < 0.0001$.

Ecotone distance was in most cases (except for forest and fynbos) significantly and negatively correlated with environmental heterogeneity variables, although the regions investigated differed with regard to which combination of the variables topographical, geological and total rainfall heterogeneity best represented ecotonal heterogeneity (explanatory power ranged between 3.6% and 29%, Table 3). In most regions, alien species richness was significantly and positively correlated with the same combination of predictor variables that best explained ecotone distance, also showing similar levels of explanatory power (ranging between 11% and 30%, Table 3). Spatial autocorrelation had a significant effect on all regions except the forest biome, especially for the grassland and savanna biomes where certain predictor variables became non-significant in spatial models (and are thus not included) (Table S5).

Table 3 Indicators of spatial heterogeneity – topographical variation (elevation range in m), geological variation (number of geological zones present) and total rainfall variation (range in total annual precipitation in mm) – were analysed as predictors of (step 1) distance to the nearest ecotone (a negative correlation implies greater heterogeneity closer to ecotones) and (step 2) of invasive alien species richness. We present here, for each multiple regression model, the coefficient of determination (r^2) indicating the explanatory power of all relevant predictors in that model, as well as the F ratio, significance level and the sign of the slope estimate (positive or negative relationship) for each predictor. Alien plant species richness was logarithmically transformed prior to analysis to improve heteroscedasticity. Similarly, a log transformation of a predictor variable, or the addition of its squared term, is used if it substantially improved model fit, and this is indicated for each relevant predictor

Response variable per region	d.f.	Elevation range	Geological variation	Rainfall variation	r^2
South Africa					
Ecotone distance	1, 1835	$F = 108.37 \dagger \dagger \dagger \dagger$; L	$F = 80.02 \dagger \dagger \dagger \dagger$; L	$F = 17.84 \dagger \dagger \dagger \dagger$; L	26
Alien richness	1, 1311	$F = 9.85^{**}$; L	$F = 21.47^{****}$; L	$F = 138.68^{****}$; L	30
Savanna					
Ecotone distance	1, 623	$F = 161.21 \dagger \dagger \dagger \dagger$; L	$F = 20.54 \dagger \dagger \dagger \dagger$; L	n.i.	28
Alien richness	1, 423	$F = 170.69^{****}$; L	$F = 4.81^*$; L	n.a.	29
Grassland					
Ecotone distance	1, 452	$F = 103.66 \dagger \dagger \dagger \dagger$; L	$F = 27.34 \dagger \dagger \dagger \dagger$; L	n.i.	23
Alien richness	1, 398	$F = 81.29^{****}$; L	$F = 13.14^{***}$; L	n.a.	19
Nama-Karoo					
Ecotone distance	1, 456	n.i.	$F = 25.64 \dagger \dagger \dagger \dagger$; L	$F = 82.06 \dagger \dagger \dagger \dagger$; L	18
Alien richness	1, 223	n.a.	n.i.	$F = 28.47^{****}$; L	11
Succulent Karoo					
Ecotone distance	1, 130	n.i.	$F = 4.77 \dagger$; L	n.i.	3
Alien richness	1, 87	n.a.	$F = 3.01^{*n.s.}$; L	n.a.	3
Fynbos					
Ecotone distance	1, 115	n.i.	n.i.	$F = 3.53 \ddagger$ n.s.	3
Alien richness	1, 101	n.a.	n.a.	$F = 33.08 \dagger \dagger \dagger \dagger$; L	23
Forest					
Ecotone distance	1, 45	n.i.	$F = 3.28^{*n.s.}$	n.i.	7
Alien richness	1, 34	n.a.	$F = 1.14 \dagger$ n.s.; sq	n.a.	3

d.f., degrees of freedom; n.i., not included in the model; n.a., not applicable to the analysis; n.s., not significant; L, log of predictor used squared term of predictor included.

Levels of significance: positive slope: *n.s. $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$; negative slope: †n.s. $P > 0.05$, †† $P < 0.05$, †††† $P < 0.0001$.

Discussion

Our study provides support that at the regional, subcontinental scale, areas closer to transitions (ecotones) between vegetation-based ecoregions across southern Africa have a higher probability of harbouring concentrations of invasive alien plant species and higher invasibility compared with areas located further away from the ecotone. In earlier work, van Rensburg *et al.* (2009) found higher native bird and frog richness (alpha diversity) in these vegetation-based ecotonal areas and also greater bird β -diversity (species turnover) than expected by chance in biome ecotonal areas (van Rensburg *et al.*, 2004; see also Kark *et al.*, 2007; Levanoni *et al.*, 2011). Here, we find elevated native plant richness to be associated with ecotones; that is, native plant species richness increases with declining distance to ecotones. Therefore, the large-scale positive correlation between alien and native plant species richness (see e.g. Stohlgren *et al.*, 1999, 2003; Richardson *et al.*, 2005) is shown to be valid for large-scale ecotones as well. At a national scale,

our findings support the notion of Richardson *et al.* (2005) suggesting that areas with rich native biodiversity across South Africa are particularly under threat by plant invasion. Indeed, such results are important given the general lack of studies in the region focusing on the topic of plant invasions that span large spatial scales (Richardson *et al.*, 2005). This trend of increased native and invasive alien plant species richness closer to ecoregion boundaries was evident both at the large subcontinental scale when analysed for the whole of South Africa combined, and at the subregional scale for all six biomes (as shown in Fig. 1a,b). This raises the question of why ecotones are richer in invasive alien species. Several reasons might explain this pattern.

Firstly, boundaries between ecoregions are areas of sharp transition with especially high spatial and temporal heterogeneity and often show lower spatio-temporal stability and predictability compared to the core of an ecoregion (Killeen & Solórzano, 2008). Increased heterogeneity, both spatially and temporally, is well known to be positively correlated with species richness for many taxa, spatial scales and regions (Rosenzweig, 1995; van Rensburg *et al.*, 2002; Pino *et al.*, 2005; Thuiller *et al.*, 2006; Hugo & van Rensburg, 2009; Levanoni *et al.*, 2011) and is also consistent with the general theory of invasibility related to fluctuating resources proposed by Davis *et al.* (2000). We have demonstrated here that areas close to ecotones tend to be characterized by relatively abrupt spatial changes in topography and total annual rainfall and by a relatively greater geological heterogeneity (Table 3). As alien plant richness was generally positively spatially associated with these three variables, we may argue that the invasion of areas close to ecotones is promoted by ecotonal heterogeneity (Table 3). Ecologically, areas of environmental transition provide unique environments, well beyond a simple combination of the two neighbouring regions (Kark & van Rensburg, 2006). For example, habitat structure and food quality for various bird species in tropical transition zones differ dramatically from those in the adjacent rain forest (Smith *et al.*, 1997). Such diverse ecotonal environments and resources, especially at large spatial scales, may therefore allow higher richness of invasive alien plant species to establish themselves and succeed, and provide an open ‘window of opportunity’ for invading the system more easily (see e.g. Planty-Tabacchi *et al.*, 1996; Thuiller *et al.*, 2006; Kark, 2012).

High propagule pressure (Davis *et al.*, 2000) might also explain high levels of invasion in ecotones. That is, even if ecotonal environments are more susceptible to invasion by new species, whether invasion actually occurs in a particular environment depends on propagule pressure (Davis *et al.*, 2000). Following the same logic related to the tendency for increased diversity and abundance at local-scale habitat boundaries, also known as the edge effect (Odum, 1997), it is more likely that the propagule pressure, based on invasive species in the adjoining ecoregions, will be higher in ecotones compared to the core of an ecoregion. The weak relationship that was found between human density and ecotone distance ($r = -0.07$; $P < 0.05$; d.f. = 1, 1816) indicates that it is unlikely, at least in this study, for a potential increase in propagule pressure in ecotones to simply be related to more humans living closer to ecotones.

A third potential explanation for why ecotones are characterized by increased invasion relates to the notion that ecotones, at least in some cases, are sources of evolutionary variation and novelty. They are thus characterized by recently derived species that exhibit high morphological divergence (Smith *et al.*, 1997; Schilthuizen, 2000) and are in the process of expanding their ranges (neoendemics) (Fjeldså, 1994). Due to this source of evolutionary novelty in ecotones,

ecotones often support evolutionary younger communities with relatively shorter co-evolutionary histories between species. Consequently, competitive interactions between native species in ecotones may be lower, compared to that of species in non-ecotonal environments where competitively dominant, successful and widespread native species may dominate the environment over time (see e.g. Peters, 2002). If such differences in competitive interactions do occur, there will be a reduced biotic resistance in ecotonal environments compared to non-ecotonal areas, regardless of species richness, thus allowing new alien species to invade the ecotonal system and establish novel populations. Indeed, a study on invasibility of riparian plant communities in France and the USA by Planty-Tabacchi *et al.* (1996) indicated that although mature plant communities appeared to be invulnerable, young communities contained more alien species than older ones (see also Heywood, 1989).

Despite the consistent finding that alien plant richness in most ecoregions in South Africa is greater close to ecotones, it should be noted that the relationship was also relatively weak in most cases. Moreover, the relationship was much weakened, and rendered statistically insignificant in most biomes, after taking into account variation in energy availability and primary productivity (Table 2). This is unsurprising as climatic variables are known to play a major role in shaping both native and alien species richness (Currie, 1991; O'Brien, 1998; van Rensburg *et al.*, 2002; Richardson *et al.*, 2005; Levin & Shmida, 2007; but see also Srivastava & Lawton, 1998). Nevertheless, although ecotone distance is generally less important as an explanatory variable, it remains a significant predictor of alien plant richness in the whole of South Africa, the grassland and the Nama-Karoo (Table 2), and possibly explains more localized variation in alien species richness, additional to underlying gradients of productivity and energy. Further, ecotones differ widely with regard to their particular characteristics, environmental determinants and ecological processes (see e.g. Walker *et al.*, 2003), and therefore, different ecotones may affect species distributions to varying degrees. This is suggested by the form of richness-distance plots (Fig. S3), which show a range of values – small to large – close to the ecotones, instead of a simple linear relationship (i.e. many ecotones do not support greater numbers of plant species). If no distinction is made between different ecotone types (as in the current study), then the presence of ecotones with weak effects would lower the overall relationship strength of species richness–ecotone distance relationships. Considering the importance of environmental conditions to alien invasions, we speculate that ecotones with strong effects on species distributions are likely those based on abrupt temporal or spatial changes in environmental conditions (i.e. with greater inherent heterogeneity), between ecoregions that differ widely in environmental conditions. For example, ecotones at the boundaries of different biomes would likely have a stronger effect on species distribution than ecotones between vegetation types within the same biome.

One could argue that increasing plant richness with decreasing distance to ecoregion boundaries may result from the fact that we used a rather coarse (quarter-degree) grid cell size, which may capture part of one ecoregion, a transitional environment, and part of a neighbouring ecoregion, thus leading to high richness in cells that include transitions. If this were the case, we would expect to see a step function in which grid cells that fall on a transition (cells that contain more than two ecoregions) show higher richness, while all other cells do not decline further in richness with increasing distance to the boundaries. However, here we see a gradual decline in both native and invasive alien species richness with increasing distance to areas of transition (see Fig. S3).

The alien species richness–ecotone distance relationship is supported and/or moderated by different combinations of environmental variables in different biomes, which is unsurprising as the South African biomes vary greatly in their climate and ecosystem structure (see also Thuiller *et al.*, 2006). Topographical heterogeneity, for example, is most important in the savanna and grassland biomes, probably reflecting the ecotones found along the Great Escarpment and especially the Drakensberg range (Table 3). Geological heterogeneity is an important variable in nearly all biomes (except fynbos, Table 3); this is probably because the spatial distributions and boundaries of many vegetation types and geological zones are coincident (geology is often a determinant of vegetation, Low & Rebelo, 1996; Mucina & Rutherford, 2006). Of all the biomes, total rainfall heterogeneity is only associated with ecotones in the Nama-Karoo; however, it is the most important ecotonal heterogeneity variable in this biome, with a substantial influence on alien species richness (Table 3).

A potential confounding variable when comparing the results of different regions stems from the differences in spatial area of the biomes and the vegetation types within the biomes. For example, while most of the South African biomes (e.g. grassland and Nama-Karoo) are large and relatively continuous, the forest biome is naturally highly fragmented, occurring in areas along the east coast with high elevational variation. It is possible that, due to the proximity of many finely divided vegetation types, ecotone distance did not vary sufficiently in this biome (i.e. all areas are close to ecotones). Therefore, the spatial scale we used here (quarter-degree resolution), chosen due to the resolution of the plant distribution data, was likely not fine enough to capture the finer-scale patterns occurring in this biome (Table 1; Fig. 1). It would be interesting to further examine the effect of ecotones on richness in this area at a local scale applying detailed fieldwork. In any case, the weaker results from the smaller biomes (forest and fynbos) are therefore probably not comparable to that of the larger biomes.

The findings of this study have several important implications for conservation. If ecotones indeed serve as hotspots of native biodiversity, as found here for South African plants (see also van Rensburg *et al.*, 2009; for patterns related to birds and frogs) and in recent work elsewhere (e.g. see Kark *et al.*, 2007; for patterns in New World birds), then they have high conservation value in a biogeographical context (both ecological and evolutionary) (Smith *et al.*, 1997; Killeen & Solórzano, 2008; Ribalet *et al.*, 2010). In addition to the often unique biodiversity characteristics and ecosystem functions associated with ecotones, as discussed in the Introduction section, it has also been suggested that ecotones are ideal areas to mitigate the impacts of climate change due to greater physiological tolerances in ecotone species (Killeen & Solórzano, 2008), although increased invasibility in these ecotonal areas is likely to reduce these mitigation effects. If ecotones, however, generally harbour, in addition to high native richness and also high invasive alien richness, more focus should be given to ecotonal invasions in management plans and conservation decision-making. While many conservation programmes are regional (due to logistic, administrative and funding constraints) when dealing with invasive alien management, they tend to, by default, focus on specific ecological units, ecoregions and systems, often ignoring the ecotones between them. Such management approaches may prove to be an inefficient strategy, as invasive species often cross boundaries. It will be important to further evaluate the role of ecotones across spatial scales and in other continents, as areas of transition and their characteristic environmental and resource heterogeneity may serve as important potential drivers of both native and invasive alien richness patterns. If such a notion is

supported by other ecotonal studies, then much needed support will be added to the general theory of invasibility related to fluctuating resources proposed by Davis *et al.* (2000) and, as these authors suggested, to the predictive power desperately needed by decision-makers.

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Supplementary material

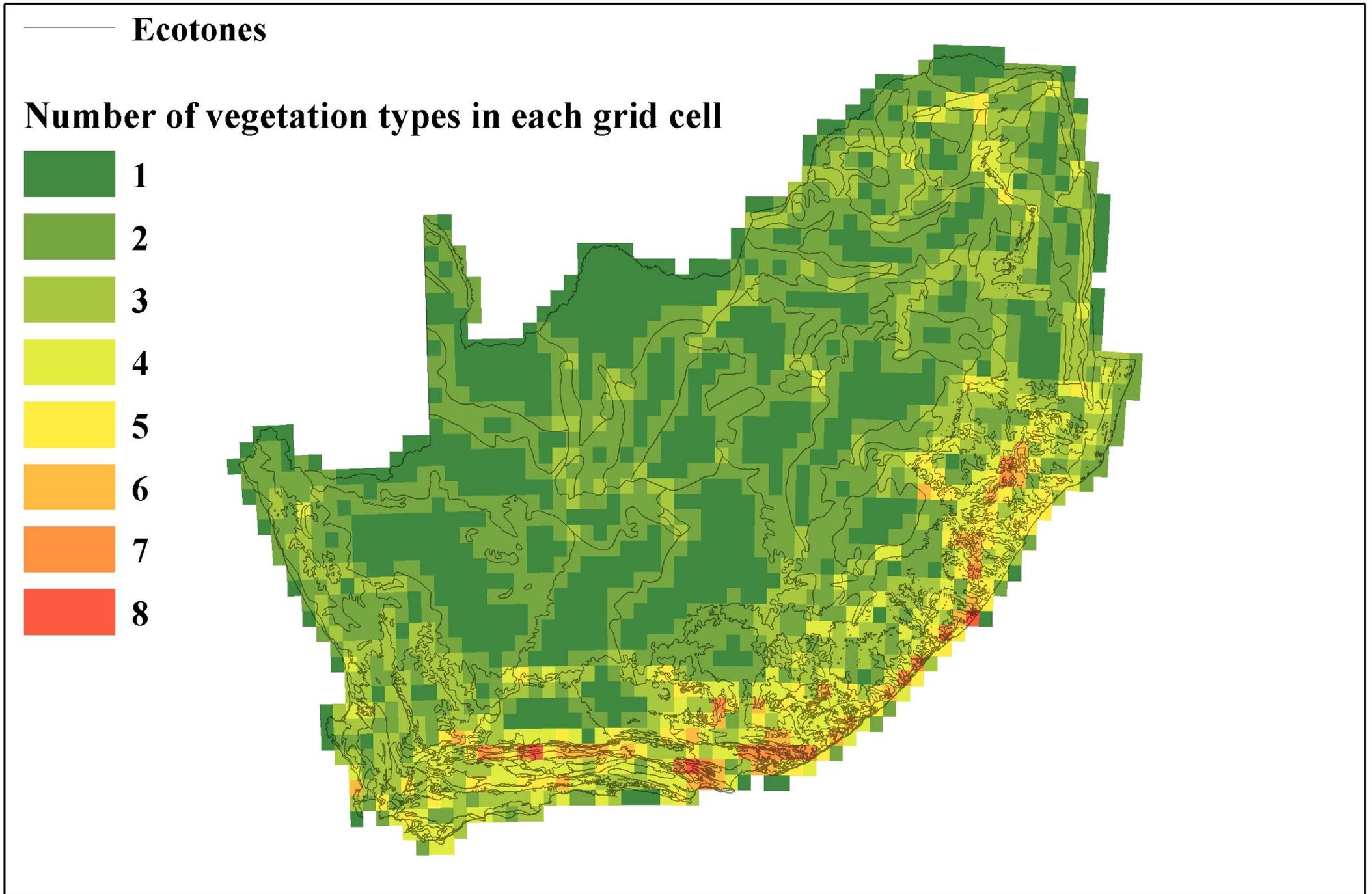


Figure S1 The spatial locations of vegetation boundaries, and the number of vegetation types per quarter-degree grid cell for South Africa and Lesotho.

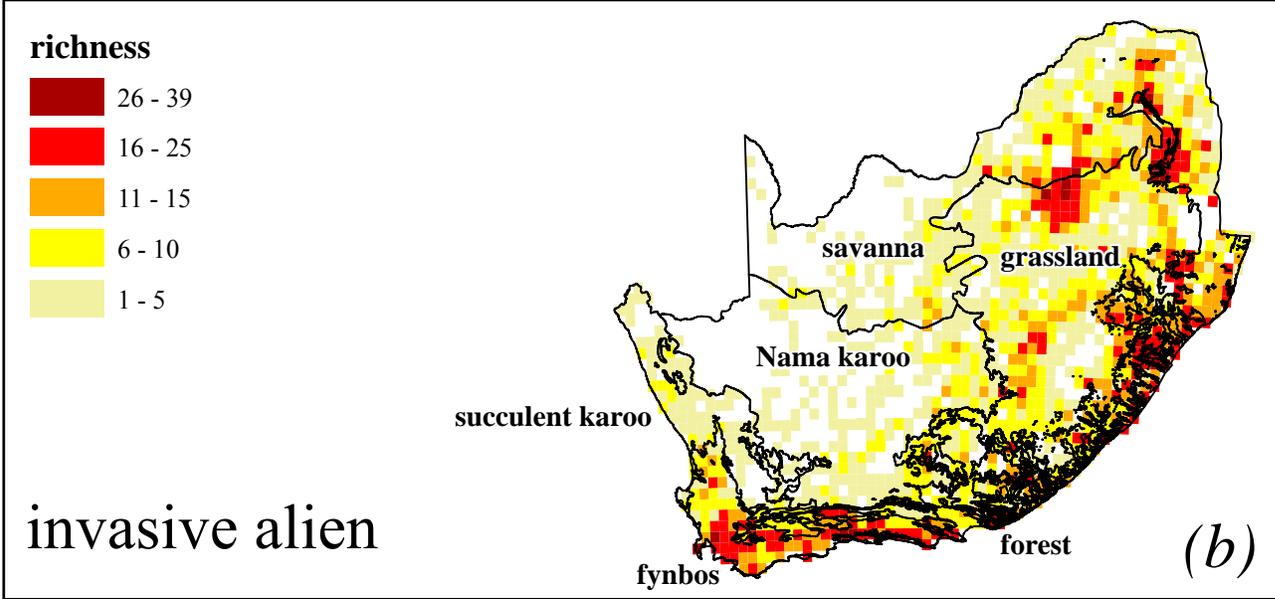
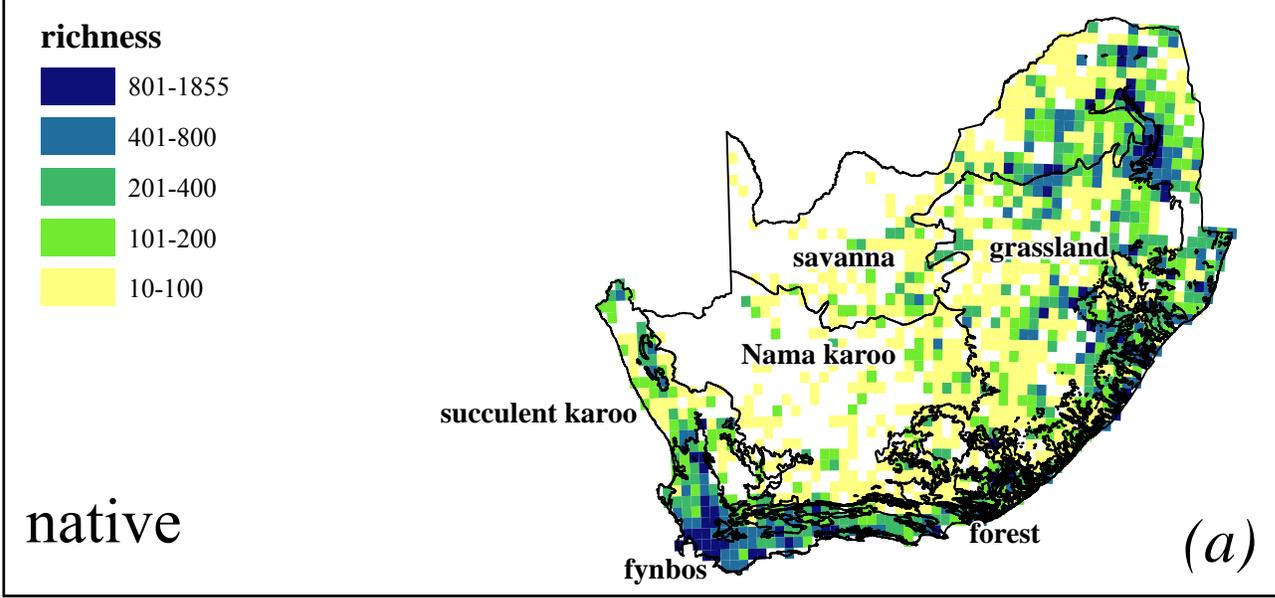


Figure S2 (a) Native and (b) invasive alien plant richness across South Africa.

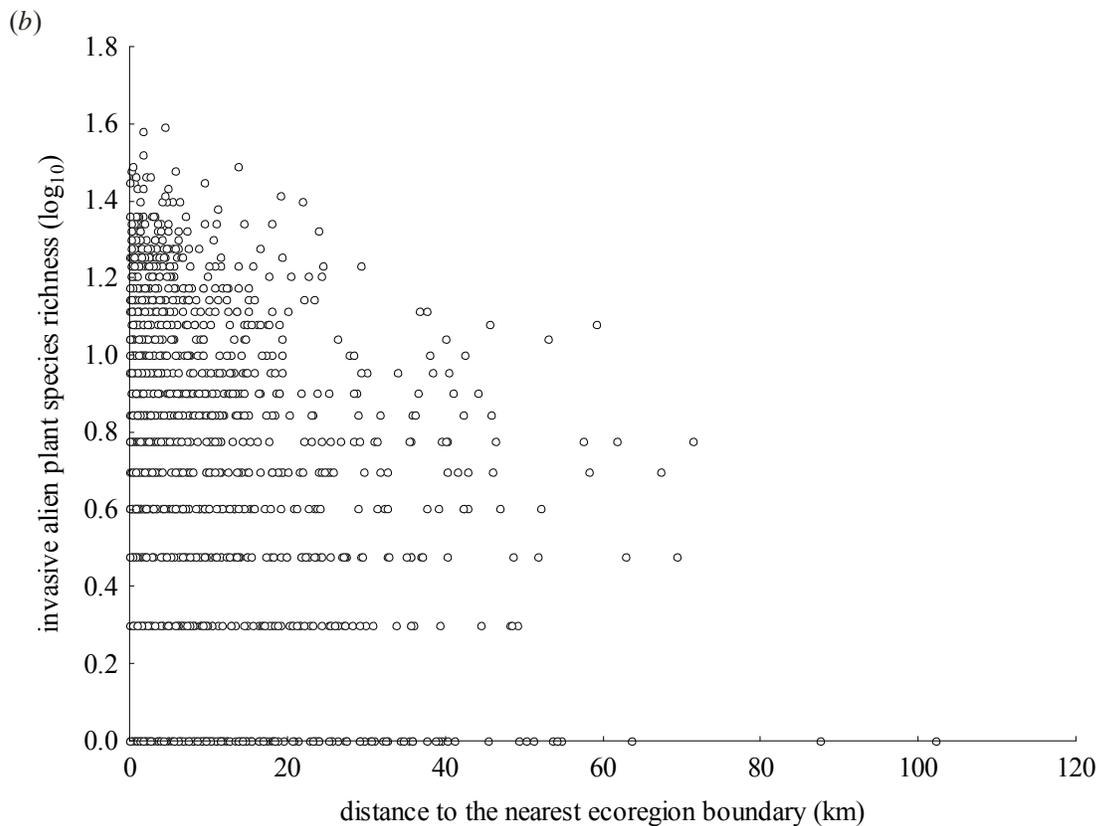
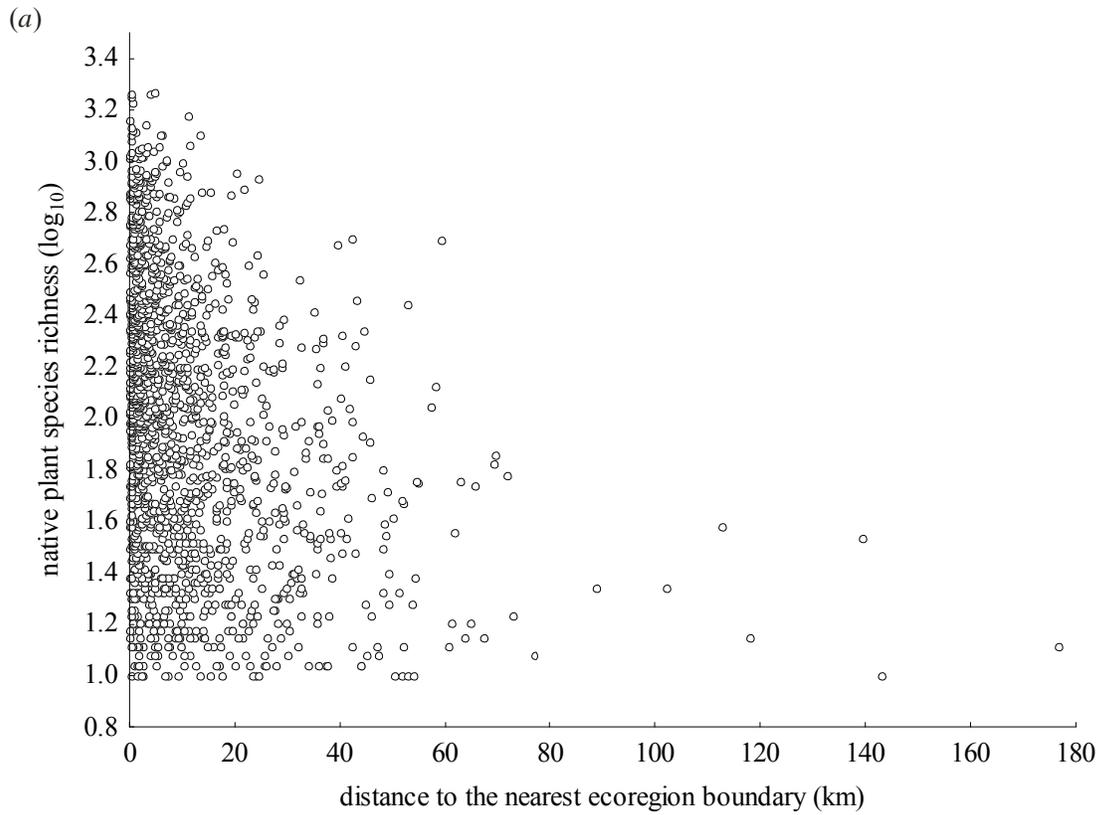


Figure S3 Relationship between (a) native, and (b) invasive alien, plant richness and distance to the nearest ecoregion boundary for the whole of South Africa.

Table S1. Analyses similar to those reported in Table 2; however, here all grid cells of which the surface area are more than 50% transformed by humans is removed from the dataset. Nama-Karoo, succulent Karoo and forest biomes are not shown here, as none of their grid cells are more than 50% transformed.

region and procedure	d.f.	ecotone distance	temp (min)	NDVI	full model r ² (%)	r ² for ecotone distance term (%)
<i>South Africa</i>						
GLM	1, 1118	$F = 29.37$ ††††	$F = 46.34$ ****; sq	$F = 331.48$ ****	29.7	7.0
Mixed spatial	1, 1118	$F = 2.91$ †n.s.	$F = 15.4$ ****; sq	$F = 111.83$ ****		
<i>Savanna</i>						
GLM	1, 360	$F = 0.02$ †n.s.	$F = 35.95$ ††††	$F = 278.73$ ****	48.3	7.6
<i>Grassland</i>						
GLM	1, 309	$F = 14.58$ †††	$F = 42.59$ ****; L	$F = 15.61$ ****; L	21.4	5.2
Mixed spatial	1, 309	$F = 2.13$ †n.s.	$F = 23.77$ ****; L	$F = 12.09$ ***; L		
<i>Fynbos</i>						
GLM	1, 78	$F = 0.09$ †n.s.; L	$F = 3.22$ *n.s.; L	$F = 87.38$ ****; L	59.5	5.0
Mixed spatial	1, 78	$F = 0.18$ †n.s.; L	$F = 1.75$ *n.s.; L	$F = 38.43$ ****; L		

Abbreviations: d.f. = degrees of freedom; temp (min) = minimum temperatures (°C); NDVI = normalised difference vegetation index; n.s. = not significant; L = log of predictor used; sq = squared term of predictor included in model.

Levels of significance: positive slope: *n.s. $P > 0.05$, *** $P < 0.001$, **** $P < 0.0001$; negative slope: †n.s. $P > 0.05$, ††† $P < 0.001$, †††† $P < 0.0001$

Table S2. Analyses similar to those reported in Table 3 with *ecotone distance* as response variable; however, here all grid cells of which the surface area are more than 50% transformed by humans is removed from the dataset. Nama-Karoo, succulent Karoo and forest biomes are not shown here, as none of their grid cells are more than 50% transformed.

region and procedure	d.f.	elevation	geology	rainfall	r ² (%)
<i>South Africa</i>					
GLM	1, 1607	$F = 109.7^{\dagger\dagger\dagger\dagger}; L$	$F = 68.28^{\dagger\dagger\dagger\dagger}; L$	$F = 12.27^{\dagger\dagger\dagger}; L$	27.2
Mixed spatial	1, 1607	$F = 13.96^{\dagger\dagger\dagger}; L$	$F = 50.02^{\dagger\dagger\dagger\dagger}; L$	$F = 3.01^{\dagger n.s.}; L$	
<i>Savanna</i>					
GLM	1, 535	$F = 143.19^{\dagger\dagger\dagger\dagger}; L$	$F = 14.42^{\dagger\dagger\dagger}; L$	n.i.	29.7
Mixed spatial	1, 535	$F = 18.48^{\dagger\dagger\dagger\dagger}; L$	$F = 9.24^{\dagger\dagger}; L$	n.i.	
<i>Grassland</i>					
GLM	1, 340	$F = 89.78^{\dagger\dagger\dagger\dagger}; L$	$F = 22.93^{\dagger\dagger\dagger\dagger}; L$	n.i.	26.4
Mixed spatial	1, 340	$F = 6.83^{\dagger\dagger}; L$	$F = 11.35^{\dagger\dagger\dagger}; L$	n.i.	
<i>Fynbos</i>					
GLM	1, 84	n.i.	n.i.	$F = 0.89^{\dagger n.s.}$	1.1

Abbreviations: d.f. = degrees of freedom; n.i. = not included in the model; n.s. = not significant; L = log of predictor used.

Levels of significance: negative slope: †n.s. $P > 0.05$, †† $P < 0.05$, ††† $P < 0.01$, †††† $P < 0.0001$

Table S3. Analyses similar to those reported in Table 3 with *alien species richness* as response variable; however, here all grid cells of which the surface area are more than 50% transformed by humans is removed from the dataset. Nama-Karoo, succulent Karoo and forest biomes are not shown here, as none of their grid cells are more than 50% transformed.

region and procedure	d.f.	elevation	geology	rainfall	r ² (%)
<i>South Africa</i>					
GLM	1106	$F = 4.92^*$; L	$F = 21.03^{****}$; L	$F = 102.94^{****}$; L	27.0
mixed spatial	1106	$F = 11.38^{***}$; L	$F = 2.24^*$ n.s.; L	$F = 18.22^{****}$; L	
<i>Savanna</i>					
GLM	360	$F = 154.34^{****}$; L	$F = 2.05^*$ n.s.; L	n.a.	31.1
mixed spatial	360	$F = 73.22^{****}$; L	$F = 0.04^*$ n.s.; L	n.a.	
<i>Grassland</i>					
GLM	297	$F = 51.85^{****}$; L	$F = 14.6^{***}$; L	n.a.	19.5
mixed spatial	297	$F = 17.95^{****}$; L	$F = 6.11^*$; L	n.a.	
<i>Fynbos</i>					
GLM	78	n.a.	n.a.	$F = 17.76^{****}$; L	18.7
mixed spatial	78	n.a.	n.a.	$F = 4.64^*$; L	

Abbreviations: d.f. = degrees of freedom; n.a. = not applicable to the analysis; n.s. = not significant; L = log of predictor used.

Levels of significance: positive slope: *n.s. $P > 0.05$, * $P < 0.05$, *** $P < 0.001$, **** $P < 0.0001$

Table S4. Spatial multiple regression models corresponding to the non-spatial models reported in Table 2, where ecotone distance and energy availability variables are analysed as predictors of invasive alien species richness. We found no significant influence of spatial autocorrelation for the savanna, Nama-Karoo and forest biomes.

region	d.f.	ecotone distance	temp (min)	NDVI
South Africa	1, 1326	$F = 10.56^{\dagger\dagger}$	$F = 18.02^{****}; sq$	$F = 147.86^{****}$
Grassland	1, 412	$F = 16.82^{\dagger\dagger\dagger\dagger}$	$F = 43.20^{****}; L$	$F = 29.70^{****}; L$
Succulent Karoo	1, 87	$F = 0.20^{\dagger}n.s.$	n.i	$F = 7.85^{**}$
Fynbos	1, 101	$F = 0.73^{\dagger}n.s.; L$	$F = 5.51^{\dagger}; L$	$F = 62.48^{\dagger\dagger\dagger\dagger}; L$

Abbreviations: d.f. = degrees of freedom; n.i. = not included in the model; temp (min) = minimum temperatures (°C); NDVI = normalised difference vegetation index; L = log of predictor used; n.s. = not significant

Levels of significance: positive effects: ** $P < 0.01$, **** $P < 0.0001$; negative effects: †n.s. $P > 0.05$, † $P < 0.05$, †† $P < 0.01$, †††† $P < 0.0001$

Table S5. Spatial multiple regression analyses corresponding to the non-spatial models reported in Table 3, where the relationships between ecotone distance, environmental heterogeneity and invasive alien species richness are examined. We found no significant influence of spatial autocorrelation for the forest biome.

region	d.f.	elevation	geology	rainfall
<i>South Africa</i>				
distance	1, 1835	$F = 22.58\ddagger\ddagger\ddagger\ddagger; L$	$F = 56.66\ddagger\ddagger\ddagger\ddagger; L$	n.i.
alien richness	1, 1311	$F = 19.12****; L$	$F = 5.19*; L$	$F = 25.29****; L$
<i>Savanna</i>				
distance	1, 623	$F = 16.73\ddagger\ddagger\ddagger\ddagger; L$	$F = 13.37\ddagger\ddagger\ddagger\ddagger; L$	n.i.
alien richness	1, 423	$F = 73.64****; L$	n.i.	n.a.
<i>Grassland</i>				
distance	1, 452	$F = 103.66\ddagger\ddagger\ddagger\ddagger; L$	$F = 27.34\ddagger\ddagger\ddagger\ddagger; L$	n.i.
alien richness	1, 398	$F = 81.29****; L$	$F = 13.14****; L$	n.a.
<i>Nama-Karoo</i>				
distance	1, 456	n.i.	$F = 27.58\ddagger\ddagger\ddagger\ddagger; L$	$F = 7.42\ddagger\ddagger; L$
alien richness	1, 223	n.a.	n.i.	$F = 16.70****; L$
<i>Succulent Karoo</i>				
distance	1, 130	n.i.	$F = 7.75\ddagger\ddagger; L$	n.i.
alien richness	1, 87	n.a.	$F = 0.15*n.s.; L$	n.a.
<i>Fynbos</i>				
distance	1, 115	n.i.	n.i.	$F = 3.53\ddagger n.s.$
alien richness	1, 101	n.a.	n.a.	$F = 13.64\ddagger\ddagger\ddagger; L$

Abbreviations: d.f. = degrees of freedom; n.i. = not included in the model; n.a. = not applicable to model; L = log of predictor used; n.s. = not significant

Levels of significance: positive effects: *n.s. $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$; negative effects: $\ddagger n.s. P > 0.05$, $\ddagger P < 0.05$, $\ddagger\ddagger\ddagger\ddagger P < 0.0001$