Biogeographical insights from ecotones and phytogeographic regions in southern Africa: case studies on invertebrates and alien plants

by

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Abstract

This thesis addresses questions within the research fields of invasion biology and spatial ecology, with a focus on species distribution patterns, biogeographical regions and ecological transition zones, or ecotones. More specifically, species distribution patterns in alien plants at large spatial scales using atlas data, and invertebrate patterns making use of field data collected at a smaller scale (total extent *ca*. 30 km). First I show that alien plants form large-scale geographically differentiated species assemblages in southern Africa (i.e. South Africa, Lesotho, Swaziland, Namibia and Botswana). I demonstrated this by mapping and describing several alien phytogeographic regions at a quarter-degree spatial resolution, and further suggest possible environmental and human-caused determinants of each of these regions. Second, at the same spatial resolution (for South Africa and Lesotho combined, and each of the plant biomes), I show that relatively higher levels of alien plant species richness occur at or near to ecotones, compared to areas that are spatially further away from these ecotones and that typically represent the core habitat of the ecoregions examined. This finding remained valid after taking into account the underlying positive relationships between alien plant richness and energy availability. I also suggest that it is the relatively higher environmental heterogeneity at ecotones (represented here by spatial variation in altitude, rainfall and geology) that promote high alien plant richness. Third, at a smaller spatial scale I report several examples of change in beetle and spider species composition across a savanna-grassland ecotone in the west of South Africa’s Free State Province, with the ecotone itself supporting comparatively lower levels of species richness and abundance. This contrasts with a popular assumption that ecotones are characterised by high species richness. Data gained from long-term intensive sampling is preferable for ecological studies, but not always available or practical to acquire; however with the three studies in this thesis I show that data from existing species atlases and feasible short-term surveys can be successfully applied to answer a variety of ecological questions.

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I would like to thank two co-authors, Salit Kark and Noam Levin, for their valuable contributions on the research findings reported in Chapter 3 of this thesis.

I thank the farmers and landowners of the Boshof area in the Free State, for allowing fieldwork on their land, especially Callie van der Merwe who went out of his way to make us comfortable at his guest house and provided help with any problems and mishaps.

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Disclaimer

This thesis mainly comprises three chapters representing studies that have been published in, or prepared for submission to, scientific journals. As a result, some style differences and overlap in the content of the thesis may occur. Chapters 2 and 3 correspond to studies conducted by multiple collaborators.

For Chapter 2 my main contributions included conceiving the research questions and tests in conjunction with the co-authors, conducting all statistical analyses and creating the maps, interpreting the results along with co-author Abraham E. van Wyk, writing the first draft manuscript of the published version (journal article), and ongoing editing and revision where needed.

For Chapter 3 my main contributions, as second author, included designing, implementing and interpreting all multivariate analyses, supplying relevant environmental data for the multivariate analyses, and incorporating this substantial aspect into all relevant sections of the accepted journal article (currently “in press”). The first author, Berndt J. van Rensburg conceived the main research question, supplied the relevant species and ecotone data, wrote the first draft manuscript, and applied ongoing editing and revision where needed.

Declaration

I, Sanet Hugo, declare that the thesis, which I hereby submit for the degree PhD (Zoology) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

SIGNATURE:

DATE:

CHAPTER 1

General Introduction

Broad-scale patterns of spatial variation in biotic diversity have received the attention of ecologists and biogeographers for almost two centuries (Nelson, 1978; Gotelli & Graves, 1996; Cox, 2001; Hawkins, 2001). Interest in biogeography and macroecology continues to grow, and recently improved methods of statistical analysis (including spatial analyses) coupled with powerful computer programs and a growing number of extensive digital datasets (i.e. species atlases and digitised museum collections) have enabled more objective studies and clearer understanding of biogeographical and biodiversity patterns (Blackburn & Gaston, 2003; Robertson *et al*., 2010). Spatial analysis and biogeography often have practical applications, in that these fields have recently had a great influence on conservation-related studies (e.g. McKinney & Lockwood, 1999; Da Silva & Bates, 2002; Koh *et al*., 2006). Spatial conservation planning is especially closely entwined with biogeography and studies on the broad-scale spatial variation in biodiversity and/or richness of endemic species (e.g. Chown *et al*., 2003; Ebach, 2003; Warman *et al*., 2004). Spatial analysis and biogeography concepts are also increasingly used to investigate threats to biodiversity such as harmful human activities or alien species (McKinney & Lockwood, 1999; Koh *et al*., 2006).

In this thesis I address the spatial distribution patterns of alien plant species, and species distribution patterns across ecotones (transition zones between adjacent ecological systems, Kark & Van Rensburg, 2006; see more information on ecotones below), which are themes of urgent enquiry in terms of their value to conservation. I report on three studies with the following aims: (i) to describe and evaluate phytogeographic regions of alien plant species in southern Africa (i.e. South Africa, Lesotho, Swaziland, Namibia and Botswana), (ii) to test whether ecotones in South Africa and Lesotho harbour higher numbers of alien plant species than more homogeneous core habitats, and (iii) to test if beetles and spiders (in the west of the Free Sate Province, South Africa) show a change in species composition, and a relatively higher species richness and diversity, at a savanna-grassland ecotone compared to the adjacent savanna and grassland habitats.

The first two studies were based on pre-existing species and environmental atlases and conducted at a broad multinational spatial scale at a quarter-degree resolution. The datasets used were plant species atlases based on herbarium collections (Pretoria herbarium's Computerised Information System, or PRECIS) and sight records along roads (South African

Plant Invaders Atlas, or SAPIA) (see e.g. Richardson *et al*., 2005; Henderson, 2007). A variety of other species atlases and ongoing species mapping programmes are also available for southern African countries, and in particular South Africa, including several vertebrate (e.g. birds, frogs and reptiles) and invertebrate (butterflies and arachnids) atlases (see Robertson *et al*., 2010, for more information). The currently available atlases, together with environmental and human demographic atlases that are also relatively easy to acquire, have led to a variety of macroecological and biogeography studies aimed at answering broad ecological questions at large spatial scales (e.g. Chown *et al*., 2003; Richardson *et al*., 2005; Steenkamp *et al*., 2005; Van Rooy & Van Wyk, 2010; Mokhatla *et al*., 2012). To my knowledge, alien phytogeographic regions have not been described for southern Africa at large spatial scales, although the endemic phytogeographic regions have been examined in several previous studies (e.g. Steenkamp *et al*., 2005; Van Rooy & Van Wyk, 2010). Further, although Richardson *et al*. (2005) have examined large-scale alien and native plant species richness patterns across South Africa in relation to natural and anthropogenic drivers, I am unaware of any studies on the possible role of ecotones in structuring these plant richness patterns. Many of the invasive alien plants in southern Africa are great ecological and economical threats, and knowledge gained from such large-scale studies could contribute to the effective management of harmful invasives (e.g. Van Wilgen *et al*., 2001; Richardson & Van Wilgen, 2004; Nel *et al*., 2004; Le Maitre *et al*., 2011).

The third study was based on a species survey conducted over two years at a much finer spatial scale, covering a distance of about 30 km across savanna and grassland vegetation types and the ecotone between them, in the west of the Free State Province of South Africa. To my knowledge, no previous studies have investigated this area in terms of its ecotonal characteristics, although the vegetation types have been classified by Mucina & Rutherford (2006). Ecotones are often seen as unique habitats with ecosystem processes and species assemblages of interest to research and conservation, as they are generally associated with relatively high levels of species and genetic diversity, high rates of speciation, and great temporal and spatial environmental heterogeneity (Gosz, 1993; Kolasa & Zalewski, 1995; Smith *et al*., 1997; Schilthuizen, 2000; Spector, 2002; Kark & Van Rensburg, 2006). Nevertheless, ecotones differ widely from one another (e.g. Walker *et al*., 2003), and as a research topic could benefit from an increased supply of studies testing the applicability of common assumptions in various regions, spatial scales and environmental conditions. South Africa is not only renowned for its wide diversity in plant and animal species (WCMC, 1992; Conservation International, 1998), but also its variety of climatic zones, vegetation types, plant biomes and ecosystems (e.g. Mucina & Rutherford, 2006), which also implies a great variety of ecotones. South Africa is therefore highly suitable for ecotone research; however, the ecotones in South Africa have up to date been relatively poorly studied (some examples are Kotze & Samways, 2001; Davis & Scholtz, 2004; Van Rensburg *et al.*, 2004). For this reason, and considering the proposed conservation value of ecotones, the second and third studies named here (research findings of these studies are reported, respectively, in the third and fourth Chapters of this thesis) would contribute timely knowledge to this research topic.

All three studies are based on the types of data that can be relatively easily and rapidly acquired by researchers with limited time and budget (i.e. short-term survey data and atlas data). It is true that data generated from long-term and/or intensive studies are most reliable (Davis, 2002; Lawes & Obiri, 2003) and such studies have become more prevalent over the past few decades (Blackburn & Gaston, 2003). Unfortunately, considering the urgent need for spatial biodiversity information for conservation purposes and the frequent restrictions on time and money for such research, short-cuts in the form of low-cost and non time-consuming data acquisition methods are still prevalent in biogeography and biodiversity studies (Gaston & Blackburn, 2000; Davis, 2002). These short-cuts may be classified as (i) using pre-existing species atlases, where these are available, or using mapped habitat characteristics (e.g. land use classes, ecosystems or habitat types) as surrogates for species diversity (e.g. Kiester *et al.*, 1996; Davis, 2002; Chown *et al.*, 2003; Lawler *et al.*, 2003; Lombard *et al.*, 2003; Warman *et al.*, 2004; Stoms *et al.*, 2005; Koh *et al.*, 2006), and (ii) conducting short-term (i.e. covering a few years only) and simple field surveys on one or a few easily sampled taxa representing biodiversity in general (e.g. McGeoch, 1998; Pik *et al.*, 1999, 2002; Davis, 2002; Van Rensburg *et al.*, 2009). Although less reliable, these less time-consuming methods often provide useful information for urgent conservation efforts (see e.g. Pik *et al.*, 1999, 2002; Chown *et al.*, 2003), or they might at least provide a base for more intensive and long-term research (Gaston & Blackburn, 2000). In some cases, however, these short-cut methods have also by themselves contributed to our understanding of general ecological questions; in this regard see the important contributions made by the relatively short-term field-based surveys of Krasnov & Shenbrot (1998), Walker *et al.* (2003) and Van Rensburg *et al.* (2009), and see Gaston (2005) and Robertson *et al.* (2010) for reviews of the contributions made by larger scale atlas-based studies. Similarly, in this thesis I successfully address general ecological questions with currently available (atlas data, Chapters 2 and 3 of this thesis) or rapidly acquired (simple short-term survey, Chapter 4 of this thesis) data.

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CHAPTER 2

Alien Phytogeographic Regions of Southern Africa: Numerical Classification, Possible Drivers, and Regional Threats

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ABSTRACT

The distributions of naturalised alien plant species that have invaded natural or semi-natural habitat are often geographically restricted by the environmental conditions in their new range, implying that alien species with similar environmental requirements and tolerances may form assemblages and characterise particular areas. The aim of this study was to use objective numerical techniques to reveal any possible alien phytogeographic regions (i.e. geographic areas with characteristic alien plant assemblages) in southern Africa. Quarter degree resolution presence records of naturalised alien plant species of South Africa, Lesotho, Swaziland, Namibia and Botswana were analysed through a divisive hierarchical classification technique, and the output was plotted on maps for further interpretation. The analyses revealed two main alien phytogeographic regions that could be subdivided into eight lower level phytogeographic regions. Along with knowledge of the environmental requirements of the characteristic species and supported by further statistical analyses, we hypothesised on the main drivers of alien phytogeographic regions, and suggest that environmental features such as climate and associated biomes were most important, followed by human activities that modify climatic and vegetation features, such as irrigation and agriculture (multivariate regression analyses explained between 9% and 47% of variation in the response variables, i.e. the phytogeographic regions' spatial distributions). Most of the characteristic species are not currently well-known as invasive plant species, but many may have potential to become troublesome in the future. Considering the possibility of biotic homogenization, these findings have implications for predicting the characteristics of the plant assemblages of the future. However, the relatively low quality of the dataset necessitates further more in-depth studies with improved data before the findings could be directly beneficial for management.

INTRODUCTION

Broad-scale patterns of spatial variation in biotic diversity have received the attention of ecologists and biogeographers for almost two centuries (Nelson, 1978; Gotelli & Graves, 1996; Hawkins, 2001; Ebach, 2003). More recently, improved methods of statistical analysis, coupled with powerful computer programs have enabled more objective macroecology and biogeography studies (Blackburn & Gaston, 2003). For example, macroecology and biogeography have recently been employed in spatial conservation planning studies, to indicate the regions where conservation efforts should be maximised (e.g. species rich areas) as well as the regions that are threatened by human activities that are detrimental to biodiversity (McKinney & Lockwood, 1999; Chown *et al*., 2003; Ebach, 2003; Gaston & Blackburn, 2003). One of these threats is the deliberate or accidental human-facilitated introduction of species into regions where they do not occur naturally (Gaston & Blackburn, 2003). Although most introduced or alien species do not form viable populations in the introduced range, many have become naturalised in the new environment and some are able to invade natural or semi-natural ecosystems, often causing loss of natural biodiversity, water shortages, loss of crop and forest production, and increased soil erosion (Higgins *et al*., 2000; Robertson *et al*., 2003; Nel *et al*., 2004; Van Wilgen *et al*., 2008; Le Maitre *et al*., 2011).

Management intervention of harmful alien species is expensive, often labour intensive, and not always effective (Coblentz, 1990; Van Wilgen *et al*., 2001; Richardson & Van Wilgen, 2004). To reduce cost and increase efficiency it is necessary to identify priority areas and species on which to focus research and control efforts (Higgins *et al*., 2000; Robertson *et al*., 2003; Nel *et al*., 2004; Van Wilgen *et al*., 2008). To this end, researchers have attempted to track the ability of certain alien species to invade areas (e.g. predictions of future spatial range, through niche modelling methods), the potential for invasive species to transform their introduced habitat, or the vulnerability of certain areas to invasion (Higgins *et al*., 1999, 2000; Robertson *et al*., 2003; Rouget & Richardson, 2003; Nel *et al*., 2004; Henderson, 2007; Wolmarans *et al*., 2010). However, with hundreds of naturalised alien species recorded from southern Africa for example (Robertson *et al*., 2003; Richardson *et al*., 2005; Henderson, 2007), timely identification and control of each potentially harmful invasive species seems to be a futile task. Several South African reviews delineated whole sets of priority species, by listing and describing alien species that are currently of most concern (i.e. with known economical and ecological impacts), often organising these species lists according to the biomes or occasionally the political provinces in which they are most troublesome (Le Maitre, 2000; Van Wilgen *et al*., 2001, 2008; Henderson, 2007). Conservation actions are often undertaken at a provincial level thereby justifying the organisation of alien species into political provinces; however it makes little sense ecologically, to impose artificial boundaries on naturally established species distributions. In this study, by ‘natural establishment’, we mean the spontaneous colonisation of alien plants in response to natural environmental conditions (which may or may not be spatially coincident with the biomes) as well as human-caused conditions/transformations, but without deliberate aid by humans (Hobbs & Huenneke, 1992; Richardson *et al*., 2005).

Naturalised alien species may adapt successfully to a new set of environmental conditions (Lavergne & Molofsky, 2007) and many invasive alien species are widespread and present in a range of habitats (e.g. *Acacia mearnsii* in southern Africa, Henderson, 2007). Nevertheless, the spatial distributions of naturalised and invasive alien plants are generally constrained by environmental factors similar to those constraining native plant species. Studies have shown that the distribution of such species in the introduced range (adventive range) is often a reflection of the prevalent environmental conditions in their native range (Higgins *et al*., 1999; Stohlgren *et al*., 1999, 2003; Daehler, 2003; Rouget & Richardson, 2003; Richardson *et al*., 2005; Henderson, 2007; Van Wilgen *et al*., 2008). For example, in southern Africa species of *Prosopis* are prominent invaders of arid areas (Milton & Dean, 1998). Consequently, we may expect to find that groups of alien plants with similar environmental requirements and tolerances are associated with specific areas, thereby forming assemblages of alien plant species that characterise those areas (Milton & Dean, 1998; Henderson, 2007).

The possibility that naturally established alien species assemblages could exist in the introduced range encourages much further research (e.g. on their spatial distributions, characteristics and determinants) and we propose that such assemblages could be prioritised for invasive species management. In this regard, previous studies in South Africa, by Richardson *et al*. (2004) and Thuiller *et al*. (2006), explored the link between the shared traits of successful alien plant species and their spatial distributions. They used classification analysis to describe clusters of invasive alien plant species as species assemblages with ecologically meaningful spatial distributions, and revealed some intrinsic and extrinsic factors that determine the invasive potential of alien species in those particular geographic areas where their niche requirements are met (Richardson *et al*., 2004; Thuiller *et al*., 2006). For both studies, the clusters could not share species although the spatial distributions of the clusters may overlap geographically (Richardson *et al*., 2004; Thuiller *et al*., 2006). What has not yet been considered, at least for southern Africa, is whether the study area itself may be spatially partitioned into non-overlapping geographical areas characterised by their alien plant species compositions, which might serve as more ecologically sensible alien species management districts than political provinces. However, before such a venture could be considered, we need to first find and describe such regions, if they exist.

Non-overlapping geographic regions characterised by distinct floristic compositions are termed phytogeographic regions (Steenkamp *et al*., 2005). This method of classifying different regions according to their species compositions has a long history with regard to endemic plant species of Africa (White, 1993; Van Wyk & Smith, 2001; Linder *et al*., 2004; Steenkamp *et al*., 2005); however, to our knowledge, alien plant species have not been studied in this way. The designation of phytogeographic regions is often based on expert opinion, for example, Van Wyk and Smith (2001) relied on expert opinion to designate the Cape Floristic Region, the Succulent Karoo Region, and the Maputaland-Pondoland Region as larger phytogeographic regions in southern Africa encompassing a series of local centres of endemism (see also White, 1993). However, more objective methods of numerical analysis are available, one of which was successfully used by Van Rooy & Van Wyk (2010) on the moss flora of southern Africa, and by Steenkamp *et al*. (2005) on the native plant genera of southern Africa (see also Linder *et al*., 2004). In these numerical studies a grid is applied to the analysed geographical area, and therefore the term ‘phytogeographic region’ would then be defined as a group of grid cells of similar floristic composition (Steenkamp *et al*., 2005). Endemic phytogeographic regions are often evaluated with regard to broad-scale current and prehistoric climatic and geological factors that have likely formed the endemic plant assemblages over the long term (Van Wyk & Smith, 2001; Linder *et al*., 2004; Steenkamp *et al*., 2005). In contrast, the adventive spatial ranges of alien plant species are probably shaped by recent or current environmental and human-related factors that were prevalent during and after the introduction of these species.

The aim of this study was to reveal ecologically meaningful phytogeographic regions of alien plant species in southern Africa, by means of numerical classification analysis. We then hypothesise on the possible drivers of these regions, and discuss their implications for alien species management and research in the future. We considered only naturalised and invasive alien plant species – casual introduced species were not included in the data. Throughout the article, we use the terms ‘naturalised’ and ‘invasive’ in accordance with the definitions in Richardson *et al*. (2000).

METHODS

Study area and data

The data we used were records of all naturalised alien plant species from the National Herbarium, Pretoria Computerised Information System (PRECIS), for Namibia, Botswana, South Africa, Lesotho and Swaziland. Distribution records in PRECIS are currently most complete for these southern African countries (Steenkamp *et al*., 2005) and of these, South

Africa, Lesotho and Swaziland provide the best data. Analyses were conducted at the quarter degree square resolution because PRECIS data are mainly available at this resolution. The species rank was the lowest taxonomic level which was analysed: records of different infraspecific taxa were pooled and hybrids were not considered. Ultimately, 861 alien plant species were included in the analysis.

Southern Africa is a geologically and climatically diverse region. Notable drivers of floristic composition are the topographical and geological variation between the interior plateau of relatively high altitude, that is bordered on three sides by mountain ranges forming the Great Escarpment, beyond which is a sharp drop in altitude towards the coastal plains (Fig. 1; Steenkamp *et al.*, 2005; Mucina & Rutherford, 2006). Notable climatic drivers include a strong moisture gradient from arid regions in the west to humid regions in the east, and a variation in the seasonality of rainfall, from summer rainfall comprising most of southern Africa, to a smaller winter rainfall area in the west, and year-round rainfall on the south-west coast between the winter and summer rainfall areas (Steenkamp *et al.*, 2005; Mucina & Rutherford, 2006). Finally, eight biomes have been described for South Africa, the grassland, savanna, Albany thicket, Nama-Karoo, succulent Karoo, forest, fynbos and Indian Ocean coastal belt (Fig. 1; Mucina & Rutherford, 2006). The Nama-Karoo, succulent Karoo and savanna biomes continue north into Namibia, which also includes the desert biome (Irish, 1994; Van Wyk & Smith, 2001). Botswana is mainly covered by savanna biome with a smaller area of Nama-Karoo (Van Wyk & Smith, 2001; Ringrose *et al.*, 2002).

Analyses

The presence and spatial distributions of discernable phytogeographic regions in the study area were assessed based on a divisive hierarchical classification technique (Steenkamp *et al.*, 2005). Grid cells were grouped into clusters based on the combination of alien plant species present in each cell as recorded in the PRECIS dataset. The statistical program TWINSPAN (two-way indicator species analysis; Hill, 1979) was used to conduct this classification. The dataset was converted to a binary presence/absence data matrix and then inputted, via the programs Turboveg 1.97 (International Single User Version, Stephen Hennekens) and Megatab 2.2 (Elsware), into TWINSPAN.

Despite criticisms directed at TWINSPAN, it is still widely used and has been shown by many previous studies from many parts of the world to be robust, effective, relatively objective, and successful in distinguishing geographic areas with characteristic assemblages

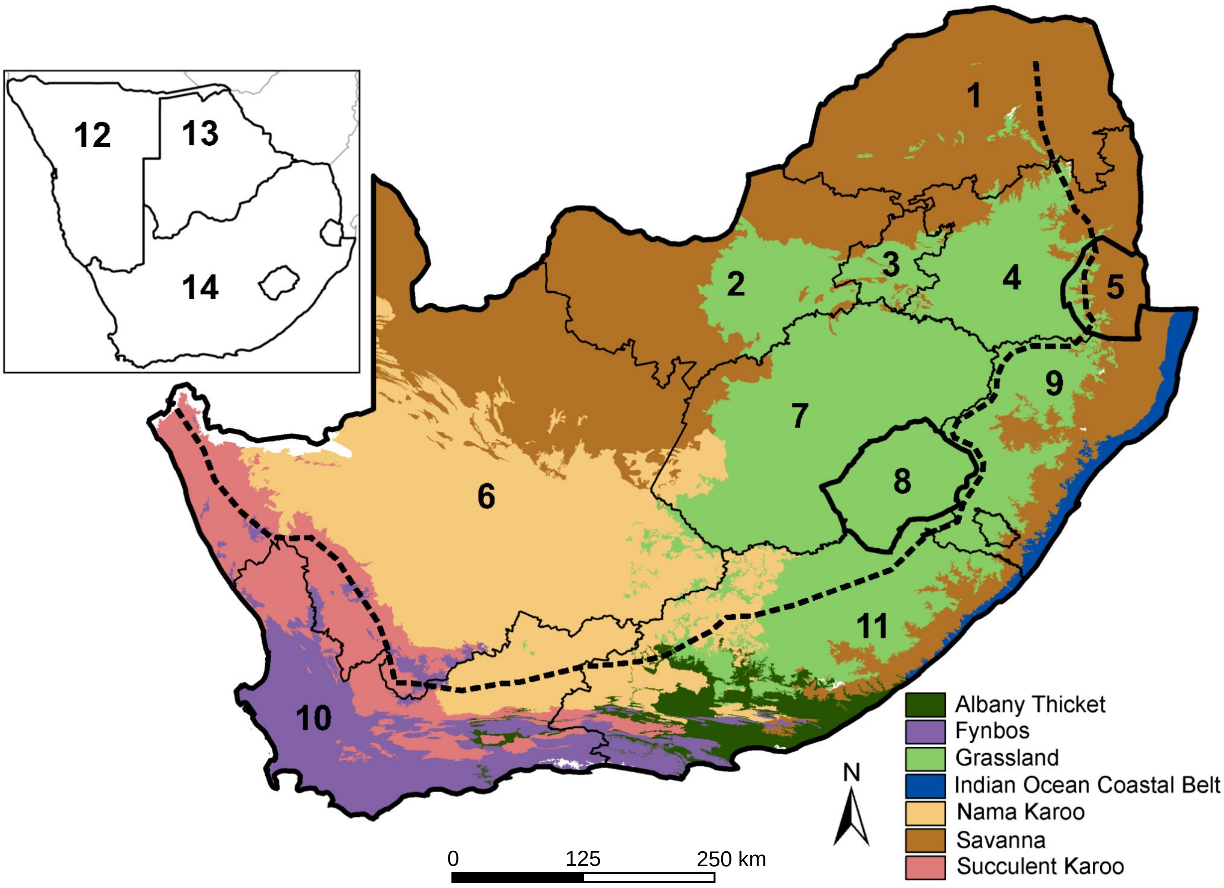

Figure 1 Here we represent the political boundaries of the general study area (i.e. including Namibia and Botswana) and the spatial distributions of seven of the biomes in South Africa, Lesotho and Swaziland, as based on the biome classifications of Mucina & Rutherford (2006). The forest and desert biomes occupy very little of South Africa's surface area, and are not shown here. The approximate position of the Great Escarpment in South Africa is represented by the dashed line. The numbers indicate the following political regions: 1. Limpopo Province, 2. North West Province, 3. Gauteng Province, 4. Mpumalanga Province, 5. Swaziland, 6. Northern Cape Province, 7. Free State Province, 8. Lesotho, 9. KwaZulu-Natal Province, 10. Western Cape Province, 11. Eastern Cape Province. The insert shows the countries 12. Namibia, 13. Botswana, and 14. South Africa.

of species or higher taxa (Gauch & Whittaker, 1981; Ojeda *et al*., 1998; Saiz *et al*., 1998; Lawesson & Skov, 2002; Steenkamp *et al*., 2005; Kent, 2006; Van Rooy & Van Wyk, 2010). Also, TWINSPAN is particularly suitable for datasets that are complex, large and noisy (Gauch & Whittaker, 1981; Steenkamp *et al*., 2005; Kent, 2006; Van Rooy & Van Wyk, 2010). This is essentially the state of the PRECIS dataset, which, as with many species atlas datasets, contains many gaps in terms of locations for which no records are available or for which the available data are not particularly reliable or representative (Richardson *et al*., 2005; Steenkamp *et al*., 2005; Van Rooy & Van Wyk, 2010).

The successive clusters of grid cells derived from the initial dendrogram provided by TWINSPAN were depicted on maps representing the study area (ArcView GIS 3.3, ESRI Inc., 2002). We report only those clusters of grid cells that we considered to be ecologically meaningful with the potential for further interpretation. Successive divisions in TWINSPAN were continued until no further interpretable or meaningful geographic regions could be identified. Clusters at any level of division in the hierarchical classification analysis that were too small or too randomly spaced across the study area to allow for meaningful interpretation were disregarded; however such clusters altogether comprised only a small part of the study area.

To select environmental factors that we considered to be possible drivers of these phytogeographic regions, we subjectively assessed the discernable phytogeographic regions as plotted on the maps, together with knowledge of the spatial distributions of environmental and human factors known to drive plant species distribution at the spatial scale studied and at the recent timescales governing alien species (Van Wyk & Smith, 2001; Richardson *et al*., 2005). Additional insight is provided by knowledge of the environmental requirements of the alien species that characterise each phytogeographic region. “Characteristic” species were considered to be those whose spatial distributions coincide more with specific phytogeographic regions than with the rest of the study area (corrected for the size of the region), and that therefore likely contributed most to TWINSPAN’s classification of grid cells into clusters. Some of these species are mentioned in the discussion; more complete lists of the characteristic species of all phytogeographic regions are provided in Table S1, Appendix 1.

We relied mainly on subjective expert opinion to refine and interpret the output of the TWINSPAN analysis (see White, 1993, and Van Wyk & Smith, 2001, for discussions of the benefits of this method); however, we based these interpretations on a wealth of published and mapped information on the areas and species studied. We still consider the TWINSPAN method to be more objective than relying solely on expert opinion for the demarcation of phytogeographic regions, as none of the alien phytogeographic regions described here were expected *a priori*. Nevertheless, although Namibia and Botswana contain too few datapoints to justify further analysis, South Africa, Lesotho and Swaziland, for which better PRECIS data coverage and spatial environmental data are available, were further examined through calculations of percentage overlap and multiple regression analyses to support our inferences of the possible environmental drivers of alien phytogeographic regions.

Mucina & Rutherford (2006) published geographic information system (GIS) maps depicting the spatial distributions of the biomes in South Africa, Lesotho and Swaziland. To convert these biome GIS maps to a quarter degree resolution that may be compared with the various phytogeographic regions, we assigned each quarter degree grid cell from the PRECIS dataset to a particular biome if more than 50% of the area of the grid cell is overlapped by that biome. Grid cells that were not more than 50% covered by any single biome (i.e. could not be assigned to any biome) were disregarded as they were few in number and unlikely to have a notable influence on the results. We then estimated and ranked the relative importance of each of the biomes in the various phytogeographic regions by calculating for each phytogeographic region the percentage of its grid cells that were assigned to each particular biome. The forest and desert biomes were excluded, as these biomes occupied very little or none of the surface area of South Africa, Lesotho or Swaziland.

The spatial distribution of each individual phytogeographic region was analysed using the SAS version 9.2 (SAS Institute Inc., 2008) procedure ‘PROC LOGISTIC’, which is a logistic regression procedure that allows the use of presence-absence (i.e. binary) data to model the probability that a grid cell belonging to a particular phytogeographic region coincides spatially with selected environmental factors (Evans *et al*., 2006). Based on our subjective interpretation as explained previously and after conducting tolerance tests for collinearity (Neter *et al*., 1996; Evans *et al*., 2006) we selected mean annual precipitation, mean monthly maximum and minimum temperatures for the hottest and coldest months respectively, and the percentage of the surface area of each grid cell that is cultivated, degraded or irrigated, as predictors of phytogeographic regions. All of these factors were represented at a quarter degree resolution. Precipitation and mean monthly maximum and minimum temperatures were calculated from monthly data based on interpolated climate surfaces for the past 30–50 years, and supplied by the South African Computing Centre for Water Research (Schulze, 1997). Cultivated area and degraded area were from the National Land Cover Database as captured by Landsat TM satellite imagery mainly between 1994 and 1995 (Thompson, 1996). A spatial distribution map of irrigated areas for South Africa was published by the Agricultural Research Council – Institute for Soil, Climate, and Water (2000) and was downloaded at the Agricultural Geo-Referenced Information System (AGIS) website (www.agis.agric.za).

In some cases, certain predictors had nonlinear correlations with the response variable and this was revealed if the inclusion of the square terms of those predictor variables significantly improved the model (Evans *et al*., 2006). In some of the models, a log transformation was applied to certain predictors to improve heteroscedasticity (Evans *et al*., 2006). To test which combination of predictor variables best explain variation in the response variable (i.e. which model is best), 'PROC LOGISTIC' supplies Akaike's Information Criterion (AIC) values, of which smaller (or more negative) values indicate a better model. AIC values do not mean anything by themselves and are used to compare models with different predictor variables and the same response variable to select the best available model. Thus, AIC values could not be used to compare different subsets of a dataset, i.e. different phytogeographic regions, and were not reported. To indicate the amount of variation in the response variables that is explained by the predictor variables of the 'best' models, we report Max-rescaled R-square values (R^2) that are appropriate for logistic regression (see Nagelkerke, 1991, for an explanation of this adjusted *R*-square value). Spatial autocorrelation in spatial studies could potentially violate assumptions of independent errors; unfortunately, we could not test or control for spatial autocorrelation, as such a procedure has not yet been developed for logistic regression analysis (Evans *et al*., 2006).

RESULTS

The meaningful clusters resulting from successive divisions of the presence records of naturalised alien plant species were depicted in a dendrogram (Fig. 2), and the clusters of two levels of division in this dendrogram were chosen to be depicted on the maps in Figs 3 (higher level of division) and 4 (lower level).

Here we summarise the process of division in the order in which the clusters of grid cells forming phytogeographic regions became separated from the main dataset. See the Discussion section for more information on the names assigned to the phytogeographic regions (see also the spatial features depicted in Fig. 1). The first meaningful division by TWINSPAN (i.e. the higher level division) showed two clusters that could be defined as phytogeographic regions (Figs 2 and 3), and that could be assumed to be the regions that differed most strongly from one another in terms of their characteristic alien plant species compositions (Table S1, Appendix 1). The larger of the two regions, the Multiclimate Phytogeographic Region, was spread over the entire study area (Fig. 3) and surrounded a smaller phytogeographic region, the Greater Arid Region.

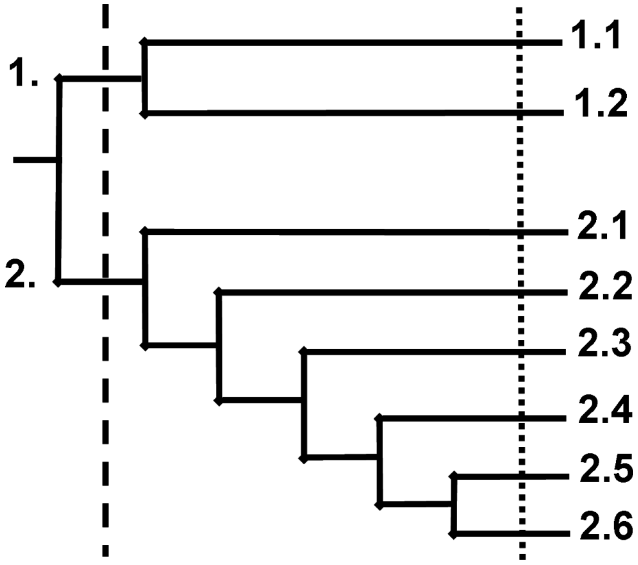

Figure 2 The initial TWINSPAN results was a dendrogram, which is represented here in a simplified form showing only the ecologically meaningful clusters (i.e. phytogeographic regions) from two levels of division (– – – – higher level; •••••• lower level). These phytogeographic regions were: 1. the Greater Arid Region, which includes the 1.1 Arid, and 1.2 Orange River Regions; and 2. the Multiclimate Region, which includes the 2.1 Escarpment, 2.2 Northern, 2.3 Agricultural, 2.4 Western Cape, 2.5 Grassland, and 2.6 Savanna Regions.

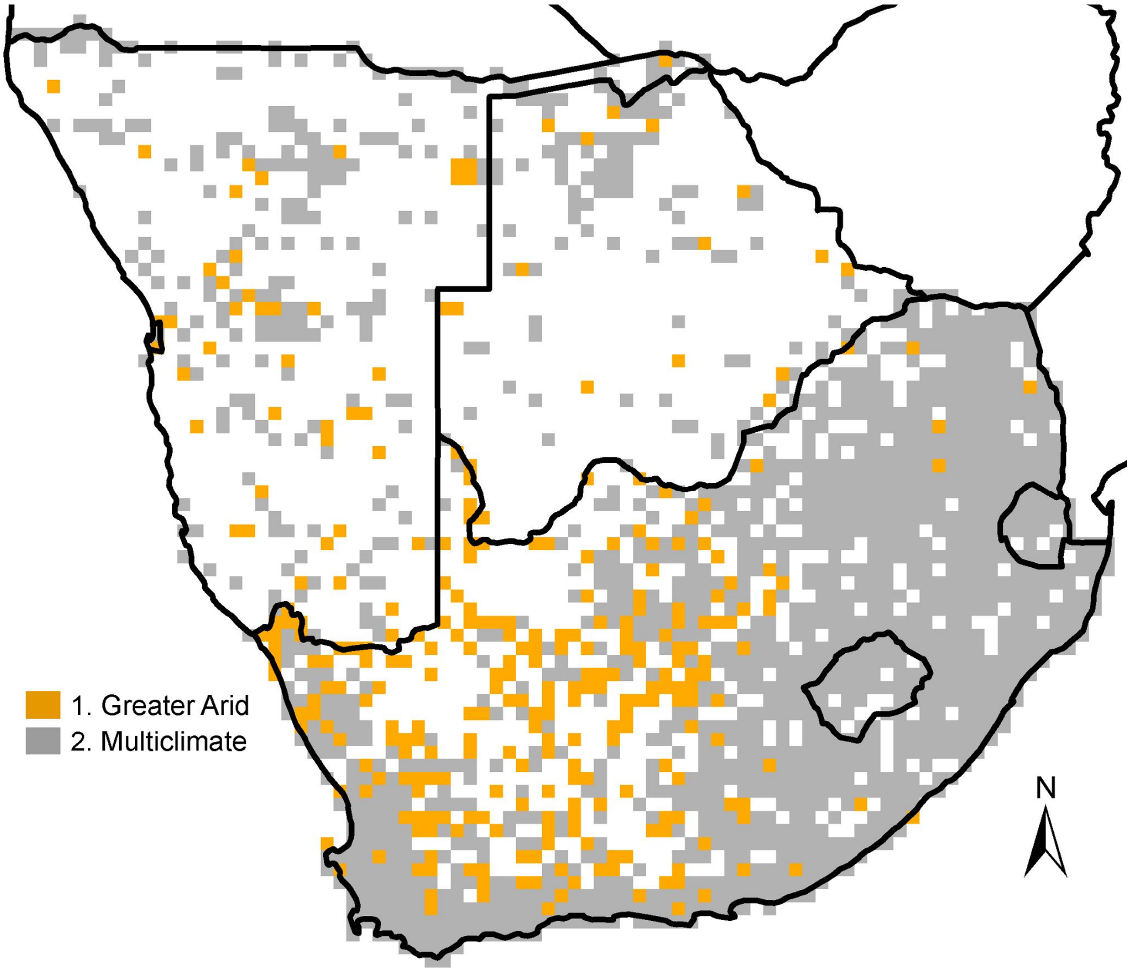

Figure 3 The grid cells comprising the two main ecologically meaningful clusters (higher level phytogeographic regions) as derived from the TWINSPAN cluster analysis (see Fig. 2), were plotted on a map to indicate the spatial distributions of the 1. Greater Arid and 2. Multiclimate Phytogeographic Regions.

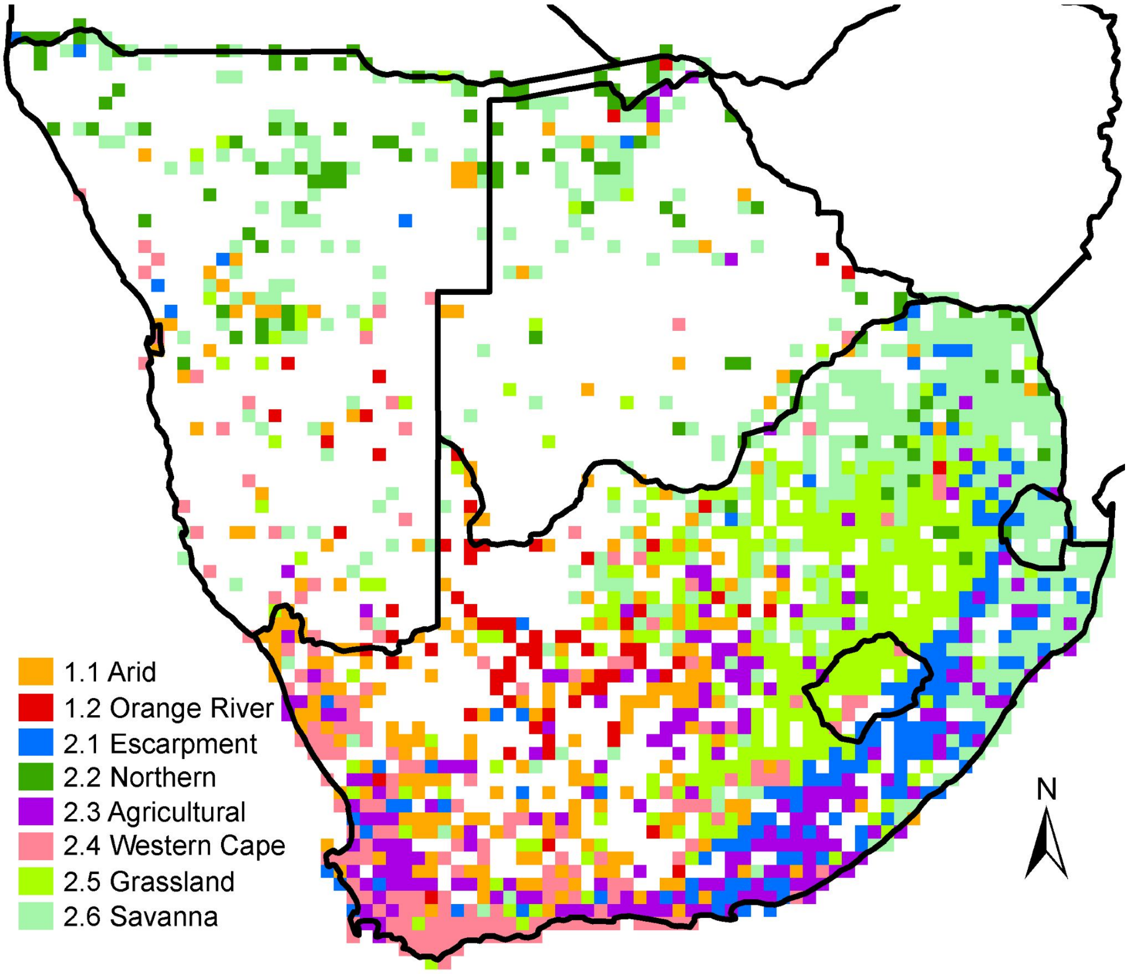

Figure 4 Similar to Fig. 3, the grid cells comprising the lower level phytogeographic regions as derived from the cluster analysis (Fig. 2) are depicted: the 1.1 Arid and the 1.2 Orange River Phytogeographic Regions were subdivided from the Greater Arid Region, and the 2.1 Escarpment, 2.2 Northern, 2.3 Agricultural, 2.4 Western Cape, 2.5 Grassland and 2.6 Savanna Regions were subdivided from the Multiclimate Region.

After further subdividing the Greater Arid Region, two more phytogeographic regions, the Arid Region and the Orange River Region, were revealed (Figs 2 and 4). After subdivision of the Multiclimate Region, six more phytogeographic regions were revealed: the Escarpment Region, followed by the Northern Region, the Agricultural Region, the Western Cape Region, and finally, the Grassland and Savanna Regions (Figs 2 and 4). Any further subdivisions of these eight lower level phytogeographic regions yielded small, vague, spread-out clusters that likely represent noise. Therefore, no further subdivisions are reported.

Table 1 lists the percentages of grid cells of each phytogeographic region that were assigned to each biome in South Africa, Lesotho and Swaziland. The Greater Arid Phytogeographic Region spatially coincided mainly with the arid Nama-Karoo and succulent Karoo biomes, although arid parts of the savanna biome also made a large contribution especially within the lower level Orange River Region. Within the Multiclimate Phytogeographic Region, *ca*. 68% of the Grassland Phytogeographic Region coincided with the grassland biome, and *ca*. 71% of the Savanna Phytogeographic Region coincided with the savanna biome. Around 50% of the Escarpment Phytogeographic Region coincided with the grassland biome and *ca*. 20% with the savanna biome. Further, nearly 50% of the Western Cape Phytogeographic Region coincided with the fynbos biome, with large contributions also made by the succulent Karoo (*ca*. 20%) and the Nama-Karoo (*ca*. 15%). Several biomes were prominent in the Agricultural Phytogeographic Region, most notably the grassland (almost 30% of the Agricultural Phytogeographic Region) and fynbos (more than 20%) biomes. The Northern Region was not analysed as only a few scattered outliers are present in South Africa, Lesotho and Swaziland.

Table 2 shows, for each phytogeographic region, the combination of environmental and human variables that best predicted the spatial distribution of that phytogeographic region (i.e. the best logistic regression model) together with the Max-rescaled R-square (R^2) values. Overall, the natural environmental factors (precipitation and mean maximum and minimum monthly temperatures) seemed to be more important than the human-caused factors (irrigated, cultivated and degraded area) in that they were more often included into the best models and also had greater Chi-square values (Table 2). Between 22% and 47% of variation in the response variables (i.e. distributions of phytogeographic regions) was explained by the relevant predictors in the reported models, except for the Agricultural Region where only 9% was explained (see the R^2 values in Table 2). Judging by this, it is likely that the phytogeographic regions are partly determined by factors that we have not considered in the current study. The ‘best’ models of individual phytogeographic regions are further discussed in the discussion section.

Table 1 The percentage of grid cells of each phytogeographic region that has been assigned to each particular biome (Mucina & Rutherford 2006; see the Methods section for more details).

	Albany thicket	Indian Ocean coastal belt	Grassland	Savanna	Fynbos	Succulent Karoo	Nama-Karoo
1. Greater Arid	1.25	0.42	6.67	20.83	5.83	18.75	42.92
1.1 Arid	1.12	0.56	7.82	16.76	7.26	24.58	37.99
1.2 Orange River	1.67	1.67	3.33	31.67	1.67	1.67	58.33
2. Multiclimate	3.45	3.45	35.77	31.82	11.87	5.13	8.16
2.1 Escarpment	8.50	3.92	50.98	21.57	7.84	3.92	3.27
2.2 Agricultural	11.46	3.13	28.65	11.98	23.44	7.29	14.06
2.3 Western Cape	1.92	0	8.97	4.49	47.44	19.87	15.38
2.4 Grassland	0.64	0.64	68.17	17.04	2.25	1.61	9.97
2.5 Savanna	0.31	8.90	15.95	71.17	0.61	0.92	2.15

Table 2 The Chi-square values, significance levels, and Max-rescaled R-square values (R^2, see Nagelkerke 1991) of natural and human-caused factors that were included in the logistic regression models that best explained (in terms of probability of co-occurrence) the spatial distribution of each phytogeographic region. Degrees of freedom for each model are equal to the number of predictors included in the model (SAS Institute Inc., 2004).

	Irrigated area	Cultivated area	Degraded area	Maximum temperature	Minimum temperature	Precipitation	R^2 (%)
1. Greater Arid	n.i.	n.i.	n.i.	****33.90	†††13.35	††††159.16	46.7
1.1 Orange River	n.i.	*5.48	n.i.	****40.25	†††11.04	††††26.15	38.7
1.2 Arid	n.i.	n.i.	n.i.	n.i.	n.i.	††††156.55	33.0
2. Multiclimate	n.i.	n.i.	n.i.	††††33.90	***13.35	****159.16	46.7
2.1 Escarpment	*4.08 L	††††17.43	****22.81 sq	††††54.05 L	****20.17 sq	*4.54 L	25.7
2.2 Agricultural	*5.81 L	n.i.	n.i.	****21.65	n.i.	n.i.	9.3
2.3 Western Cape	n.i.	††7.25	n.i.	††††60.64	*6.64	****26.26	22.2
2.4 Grassland	††9.96	*5.61 L	††7.83	**8.61 L, sq	††††116.78	****25.27 sq	38.8
2.5 Savanna	n.i.	n.i.	†5.30	****18.46	****23.78	****56.18	46.5

Note: Abbreviations: n.i = not included in the model, L = log of predictor used, sq = square term of predictor included (nonlinear relationship). Levels of significance: positive slope: *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, ****$p < 0.0001$; negative slope: ††$p < 0.01$, †††$p < 0.001$, ††††$p < 0.0001$.

DISCUSSION

Several alien plant phytogeographic regions were identified based on the PRECIS data, which we considered ecologically meaningful based on their spatial associations with various habitat, climatic and human-related factors. At the lowest meaningful level of division, a total of eight alien phytogeographic regions were revealed, two of which were subdivided from the Greater Arid Phytogeographic Region, and six from the Multiclimate Phytogeographic Region.

Our subjective interpretations of the determinants of these phytogeographic regions, as discussed further on in the article, were generally supported by further statistical analyses. Compared to human-related factors, natural environmental factors were generally more important predictors of the spatial distributions of alien phytogeographic regions in logistic regression models. It is possible that the alien species that characterise the various phytogeographic regions (Table S1, Appendix 1) are less dependent on human activities because they are invasive species that thrive in the natural habitat of their introduced range (Richardson *et al*., 2005). However, this contrasts with previous studies stressing the importance of human activities for explaining invasive alien plant spatial distributions (Richardson *et al*., 2004; Thuiller *et al*., 2006). Other possible reasons for the weaker influence of human-related factors in the current study are that these variables might be more important at finer spatial resolutions than that of the current study (scale-dependent effects, Richardson *et al*., 2005), or that the phytogeographic regions might be associated with human activities that had not been considered in the current study.

Other atlases of the geographic distribution of alien plants are available for at least parts of the study area, most notably the Southern African Plant Invaders Atlas, or SAPIA, database; however, this database is based on sight records of easily visible species along roads and as such is particularly biased towards larger woody species and human-disturbed environments (Henderson, 2007). Considering that we were more interested in the natural spread of *all* naturalised alien plant species, the SAPIA database is less suitable for the study because it introduces those biases that we would most like to avoid (but see Richardson *et al*., 2004; Thuiller *et al*., 2006). Therefore, we considered the PRECIS dataset more suitable, as it was based on specimen collection of all plants regardless of invasive status and growth form, more randomly placed with regard to natural and human-made landscape features, and has been shown to be useful for large-scale spatial numerical classification studies (Steenkamp *et al*., 2005).

Greater Arid phytogeographic region

The Greater Arid Phytogeographic Region (Fig. 2) is associated mainly with hot, low rainfall areas (Table 2), like the arid and semi-arid Nama-Karoo biome and Kalahari regions in the west of South Africa and in Namibia, extending further west into the succulent Karoo biome (Table 1; Figs 1 and 3; Irish, 1994; Ringrose *et al*., 2002; Mucina & Rutherford, 2006). In accordance with Milton & Dean's (1998) survey in arid and semi-arid regions of South Africa, the Greater Arid Phytogeographic Region is characterised by arid-adapted taxa such as *Atriplex* spp., *Prosopis* spp., *Verbesina encelioides* and *Salsola kali*. The native ranges of these species are generally tropical or subtropical arid regions, especially in South and Central America and Australia (Gates, 1972; Stromberg, 1993; Feenstra & Clements, 2008).

The lower level Arid Phytogeographic Region spans the Greater Arid Region, encloses the Orange River Region, and closely matches the Greater Arid Region in terms of characteristic species and biomes, except that species of *Prosopis* are much less important in the Arid Region (Table 1; Figs 1, 3 and 4). The Orange River Region is found on the border between the savanna and Nama-Karoo biomes where these biomes are separated by the Orange River (Table 1; Figs 1 and 4; Mucina & Rutherford, 2006). In contrast to the Arid Region, which is characterised mainly by *Atriplex* and *Salsola* species, we consider *Prosopis glandulosa*, or honey mesquite, to be the most significant characteristic species of the Orange River Region (present in 59% of the grid cells of this region), followed by *P. velutina*, or velvet mesquite (present in 52% of grid cells). Less important, but still noteworthy, are *Persicaria limbata* (third most characteristic species) and *Prosopis chilensis* (fourth most characteristic). These four characteristic species commonly colonise the water edge and the banks of permanent or temporary rivers or dry riverbeds, and are probably dependent on the Orange River and other water sources such as irrigation dams. Therefore, we suggest that permanent and temporary sources of water are essential drivers of the alien species found in the Orange River Region, although irrigated area is not included in the best model for this region (Table 2).

Multiclimate phytogeographic region

The Multiclimate Phytogeographic Region is not distinctly associated with any specific biome or habitat (Table 1; Figs 1 and 3), although the climatic variables best predicting its distribution are exactly opposite to that of the Greater Arid Region, i.e. milder and wetter (Table 2). The six lower level phytogeographic regions embedded within this main region are more distinct in terms of climate and environmental features.

Escarpment Phytogeographic Region

This region is distributed mainly along the length of the eastern and southern side of the Great Escarpment, being most concentrated at the Drakensberg range in KwaZulu-Natal Province, bordering (and overlapping) Lesotho, and to a lesser extent, the Lebombo mountains on the border between Mpumalanga and the west of Swaziland (Figs 1 and 4). It is mainly covered by grassland, with a smaller contribution by savanna and other biomes (Table 1, Fig. 1). It shows spatial congruence with the mistbelt on the eastern side of the escarpment, which is a cool, moist temperate region within the grassland biome that is characteristically wetter than other grasslands (consistent with the regression model for this region, Table 2) and includes many small patches of natural forest. The Escarpment Phytogeographic Region is characterised by alien plant species that originate from cool, moist temperate regions such as northern Europe. This includes mainly temperate C_3 grasses such as *Bromus catharticus*, *Poa annua*, *Poa pratensis*, *Holcus lanatus*, *Phalaris arundinacea*, and *Phalaris dilitatum*. The phytogeographic region forms a sharp border on the escarpment, especially at Lesotho and the KwaZulu-Natal Drakensberg, which is unsurprising because the alien species named probably require year round moisture, as found in the mistbelt, whereas the environmental conditions on the adjacent high-altitude Afroalpine grasslands are harsh, with cold, dry winters. Irrigated area and degraded area are also coincident with this region according to the regression model, suggesting a possible human influence (Table 2).

Northern Phytogeographic Region

This region is distributed mainly in the north of Namibia and Botswana, with some outliers in the north of South Africa (Figs 1 and 4). It is the most geographically dispersed of all clusters of grid cells that we reported as phytogeographic regions. It is characterised by tropical alien plants that do not tolerate cold conditions (e.g. frost), and includes tropical water plants such as *Salvinia molesta* and *Persicaria limbata*, and riverside plants such as *Mimosa pigra* and *Sesbania bispinosa*. This region appears to be found in relatively arid low altitude areas with water sources, such as the Okavango Delta and Kunene River on the northern boundaries of Namibia and Botswana, and seems to constitute the southern outliers of a tropical phytogeographic region with its core situated to the north of the study area. However, the paucity of data in this area precludes any further analysis and interpretation.

Agricultural Phytogeographic Region

This region is associated with several biomes and different rainfall patterns and does not appear to be a consistent, spatially unified phytogeographic region, except that it is associated with high mean maximum temperatures throughout its range (Tables 1 and 2). It is closely associated with the Escarpment Phytogeographic Region in certain areas, and continues along the escarpment to the south of the mistbelt where it is most concentrated in the summer rainfall region of the Eastern Cape Province, bordering much of the coastline (Figs 1 and 4; Mucina & Rutherford, 2006). However, the Agricultural Region is also prominent in the Western Cape Province, where it is concentrated in the centre of the fynbos biome and winter rainfall zone, especially in the Breede River valley and Swartland areas (Figs 1 and 4; Mucina & Rutherford, 2006). In addition, a substantial group of grid cells are concentrated in the summer rainfall interior of South Africa, in the Northern Cape and Free State Provinces (Figs 1 and 4). The Agricultural Region is characterised by temperate C_3 alien grasses, such *Briza maxima*, *B. minor*, *Hordium murinum*, *Bromus diandrus*, *Vulpia myuros*, and *Phalaris minor*, and a few species such as *Poa annua* that are shared with the Escarpment Region. These species require winter precipitation and are often planted for winter fodder and encouraged by irrigation to grow where there is naturally no winter rainfall, such as in the Northern Cape, Free State and Eastern Cape Provinces where irrigation is common along rivers. Further, agriculture reduces competition by clearing native vegetation, and changes soil nutrient input and edaphic features, and may thereby encourage pioneer alien grasses that are able to quickly colonise disturbed land (Hobbs & Huenneke, 1992). These may be important factors for this phytogeographic region in the Swartland and Breede River Valley regions in the Western Cape Province, where the native vegetation had mostly been converted to agricultural land such as winter wheat fields and vineyards (Rebelo *et al*., 2006). These observations suggest that human activities, such as agriculture and irrigation that artificially manipulate vegetation cover and edaphic and climatic factors, are important unifying features that link the various clusters of this phytogeographic region across the study area. This suggestion is not well supported by the regression model for this region, as cultivated and degraded area is not included in the model and irrigated area makes only a small positive contribution (Table 2). However, the small Max-rescaled R-square value of this model (9%, Table 2) suggests that the spatial distribution of this region is very likely determined by variables that have not been considered in the current study, which might be human-related variables. Further, as mentioned previously, perhaps a human influence on this phytogeographic region may be obscured at the coarse spatial resolution of this study (Richardson *et al*., 2005). For example, in the dataset used for the logistic regression model, irrigated area usually comprise less than 10% of the surface area of the grid cells in which it is present. Therefore, alien plant species that are facilitated by irrigation might be spatially associated with small patches of irrigated area within the quarter degree grid cells in which they were recorded. A finer spatial resolution might reveal this association more explicitly; nevertheless, irrigated area would remain an important factor in the overall phytogeographic region.

Western Cape Phytogeographic Region

This region is most concentrated in the Western Cape Province, but extends north into the Northern Cape Province and east into the Eastern Cape Province (Figs 1 and 4). It borders most of the coastline in the region covered and is mainly a temperate area with mild winters, including areas with relatively high winter and year-round rainfall and the fynbos and succulent Karoo biomes (Tables 1 and 2; Figs 1 and 4; Mucina & Rutherford, 2006; Rebelo *et al.*, 2006). It is characterised by herbs that are weeds in agricultural areas and disturbed valleys and annuals that are strongly dependent on winter rain, such as *Hordium murinum*, *Briza maxima*, *B. minor*, *Phalaris minor*, *Vulpia myuros*, *V. bromoides*, *Fumaria muralis* and *Lolium rigidum*. Many accidentally introduced species characterise this region; however, although cultivated area is not particularly strongly associated with this region (Table 2), deliberate introduction also seemed to have had a great influence here, and the Agricultural and Western Cape Phytogeographic Regions share several C_3 grass species.

Grassland Phytogeographic Region

This region mainly comprises the grassland biome in the interior of South Africa north and west of the escarpment and bordering the Escarpment Phytogeographic Region, in the provinces North West, Gauteng, Mpumalanga, the west of KwaZulu-Natal, the northern edge of the Eastern Cape and most of Lesotho (Table 1; Figs 1 and 4; Mucina & Rutherford, 2006). It also extends north into the savanna biome of North West Province, Namibia and Botswana (Figs 1 and 4; Irish, 1994; Ringrose *et al.*, 2002; Mucina & Rutherford, 2006). The Grassland Region is mainly characterised by cold, dry winters with frost and warm temperate summers with summer rainfall (see Mucina *et al.*, 2006, and the regression model for this region, Table 2), and is characterised by herbs and grasses that are associated with agriculture, cultivation and abandoned agricultural fields, e.g. *Oenothera rosea*, *O. tetraptera*, *Salvia stenophylla*, *Medicago laciniata*, *Hibiscus trionum*, *Persicaria lapathifolia* and *Cirsium vulgare*. The first four species named most likely invade specifically moist areas within the grassland biome, and *C. vulgare* is mainly associated with wetlands.

Savanna Phytogeographic Region

This region is mainly situated in warm frost-free savanna biome areas of South Africa in the provinces North West, Limpopo, Mpumalanga, the east of KwaZulu-Natal, a small eastern part of the Northern Cape, and also most of Swaziland (Tables 1 and 2; Figs 1 and 4; Mucina & Rutherford, 2006). It extends north into, and is spread over, the entire Botswana and

Namibia, where it is the most prevalent phytogeographic region (Figs 1 and 4). It is also associated with the coast in KwaZulu-Natal Province and covers the Indian Ocean coastal belt biome and the adjacent savanna biome where it is probably associated with the numerous dry river valleys (Table 1; Figs 1 and 4; Rutherford *et al*., 2006). It includes all kinds of savanna habitat: from dry to moist, and from fertile to infertile (Rutherford *et al*., 2006). The alien plant species characterising this phytogeographic region are mainly herbs that colonise disturbed areas and are found at roadsides (e.g. *Lantana camara*), although degraded area has a weak negative correlation with this region (Table 2). Temperate C_3 grasses and species characterising the Greater Arid Region are least likely to be found in the Savanna Region (Table S1, Appendix 1).

Further research and implications for management

The alien species that appeared to be most characteristic of the phytogeographic regions (Table S1, Appendix 1) were generally relatively range-restricted invaders, a few of which were well-known harmful invaders (e.g. *Prosopis* spp., Robertson *et al*., 2003), whereas most were currently of less concern. However, some of the species of less concern, such as the alien grasses that play an important role in several of the alien phytogeographic regions described, have the potential to become increasingly harmful in the future and warrant more research and management attention than they are currently given (Milton, 2004; Richardson & Van Wilgen, 2004; Henderson, 2007; Lavergne & Molofsky, 2007; Parker-Allie *et al*., 2009). Unsurprisingly, alien species that have small ranges (only a few grid cells) did not influence the designation of phytogeographic regions. Conversely, the very widespread harmful invaders (e.g. *Acacia* spp., *Opuntia* spp. and *Pinus* spp.; Higgins *et al*., 1999; Robertson *et al*., 2003) individually covered many of the alien phytogeographic regions together, which would mean that these species did not have a strong influence on TWINSPAN in grouping grid cells into phytogeographic regions (abundance or dominance is not taken into account when a presence/absence dataset is used). The analysis methods of Richardson *et al*. (2004) and Thuiller *et al*. (2006), as described in the introduction section, are probably more suitable than the current study’s methods for revealing the spatial patterns of these widespread species.

As mentioned in the introduction, the presence of phytogeographic regions may be helpful in organising alien species management; however, the current study is mainly an explorative study, and the findings need to be refined before it will be useful for practical applications. Nevertheless, the findings provide a framework for further research, enabling further refinement of the spatial distributions and species compositions of the described phytogeographic regions (contingent on improved data at a finer spatial resolution) and more in-depth understanding of the environmental factors (natural and human-related) that determine each region. Future studies could explore the link between alien phytogeographic regions and the species traits that had predisposed the alien species to colonise those regions and exploit the available niche space. In particular, considering that alien phytogeographic regions formed over a much shorter time period (i.e. since the introduction of the characteristic species) than endemic phytogeographic regions (Van Wyk & Smith, 2001; Steenkamp *et al*., 2005), were alien phytogeographic regions shaped in the introduced range by original alien species traits (i.e. those traits that had evolved in their original home range) or by rapid adaptation to new conditions (i.e. new or changed traits)?

It is likely that the spatial ranges of alien phytogeographic regions might shift in the near future as the spatial ranges of the characteristic species shift in response to changes in general climatic conditions (i.e. global climate change) as well as projected increases in human-induced microclimates and transformed habitats (e.g. irrigation and agriculture) that favour invasive alien plant species (Hobbs & Huenneke, 1992; McCarty, 2001; Daehler, 2003; Thuiller *et al*., 2006; Lavergne & Molofsky, 2007). Similarly, climate change and local human activities are predicted to cause range shifts of plant species in general in the near future, thereby reorganising current plant assemblages to create new assemblages consisting mainly of plants with rapid colonisation abilities (a common characteristic of alien plant species) where the ranges of specialised native species have retreated, a process known as biotic homogenisation (Hobbs & Huenneke, 1992; McKinney & Lockwood, 1999; Sax & Gaines, 2003; Olden *et al*., 2004; Lavergne & Molofsky, 2007). The alien phytogeograpic regions revealed in the current study might indicate some of the characteristics of future plant assemblages if such a scenario prevails. Correspondingly, this prediction also implies that short-term anthropogenic processes could influence the ranges and compositions of phytogeographic regions of endemic plant species (Linder *et al*., 2004) or genera (Steenkamp *et al*., 2005), along with long-term natural climatic and geological changes.

Conclusions

We found that the study area could be partitioned into several ecologically interpretable phytogeographic regions. These phytogeographic regions primarily follow natural climatic, biome and habitat features, but are also influenced by anthropogenic modification and activities to varying degrees. Although this study is mainly explorative, our findings generate a suite of new hypotheses, and so open many possibilities for further research to refine and explain the spatial distributions and determinants of these phytogeographic regions. This is contingent on improved species presence data at a finer resolution. We suggest that, after appropriate further research, these phytogeographic regions could provide information benefitting the organisation of effective local management of currently or potentially harmful alien plant species. Further, we suggest that the characteristics (i.e. the species and the associated natural and anthropogenic factors) of these phytogeographic regions provide a glimpse of the likely floristic composition of regional plant assemblages of the future in a scenario where biotic homogenisation and range shifts have reorganised the current plant assemblages.

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CHAPTER 3

Are Environmental Transitions More Prone To Biological Invasions?

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ABSTRACT

The aim of this study was to examine whether at a sub-continental scale for South Africa and Lesotho, ecotonal areas of transition between vegetation communities are at higher risk of plant invasion. 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. Both alien (r = -0.26) and native (r = -0.31) richness becomes 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 relationship between ecotone distance and alien species richness remained negative and significant for the whole of South Africa (partial R^2 for 'ecotone distance' = 8.2%, $p < 0.0001$), grassland (partial R^2 = 4.6%, $p < 0.0001$) and Nama-Karoo (partial R^2 = 5.1%, $p < 0.05$), after controlling for environmental variables. Several sources of environmental heterogeneity that were associated with ecotones, were also found to be important determinants of alien species richness (R^2 varied between 3.1% for the succulent Karoo and 29.7% for the savanna). 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.

INTRODUCTION

Fifty years ago, Elton discussed the relationship between environmental conditions and native and alien species richness, suggesting that species-rich communities are more resistant to invasion (Elton, 1958). 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, i.e. 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: (i) tend to show high spatial and temporal variability due to greater fluctuations in environmental variables, (ii) are small in area, (iii) experience high edge or mass effects, and (iv) 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: (i) levels of rare species (Kark *et al.*, 2007; Ribalet *et al.*, 2010), (ii) speciation rates (Schilthuizen, 2000), (iii) evolutionary novelty (Smith *et al.*, 1997), and (iv) 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 hypothesised 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; Tuiller *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 *vs*. 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. 1 of Chapter 1), 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 (*ca*. 20 000 species) and plant endemism (*ca*. 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 *ca*. 21 962 species listed as native, and the distribution of each species is indicated using a grid reference system at a quarter-degree resolution (~15' x 15' ≈ 676 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 that 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 prioritised 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, Appendix 2). 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, Appendix 2, 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 (i) 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 (ii) those that indicate the higher environmental heterogeneity that are reputedly associated with the ecotones themselves. In the first class, we investigated mean January normalised difference vegetation index (NDVI) as surrogate of productive energy availability (Hurlbert & Haskell, 2003) and minimum mean annual temperature (ºC) as a surrogate for solar energy (see Van Rensburg *et al*., 2009, for more information on these data sets). In the second class, we investigated topographic heterogeneity (the maximum elevation above sea level minus minimum elevation above sea level, in meters, 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 Data Set does 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). GIS (Geographical Information System) 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.

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 (Table 1; Fig. 1; Fig. S1, Appendix 2).

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 (i) all grid cells and (ii) 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 standardised 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. Results using these two data sets (with and without some level of land transformation) were qualitatively similar (see e.g. Tables S1-S3, Appendix 2) and therefore we only present those from analyses that used the entire data set.

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, i.e. 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

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). *SD* = standard deviation.

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

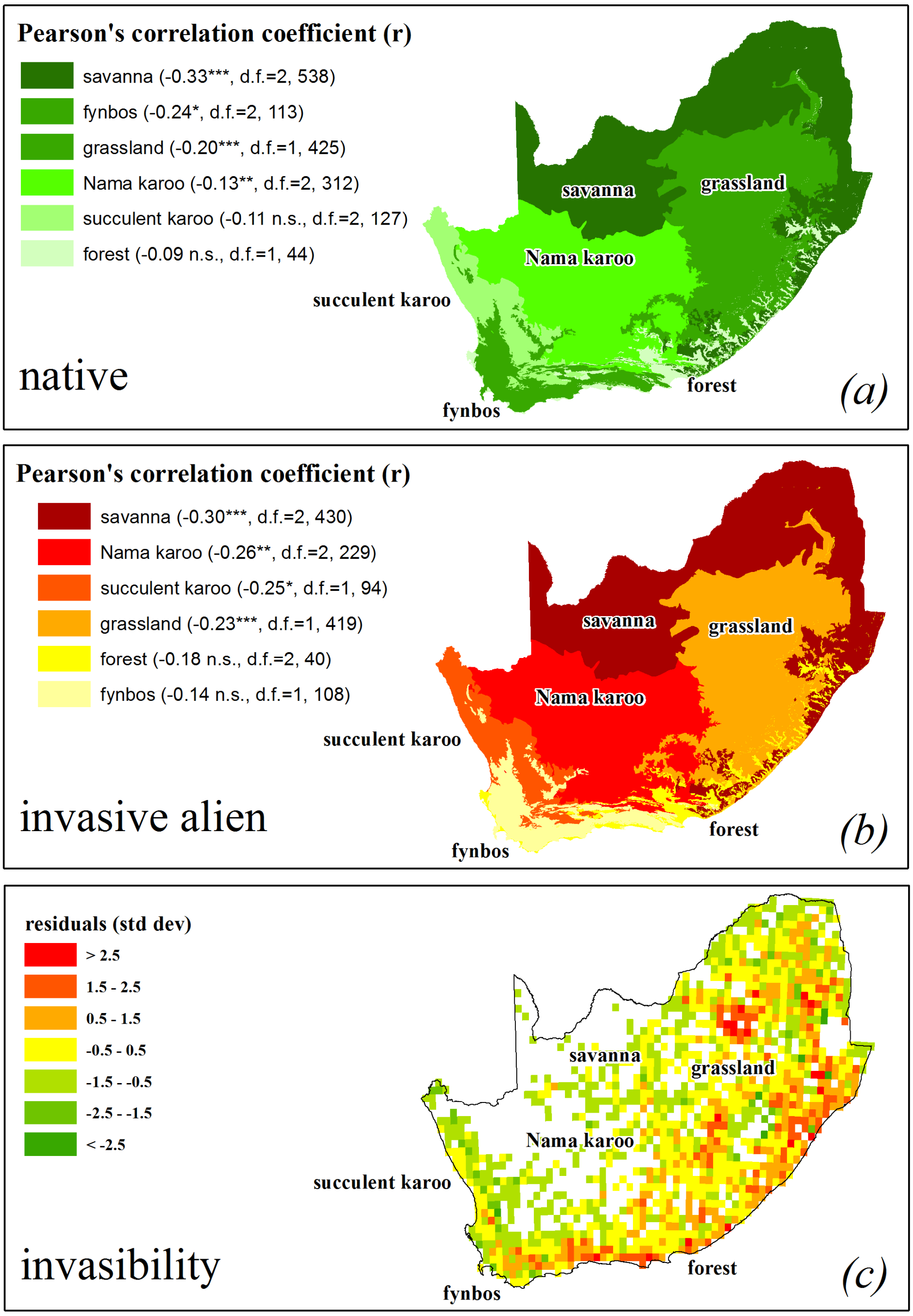

Figure 1 Pearson's correlation coefficients between distance to the nearest ecotone (boundary between vegetation communities) and (a) native plant richness, and (b) invasive alien plant richness. Results are shown for each of the major plant biomes of South Africa and Lesotho. Significance levels show 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, i.e. 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 evaluate the relationship between distance to nearest ecotone and invasibility. This was done 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 to 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 indicates model fit (AIC; Burnham & Anderson, 1998; the model with the best fit is the model with the lowest value). 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. In addition, we re-examined all models with PROC MIXED to determine the effect of spatial autocorrelation. This procedure fits a spatial covariance matrix to the data (an exponential spatial covariance structure provides the best fit) to detect autocorrelation in the response variable and adjust the test statistic, if necessary (see Littell *et al.*, 1996, for more information). Unfortunately, to date there are no statistical procedures available that provides coefficients of determination for spatial models. 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, Appendix 2). 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 number of ecotones 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 is 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, e.g. 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, Appendix 2). 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, Appendix 2). 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 though 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 variables remained significant in spatial models (Table S4, Appendix 2).

Ecotone distance was in most cases (except for forest and fynbos) significantly and negatively correlated to 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 to 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 nonsignificant in spatial models (and are thus not included) (Table S5, Appendix 2).

DISCUSSION

Our study provides support that at the regional sub-continental 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 and Levanoni *et al*., 2011). Here, we find elevated native plant richness to be associated

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	††††53.57	****51.65; sq	****422.26	31.3	8.2
Savanna	1, 424	n.s.† 0.28	††††30.97; L	****313.12	47.4	7.9
Grassland	1, 412	††††16.82	****43.20; L	****29.70; L	20.3	5.1
Nama-Karoo	1, 223	†4.85; L	n.i.	****43.74; L	19.9	4.6
Succulent Karoo	1, 87	n.s.†0.35	n.i	****39.20	34.2	6.5
Fynbos	1, 101	n.s.†1.01; L	†6.38; L	††††116.91; L	55.3	2.3
Forest	1, 34	n.s.*1.61; L	n.i.	**9.37	19.5	3.4

Note: Abbreviations: d.f. = degrees of freedom, temp (min) = minimum temperatures (°C), NDVI = normalised 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: n.s.† $p > 0.05$, † $p < 0.05$, †††† $p < 0.0001$

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	††††108.37; L	††††80.02; L	††††17.84; L	26.3
Alien richness	1, 1311	**9.85; L	****21.47; L	****138.68; L	30.2
Savanna					
Ecotone distance	1, 623	††††161.21; L	††††20.54; L	n.i.	28.9
Alien richness	1, 423	****170.69; L	* 4.81; L	n.a.	29.7
Grassland					
Ecotone distance	1, 452	††††103.66; L	†††† 27.34; L	n.i.	23.2
Alien richness	1, 398	****81.29; L	***13.14; L	n.a.	19.9
Nama-Karoo					
Ecotone distance	1, 456	n.i.	††††25.64; L	††††82.06; L	18.5
Alien richness	1, 223	n.a.	n.i	****28.47; L	11.0
Succulent Karoo					
Ecotone distance	1, 130	n.i.	†4.77; L	n.i.	3.6
Alien richness	1, 87	n.a.	n.s.* 3.01; L	n.a.	3.1
Fynbos					
Ecotone distance	1, 115	n.i.	n.i.	n.s.†3.53	3.0
Alien richness	1, 101	n.a.	n.a.	††††33.08; L	23.5

Table 3 continues

Forest					
Ecotone distance	1,45	n.i.	n.s.*3.28	n.i.	7.0
Alien richness	1, 34	n.a.	n.s.†1.14; sq	n.a.	3.4

Note: Abbreviations: 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, sq = 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.† $p > 0.05$, † $p < 0.05$, †††† $p < 0.0001$.

with ecotones; that is, native plant species richness increase 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 at both the large sub-continental scale when analysed for the whole of South Africa combined, and at the sub-regional scale for separate biomes (as shown in Fig. 1a,b). This raises the question, why are ecotones 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; 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 rainforest (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 provides an open "window of opportunity" for invading the system more easily (see e.g. Planty-Tabacchi *et al.*, 1996; Thuiller *et al.*, 2006; Kark, in press).

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 characterised 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 (neo-endemics) (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 invasible, 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; 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 localised 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, Appendix 2), 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, Appendix 2).

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 field work. In any case, the weaker results from the smaller biomes (forest and fynbos) are therefore probably not comparable to those 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 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 also high invasive alien richness, more focus should be given to ecotonal invasions in management plans and conservation decision making. While many conservation programs 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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CHAPTER 4

Patterns of Beetle and Spider Richness and Composition across a South African Savanna-Grassland Ecotone

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ABSTRACT

Ecotones, or transition zones between adjacent ecological systems, may differ widely from one another, each with a unique combination of causes, characteristics and ecosystem processes. In this study, we tested two common assumptions about ecotones, namely, that ecotones represent transition zones between different assemblages of species, and that ecotones support higher biodiversity than the adjacent ecosystems. We based the study on the vegetation and invertebrate (beetles and spiders) attributes of a semi arid savanna-grassland ecotone in the west of the Free State Province of South Africa, where we conducted vegetation and invertebrate surveys over a distance of approximately 30 km across the ecotone and the adjacent habitats. We used analysis of variance, analysis of similarity, and cluster analysis to reveal patterns among the habitats, and correlations to reveal relationships between invertebrates and vegetation variables. We found that the different habitats can be distinguished according to vegetation and invertebrate attributes, that the ecotone is a unique habitat in terms of vegetation composition (red grass, *Themeda trianda*, covered >50% of the ecotone habitat) but not invertebrate composition, and that invertebrate abundance, richness and diversity is never higher at the ecotone but rather lower than the other habitats (for species richness and abundance) or intermediate between the other habitats (for overall species diversity in 2009). Vegetation attributes as predictors (height, density, bare ground cover and diversity) were significantly related to invertebrate richness, abundance and diversity for eight of 18 cases, and explained between 18% and 44% of variation in the response variables. Nevertheless, many of the patterns were unclear or unexpected, and more intense long-term study is required to reveal the underlying ecological processes and their relative importance.

INTRODUCTION

Ecotones are defined as transition zones between adjacent ecological systems (Gosz, 1993; Risser, 1995; Kark & Van Rensburg, 2006; but see Van der Maarel, 1990). They are determined by a wide variety of ecological processes, and the characteristics of ecotones may vary depending on the particular combination of ecological conditions present (e.g. Lloyd *et al*., 2000; Walker *et al*., 2003). Observed ecotone characteristics also vary depending on the spatial scale at which they are viewed, with different constraints, characteristics and processes operating at different scales (Gosz, 1993; Kark & Van Rensburg, 2006). Also, although it is characteristic of some ecotones to form an abrupt edge or a smooth transition, many ecotones form a mosaic of patches of either abutting ecosystem type (Gosz, 1993).

Despite the great variety in ecotone types and ecological processes, ecotone research is often based on two general assumptions in terms of the distribution of taxa across ecotones (reviewed in Kark & Van Rensburg, 2006), namely (i) that ecotones signify areas where species composition changes between the ecosystems abutting an ecotone (e.g. Krasnov & Shenbrot, 1998; Kotze & Samways, 1999a; Baker *et al*., 2002); in some cases, this implies that the ecotonal area supports a distinct species composition (e.g. Spector & Ayzama, 2003), and (ii) that biodiversity at all levels (i.e. habitats, species, genes, etc.) is likely to be higher at ecotones than in the adjacent ecosystems (Gosz, 1993; Smith *et al*., 1997; Kark *et al*., 1999, 2002, 2007; Kotze & Samways, 2001; Van Rensburg *et al*., 2004).

The second assumption is of conservation interest due to the recent trend of prioritising the protection of high biodiversity areas to maximise the overall level of biodiversity that would be conserved (e.g. Chown *et al*., 2003; Luck *et al*., 2004; Gaston, 2005; Kark *et al*., 2007). The reasoning behind this assumption is that habitat features and species assemblages of different habitats meet, interact and overlap at ecotones and that elements (e.g. genes, species or microhabitats) unique to the ecotone may be found, thereby inflating the overall levels of biodiversity at ecotones (Gosz, 1993; Smith *et al*., 2001; Kark *et al*., 1999, 2007; Van Rensburg *et al*., 2004; Kark & Van Rensburg, 2006; but see Tamme *et al*., 2010). Apart from this proposed high biodiversity, ecotones are also generally recognised as unique dynamic ecosystems, containing unique habitat features and ecosystem processes that warrant conservation and research attention (Risser, 1995; Smith *et al*., 2001; Kark & Van Rensburg, 2006; but see Brooks *et al*., 2001).

Although South Africa contains a very diverse set of habitats and ecosystems, and by implication a wide variety of ecotones, these ecotones have been poorly investigated (for examples, see Kotze & Samways, 1999a, 2001; Davis & Scholtz, 2004; Van Rensburg *et al*., 2004; Davis *et al*., 2008). In this study, we investigate an ecotone between the savanna and grassland biomes in the west of the Free State Province of South Africa. The main aim of this study was to investigate variation in biodiversity and composition across this ecotone, and how these patterns relate to vegetation and habitat features. We used invertebrates to represent biodiversity, because they are known to be sensitive to environmental conditions that differ between habitats, such as vegetation structure and composition, and are easy to sample in the field (Kotze & Samways, 1999b; Foord *et al.*, 2002, 2003; Davis, 2002; Szövényi, 2002; Pik, *et al*. 1999, 2002). We specifically focused on beetles (Coleoptera) and spiders (Araneae), as they were abundant and commonly trapped in the study area.

To investigate this aim, we addressed the following questions. First, how does invertebrate species composition vary across the ecotone and adjacent habitats, i.e. does the ecotone support an intermediate or a distinct invertebrate assemblage compared to those of the savanna and grassland? Second, is biodiversity, as indicated by invertebrate species richness and diversity, greater at the ecotone than in the adjacent habitats? Third, which roles, if any, do vegetation attributes play in determining variation in invertebrate species?

METHODS

Study area

The ecotone runs mainly north-south between the savanna and grassland biomes as described by Mucina & Rutherford (2006), in a semi-arid region (Fig. 1, see also Fig. S1 in Appendix 3). Although the climate of the study area is similar across habitats, the different vegetation types associated with the ecotone are spatially associated with different soil types (Mucina *et al.*, 2006; Rutherford *et al.*, 2006), which probably led to differences in the vegetation supported. The study spans approximately 30 km and was conducted on privately owned game farms and mixed cattle and sheep farms with wildlife and natural vegetation that was largely undisturbed by humans. The savanna and grassland biomes bordering the ecotone are each represented by a distinct vegetation type described by Mucina & Rutherford (2006), and for the interest of simplifying the study we recorded data only in these vegetation types and avoided the other vegetation types as far as possible (Fig. 1). The savanna is represented by Kimberley Thornveldt which is characterised by slightly irregular plains with a well-developed tree layer, a well-developed shrub layer and a sparse grass layer with much uncovered soil (Rutherford *et al.*, 2006). This vegetation type is based on a deep layer (0.6 - 1.2 m) of sandy to loamy soils (Rutherford *et al.*, 2006). The grassland is represented by Western Free State Clay Grassland, which is based on a clay soil supporting a grass layer with dwarf shrubs (Mucina *et al.*, 2006). The climate is similar across all vegetation types in the general study area – semi-arid, with mean annual precipitation about 450 mm, and a late

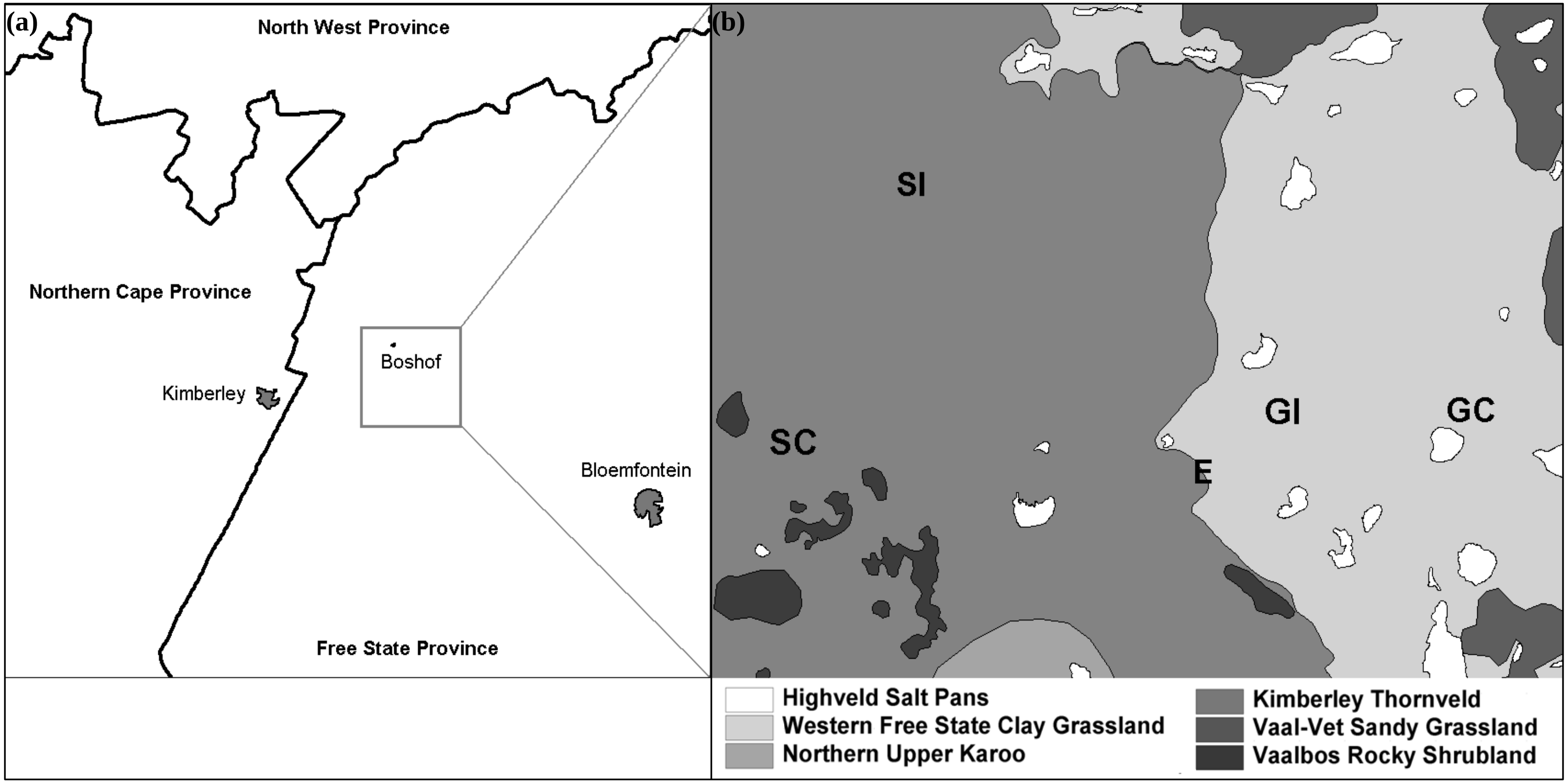

Figure 1 The general study area, showing a) its location (the central square) in relation to provincial boundaries (compare to Chapter 2’s Fig. 1), the cities Kimberley and Bloemfontein, and the town Boshof, and b) the vegetation types as illustrated in Mucina & Rutherford (2006) and the spatial locations of the sampling sites, as indicated by the abbreviations on the map: SC – Savanna core (about 16 km from the nearest relevant ecotone); SI – Savanna intermediate (about 5.5 km from the ecotone in the north east); E – Ecotone (across the ecotone); GI – Grassland intermediate (about 3.5 km from the ecotone); GC – Grassland core (about 12 km from the ecotone). See the text for more details on the placement and layout of the sampling sites.

summer and autumn rainy season that peaks in March (Mucina *et al*., 2006; Rutherford *et al*., 2006).

We used a vegetation type GIS (geographical information system) map published by Mucina & Rutherford (2006) together with topographical maps (South African Trigonometric Survey, 1986b,d), to identify the spatial coordinates of the ecotone prior to fieldwork. Compared to the savanna, the grassland generally occurs at lower elevations within the study area (South African Trigonometric Survey, 1986b,d), as indicated in the topography maps and also verified by personal observations in the field. The different soil types reported by Rutherford *et al*. (2006) and Mucina *et al*. (2006) were easily identified at local scales (e.g. 20m^2) with the naked eye – apart from the obvious difference in texture, the sandy savanna soil is usually reddish whereas the clay is grey in most locations in the study area. Trees and large shrubs were useful indicators of habitat type as they were present only on sandy soil, with the ecotone being the margin of the savanna distribution of trees in the study area. This agrees with previous research indicating that, where rainfall and climate are similar across different soil types (as in the current study), trees are often outcompeted by grass on clay soil, whereas deeper water infiltration on sandy soil allows trees to thrive as the water is more likely to reach their deeper root systems (see Walter, 1971; Knoop & Walker, 1985; Scholes & Archer, 1997).

The ecotone habitat appeared to be based on a mosaic of patches of sandy soil and clay soil and consisted mainly of grassland with some savanna vegetation features (i.e. sparse tree and shrub cover). This mosaic extends several kilometres into the savanna vegetation type where we found patches of clay soil without trees, several hundred metres across, and not revealed at the coarser resolution of the Mucina & Rutherford (2006) vegetation maps. Should the ecotone be studied at larger spatial scales, these clay soil patches may be considered as part of a broad mosaic ecotone that is several kilometres wide. Nevertheless, despite this ecotone’s complicated mosaic configuration which would require a more in-depth spatial study to describe fully, the general location of ecotone habitat was easily identified visually and with the help of maps.

Spatial experimental design

Five sampling sites were placed several kilometres apart depending on the availability of farmland for sampling (i.e. more than 4 km between the two sites that are closest to each other) across a distance of about 30 km. The sampling sites included two ‘core’ habitat sites (one in the grassland and one in the savanna) that were furthest from the ecotone, a site at the ecotone, and two sites in the savanna and grassland at intermediate distances to the ecotone

(Fig. 1). Due to a number of practical limitations, including travelling distance, accessibility, and availability of farmland for sampling, the sampling sites were not placed at regular intervals in a straight transect across the ecotone, but rather in relation to the ecotone, *a priori* on habitat representing the vegetation types associated with the ecotone (i.e. based on personal observations and Mucina & Rutherford, 2006; see Fig. 1). The intermediate savanna sampling site was situated partly on a treeless clay soil patch surrounded by savanna vegetation and sandy soil (personal observation), thereby capturing the ecotone's mosaic effect.

Each sampling site consisted of five 20 m by 20 m trapping grids (see under "study taxa, trapping and sorting") which served as replicates for each site, with the replicates positioned at 250 m intervals along a 1 km transect for each site. We ensured that all five replicates were included within one field, and we avoided fences, dams, buildings and human-transformed areas (e.g. cultivated area) as far as possible. At the ecotone sampling site (Fig. 1), we placed the transect line approximately perpendicularly across the ecotone. Throughout the rest of this chapter we refer to the replicates as "grids" and to individual replicates by consistent numbers, e.g. grid 1, grid 2, etc.

Study taxa, trapping and sorting

We collected the beetles and spiders in March of 2009 and 2010 during the peak rainfall and growing season, as they are likely to be most active during this time (Davis, 2002; Davis & Scholtz, 2004; Davis *et al.*, 2008). For this study we used pitfall trapping, which is a popular invertebrate trapping method as, compared to other methods, it is relatively less labour-intensive and captures invertebrates continuously thereby including those species that are active in the absence of the researchers, such as nocturnal species (e.g. Pik *et al.*, 1999, 2002; Parr & Chown, 2001; Davis, 2002; but see Melbourne, 1999, for an evaluation of sampling biases linked to pitfall traps).

The pitfall traps were not baited and consisted of a 20 ml plastic cup sunk into the ground with the rim level with the ground. Nine pitfall traps were each spaced 10 m apart (e.g. Yaacobi *et al.*, 2007) in a 3 by 3 grid configuration (i.e. 20 m by 20 m grids), and they were half-filled with a mixture of one part propylene glycol (as preservative) and three parts water with some detergent (to reduce surface tension) (Schmidt *et al.*, 2006). The traps were each covered by a roof made of a plastic lid propped on wire to prevent evaporation of the trapping liquid or flooding with rainwater (Durães *et al.*, 2005).

Depending on accessibility to a particular sampling site (i.e. depending on weather or road conditions), the traps were active for a total of six (2009) or eight (2010) days, with a renewal of the traps in the middle of this trapping period, i.e. after three or four days. Captured invertebrates from each trapping session were pooled for each particular grid and stored in 70% ethanol (Durães *et al.*, 2005) to facilitate storage and transportation of the samples. Spiders and beetles were sorted to morphospecies level and number of species and abundance of each species was recorded (Oliver & Beattie, 1996; Samways *et al.*, 1996; Pik *et al.*, 1999, 2002; Dangerfield *et al.*, 2003; Foord *et al.*, 2003; Spector & Ayzama, 2003).

Vegetation survey

The understory vegetation level was probably most relevant to the ground-level trapping method and captured invertebrates of this study (e.g. Szövényi, 2002; Foord *et al.*, 2003; Matern *et al.*, 2007). Therefore, the vegetation survey focused on understory vegetation structure and dominant understory plant species composition, which were measured and recorded at each grid. Plant density (represented here by above-ground standing biomass) at each grid was measured with a disc pasture meter at 20 random points along the perimeter of the grid, which provides an index value that could be compared between grids and sites (Bransby & Tainton, 1977; Dörgeloh, 2002). A similar method was used to measure plant height (cm), except that the measuring equipment consisted of a thin pole and a light-weight plastic bucket lid with a hole cut in the middle along which the pole can slide (based on the disc pasture meter) (see Szövényi, 2002, for a similar method). The dominant plant species were recorded by dividing the grid into four quadrants and then placing a 2 m by 2 m quadrat in the middle of each quadrant (see e.g. Bredenkamp *et al.*, 1999; Walker *et al.*, 2003). The identities of plant species and the percentage of ground surface that they cover (visual estimates) were then recorded in each quadrat for all plant species that cover more than 5% of the quadrat. Percentage bare ground in the quadrats was also recorded and represented another measure of vegetation structure (Walker *et al.*, 2003). Because of time and labour constraints, the vegetation measurements were not repeated at both years – plant height and composition were recorded during 2009 and plant density was recorded during 2010. All of these vegetation variables were averaged for each grid, and the average values were used in analyses.

Analyses

To evaluate the relationships between sampling sites according to the species composition of invertebrates and dominant understory plant species, we constructed Bray-Curtis similarity matrices (data were not transformed, as transformation did not improve the results) and conducted analyses of similarity (ANOSIM) and cluster analyses (Bredenkamp *et al.*, 1999;

Kotze & Samways, 1999a,b, 2001; Primer 5.2, Primer-E Ltd., 2000; Szövényi, 2002; Pik *et al*., 2002; Foord *et al*., 2003; Spector & Ayzama, 2003; Davis & Scholtz, 2004; Davis *et al*., 2008). For the dendrograms resulting from cluster analyses we used rank similarities on the y axis, as these seemed to provide visually clearer results in every case, and we were more concerned with delineating main clusters than with showing the strength of the relationships between individual grids. We evaluated the dendrograms subjectively, seeking one or more coherent clusters of sampling grids, especially where sampling grids from specific vegetation types have clustered together, i.e. we searched for ecologically or at least logically meaningful clusters. For the sake of brevity and to avoid repetition, multi-dimensional scaling (MDS) plots corresponding with the cluster analyses are not reported in this chapter; however, they are available in Appendix 3 (Figs S2-S5). For plant species, we used estimated percentage cover as a surrogate for abundance when constructing similarity matrices.

Preliminary analyses with Estimate S v. 8.2 (Colwell, 2006) showed that trapping effort was insufficient to sensibly estimate species richness. Therefore, instead of relying on richness estimators from Estimate S (see e.g. Kotze & Samways, 1999a,b; Parr & Chown, 2001; Durães *et al*., 2005; Davis *et al*., 2008), we decided it was more appropriate to compare the different sites and grids according to relative per-trap species richness and abundance values, where any unplanned variations in sampling effort (i.e. failed traps at some grids) were taken into account (see also Krasnov & Shenbrot, 1998; Durães *et al*., 2005). Although these relative corrected per-trap values cannot be compared with species richness estimates from other studies, it ensured that the sampling sites could still be compared with one another. Throughout the rest of this chapter the terms “species richness” and “species abundance” refer to these relative per-trap values.

We used one-way analyses of variance (ANOVA) to assess whether the sampling sites differed in invertebrate species richness, abundance and diversity (indicated by Shannon-Wiener diversity index values). We also evaluated the sampling sites by one-way ANOVA to detect differences in vegetation height, vegetation density, percentage bare ground cover, and dominant understory plant species diversity (Shannon-Wiener diversity index). Again, we used percentage cover as a surrogate of abundance when calculating plant species diversity. Data that were not normally distributed were analysed with a Kruskal-Wallis nonparametric one-way ANOVA.

We further evaluated the possible influence of vegetation on invertebrate species richness, abundance and diversity, through general linear models (GLM) with the four vegetation attribute variables – dominant vegetation diversity, average vegetation height and density and percentage bare ground cover – as predictors. We also used mixed modelling and Akaike’s Information Criterion (AIC) to compare different models (i.e. different combinations of the predictor variables) for each response variable, to ascertain which predictor variables best explained variation in each response variable (a smaller AIC value indicate a better model). For the sake of brevity, however, we only reported the GLM results of the best models. We found no indication of nonlinearity in the relationships and collinearity between predictors was not great enough to render any of the predictors redundant (see Quinn & Keough, 2002; Evans *et al.*, 2005). We also found no indication of an interaction effect with sampling site or of any form of autocorrelation (including spatial autocorrelation, see Chapter 3; Legendre, 1993; Keitt *et al.*, 2002; Evans *et al.*, 2005; Baker & Barmuta, 2006) between grids and sites (i.e. all records were statistically independent). Finally, all of the GLM models that we reported were based on normally distributed data.

RESULTS

In total, we identified 127 invertebrate species (94 beetle species and 33 spider species) and 2803 individuals (1727 beetles, 1076 spiders).

Preliminary analyses indicated that species abundance and composition generally differed strongly between the two years with only a few species showing similar patterns of abundance and distribution between the two years, thus indicating strong temporal fluctuations in most of the beetle and spider populations examined. The invertebrate data for each year were therefore analysed separately.

Invertebrate composition across habitats

An analysis of similarity (ANOSIM, Table 1; see also the results of the pairwise tests in Table S1, Appendix 3) showed that, for both years and both taxa separately and combined, species composition of grids were generally more similar within sampling sites than between sampling sites, i.e. there were significant differences between different sampling sites in terms of their species compositions. We describe these relationships further using cluster analyses as illustrated with dendrograms in Figs 2 to 4 (see also the MDS plots in Figs S2-S4, Appendix 3). In these dendrograms we indicate the rank level at which we have subjectively observed the most meaningful clusters. The ANOSIMs and cluster analyses varied widely between the two taxa and two years; however, a few distinct patterns could be seen in the way the different grids were related to one another which indicated ecologically or at least logically meaningful relationships between sampling sites (Figs 2 to 4).

The two most prominent patterns were: (i) the core (GC) and intermediate grassland (GI) grids were generally separated from the core (SC) and intermediate savanna (SI) grids

Table 1 The global *R* statistics and significance levels (*p*) for analyses of similarity (ANOSIM) comparing sampling sites (habitat types) in terms of their invertebrate species composition for beetles and spiders, separately and combined, in each year.

	2009	2010
Beetles	*R*=0.42; *p*=0.001	*R*=0.29; *p*=0.001
Spiders	*R*=0.20; *p*=0.015	*R*=0.33; *p*=0.001
Combined	*R*=0.43; *p*=0.001	*R*=0.43; *p*=0.001

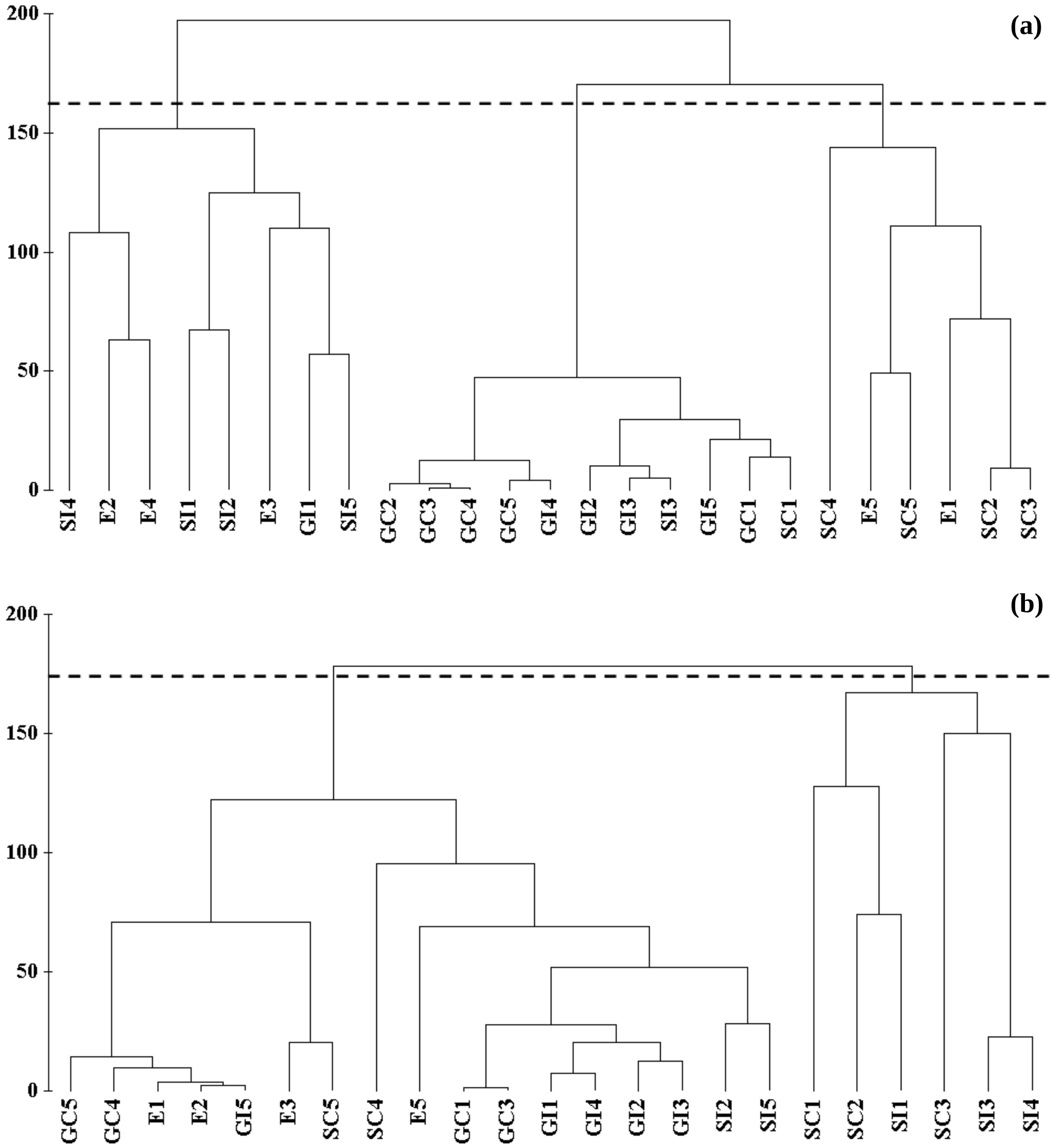

Figure 2 Dendrograms representing cluster analyses, showing the relationships between the grids of sampling sites in terms of (a) beetle and (b) spider composition for 2009. Rank similarities are on the y axis and the dashed lines indicate where the clusters may be divided into meaningful subsets. The abbreviations are: SC – Savanna core; SI – Savanna intermediate; E – Ecotone; GI – Grassland intermediate; GC – Grassland core. The numbers denote different sampling grids. Note that, for the spider composition dendrogram (b), grids GC2 and E4 have been removed prior to the analysis, as these grids appeared to be outliers that could distort the MDS plot (Fig. S2b, Appendix 3).

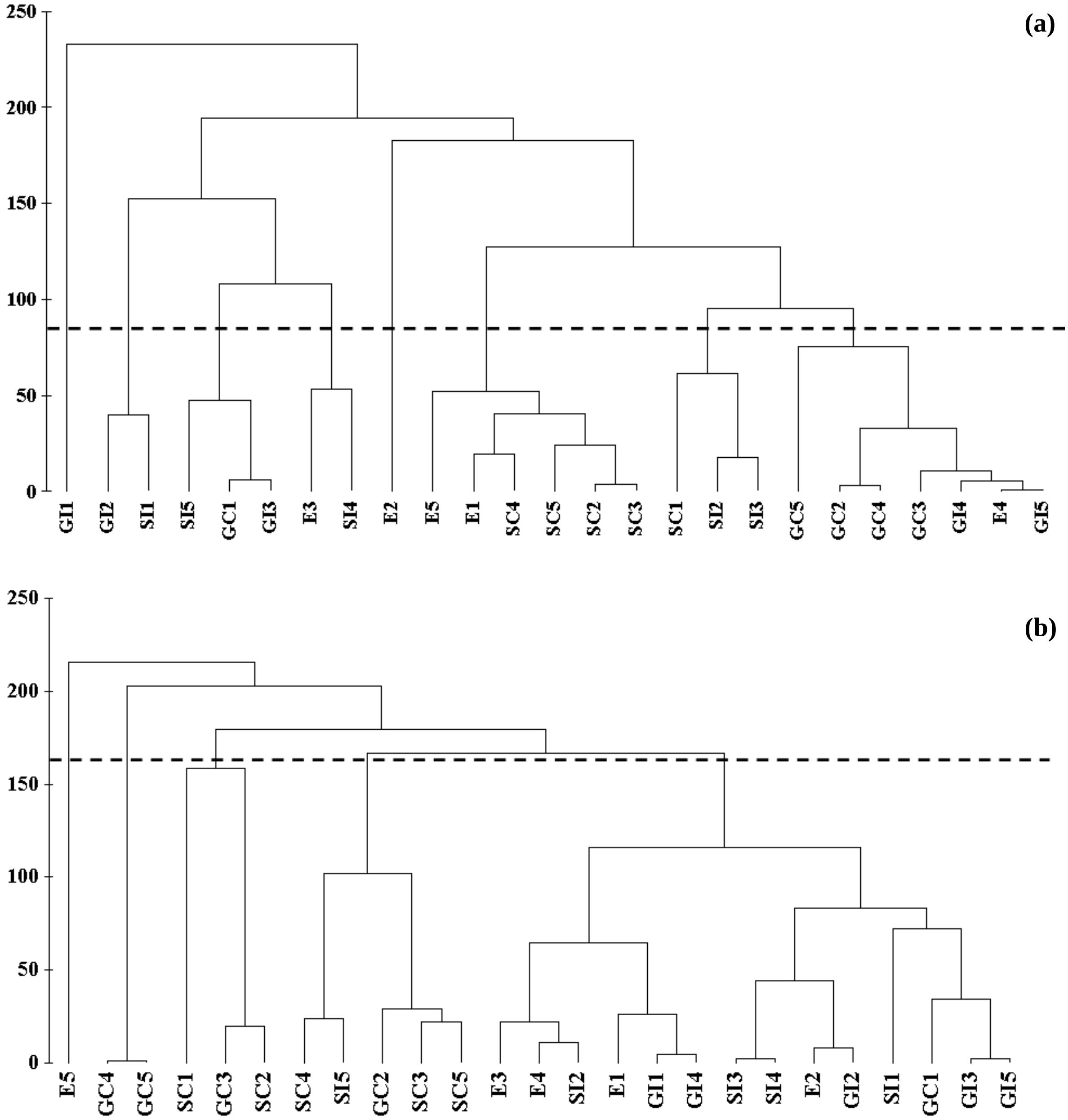

Figure 3 Dendrograms representing cluster analyses, showing the relationships between the grids of sampling sites in terms of (a) beetle and (b) spider composition for 2010. Rank similarities are on the y axis and the dashed lines indicate where the clusters may be divided into meaningful subsets. The abbreviations are: SC – Savanna core; SI – Savanna intermediate; E – Ecotone; GI – Grassland intermediate; GC – Grassland core. The numbers denote different sampling grids.

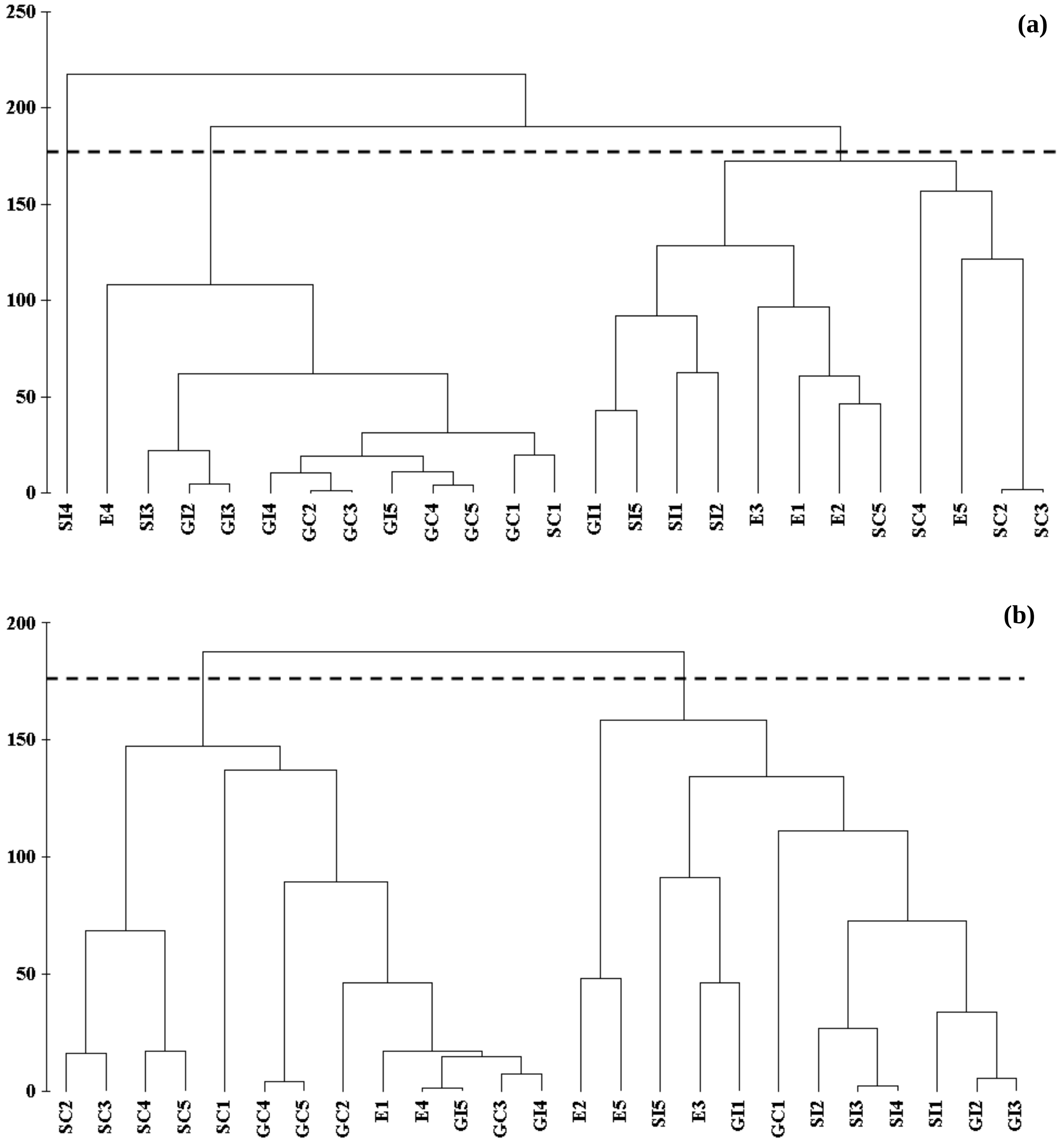

Figure 4 Dendrograms representing cluster analyses, showing the relationships between the grids of sampling sites in terms of invertebrate species composition (beetles and spiders combined) for (a) 2009 and (b) 2010. Rank similarities are on the y axis and the dashed lines indicate where the clusters may be divided into meaningful subsets. The abbreviations are: SC – Savanna core; SI – Savanna intermediate; E – Ecotone; GI – Grassland intermediate; GC – Grassland core. The numbers denote different sampling grids.

(beetles, spiders and both taxa combined in 2009, Figs 2 and 4), and (ii) the savanna and grassland intermediate grids were generally separated from the savanna and grassland core grids (spiders and both taxa combined in 2010, Figs 3 and 4). Another noteworthy relationship found for beetles in 2009, is that savanna core and savanna intermediate grids are included in separate clusters, with the savanna core cluster being more closely related to a cluster comprising mainly intermediate and core grassland grids (Fig. 4). Also, the savanna core and grassland core grids are generally separated for beetles in 2010 (Fig. 3) and, at a lower level of division (e.g. rank 100 in the dendrogram, Fig. 4), for combined taxa in 2010.

Ecotone grids did not form a unique cluster for any year or taxon. Instead, the ecotone grids were usually clustered with grids from other sampling sites (Figs 2 to 4). In some cases the ecotone grids seemed to be mainly (i.e. four or five grids) grouped with clusters characterised by specific habitat or spatial characteristics, such as with the savanna clusters for beetles and both taxa combined in 2009 (Figs 2 and 4), and with either the grassland clusters (2009, Fig. 2b) or the intermediate clusters (2010, Fig. 3b) for spiders. For beetles and both taxa combined for 2010 (Figs 3 and 4), the ecotone grids were not particularly associated with other vegetation types or habitats.

Invertebrate species richness, abundance and diversity

Abundance of beetles and of both taxa combined in both years, and 2009 spider species richness, differed significantly between sampling sites (Table 2), with all, except beetle abundance in 2010, reaching their lowest values at the ecotone (Table 2; Figs 5 and 6; Tables S3 and S4, Appendix 3). Similar patterns of variation in richness and abundance across sites could also be observed for other cases (Table 2; Figs 5 and 6), even though the variation was not significant (Table 2). For example beetle richness in both years, spider abundance in 2010, and species richness of both taxa combined in 2009, were all lowest at the ecotone (Table 2; Figs 5 and 6). Further, as with beetle abundance in 2010, species richness of both taxa combined in 2010 was greater in the core habitats compared to the other sites (Table 2; Figs 5 and 6). Although we observed substantial differences between taxa and years, overall the most common pattern of variation across sampling sites was a reduced value at the ecotone compared to the core habitats (Figs 5 and 6).

There were no significant differences in invertebrate species diversity (Shannon-Wiener index) between the sites, regardless of year or taxon (Table 2); nevertheless, some meaningful patterns could be observed for 2009 (Table 2; Fig. 7; Tables S3 and S4, Appendix 3). Beetle diversity appeared to be higher in the savanna habitat and the ecotone, and lower in the grassland habitat, whereas spider diversity was reduced at the ecotone compared to the

Table 2 One-way analyses of variance (ANOVA) showing the relationships between sampling sites in terms of number of species per trap (species richness), number of individuals per trap (abundance) and Shannon-Wiener diversity index values (H'). Parametric ANOVAs (*F*) were conducted for normally distributed data and Kruskal-Wallis tests (x^2) were used where the data were not normally distributed. Variables that were improved by the natural log are indicated (L). Degrees of freedom are 4 among groups and 20 within groups for each analysis.

	Beetles	Spiders	Combined
2009			
Species richness	$x^2=9.50$; $p=0.05$	$F=3.40$; $p=0.03$	$F=1.74$; $p=0.18$
Abundance	$F=4.93$; $p=0.006$	$F=0.90$; $p=0.49$	$F=5.00$; $p=0.006$
Diversity	$F=2.51$; $p=0.08$	$F=2.52$; $p=0.07$	$F=1.56$; $p=0.23$
2010			
Species richness	$F=2.41$; $p=0.08$	$F=0.91$; $p=0.48$	$F=0.54$; $p=0.71$ (L)
Abundance	$F=10.17$; $p=0.0001$	$x^2=6.83$; $p=0.15$	$F=5.26$; $p=0.005$ (L)
Diversity	$F=1.62$; $p=0.21$	$F=2.49$; $p=0.08$	$F=0.30$; $p=0.87$

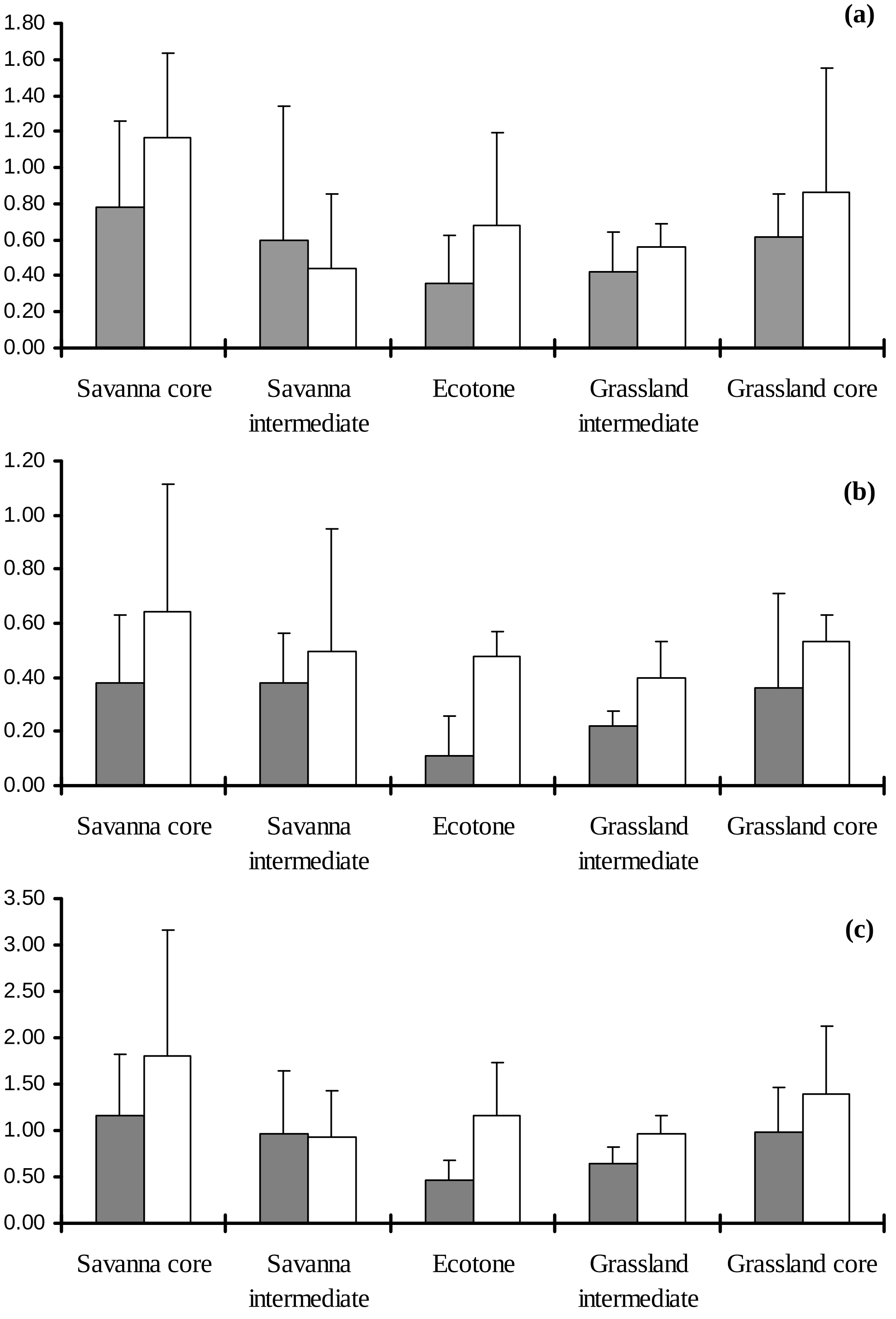

Figure 5 Number of species per trap (species richness) for (a) beetles, (b) spiders and (c) both taxa combined, recorded at each habitat (sampling site) for 2009 (shaded bars) and 2010 (unshaded bars). See all values and their standard deviations in Tables S3 and S4, Appendix 3.

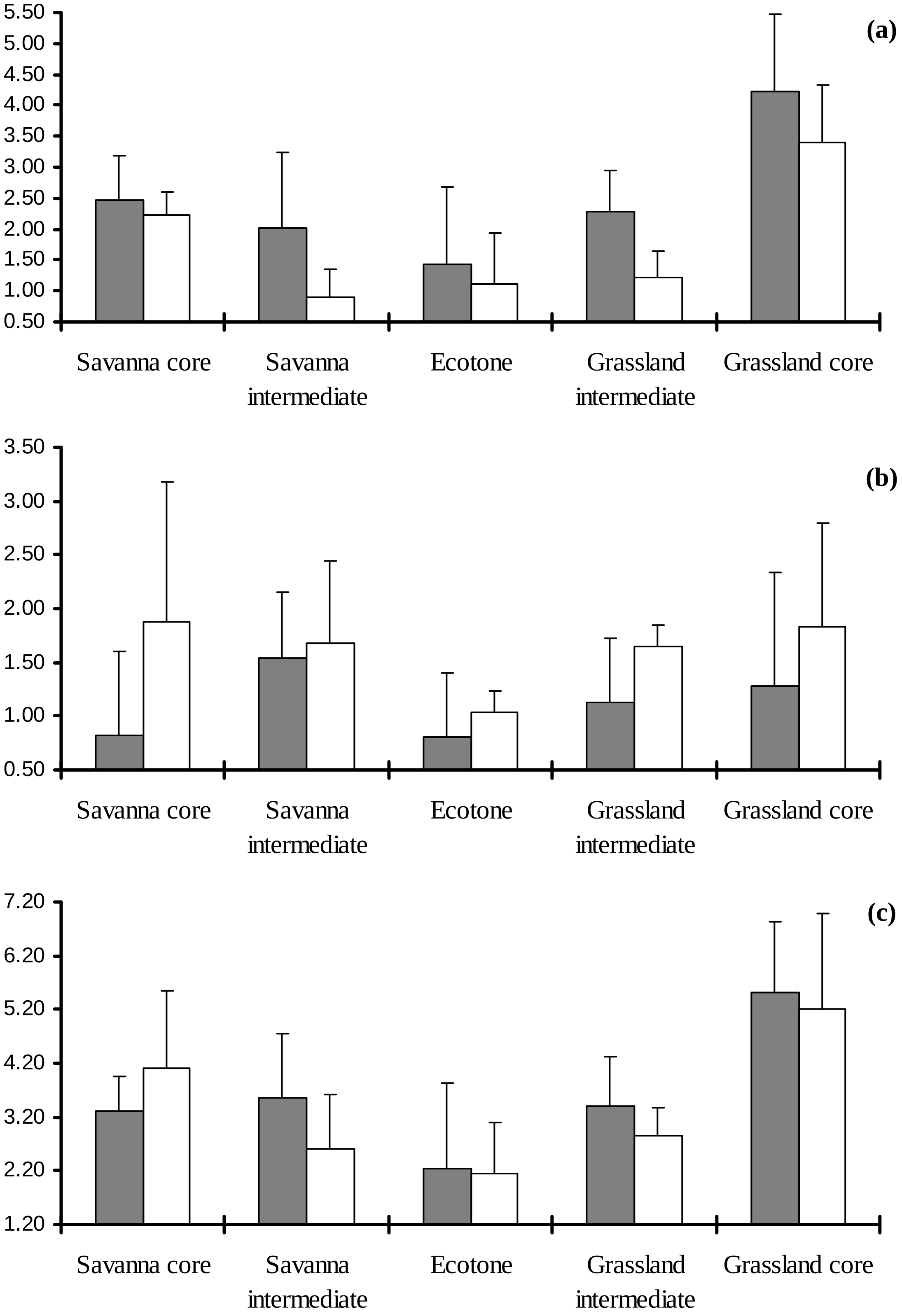

Figure 6 Number of individuals per trap (abundance) for (a) beetles, (b) spiders and (c) both taxa combined, recorded at each habitat for 2009 (shaded bars) and 2010 (unshaded bars). See all values and their standard deviations in Tables S3 and S4, Appendix 3.

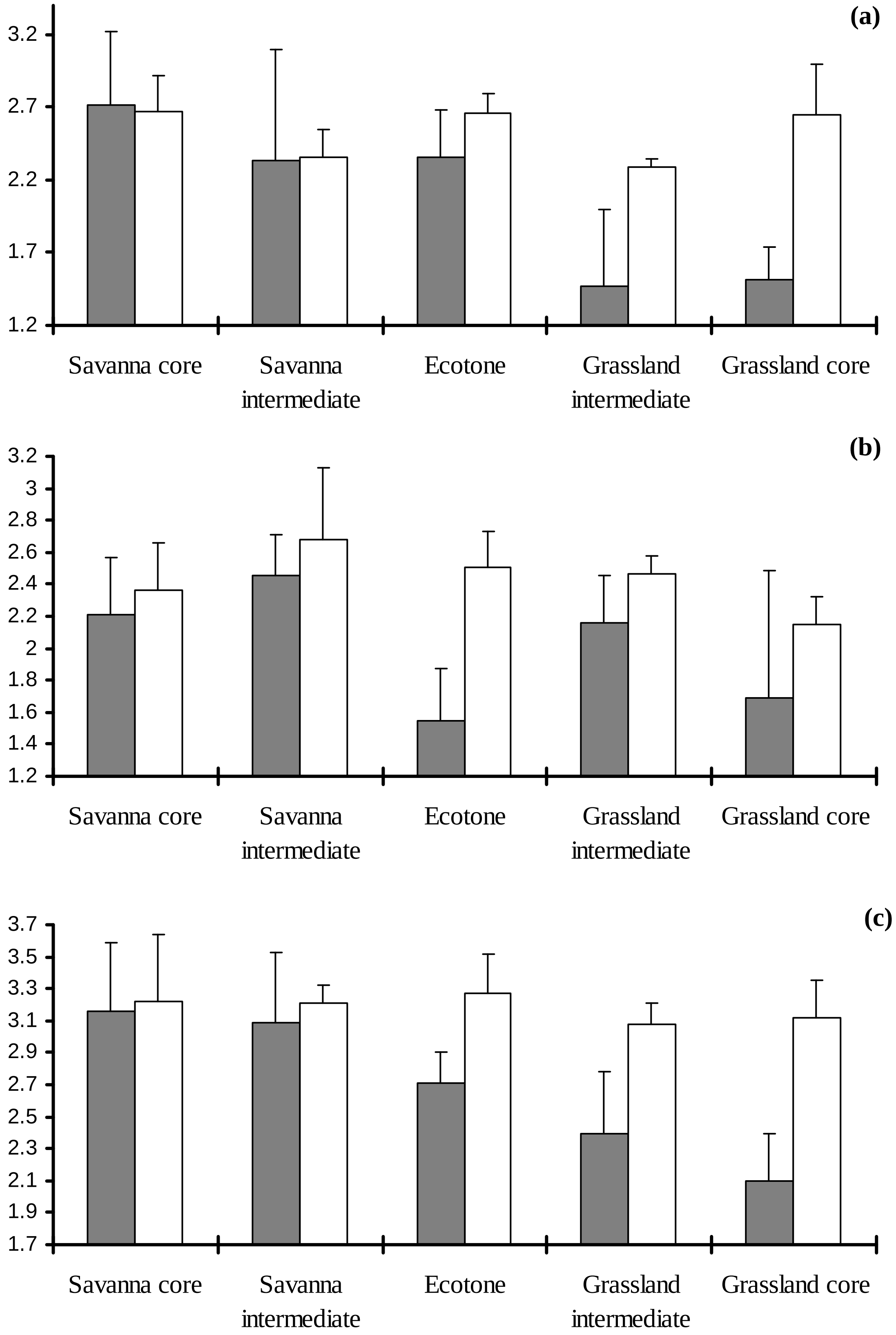

Figure 7 Shannon-Wiener diversity index (H') values of (a) beetles, (b) spiders and (c) both taxa combined, recorded at each habitat for 2009 (shaded bars) and 2010 (unshaded bars). See all values and their standard deviations in Tables S3 and S4, Appendix 3.

other sites (Table 2; Fig. 7). For both taxa combined, diversity in 2009 was lowest at the grassland core habitat, and increased gradually through the other sites to the savanna core site, with an intermediate value at the ecotone (Table 2; Fig. 7). Diversity values in 2010 did not show clear patterns for either taxon, with generally less variation across sites (Table 2; Fig. 7).

Vegetation attributes and their relationships with invertebrates

An ANOSIM showed that sampling sites generally differed significantly in terms of dominant understory plant species composition (Global *R*: 0.55, *p*=0.001; see also Table S2, Appendix 3, for the results of the pairwise tests). A cluster analysis (Fig. 8; see also the MDS plot in Fig. S5, Appendix 3) shows that the grids could be divided into three meaningful clusters containing (i) four of the five ecotone grids, (ii) only core site grids (grassland and savanna), and (iii) mainly intermediate site grids (grassland and savanna).

Sampling sites differed significantly (ANOVA) in terms of vegetation height (*F*=4.73; *p*=0.0075), vegetation density (*F*=11.22; *p*<0.0001) and bare ground cover (*F*=8.54; *p*=0.0003), although the patterns of variation of these variables among sites did not seem ecologically meaningful (Table 3). By “ecologically meaningful”, we mean a pattern of change across the different sampling sites that is either directional (e.g. highest values in one biome, lowest values in the other biome and intermediate values at the ecotone) or that show that the ecotone sampling site’s habitat characteristics are clearly distinguishable from the sampling sites representing other habitats. The diversity of dominant understory plant species (Shannon-Wiener) at each grid was not significantly different between sites (*F*=2.61; *p*=0.07); however, it is noteworthy that vegetation diversity at the ecotone site (1.56) and grassland intermediate site (1.67) was lower than the other three sites (grassland core = 2.62; savanna intermediate = 2.36; savanna core = 2.21). For all ANOVA tests of vegetation variables, the degrees of freedom were 4 among groups and 20 within groups.

General linear models showed that variation among grids in terms of vegetation attributes significantly explained variation in eight of the 18 different response variables (invertebrate richness, abundance and diversity of the different taxa and years were the response variables, Table 4). Five out of these eight response variables were invertebrate abundance variables (i.e. as opposed to richness or diversity) (Table 4). Vegetation height generally contributed most towards explaining invertebrate variation and was most often included in models, usually with a negative correlation and the highest *F* statistics and R^2 values. Vegetation height was followed by density (positive and negative correlations), bare ground cover (positive correlations), and vegetation diversity (being included with vegetation height in only one model for spider abundance in 2009, Table 4). We only report the models

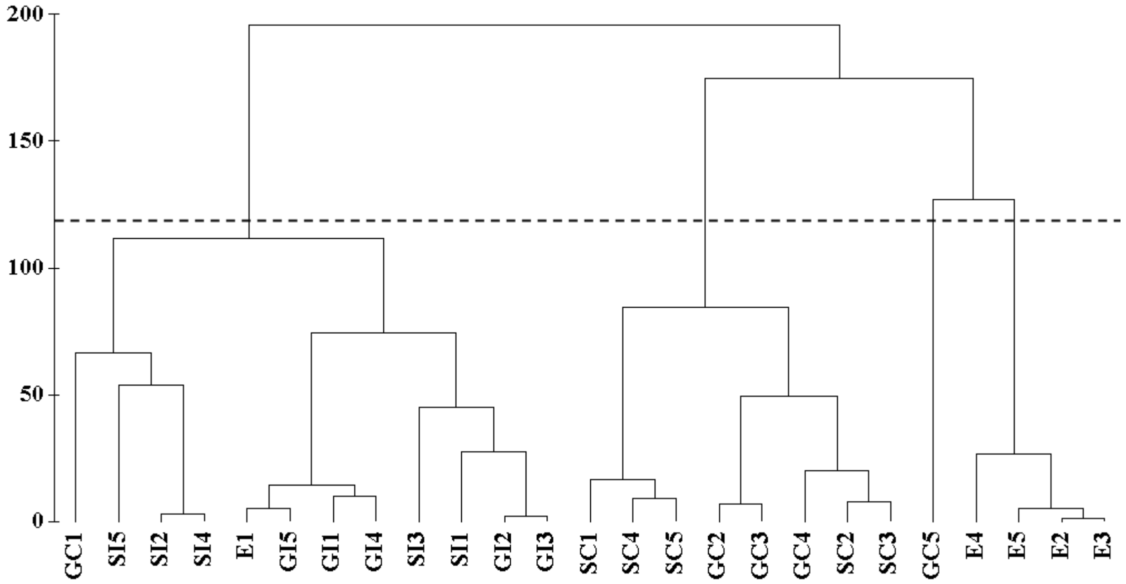

Figure 8 A cluster analysis with rank similarities on the y-axis showing the relationships between sampling grids and sites in terms of dominant plant species composition. The dashed line indicates where clusters may be divided into meaningful subsets. The abbreviations are: SC – Savanna core; SI – Savanna intermediate; E – Ecotone; GI – Grassland intermediate; GC – Grassland core. The numbers denote different sampling grids.

Table 3 The vegetation structure of sampling sites in terms of average and standard deviation of vegetation height (cm), vegetation density (relative index) and percentage of ground cover that is bare of vegetation.

	Height (cm)	Density	Bare ground (%)
Savanna core	17.69±1.77	10.27±1.54	32.10±5.56
Savanna intermediate	10.58±5.22	5.28±2.03	43.00±9.71
Ecotone	15.00±3.96	8.35±1.06	24.20±16.80
Grassland intermediate	14.25±3.04	6.21±1.11	27.00±5.20
Grassland core	8.99±3.08	5.80±0.92	63.75±17.96

Table 4 General linear models showing combinations of vegetation variables – dominant vegetation diversity (Shannon-Wiener index, H'), vegetation height (cm), relative density, and percentage bare ground cover – that best explain variation in invertebrate species richness, abundance and diversity (H'), across sampling sites. We present here, for each 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. Only the best models (lowest Akaike's Infromation Criterion values, see text) where all predictors contributed significantly, are shown.

	Height (cm)	Density	Bare ground (%)	Vegetation diversity	R^2 (%)
2009					
Spider richness	n.i.	†5.85	n.i.	n.i.	20.3
Beetle abundance	n.i.	n.i.	*5.00	n.i.	17.8
Spider abundance	††12.95	n.i.	n.i.	†4.93	43.7
Combined abundance	†††15.45	n.i.	n.i.	n.i.	40.2
Spider diversity	*4.44	†4.72	n.i.	n.i.	18.7
2010					
Beetle richness	†6.95	*5.03	n.i.	n.i.	24.1
Beetle abundance	†4.83	*4.52	n.i.	n.i.	19.0
Combined abundance	n.i.	n.i.	**9.3	n.i.	29.0

Note: Abbreviations: n.i. = not included in model. Levels of significance: positive slope: * $p < 0.05$, ** $p < 0.01$; negative slope: † $p < 0.05$, †† $p < 0.01$, ††† $p < 0.001$.

that best explained variation in each dependent variable, where all of the predictor variables made significant contributions to the model (Table 4).

DISCUSSION

The ecosystems represented in the study area (i.e. grassland and savanna vegetation types adjoining an ecotone habitat), are generally characterised by the spatial variation in richness, abundance, diversity and composition of ground-dwelling beetles and spiders. This may be linked to the distinguishing characteristics (e.g. spatial location and vegetation attributes) of the habitats investigated. However, the patterns of variation in invertebrates across the different habitats varied markedly between taxa and years, and the roles played by the different habitats and vegetation attributes were not always clear. We discuss the findings in relation to the three questions listed in the Introduction.

1) Variation in invertebrate composition across the ecotone

Ecologically meaningful relationships between habitats in terms of invertebrate composition were found in several cases. For example, grassland habitat differs from savanna habitat for beetles, spiders and both taxa combined in 2009, and (at least for the core savanna and grassland habitats furthest from the ecotone) beetles and both taxa combined in 2010. These patterns indicate that there is a change in species composition between the savanna and grassland (consistent with e.g. Durães *et al.*, 2005), although the patterns varied widely between taxa and years.

The ground-dwelling invertebrate species composition of the ecotone was not unique, with no ecotonal invertebrate species that were restricted to or more common at the ecotone (consistent with Durães *et al.*, 2005; but see Lloyd *et al.*, 2000, and Walker *et al.*, 2003). Instead, ecotone invertebrate composition was usually related to one or more of the other habitats (e.g. related to the savanna habitat for both taxa combined in 2009). However, in some cases (e.g. spiders and both taxa combined in 2010) both intermediate habitats (i.e. savanna and grassland habitat closer to the ecotone) were grouped with the ecotone, possibly indicating an ecotone effect on invertebrate composition that is spatially broader than what is expected from the observed habitat and spatial characteristics of this study area (see also Dangerfield *et al.*, 2003).

Unexpected or unclear relationships were also found. For example for beetles and both taxa combined in 2010, the savanna and grassland core habitats (which were expected to be most dissimilar) were more closely related to each other than to other sites. Unclear or unexpected invertebrate composition patterns might be attributed to several possible confounding factors (discussed in more detail further on in this chapter), namely (i) the presence of generalist invertebrates that are not restricted by habitat type, (ii) fluctuations in species population sizes and distributions, (iii) the exact locations of the sampling sites in relation to the ecotone mosaic, or (iv) inadequate sampling effort in terms of intensity and spatial cover (Foord *et al.*, 2003).

2) Variation in invertebrate richness, diversity and abundance across the ecotone

The current study did not show the expected increase in biodiversity at the ecotone compared to the adjacent habitats. The most common overall trend found for invertebrates in this study area was a reduction in species richness and abundance at the ecotone. Reduced spider diversity at the ecotone in 2009 was also found. Compared to savanna and grassland core habitats, richness and abundance values were often also smaller in the savanna and grassland habitats that were closer to the ecotones (i.e. the intermediate habitats), which possibly indicates a spatially broader ecotone influence on invertebrate richness and abundance (as with species composition in point 1; see also Durães *et al.*, 2005). Further, combined invertebrate taxa in 2009 showed an intermediate diversity at the ecotone compared to a lower diversity in the grassland sites and a higher diversity in the savanna sites, whereas the diversity at the ecotone for beetles in 2009 is similar to that for the savanna sites (i.e. higher than for the grassland sites).

Although the commonly expected increased ecotone biodiversity and richness (i.e. diversity and richness in species, genes, and morphological characteristics) has been found in previous studies (e.g. Kark *et al.*, 1999, 2002, 2007; Walker *et al.*, 2003; Van Rensburg *et al.*, 2004), other patterns have also been found, such as a reduced biodiversity level (e.g. Spector & Ayzama, 2003) or an intermediate biodiversity level (e.g. Lloyd *et al.*, 2000; Kotze & Samways, 2001; Baker *et al.*, 2002; Walker *et al.*, 2003). The particular pattern found at an ecotone may depend on which taxa and spatial scale are used, as well as on the ecological characteristics and temporal and spatial dynamics found at that ecotone (e.g. Lloyd *et al.*, 2000; Spector & Ayzama, 2003; Van Rensburg *et al.*, 2004; Durães *et al.*, 2005; Kark *et al.*, 2007).

If this ecotone can truly be linked to a consistent (i.e. long-term and widespread) pattern of reduced invertebrate richness and abundance, and by implication a suboptimal environment for invertebrates compared to the adjacent habitats, then the ecotone is likely an important environmental component regulating the movement and distribution of at least less mobile (e.g. flightless) ground-dwelling invertebrates between the savanna and grassland habitats in the study area. The significance of this is that the ecotone may act as a selective filter that moderates or reduces gene flow between different populations of species that are found in savanna and grassland habitats (e.g. Kark *et al.*, 1999; Brouat *et al.*, 2003; Pfenninger *et al.*, 2003).

3) The relationships between vegetation and invertebrates

Spatial variation in richness, abundance and diversity for both invertebrate taxa (separately and combined) and both years separately (i.e. 18 different response variables) were correlated to variation in four understory vegetation attributes, namely, dominant plant species diversity, vegetation height and density and bare ground cover. Understory vegetation attributes, of which vegetation height seemed to have the greatest influence, explained between 18% and 44% of spatial variation in invertebrates for eight of all 18 different invertebrate response variables (see details in Table 4; see also Szövényi, 2002). Despite these findings, vegetation attributes appeared to vary arbitrarily among the different habitats (Table 3), whereas invertebrates were shown to vary among the habitats in ecologically meaningful patterns (e.g. the reduction in richness and abundance at the ecotone, point 2). It is therefore still unclear whether or how vegetation attributes influenced the overall patterns of change in invertebrate richness, abundance and diversity across the different habitats.

For the most part, composition of invertebrates and composition of dominant plant species did not show similar patterns across the habitats, with two exceptions. As discussed in point 1 (Figs 3 and 4) we found unexpected patterns for beetles in 2010, and both invertebrate taxa combined in 2010, which were similar to the pattern found for plant species composition – the savanna and grassland core habitat sampling sites were more closely related to one another than to the other sites (Fig. 8). Therefore, like other vegetation attributes discussed previously, plant species composition also did not vary predictably or meaningfully among habitats and did not indicate an ecotonal change in plant species assemblages between the two biomes.

Unlike invertebrates, plant species composition of the ecotone was found to be very distinct compared to the other habitats. In particular, an overview of the dominant plant species recorded for each grid reveals that four of the five ecotone grids were dominated by red grass (*Themeda trianda*), which is unlike the other habitats (or any other grids) that were generally covered by a variety of grass and shrub species. Red grass cover ranged between 16% and 77% (average more than 50%) in these four ecotone grids, while it was absent from the one ecotone grid that was not included in the ecotone cluster (E1 was included in the intermediate habitats cluster, Fig. 8). Further, personal observations revealed that a mosaic of patches dominated by red grass is a pervasive characteristic of the ecotone in the study area, at the ecotone sampling site as well as at all of the other locations along the ecotone (in various fields, with or without livestock) that had been visited, but not sampled, during field work. The environmental factors and mechanism promoting the dominance of red grass at the ecotone are currently unknown, and requires a more thorough botanical survey at the study area.

Considering that the current study's ecotone is associated with reduced invertebrate abundance and richness values (see point 2), it might be revealing to specifically investigate the influence that the red grass dominated patches in this study area might have on the colonisation and dispersal of invertebrates at a local scale (see e.g. Wiens *et al*., 1997). One possible finding from such an investigation could be that habitat structure, especially vegetation density, influences trappability and consequently biases records of species richness, abundance and composition in the different habitats (Melbourne, 1999); however, given that vegetation structure at the ecotone was not particularly distinct from other habitats (Table 3), and vegetation density (the ecotone has the second densest vegetation, Table 3) does not seem to have negative effects on abundance (Table 4), this explanation is currently no more likely than that invertebrate richness and abundance, and perhaps dispersal rate, are negatively influenced by red grass domination.

By focusing on ground-dwelling invertebrates in the current study, we did not sample the biodiversity associated with the trees and large shrubs, which are likely to support a wealth of tree-dwelling invertebrate species that are present only in the ecotone and savanna habitats (e.g. Ribas *et al*., 2003). Trees and large shrubs also provide additional habitat resources (e.g. improved soil fertility) and increased habitat complexity, thereby possibly locally increasing ground-dwelling invertebrate species richness, abundance and diversity in the savanna and ecotone habitats (Vetaas, 1992; Campbell *et al*., 1994; Scholes & Archer, 1997; Ribas *et al*., 2003). It would be interesting to investigate how many more invertebrate species are supported by trees and large shrubs in the savanna and ecotone habitats, and whether the overall (i.e. flying, ground and tree-dwelling) recorded invertebrate diversity, richness and abundance would then be greater in the tree-supporting habitats than the grassland habitats.

Complicating factors in the study

Although obvious human-caused factors were avoided, many of the dominant understory plant species recorded in the study area, such as the grass species *Schmidtia pappophoroides* (abundant in the savanna core habitat), *Enneapogon desvauxii* (savanna intermediate), and

Cynodon dactylon (grassland intermediate), indicate overgrazing (Trollope *et al.*, 1989; Dorgelöh, 1999; Rutherford *et al.*, 2012), and there are many more examples of disturbed habitat patches (e.g. abandoned agricultural fields) throughout the study area that could possibly affect invertebrates (as found in Samways *et al.*, 1996, and Kotze & Samways, 1999a).

Further, it is conceivable that the particular location of sampling sites in relation to mosaic configuration of vegetation types at and close to the ecotone have influenced the current results and obscured underlying patterns of change in invertebrates and vegetation between biomes (see also Krasnov & Shenbrot, 1998). For example, if the entire intermediate savanna sampling site was located on more typical savanna habitat (i.e. not with four out of the five grids located on a clay soil patch, see Methods section), then invertebrate and vegetation variables from this site might have been more similar to the core savanna sampling site. Similarly, as the importance of ecotone mosaics are scale-dependent, a change in species assemblages between the two biomes might be more apparent at larger spatial scales, where the entire ecotone mosaic and all its habitat patches would be viewed as one comprehensive ecotonal zone (Gosz, 1993; Walker *et al.*, 2003). By this argument, it is also likely that an increased invertebrate biodiversity could be observed when investigating this ecotone at larger spatial scales (see Willis & Whittaker, 2002).

More generally, despite the fact that a few meaningful patterns were found for the current study, a pervasive characteristic of the study is that all results for invertebrates varied widely according to taxon and year. This possibly indicates that beetles and spiders respond differently to environmental variables (e.g. Kotze & Samways, 1999b; Dangerfield *et al.*, 2003; Durães *et al.*, 2005), and that their populations fluctuate strongly between years. In fact, it is conceivable that differences between the ecosystems of the study area might manifest as differences in the ecosystem temporal dynamics and stability, causing populations to fluctuate at different frequencies or amplitudes in different habitats. However, two years' worth of data is inadequate to investigate such temporal effects. Further, it is possible that the simple sampling design does not capture true patterns of variation across the ecotone, and clearer results could be gained from a design covering a larger area, with a larger number of sampling sites in each habitat type, and also a larger number replicates per site. A long-term study and more intense sampling at different spatial scales is needed to clarify the characteristics and environmental determinants (e.g. variable ecosystem responses to rainfall patterns) of such population fluctuations and inconsistent patterns, and allow us to observe more general underlying ecological trends.

Conclusions

This vegetation and invertebrate survey of a savanna-grassland ecotone revealed several general characteristics of this ecotone. First, the habitats differ with regard to their vegetation attributes, as well as invertebrate species richness, abundance, diversity and composition, to varying degrees depending on year and taxon investigated, but not always in expected ways. For invertebrates, in some cases, habitat differences indicated a turnover in species composition between the savanna and grassland. Second, the vegetation composition of the ecotone is distinct compared to the other habitats due to the dominance of red grass; however the invertebrate composition of the ecotone is not distinct. Third, biodiversity at the ecotone is not higher than the other habitats; rather, results mainly indicate lower levels of species richness and abundance compared to the other habitats. These lower levels might indicate that the ecotone is a suboptimal environment that could act as a selective filter moderating the movement of individuals and genes across the ecotone, at least of less mobile species.

Despite these insights, the study is restricted by the low intensity and short time span of the sampling, which was probably responsible for some of the unclear patterns across the different habitats and the uninformative variation between years. In addition, although certain patterns of spatial variation in invertebrates (e.g. richness, abundance and diversity) covary with vegetation attributes to some extent, it is unclear what role vegetation plays in determining invertebrate variation across habitats.

As with many short-term studies based on rapid species surveys, the accuracy with which each habitat of the current study is represented by the data from the sampling sites is questionable (e.g. Foord *et al*., 2003). Biodiversity studies, especially those with a conservation aim, are commonly constrained by available time, budget and labour, which results in a growing pool of simple short-term surveys (e.g. Szövényi, 2002; Foord *et al*., 2003) that may all contribute valuable insights, provided that their limitations are recognised (see e.g. Pik *et al*., 2002). Nevertheless, a more intensive and long-term survey (including a thorough botanical survey) at several spatial scales would more explicitly reveal the underlying ecological processes of this ecotone.

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CHAPTER 5

General Discussion

At large spatial and temporal scales the geographical distributions of taxa are a product of the evolutionary, geological and geographical history of the earth (Cox, 2001; Ebach, 2003; Ebach & Humphries, 2003); however, short-term processes such as human-caused habitat modifications and species introductions may substantially modify these distributions (e.g. McKinney & Lockwood, 1999; Real *et al*., 2003; Olden *et al*., 2004). These basic insights served as a background for the three studies comprising this thesis. In these studies I (i) describe various alien phytogeographic regions for southern Africa (Chapter 2), (ii) show that ecotones, in South Africa as a whole and in individual biomes, harbour relatively higher numbers of alien plant species compared to areas that are spatially distant from ecotones (Chapter 3), and (iii) show that the savanna-grassland ecotone in the west of the Free State Province in South Africa generally represents a zone where invertebrate composition changes between these two biomes, although the ecotone itself harboured relatively fewer invertebrate species and at lower abundances (Chapter 4).

Chapters 2 and 3 benefit the research field of invasion biology, by revealing new aspects of the large-scale spatial distribution patterns of alien plant species in southern Africa (for previous studies on this subject, see Richardson *et al*., 2004, 2005; Thuiller *et al*., 2006). Seeing that alien plant species are generally considered to be a major threat to native biodiversity and ecosystems, both studies provide information that is potentially useful for conservation efforts and especially the prioritisation of areas in terms of management and conservation needs (see e.g. Nel *et al*., 2004; Le Maitre *et al*., 2011). Chapters 3 and 4 provide contrasting evidence on biodiversity levels at ecotones; however, this could simply reflect the scale-dependence of the ecological patterns and processes operating at ecotones (Gosz, 1993; Kark & Van Rensburg, 2006; Davis *et al*., 2008). Indeed, as mentioned in the General Introduction (Chapter 1), even though ecotones may be caused and characterised by a wide variety of ecological processes, ecotone research is often based on, or recapitulates, several common assumptions concerning biodiversity, speciation and other ecological processes at ecotones (Walker *et al*., 2003; Kark & Van Rensburg, 2006). To test the universality and applicability of these assumptions, sufficient research on ecotones is needed for various taxa and spatial scales and in different locations around the world. Such research is especially important as many of the characteristics commonly attributed to ecotones (e.g. exceptional species richness, unique species/genotypes) are of interest to conservation.

Even considering the contributions made by this thesis, I anticipated and observed a similar problem with each of the three studies, namely data inadequacy, which reduces the robustness and consistency of the results and restricts comparability with other similar studies. As I have explained in Chapter 1, data inadequacy has been in the past and is still a common and persistent problem in ecological research, especially considering the difficulties in obtaining ecological data at appropriate spatial resolutions and time scales (Gaston & Blackburn, 2000; Davis, 2002; Blackburn & Gaston, 2003). For example, at any spatial scale, it is challenging to choose appropriate taxa representing biodiversity. It is always possible that the distribution patterns observed for the chosen taxon or taxa do not represent overall biodiversity distribution patterns, as other taxa in the study area might not be similarly distributed, due to e.g. taxonomic differences in mobility and environmental requirements and tolerances (e.g. McGeoch, 1998; Stoms *et al.*, 2005).

Two principal forms of data-inadequacy may be found in atlas-based studies. First, atlases often suffer from incomplete data and/or inadequate data coverage, where certain locations might have no data available or where the available data are not particularly representative (Richardson *et al.*, 2005; Robertson *et al.*, 2010). The alien phytogeographic regions mapped in Chapter 2 show a fair amount of unresolved noise in the form of outlier grid cells situated some distance away from the regions (spatial clusters of grid cells) to which they belong, which could be a result of poor data quality in these grid cells. Second, the spatial resolution of atlas data is in many cases too coarse to answer certain ecological questions (see e.g. Hugo & Van Rensburg, 2008). For example, in Chapter 3, the spatial relationships between alien plant richness and ecotones were insignificant in the relatively smaller fynbos and forest biomes, which should probably have been studied at a much finer spatial resolution. Also, the coarse resolution of atlas-based studies is often inappropriate for practical conservation and/or management decisions and useful as a guideline only, as local conservation projects and protected areas are often much smaller than the spatial resolution of the atlas. For example, a study based on the first bird atlas project in South Africa (SABAP 1; Chown *et al.*, 2003; Robertson *et al.*, 2010) might identify a particular quarter-degree grid cell as an urgent conservation priority; however, due to processes operating at a smaller spatial scale (e.g. local competition with the human population and development), only part of that grid cell will be conserved. Quarter-degree resolution is currently the finest resolution biological atlas data for southern Africa, although the second unfinished bird atlas project (SABAP 2) aims to record national-scale data at a finer 5 minute resolution (Chown *et al.*, 2003; Robertson *et al.*, 2010).

Studies based on data gained from field-based surveys are also subject to certain limitations. For example, species surveys such as that of Chapter 4 are often conducted at spatial resolutions and extents that are too small to be representative of the areas that are of conservation interest, although such surveys are routinely conducted in rehabilitation or ecological impact studies (McGeoch, 1998; Pik *et al.*, 1999, 2002). Moreover, the limited spatial coverage and short time-spans that are common in such studies do not adequately incorporate fluctuations over time in the characteristics of the habitats, population sizes of individual species, or the composition of the species assemblages (Davis, 2002; Blackburn & Gaston, 2003). For example, in Chapter 4 I had noted great differences between the two years and the two taxa; however, it was unclear whether these differences were caused by under-sampling or by an undiscovered temporally changeable natural factor.

Despite these possible limitations, the wealth of species survey collections and atlases that are growing in number, scope and quality across the globe are still in great demand for research and applied conservation efforts (Blackburn & Gaston, 2003). As shown by the three studies in this thesis, the data can be successfully applied to answer a variety of ecological questions and to improve our understanding of diverse ecological systems. Indeed, the complexity of interacting factors that determine species distributions, which often differs between regions, taxa and the spatial and temporal scale at which an ecosystem is viewed (e.g. Davis *et al*., 2008), leaves us with a range of unanswered questions in the quest to find general ecological theories to explain the distribution of species across the earth. This complexity is one more reason for the continued and growing interest in biogeography and macroecology (Blackburn & Gaston, 2003).

Authors of macroecology research articles often express the need for improved data at finer spatial resolutions, with which to confirm and further examine their findings (see e.g. Van Rensburg *et al*., 2004; Richardson *et al*., 2005; Hugo & Van Rensburg *et al*., 2008; and also Chapters 2 to 4 in this thesis). However, researchers should also aim to develop innovative approaches towards using any data that are already available or that can be feasibly acquired within an allotted time period and budget. For example, researchers could make full use of all available species atlas programmes available for a particular geographical area, to investigate common ecological questions (e.g. describing biogeographical regions and centres of endemism, or determining relationships between species richness and energy availability or human activities) across a range of different taxa (e.g. for South Africa, Robertson *et al*., 2010). Data acquired through smaller-scale species surveys from different studies could also be added to a common database and made available for multiple research projects, which would enable better coordination in research efforts and also help to systematically identify undersampled areas (e.g. Davis, 2002). In any case, researchers should always proceed with due caution in interpreting findings by taking into account data limitations. Ultimately, a sustained research interest in diverse systems around the world is vital to identify research questions requiring more intensive examination and more rigorous sampling efforts, and to eventually reveal our way forward in terms of macroecology and biogeography research and our pursuit to formulate generally applicable theories and natural laws.

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APPENDIX 1

Supporting information for Chapter 2

Table S1 The phytogeographic regions of the current study were differentiated from one another and classified according to the alien plant species that were most characteristic of each particular region, i.e. that were more likely to occur in that particular region than in the rest of the study area. With the method used in the current study, the different regions could not overlap geographically but often shared characteristic species. Here we list, for each phytogeographic region, the species that occupied a greater proportion of a particular phytogeographic region than the rest of the study area (corrected for the sizes of the areas). We list only those species that occupied 5% or more of a region and were within the top twenty species, ranked according to the difference between the phytogeographic region and rest of the study area in percentage of grid cells occupied. The percentage of grid cells occupied by a species in a phytogeographic region is included in brackets.

Rank	1. Greater Arid	1.1 Arid	1.2 Orange River	2. Multiclimate
1	*Atriplex lindleyi* (23)	*Atriplex lindleyi* (32)	*Prosopis glandulosa* (59)	*Hibiscus trionum* (13)
2	*Prosopis glandulosa* (20)	*Salsola kali* (27)	*Prosopis velutina* (52)	*Achyranthes aspera* (12)
3	*Salsola kali* (21)	*Coronopus integrifolius* (26)	*Persicaria limbata* (10)	*Persicaria lapathifolia* (9)
4	*Coronopus integrifolius* (19)	*Polypogon monspeliensis* (18)	*Prosopis chilensis* (6)	*Rumex acetosella* (7)
5	*Prosopis velutina* (16)	*Verbesina encelioides* (11)		*Oenothera rosea* (7)
6	*Verbesina encelioides* (9)	*Atriplex nummularia* (9)		*Paspalum dilatatum* (9)
7	*Polypogon monspeliensis* (14)	*Atriplex eardleyae* (5)		*Lantana camara* (6)
8	*Atriplex nummularia* (7)	*Juncus bufonius* (6)		*Verbena bonariensis* (7)
9		*Puccinellia fasciculata* (5)		*Amaranthus hybridus* (6)
10		*Chenopodium murale* (7)		*Digitaria sanguinalis* (7)
11		*Lophochloa pumila* (5)		*Oxalis corniculata* (6)
12				*Gomphrena celosioides* (6)
13				*Schkuhria pinnata* (7)
14				*Hypochaeris radicata* (5)
15				*Oenothera tetraptera* (5)
16				*Poa annua* (5)
17				*Bromus catharticus* (7)
18				*Bidens pilosa* (5)

Table S1 continues

Rank	2.1 Escarpment	2.2 Northern	2.3 Agricultural	2.4 Western Cape
1	*Verbena bonariensis* (16)	*Mimosa pigra* (7)	*Polypogon monspeliensis* (19)	*Polypogon monspeliensis* (29)
2	*Rumex acetosella* (15)	*Senna obtusifolia* (5)	*Briza maxima* (11)	*Hordeum murinum* (25)
3	*Oenothera rosea* (13)	*Glinus lotoides* (6)	*Paspalum dilatatum* (16)	*Spergularia media* (20)
4	*Paspalum dilatatum* (15)	*Salvinia molesta* (5)	*Lolium multiflorum* (10)	*Briza maxima* (19)
5	*Persicaria lapathifolia* (15)	*Datura innoxia* (5)	*Hypochaeris radicata* (12)	*Aira cupaniana* (15)
6	*Phalaris arundinacea* (8)	*Digitaria sanguinalis* (10)	*Aira cupaniana* (10)	*Bromus diandrus* (14)
7	*Holcus lanatus* (7)	*Eclipta prostrata* (5)	*Poa annua* (12)	*Vulpia myuros* (14)
8	*Lantana camara* (12)	*Acanthospermum hispidum* (5)	*Rumex acetosella* (13)	*Brachypodium distachyon* (12)
9	*Poa annua* (10)	*Flaveria bidentis* (7)	*Vulpia bromoides* (9)	*Vulpia bromoides* (13)
10	*Poa pratensis* (7)	*Phyla nodiflora* (5)	*Digitaria sanguinalis* (12)	*Lolium rigidum* (12)
11	*Polygonum aviculare* (10)	*Persicaria limbata* (5)	*Hordeum murinum* (11)	*Anagallis arvensis* (12)
12	*Solanum nigrum* (11)	*Sesbania bispinosa* (6)	*Briza minor* (8)	*Polypogon viridis* (12)
13	*Senna septemtrionalis* (7)	*Ricinus communis* (6)	*Bromus diandrus* (8)	*Solanum americanum* (10)
14	*Acanthospermum australe* (7)	*Senna occidentalis* (5)	*Silene gallica* (7)	*Fumaria muralis* (11)
15	*Bromus catharticus* (12)		*Juncus bufonius* (6)	*Briza minor* (11)
16	*Rubus cuneifolius* (7)		*Phytolacca octandra* (8)	*Phalaris minor* (11)
17	*Bidens pilosa* (9)		*Vulpia myuros* (8)	*Medicago polymorpha* (11)
18	*Ageratum conyzoides* (7)		*Bromus catharticus* (11)	*Bromus hordeaceus* (10)
19	*Echium vulgare* (6)		*Phalaris minor* (7)	*Silene gallica* (11)
20	*Phytolacca octandra* (8)		*Medicago polymorpha* (7)	*Lotus subbiflorus* (10)

Table S1 continues

Rank	**2.5 Grassland**	**2.6 Savanna**
1	*Oenothera rosea* (21)	*Achyranthes aspera* (23)
2	*Medicago laciniata* (19)	*Alternanthera sessilis* (9)
3	*Oenothera tetraptera* (19)	*Sesbania bispinosa* (9)
4	*Hibiscus trionum* (17)	*Gomphrena celosioides* (12)
5	*Paspalum dilatatum* (25)	*Senna occidentalis* (8)
6	*Rumex acetosella* (21)	*Richardia scabra* (8)
7	*Persicaria lapathifolia* (18)	*Euphorbia indica* (8)
8	*Bromus catharticus* (20)	*Flaveria bidentis* (9)
9	*Amaranthus hybridus* (17)	*Lantana camara* (11)
10	*Cirsium vulgare* (16)	*Boerhavia diffusa* (7)
11	*Chenopodium schraderianum* (13)	*Ageratum conyzoides* (8)
12	*Oxalis corniculata* (12)	*Hybanthus enneaspermus* (7)
13	*Polygonum aviculare* (15)	*Polycarpaea corymbosa* (7)
14	*Cuscuta campestris* (13)	*Acanthospermum hispidum* (7)
15	*Rumex crispus* (13)	*Corchorus trilocularis* (7)
16	*Pseudognaphalium luteoalbum* (12)	*Hibiscus trionum* (18)
17	*Digitaria sanguinalis* (17)	*Phyla nodiflora* (7)
18	*Myosotis sylvatica* (14)	*Ethulia conyzoides* (7)
19	*Schkuhria pinnata* (10)	*Richardia brasiliensis* (10)
20	*Physalis angulata* (9)	*Malvastrum coromandelianum* (6)

APPENDIX 2

Supporting Information for Chapter 3

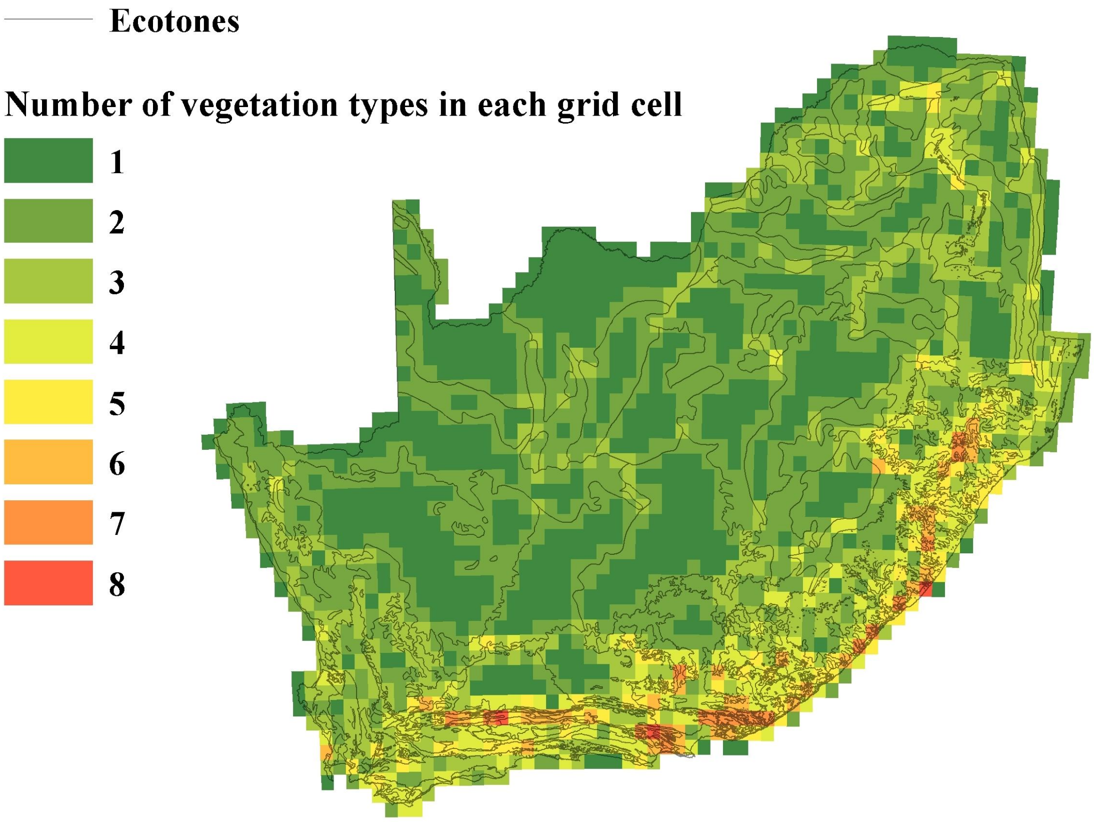

Figure S1 The spatial locations of vegetation boundaries and the number of vegetation types within each quarter-degree grid cell for South Africa and Lesotho, based on the vegetation types described by Low & Rebelo (1996).

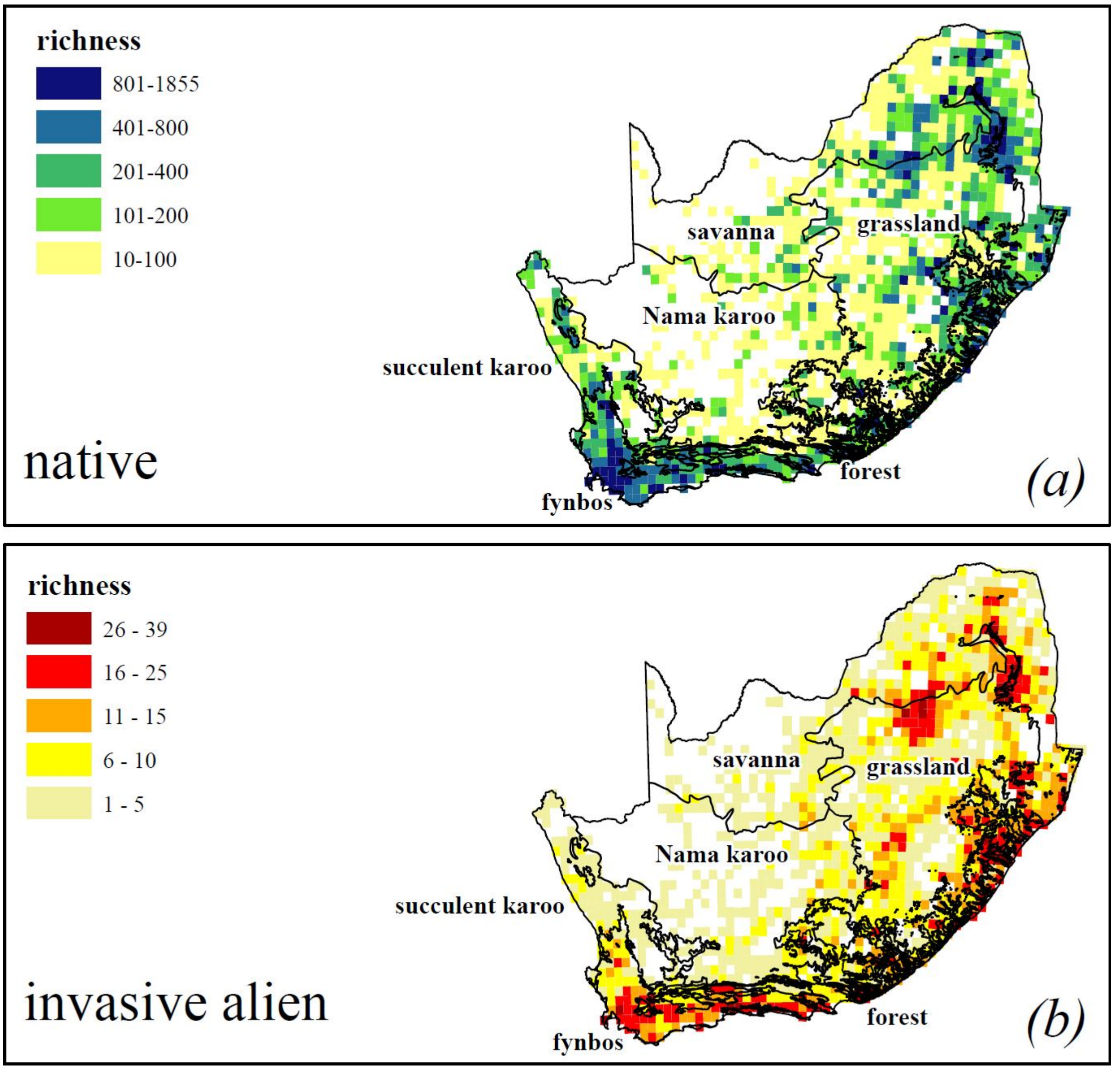

Figure S2 For South Africa and Lesotho at the quarter-degree grid cell resolution, patterns of (a) native plant richness and (b) invasive alien plant richness.

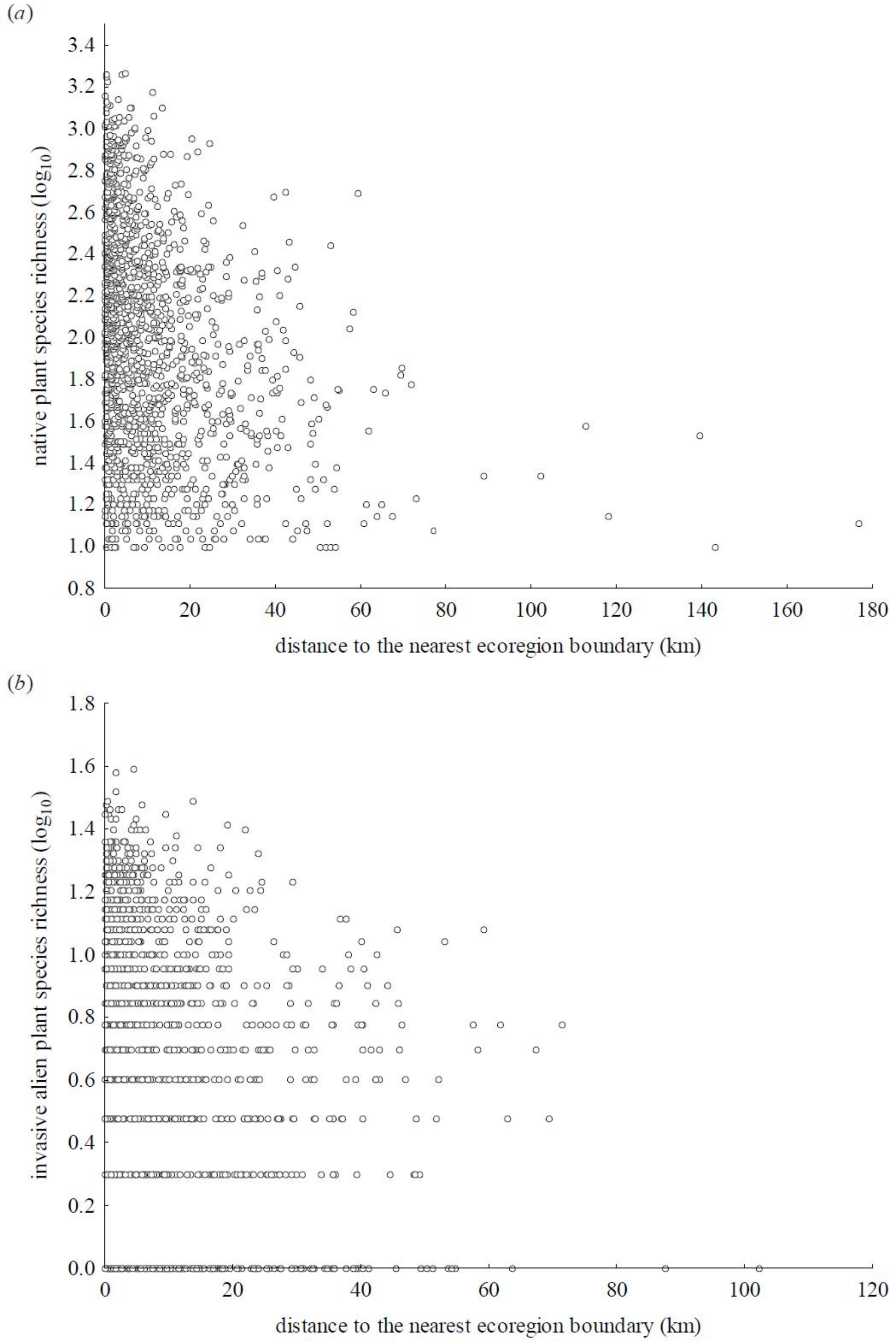

Figure S3 Relationship between plant species richness and distance to the nearest ecoregion boundary (defined as the edge between vegetation communities using Low & Rebelo's (1996) classification system of 68 vegetation types) based on data for the whole of South Africa and Lesotho. (a) Log native plant species richness = 2.0799 - 0.0105 x distance to the nearest ecotone; $r = -0.31$; $p < 0.001$; *d.f.* = 2, 1572. (b) Log invasive alien plant species richness = 0.82832 - 0.0096 x distance to the nearest ecotone; $r = -0.29$; $p < 0.001$; *d.f.* = 1, 1333.

Table S1 Analyses similar to those reported in Table 2 of Chapter 3; however, here all grid cells of which the surface area are more than 50% transformed by humans are removed from the dataset. *F* ratios, significance levels, and the sign of the slope (positive or negative relationship) of each predictor variable, are shown. 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 (%)
South Africa						
GLM	1, 1118	††††29.37	****46.34; sq	****331.48	29.7	7.0
Mixed spatial	1, 1118	n.s.†2.91	****15.4; sq	****111.83		
Savanna						
GLM	1, 360	n.s.†0.02	††††35.95	****278.73	48.3	7.6
Grassland						
GLM	1, 309	†††14.58	****42.59; L	****15.61; L	21.4	5.2
Mixed spatial	1, 309	n.s.†2.13	****23.77; L	***12.09; L		
Fynbos						
GLM	1, 78	n.s.†0.09; L	n.s.*3.22; L	****87.38; L	59.5	5.0
Mixed spatial	1, 78	n.s.†0.18; L	n.s.*1.75; L	****38.43; L		

Note: 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 of Chapter 3, with *ecotone distance* as response variable; however, here all grid cells of which the surface area are more than 50% transformed by humans are removed from the dataset. *F* ratios, significance levels, and the sign of the slope (positive or negative relationship) of each predictor variable, are shown. 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 (%)
South Africa					
GLM	1, 1607	††††109.7; L	††††68.28; L	†††12.27; L	27.2
Mixed spatial	1, 1607	†††13.96; L	††††50.02; L	n.s.†3.01; L	
Savanna					
GLM	1, 535	††††143.19; L	†††14.42; L	n.i.	29.7
Mixed spatial	1, 535	††††18.48; L	††9.24; L	n.i.	
Grassland					
GLM	1, 340	††††89.78; L	††††22.93; L	n.i.	26.4
Mixed spatial	1, 340	††6.83; L	†††11.35; L	n.i.	
Fynbos					
GLM	1, 84	n.i.	n.i.	n.s.†0.89	1.1

Note: 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 of Chapter 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 are removed from the dataset. *F* ratios, significance levels, and the sign of the slope (positive or negative relationship) of each predictor variable, are shown. 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 (%)
South Africa					
GLM	1, 1106	*4.92; L	****21.03; L	****102.94; L	27.0
mixed spatial	1, 1106	***11.38; L	n.s.*2.24; L	****18.22; L	
Savanna					
GLM	1, 360	****154.34; L	n.s.*2.05; L	n.a.	31.1
mixed spatial	1, 360	****73.22; L	n.s.*0.04; L	n.a.	
Grassland					
GLM	1, 297	****51.85; L	***14.6; L	n.a.	19.5
mixed spatial	1, 297	****17.95; L	*6.11; L	n.a.	
Fynbos					
GLM	1, 78	n.a.	n.a.	****17.76; L	18.7
mixed spatial	1, 78	n.a.	n.a.	*4.64; L	

Note: 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 of Chapter 3, where ecotone distance and energy availability variables are analysed as predictors of invasive alien species richness. *F* ratios, significance levels, and the sign of the slope (positive or negative relationship) of each predictor variable, are shown. 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	††10.56	****18.02; sq	****147.86
Grassland	1, 412	††††16.82	****43.20; L	****29.70; L
Succulent Karoo	1, 87	n.s.†0.20	n.i	**7.85
Fynbos	1, 101	n.s.†0.73; L	†5.51; L	††††62.48; L

Note: 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 of Chapter 3, where the relationships between ecotone distance, environmental heterogeneity and invasive alien species richness are examined. *F* ratios, significance levels, and the sign of the slope (positive or negative relationship) of each predictor variable, are shown. We found no significant influence of spatial autocorrelation for the forest biome.

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

Note: 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 slope: n.s.*$p > 0.05$, *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, ****$p < 0.0001$; negative slope: n.s.†$p > 0.05$, †$p < 0.05$, ††††$p < 0.0001$.

APPENDIX 3

Supporting Information for Chapter 4

Figure S1 The appearance of relevant habitat types during the peak rainy season in the study general study area, is pictured on the following page. (a) The Kimberley Thornveldt vegetation type representing the savanna biome. (b) The ecotone between the two vegetation types representing the savanna and grassland biomes. Note the sparse cover of trees and large shrubs and relatively homogeneous understory (compare e.g. to (a)). (c) The Western Free State Clay Grassland vegetation type representing the grassland biome. The undulating terrain associated with savanna vegetation in this study area can be seen in the distance.


(a)


(b)


(c)

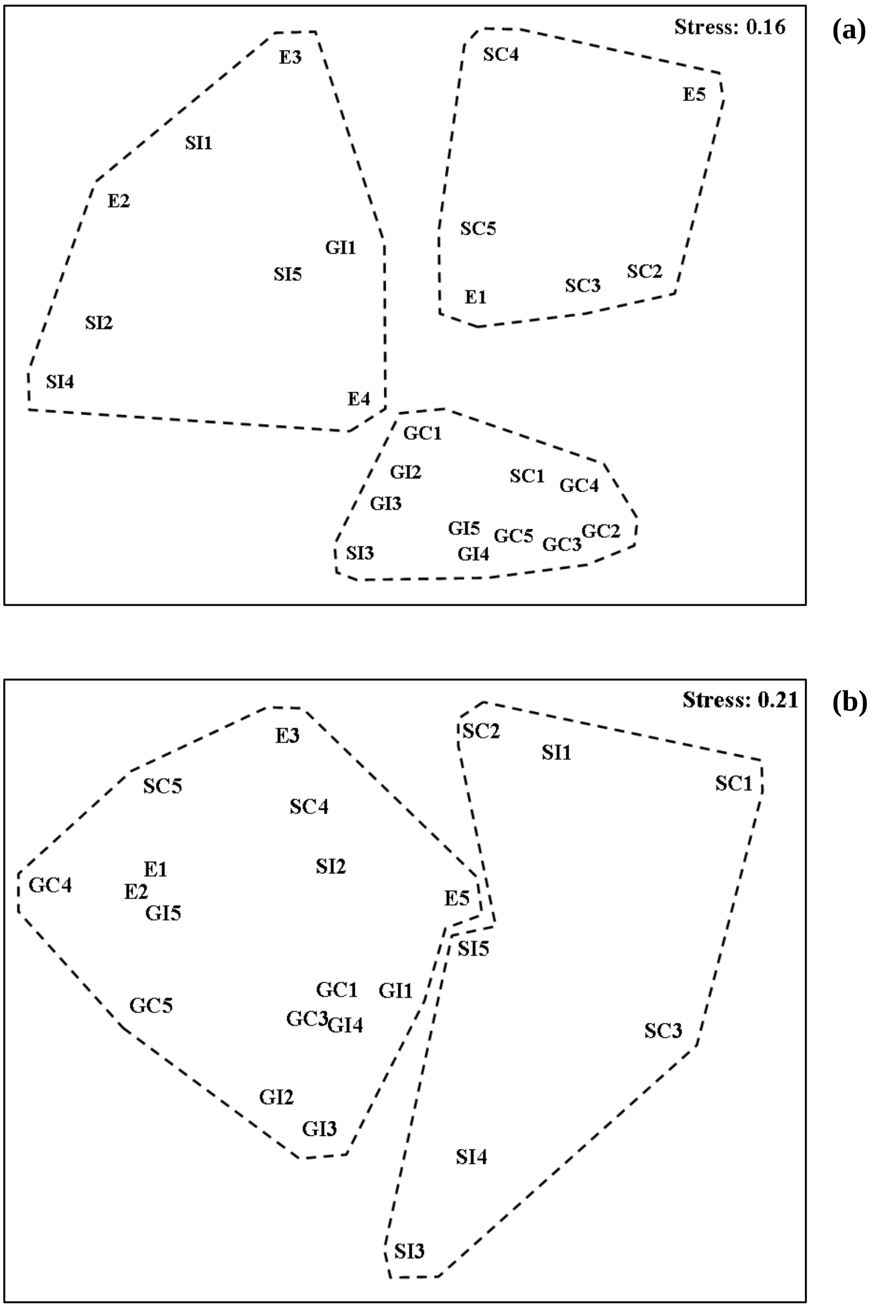

Figure S2 The Multi-dimensional scaling (MDS) plots corresponding with the dendrograms of Fig. 2 in Chapter 4, showing the relationships between the grids of sampling sites (habitat types) in terms of (a) beetle and (b) spider composition for 2009. The dashed lines correspond with those of the dendrograms and indicate where the clusters may be divided into meaningful subsets. The abbreviations are: SC – Savanna core; SI – Savanna intermediate; E – Ecotone; GI – Grassland intermediate; GC – Grassland core. The numbers denote different sampling grids.

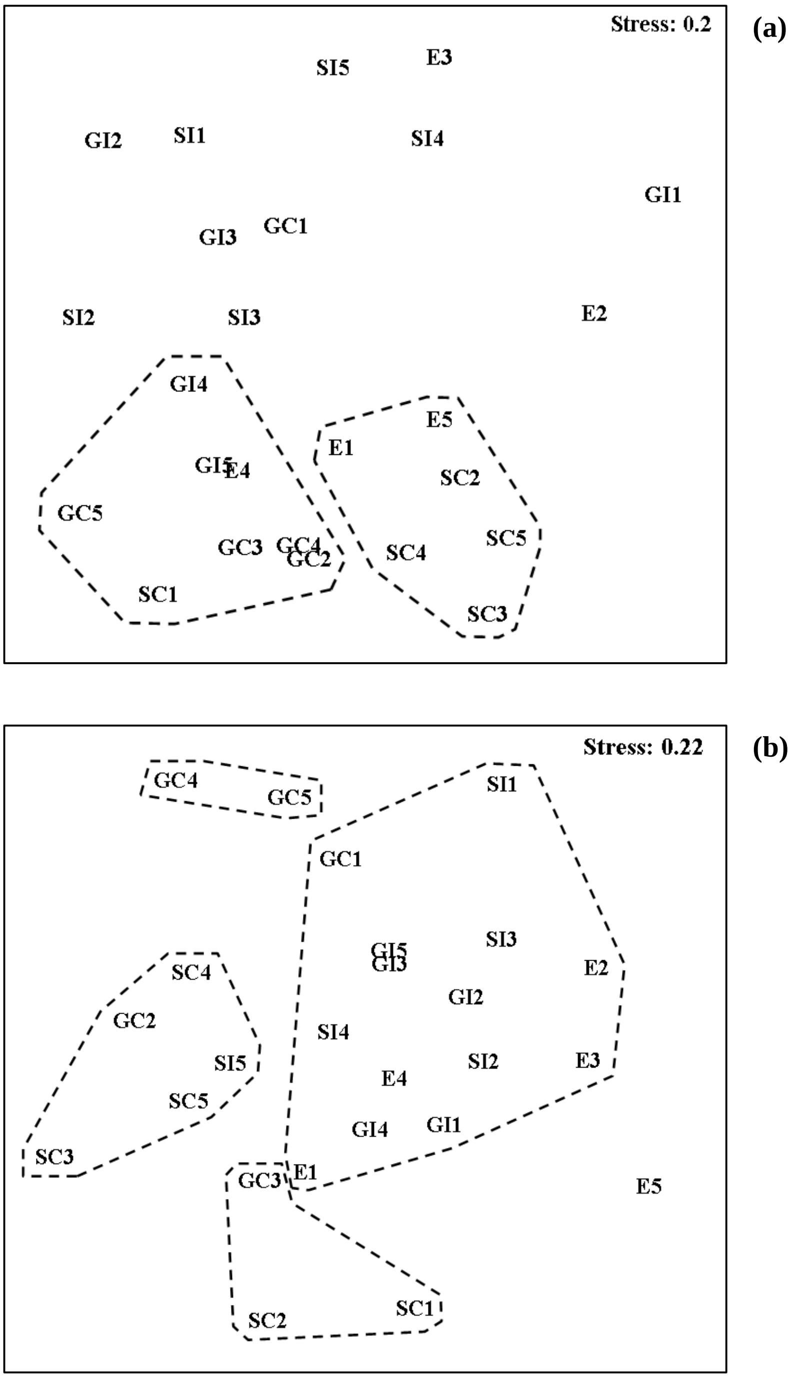

Figure S3 The Multi-dimensional scaling (MDS) plots corresponding with the dendrograms of Fig. 3 in Chapter 4, showing the relationships between the grids of sampling sites (habitat types) in terms of (a) beetle and (b) spider composition for 2010. The dashed lines correspond with those of the dendrograms and indicate where the clusters may be divided into meaningful subsets. The abbreviations are: SC – Savanna core; SI – Savanna intermediate; E – Ecotone; GI – Grassland intermediate; GC – Grassland core. The numbers denote different sampling grids.

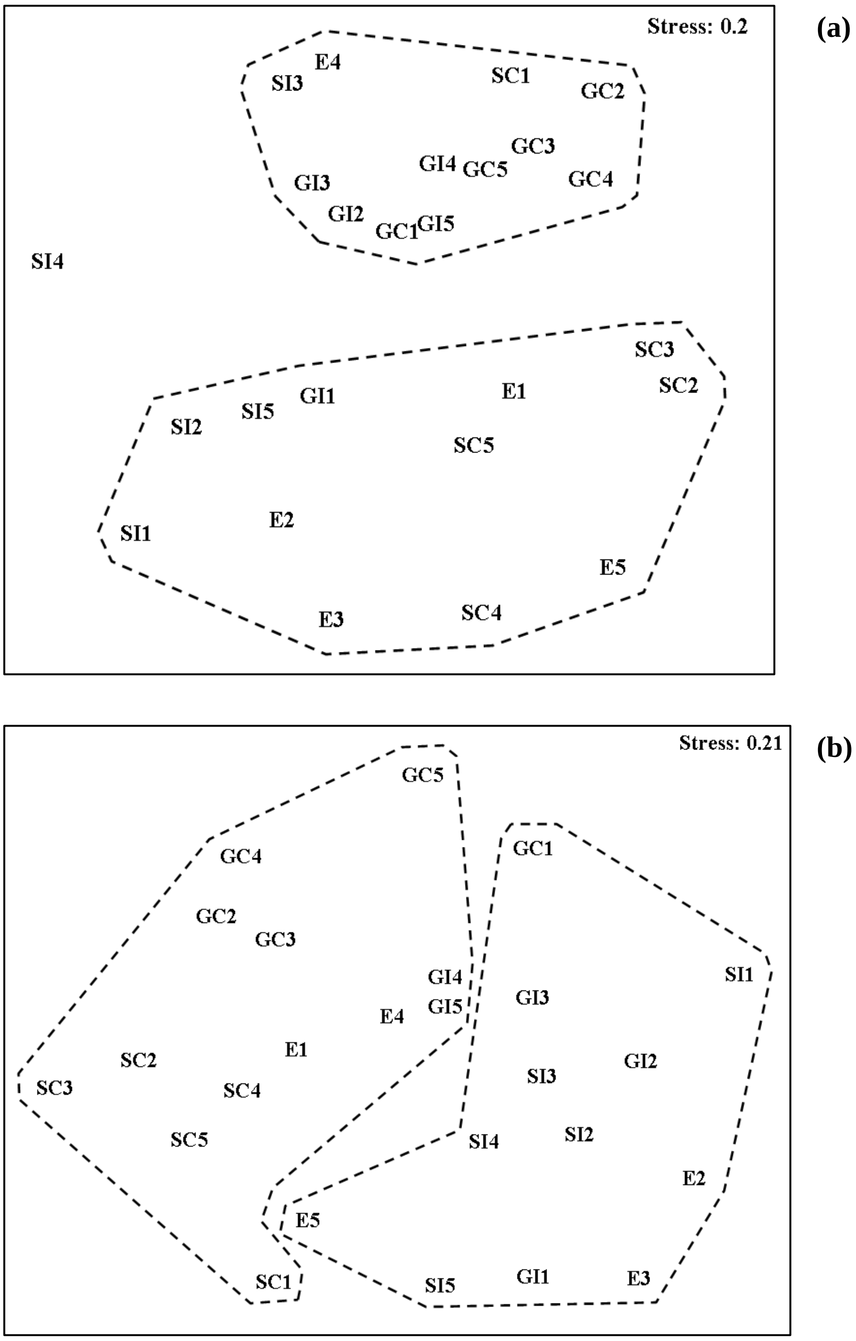

Figure S4 The MDS plots corresponding with the dendrograms of Fig. 4 in Chapter 4, showing the relationships between the grids of sampling sites (habitat types) in terms of invertebrate species composition (beetles and spiders combined) in (a) 2009 and (b) 2010. The dashed lines correspond with those of the dendrograms and indicate where the clusters may be divided into meaningful subsets. The abbreviations are: SC – Savanna core; SI – Savanna intermediate; E – Ecotone; GI – Grassland intermediate; GC – Grassland core. The numbers denote different sampling grids.

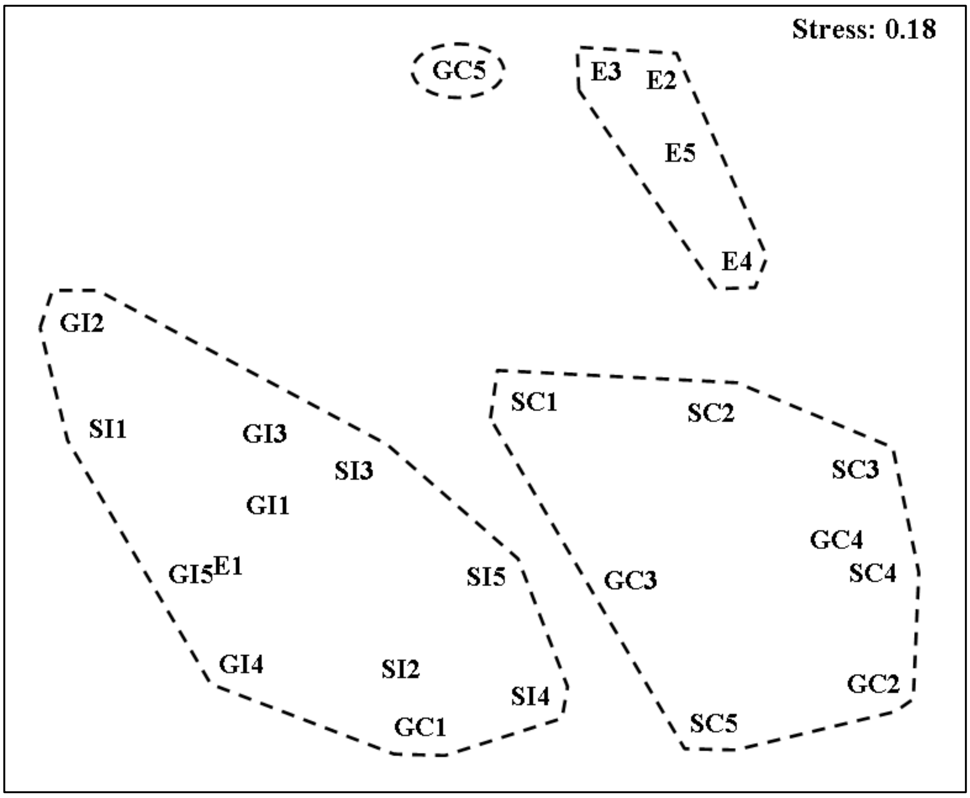

Figure S5 An MDS plot corresponding with the dendrogram of Fig. 8 in Chapter 4, showing the relationships between the grids of sampling sites (habitat types) in terms of the composition of dominant understory plant species. The dashed lines correspond with those of the dendrograms and indicate where the clusters may be divided into meaningful subsets. The abbreviations are: SC – Savanna core; SI – Savanna intermediate; E – Ecotone; GI – Grassland intermediate; GC – Grassland core. The numbers denote different sampling grids.

Table S1 Pairwise tests of an analysis of similarity (ANOSIM) reported in Chapter 4, where sampling sites (habitat types) were compared in terms of the species composition of beetles and spiders, separately and combined. The abbreviations are: SC – Savanna core; SI – Savanna intermediate; E – Ecotone; GI – Grassland intermediate; GC – Grassland core.

	2009			*2010*		
	Beetles	Spiders	Combined	Beetles	Spiders	Combined
E, GC	*R*=0.55; *p*=0.008	*R*=0.21; *p*=0.171	*R*=0.53; *p*=0.008	*R*=0.25; *p*=0.040	*R*=0.62; *p*=0.008	*R*=0.51; *p*=0.008
E, GI	*R*=0.35; *p*=0.032	*R*=0.54; *p*=0.016	*R*=0.37; *p*=0.024	*R*=0.10; *p*=0.214	*R*=0.16; *p*=0.151	*R*=0.22; *p*=0.103
E, SC	*R*=0.13; *p*=0.19	*R*=-0.10; *p*=0.786	*R*=0.10; *p*=0.222	*R*=0.16; *p*=0.095	*R*=0.28; *p*=0.048	*R*=0.32; *p*=0.032
E, SI	*R*=0.16; *p*=0.143	*R*=0.47; *p*=0.016	*R*=0.26; *p*=0.095	*R*=0.19; *p*=0.111	*R*=0.14; *p*=0.167	*R*=0.17; *p*=0.167
GC, GI	*R*=0.37; *p*=0.032	*R*=0.29; *p*=0.087	*R*=0.40; *p*=0.024	*R*=0.13; *p*=0.095	*R*=0.49; *p*=0.008	*R*=0.46; *p*=0.024
GC, SC	*R*=0.55; *p*=0.008	*R*=-0.04; *p*=0.619	*R*=0.52; p=0.008	*R*=0.37; *p*=0.024	*R*=0.36; *p*=0.032	*R*=0.41; *p*=0.016
GC, SI	*R*=0.76; *p*=0.008	*R*=0.17; *p*=0.222	*R*=0.72; *p*=0.008	*R*=0.55; *p*=0.016	*R*=0.55; *p*=0.008	*R*=0.77; *p*=0.008
GI, SC	*R*=0.62; *p*=0.016	*R*=0.28; *p*=0.016	*R*=0.64; *p*=0.016	*R*=0.49; *p*=0.008	*R*=0.50; *p*=0.008	*R*=0.77; *p*=0.008
GI, SI	*R*=0.43; *p*=0.024	*R*=0.38; *p*=0.016	*R*=0.44; *p*=0.016	*R*=-0.04; *p*=0.587	*R*=0.27; *p*=0.048	*R*=0.10; *p*=0.23
SC, SI	*R*=0.66; *p*=0.008	*R*=-0.14; *p*=0.873	*R*=0.55; *p*=0.016	*R*=0.64; *p*=0.008	*R*=0.30; *p*=0.032	*R*=0.61; *p*=0.016

Table S2 Pairwise tests of an ANOSIM reported in Chapter 4, showing the relationships between sampling sites in terms of the species composition of dominant understory plant species. The abbreviations are: E – Ecotone; GC – Grassland core; GI – Grassland intermediate; SC – Savanna core; SI – Savanna intermediate.

Site pairs	*R* statistic	*p* value
E, GC	0.37	0.048
E, GI	0.68	0.016
E, SC	0.62	0.008
E, SI	0.64	0.016
GC, GI	0.61	0.008
GC, SC	0.33	0.024
GC, SI	0.32	0.04
GI, SC	0.86	0.008
GI, SI	0.20	0.135
SC, SI	0.77	0.008

Table S3 Number of species per trap (species richness), number of individuals per trap (abundance) and Shannon-Wiener diversity index values, with standard deviations, for beetles and spiders separately and combined, in 2009 at each sampling site (habitat type) of Chapter 4.

	Taxon	Savanna core	Savanna intermediate	Ecotone	Grassland intermediate	Grassland core
Species richness	Beetles	0.78±0.48	0.59±0.75	0.36±0.27	0.43±0.22	0.62±0.24
	Spiders	0.38±0.25	0.38±0.19	0.11±0.14	0.22±0.05	0.36±0.35
	Combined	1.16±0.67	0.97±0.66	0.47±0.21	0.65±0.18	0.98±0.49
Abundance	Beetles	2.48±0.70	2.03±1.22	1.44±1.24	2.27±0.68	4.22±1.25
	Spiders	0.82±0.78	1.54±0.61	0.81±0.60	1.12±0.60	1.29±1.05
	Combined	0.82±0.79	1.54±0.62	0.81±0.61	1.12±0.61	1.29±1.06
Diversity (H’)	Beetles	2.72±0.51	2.34±0.76	2.36±0.33	1.47±0.53	1.51±0.23
	Spiders	2.21±0.36	2.46±0.25	1.55±0.33	2.16±0.30	1.69±0.79
	Combined	3.16±0.43	3.09±0.44	2.71±0.19	2.39±0.39	2.10±0.30

Table S4 Number of species per trap (species richness), number of individuals per trap (abundance) and Shannon-Wiener diversity index values with standard deviations, for beetles and spiders separately and combined, in 2010 at each sampling site (habitat type) of Chapter 4.

	Taxon	Savanna core	Savanna intermediate	Ecotone	Grassland intermediate	Grassland core
Species richness	Beetles	1.16±0.47	0.44±0.41	0.68±0.52	0.56±0.13	0.87±0.68
	Spiders	0.64±0.47	0.49±0.45	0.48±0.09	0.40±0.13	0.53±0.10
	Combined	1.81±1.35	0.93±0.49	1.15±0.58	0.96±0.20	1.40±0.73
Abundance	Beetles	2.24±0.35	0.91±0.45	1.11±0.83	1.21±0.44	3.39±0.94
	Spiders	1.88±1.30	1.68±0.76	1.03±0.20	1.65±0.20	1.83±0.97
	Combined	4.12±1.43	2.59±1.01	2.15±0.96	2.87±0.52	5.22±1.75
Diversity (H')	Beetles	2.67±0.25	2.36±0.19	2.65±0.14	2.29±0.05	2.64±0.35
	Spiders	2.36±0.30	2.68±0.45	2.51±0.23	2.47±0.11	2.14±0.18
	Combined	3.22±0.42	3.21±0.11	3.28±0.24	3.08±0.14	3.12±0.23