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Impacts of invasive plants on animal diversity in South Africa: A synthesis

Authors:
Susana Clusella-Trullas[1]
Raquel A. Garcia[1]

Affiliations:
[1]Centre for Invasion Biology, Department of Botany and Zoology, Stellenbosch University, South Africa

Corresponding author:
Susana Clusella-Trullas,
sct333@sun.ac.za

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Background: Increasing numbers of invasive alien plant (IAP) species are establishing around the globe and can have negative effects on resident animal species function and diversity. These impacts depend on a variety of factors, including the extent of invasion, the region and the taxonomic group affected. These context dependencies make extrapolations of IAP impacts on resident biota from region to region a substantial challenge.

Objectives: Here, we synthesised data from studies that have examined the effects of IAPs on animal diversity in South Africa. Our focus is on ectothermic organisms (reptiles, amphibians and invertebrates).

Method: We sourced relevant articles using keywords relating to (1) the effects of IAPs on species diversity (abundance, richness and composition), (2) the IAP and (3) the native ectotherm. We extracted the taxonomic and spatial coverage of IAPs and affected native species and assessed the extent of information given on potential mechanisms driving IAP impacts.

Results: Across the 42 studies, IAPs had a decreasing or neutral effect on native animal abundance and richness and significantly changed species composition. This review highlighted the paucity of studies and the research deficits in taxonomic and geographic coverage and in the mechanisms underlying IAP impacts on ectotherms.

Conclusion: By assessing the status of knowledge regarding the impacts of IAPs on resident animal species in South Africa, this study identifies information gaps and research priorities at the country level with a view to informing monitoring and conservation efforts, such as alien plant removal and control programmes, and ensuring that endemic terrestrial animal diversity is maintained.

Introduction

Invasive alien species are considered a major pressure on the current state of biodiversity globally (Butchart et al. 2010). Invasive alien plants (IAPs), in particular, have spread rapidly and extensively in many regions of the world, impacting resident species diversity, ecosystem processes and people's livelihoods (Levine et al. 2003; Pyšek et al. 2012; Schirmel et al. 2016; Vilà et al. 2011). South Africa is no exception and nearly two million hectares of land have been invaded by alien plants (Van Wilgen et al. 2012), with well-known impacts on hydrology, nutrient cycling and fire regimes (Kraaij, Cowling & Van Wilgen 2011; Le Maitre, Gush & Dzikiti 2015; Richardson & Van Wilgen 2004). This estimate of alien plant coverage includes 27 species, without incorporating arid and transformed land except for *Prosopis* trees in the arid northwest of the country (Kotzé et al. 2010; Van den Berg, Kotze & Beukes 2013). Alien *Acacia* species cover most of the dense areas of invasion, followed by *Eucalyptus* and *Pinus* trees, *Opuntia* cacti and *Chromolaena odorata* shrubs. These invasions extend across the country, with higher concentrations in the southwestern, southern and particularly eastern coastal belts and the adjacent interior (Henderson 2007; Kotzé et al. 2010; Van Wilgen et al. 2012). Overall, there is reasonable knowledge of alien plant occurrence in South Africa, especially at a coarse spatial resolution. Whereas their effects on native plant diversity have been fairly well assessed (e.g. Gaertner et al. 2009; Richardson & Van Wilgen 2004), fewer studies have focused on the impacts of alien plants on native animal communities (Richardson et al. 2011, but see Breytenbach 1986).

Species population and community metrics such as abundance, richness and composition can provide useful baseline data as indicators of animal diversity change between invaded and uninvaded areas. The direction and magnitude of effects of alien plant invasions on animal communities can, however, depend on a variety of factors, including the scale of the plant invasion (extent and density), the stage of invasion, and the region and taxonomic group affected

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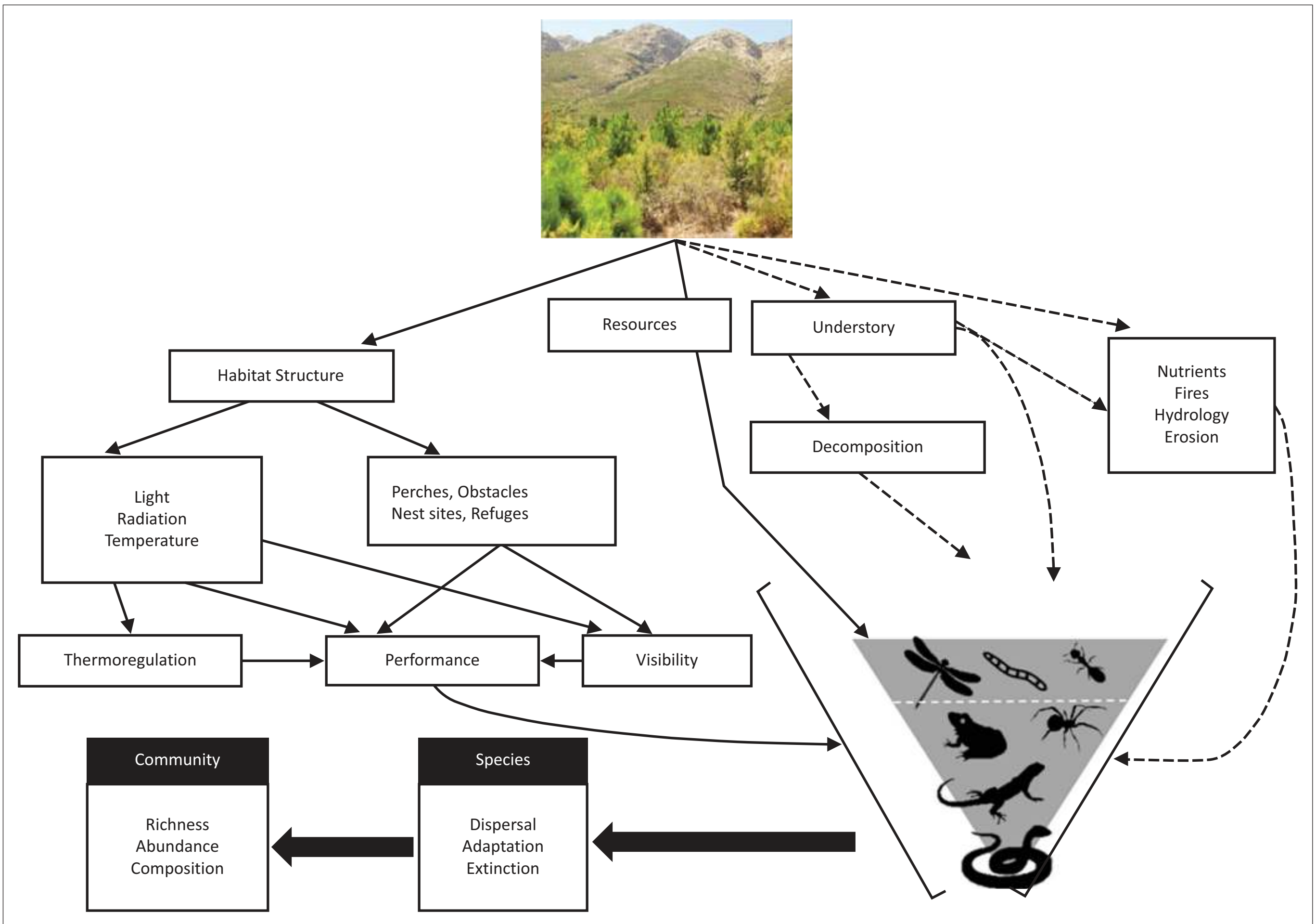
(Kumschick et al. 2015; Ricciardi et al. 2013). These context dependencies make extrapolations of the effects of IAPs on resident biota from region to region a substantial challenge, especially for the development of generalised management frameworks across diverse habitats. The invasion of alien plants into natural or previously uninvaded habitats involves a number of significant changes to the habitat, often negatively affecting resident fauna and sometimes in counterintuitive or non-obvious ways (Figure 1). Alien plants may directly modify the structure and complexity of the physical environment and, thus, restrict the opportunities for the animal to thermoregulate or hydroregulate within its microenvironment or impose barriers to essential functions such as moving, creating nests or finding refuges. Alien plants can also directly or indirectly affect food resources for animal communities (e.g. Groot, Kleijn & Jogan 2007). For example, a change in plant composition will affect herbivores directly by reducing the amount or quality of plant hosts whereas a change in habitat structure, microenvironment and litter or soil properties can indirectly affect prey availability or predator abundance and alter trophic interactions (Figure 1; e.g. Pearson 2009).

Whereas reports of negative impacts of invasive plant species are pervasive in the literature, positive effects have also been reported, for example, via increases in suitable habitat or net resources to recipient fauna (e.g. Schlaepfer, Sax & Olden 2010). Whether the latter represent rare case studies or whether any general patterns can be drawn from these is presently unclear. Thus, knowledge of the underlying mechanisms should improve the understanding of the consequences of alien plant invasions on native diversity. More importantly, knowledge of proximate and ultimate causes of species declines may enhance our ability to predict responses of animal communities in newly invaded areas of South Africa with similar characteristics to those studied previously, or facing concomitant pressures such as global climate change or habitat transformation (Ricciardi et al. 2013). Together, these are essential elements of the scientific framework that will allow invasion science to robustly predict the impacts of new and developing invasions, and not simply be viewed as a series of unique invasion case studies.

In this study, we aim to synthesise studies that have examined the effects of IAPs on animal diversity in South Africa. We concentrate this review on ectotherms (reptiles, amphibians and invertebrates) for several reasons. Firstly, their energy budgets are more directly influenced by the environment compared with endotherms (Gates 1980). Consequently, environmental factors likely play a major role in determining a suite of physiological and behavioural attributes and, at



The picture depicts the invasion of an alien plant species (e.g. *Pinus sp.*) into native fynbos vegetation (e.g. *Protea sp.*). Solid and dashed arrows refer to direct and indirect effects of IAPs on native species, respectively.

FIGURE 1: Potential mechanisms through which invasive alien plants (IAPs) affect ectotherm diversity.

least partly, influence life history and timing of key phenological events (e.g. mating and reproduction) in the group. Secondly, they typically have smaller dispersal abilities than mammals and birds (Endler 1977), likely reducing their capacity to move away from disturbance or suboptimal conditions. Finally, they make a large contribution to overall animal diversity that is mostly explained by high insect diversity and abundance (Wilson & Peter 1988), playing a central role in food webs and ecosystem function. To present a comprehensive view of the status of knowledge of impacts of IAPs on resident animal species in South Africa and identify information gaps, we ask three key questions: (1) How many studies have addressed the effects of IAPs on terrestrial ectotherm diversity and what general patterns can we draw from these?, (2) What is the taxonomic and spatial coverage of IAPs and affected native species studied so far? and (3) How much is known about the mechanisms underlying these impacts? These questions are central to assess the status of knowledge of alien plant impacts on animal species diversity and inform invasive plant monitoring and control programmes in South Africa (Wilson et al. 2017).

Methods

We searched the ISI Web of Science for relevant studies comparing abundance, richness or composition of terrestrial ectotherms between invaded and uninvaded sites in South Africa. Our search combined terms for (1) invasive plants; (2) native reptiles, amphibians and terrestrial invertebrates; and (3) effects on species abundance, richness or composition (shown in detail in Appendix 1). We included studies comparing sites with native vegetation or cleared of alien vegetation to sites invaded by alien plants or with plantations of alien species. A second search targeted studies addressing only the mechanisms underlying the potential effects on ectotherm species, without necessarily quantifying changes in species diversity. This second search thus replaced the search terms for effects with terms for mechanisms such as altered thermoregulatory behaviour, prey availability or reproductive output (Appendix 1). We retrieved articles, reviews or book chapters for all years available on the Web of Science Core Collection on 10 June 2016. The articles considered relevant for our review were then screened for additional references.

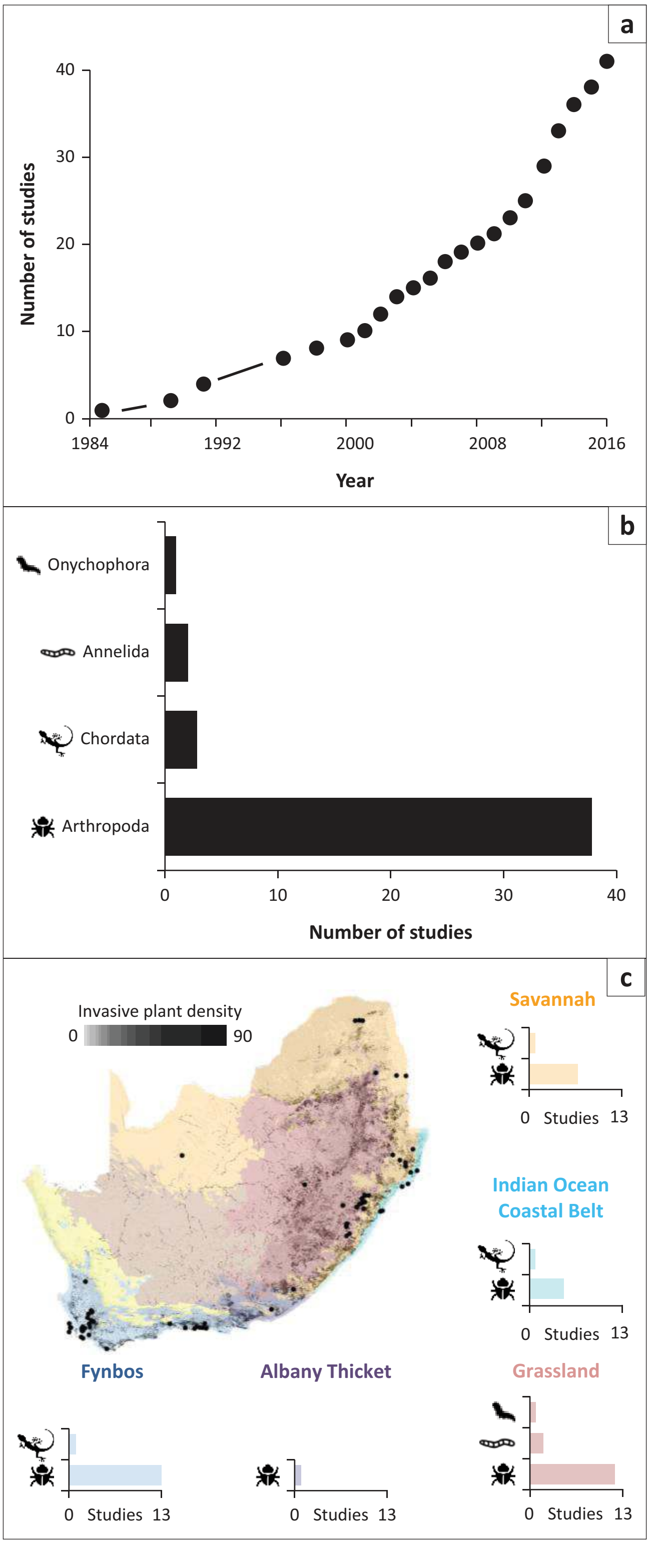
We gathered information from the studies on the location of the field sites and respective biomes (Mucina et al. 2014), and on the native animal and IAP species included. We classified the studies according to the phyla of native animals potentially affected by plant invasions (Arthropoda, Annelida, Chordata and Onychophora). For the IAP species included, we used three classifications. Firstly, we assigned IAP species to six major growth forms: tree, shrub or bush, vine, forb, grass and aquatic plant. Secondly, we used the categories of the Alien and Invasive Species (A&IS) Lists that were published under the National Environmental Management: Biodiversity Act (NEM:BA) in 2014. The NEM:BA A&IS categories include eradication targets (category 1a), widespread invasive species where a national species management programme is required (category 1b) and invasive species that can be kept under managed circumstances (categories 2 and 3). Thirdly, to assess the extent to which the existing studies focus on the invasive plants with the largest potential impacts on ectotherms, we also considered a published classification of the most prominent invasive plant species in South Africa, according to their estimated impacts on native biodiversity (Van Wilgen et al. 2008). For all classifications above, we assigned studies to multiple categories when they presented individual comparisons for more than one biome, native phylum or IAP category.

To assess the impacts of alien plants on native animal diversity, we focused on comparisons of species abundance or richness between sites with native and alien vegetation and classified the effects as positive (i.e. an increase in abundance or richness in sites with alien vegetation), negative (decrease) or neutral effect. Native vegetation sites included sites cleared of alien plants in two studies where authors indicated that sufficient time had elapsed for recovery of native vegetation. We incorporated comparisons based on original data, accumulation and rarefaction curves, and richness estimators (e.g. Chao1 and Chao2) but did not include diversity indices (e.g. Shannon's or Simpson's index) as their use was very variable across studies. For composition, comparisons were classified as alien vegetation resulting in a change or not in species composition. These comparisons were typically the result of ordination techniques based on similarity measures or cluster analyses. When studies presented the effects of alien plants on fauna for several functional or taxonomic groups (e.g. herbivores vs. predators and beetles vs. spiders) or for different habitat types (e.g. invaded by *Eucalyptus* vs. *Pinus*), we considered each comparison separately in the synthesis unless there were no statistical tests associated with these. Therefore, the number of comparisons was typically higher than the number of studies assessed. If available, we extracted information on the growth form, stand age and spatial coverage of the IAP and on mechanisms driving the impacts such as changes in habitat structure, thermal opportunities, food resources, predators and refuge or nest site availability.

Results

Our first search for studies addressing the effects of invasive plants on ectotherm diversity in South Africa yielded 358 studies. Of these, only 42 were relevant for this review (Appendix 2). Our second search for articles studying the mechanisms underlying the effects of alien plants on ectotherms in South Africa yielded 702 papers. Among these, we only retained six relevant studies (Appendix 2), partly because a large portion of the articles found investigated the viability of biological agents for invasive plant control which was outside the focus of this study.

The 42 papers reviewed were published between 1985 and 2016, with a slight increase in the annual number of publications since 2000 (Figure 2a). The vast majority of studies



Source: (c) Mucina et al. 2014; Kotzé et al. 2010

There are no studies in the Succulent Karoo (light yellow) and Nama Karoo (brown) biomes. The forest and desert biomes are not represented in the map due to their small range.

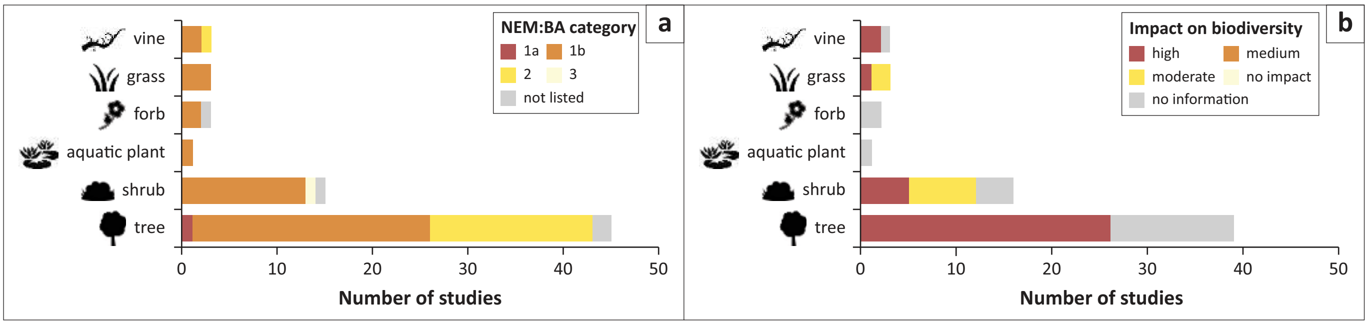
FIGURE 2: Distribution of studies (a) per year of publication, (b) per taxonomic group (phylum) of native ectothermic organisms, and (c) per biome and taxonomic group of native ectothermic organisms. The map in (c) shows the distribution of study sites (black dots) in South Africa across seven biomes, with the shades of grey indicating the density of invasive plants.

focused on arthropods (Figure 2b), particularly in the Insecta (mostly Coleoptera, Hymenoptera, Diptera, Lepidoptera and Odonata) and Arachnida (mostly Araneae) classes. A single study included Onychophora and two studies focused on earthworms. Only three studies addressed vertebrate ectotherms, covering amphibians (Order Anura), lizards and snakes (Order Squamata).

Most studies compared sites along the coastal belt and adjacent interior in the Western Cape and KwaZulu-Natal provinces (Figure 2c). The majority of studies took place in the Fynbos and Grassland biomes, whereas a few studies covered the Savanna, Indian Ocean Coastal Belt and Albany Thicket biomes (Figure 2c). Native arthropods remained the focal native class across biomes (Figure 2c). Trees, particularly those belonging to the genera *Acacia*, *Eucalyptus* and *Pinus*, were the most common growth form of invasive plants (Figure 3a), followed by shrubs such as *Chromolaena odorata*, *Hakea* species, *Lantana camara* and *Solanum mauritianum*. These alien trees and shrubs are listed as major invaders in the country (Henderson 2007; Le Maitre, Versfeld, & Chapman 2000; Van Wilgen et al. 2012). Many of them are species that need to be controlled according to the NEM:BA A&IS regulations (category 1b; Figure 3a) and are estimated to have high impacts on native biodiversity (Van Wilgen et al. 2008; Figure 3b).

Alien plants had a larger decreasing effect on native species abundance compared to species richness (Figure 4a and Table 1). Most studies found that the effects of alien plants were either neutral or decreasing for native animal species richness, but increasing effects of alien plants were rare for both species richness and abundance. Alien plants had a substantial impact on species composition (Figure 4b and Table 1). Among the 15 IAPs listed on NEM:BA, only 3 species (*Arundo donax*, *Chromolaena odorata* and *Passiflora edulis*) showed no negative effects on the arthropod species studied. However, these results refer to a single study conducted for each alien plant, highlighting the data deficiency for these species (Table 1). *Acacia mearnsii* was the IAP, most commonly studied, with negative or neutral effects on arthropod species found in four studies (Table 1). Although most studies incorporated standard metrics of species abundance and richness, accumulation and rarefaction curves were presented (or mentioned) in only 13 and 7 studies, respectively, and 10 studies provided comparisons of metrics between invaded and uninvaded sites without presenting accompanying statistical analyses.

Seventy percent of the studies investigating differences in species diversity between invaded and uninvaded habitats referred to potential mechanisms underlying the patterns found. These mechanisms included changes in habitat structure (n = 15 of 29 studies), microclimates (n = 13 of 29 studies) and food resources (including host specificity for herbivores, n = 14 of 29 studies), and the degree of species' ecological breadth (e.g. generalists vs. specialists, n = 3 of 29 studies). In the 6 publications that solely referred to mechanisms (Appendix 2), the authors highlighted habitat structure, microclimate and food resources as mechanisms affecting functional diversity (according to McGill et al.



Source: (a) National Environmental Management: Biodiversity Act (NEM:BA), 2014; (b) van Wilgen et al. 2008

FIGURE 3: Distribution of studies per growth form of the invasive plant species studied and their classification according to (a) the NEM:BA regulations for control and management of invasive species and (b) their estimated impacts on biodiversity according to a published classification.

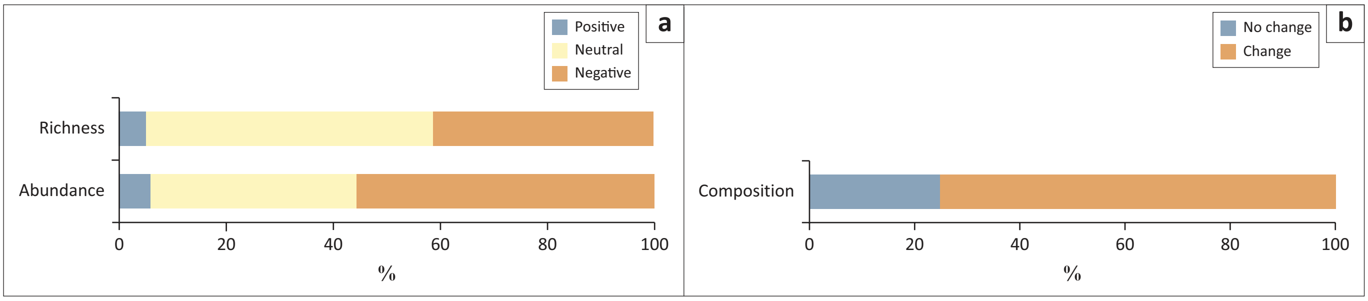


FIGURE 4: Percentage of comparisons performed in the 42 studies reviewed that found invaded sites to have (a) positive (increased diversity), neutral or negative (decreased diversity) effects on native ectotherm species richness (n = 80 comparisons) and abundance (n = 52), and (b) the same or altered species composition (n = 36) as uninvaded sites.

TABLE 1: Impacts of specific invasive alien plants on abundance, richness and composition of several taxonomic groups of ectotherms.

Invasive alien plant species	Impacts on native species		
	Abundance	**Richness**	**Composition**
Acacia dealbata	Negative: Insecta (1)	Negative: Insecta (1)	Different: Insecta (1)
Acacia mearnsii	Negative: Araneae, Lepidoptera, Formicidae (2) Neutral: Odonata (3), Coleoptera, Diptera, Hemiptera, Hymenoptera (2)	Negative: Odonata (3), Araneae and Formicidae (2), Araneae*, Coleoptera•, Diptera*, Hemiptera•, Hymenoptera• and Formicidae* (4) Neutral: Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera (2), Lepidoptera• and Orthoptera• (4)	Different: Odonata (3, 5), Orthoptera*, Formicidae•, Hymenoptera• and Hemiptera• (4) Not different: Araneae•, Coleoptera•, Diptera•, Lepidoptera• (4)
Acacia saligna	Negative: Formicidae (6)	Neutral: Formicidae (6)	Different: Formicidae (6)
Arundo donax	-	Neutral: Insecta and Arachnida (7)	-
Chromolaena odorata	-	Neutral: Araneae (8)	-
Eucalyptus camaldulensis	Negative: Araneae, Coleoptera, Hymenoptera, Lepidoptera, Formicidae (9) Neutral: Diptera, Hemiptera, Orthoptera (9)	Negative: Araneae, Orthoptera, Hymenoptera, Lepidoptera, Formicidae (9) Neutral: Coleoptera, Diptera, Hemiptera (9)	Different: Araneae, Orthoptera, Hymenoptera, Lepidoptera, Formicidae, Coleoptera, Diptera, Hemiptera (9)
Eucalyptus grandis	-	-	Different: Formicidae (10) Not different: Lepidoptera, Orthoptera, Araneae and Scarabaeidae (10)
Eucalyptus lehmannii	-	Negative: Hymenoptera, Opiliones and Amphipoda (11)	Different: Hymenoptera, Opiliones and Amphipoda (11)
Opuntia stricta	Positive: Coleoptera (12) Neutral: Araneae (12)	Neutral: Coleoptera (12), Araneae (12)	Different: Coleoptera (12) Not different: Araneae (12)
Passiflora edulis	Neutral: Coleoptera (13)	Neutral: Coleoptera (13)	
Pinus patula	-	-	Different: Formicidae and Araneae (10) Not different: Orthoptera, Lepidoptera and Scarabaeidae (10)
Pinus radiata	Negative: Squamata (14) Positive: Collembola (15)	Negative: Squamata (14) Positive: Collembola (15)	Different: Collembola (15), Squamata (14)
Prosopis glandulosa	-	Negative: Scarabaeidae (16)	Different: Scarabaeidae (16)
Rubus cuneifolius	-	Positive: Anisoptera (17) Neutral: Zygoptera (17)	Not different: Odonata (17)
Solanum mauritianum	-	Neutral: Insecta (18)	Different: Insecta (18)

(1) Coetzee, van Rensburg & Robertson 2007; (2) van der Colff et al. 2015; (3) Samways & Sharratt 2010; (4) Maoela et al. 2016; (5) Samways & Grant 2006; (6) French & Major 2001; (7) Canavan et al. 2014; (8) Mgobozi et al. 2008; (9) Roets & Pryke 2012; (10) Pryke & Samways 2012; (11) Ratsirarson et al. 2002; (12) Robertson et al. 2011; (13) Padayachi, Proches & Ramsay 2014; (14) Schreuder & Clusella-Trullas in press; (15) Liu et al. 2012; (16) Steenkamp & Chown 1996; (17) Kietzka et al. 2015; (18) Olckers & Hulley 1989.

For invasive alien plants listed in South Africa's *National Environmental Management: Biodiversity Act* (NEM:BA) of 2014, the table summarises the negative, neutral or positive impacts on native reptiles, amphibians or arthropods that were found in the studies reviewed. When reported, the reversibility or irreversibility of negative impacts after alien plant clearing or restoration is indicated with an asterisk (*) or a filled circle (•), respectively. Only statistically significant results are included.

2006) and animal behaviours such as the ability to create nests, flight dynamics and flower visitation rates. Of a total of 35 studies that addressed mechanisms, 21 studies used an observational (correlative) approach to assess the link between impact and mechanism, 4 studies followed a manipulative experimental approach (including a study that incorporated the clearing history of the invasive plant) and 10 studies speculated on potential mechanisms.

Discussion

IAPs have been recognised as a threat to South Africa's native biodiversity for more than two decades, with efforts to manage invasions underway through the Working for Water Programme since 1995 (Van Wilgen et al. 2016). Our review underscores the importance of controlling IAPs to reduce their impacts on terrestrial ectotherm diversity in the country. Although not always statistically significant, reductions in abundance and richness of native ectothermic species were found in 56% and 41% of the comparisons presented in the studies reviewed, respectively, and changes in species composition were reported in almost 75% of the comparisons. These findings echo those of global reviews and meta-analyses, which have reported significant decreases in native animal species abundance, diversity and fitness as impacts of plant invasions (Pyšek et al. 2012; Schirmel et al. 2016; Van Hengstum et al. 2014; Vilà et al. 2011). In the following three sections, we discuss key directions for future research, the context-dependent nature of the problem and issues relating to methodologies used to assess impacts.

Research gaps

The studies reviewed in this synthesis covered some of the areas of South Africa most heavily invaded by alien plants such as *Acacia*, *Eucalyptus* and *Pinus* tree species, along a southern and eastern coastal belt (Kotzé et al. 2010; Figure 2c). The extent of this coverage was, however, very small relative to the distribution of invasive plants in the country. Study locations tend to be clumped in particular areas (Figure 2c), likely associated with the accessibility of sites, management prioritisation for particular problematic alien plant species or fields of interest of research institutes and invasion biologists. The arid regions of the country, including the Succulent Karoo, Nama Karoo and Desert biomes, and the arid parts of the Savanna and Grassland biomes have not been assessed. However, these areas are invaded by dense stands of *Prosopis* spp. (Van den Berg et al. 2013), listed as NEM:BA category 1b and estimated to have high impacts on natural ecosystems. Less attention has also been given to invasive forbs, aquatic plants, vines and grasses (Figure 3). Alien grasses, for example, are recognised as understudied in South Africa (Milton 2004; Richardson & Van Wilgen 2004; Visser et al. 2017), despite their prominence in invasion science in other regions of the world (Hulme et al. 2013; Visser et al. 2016). In South Africa, however, forbs, vines and grasses tend to be less prominent than invasive shrubs and trees, and introduced grasses are not well adapted to local conditions, such as fire regimes (Van Wilgen et al. 2008, 2012; Visser et al. 2016). Overall, the 42 studies assessing alien plant impacts on native ectotherms addressed some of the major IAP species of South Africa in terms of potential impacts and control regulations in place (e.g. *Acacia*, *Eucalyptus* and *Pinus* species; Figure 3 and Table 1) but gave less or no attention to other important alien plants such as *Lantana camara* in the Savanna Biome and *Populus* species in the Grassland Biome (Henderson 2007). For each NEM:BA-listed IAP species examined individually, the evidence collated typically comes from a small number of studies and refers to a small number of native taxonomic groups (Table 1).

Our synthesis highlights a serious deficit in the knowledge of impacts of IAPs on terrestrial ectothermic groups other than arthropods, which mostly comprised insects and spiders. South Africa is known for its exceptional reptile and amphibian diversity and its high level of endemism; between 40% and 67% of its indigenous species of amphibians, chelonians, lizards and snakes are unique to the country (Bates et al. 2014; Measey 2011). Invasive alien vegetation has been highlighted as a major threat to reptile and amphibian diversity, both nationally and globally (Gibbons et al. 2000; Martin & Murray 2011; Measey 2011; Mokhatla et al. 2012), but despite this realisation, little focus has been given to the effects of alien vegetation on these organisms in South Africa. The three studies that examined the effects of alien vegetation on squamate and amphibian species found significant reductions in species richness and substantial changes in species composition (Russell & Downs 2012; Schreuder & Clusella-Trullas in press; Trimble & van Aarde 2014). A single study demonstrated that the encroachment of alien vegetation into nesting habitat of the Nile crocodile (*Crocodylus niloticus*) altered the temperatures in egg chambers, potentially affecting hatchling sex ratios, and clearing of the roots of the alien plant increased the number of females nesting (Leslie & Spotila 2001). To our knowledge, no study has been conducted to assess the impacts of alien vegetation on tortoises, a taxonomic group with high species diversity in South Africa and high endemism in the Cape region (Branch, Benn & Lombard 1995). Some of the life history characteristics of tortoises, such as herbivory, long lifespans and habitat structure needed for shelter, likely increase their vulnerability to alien plant invasions (Gray & Steidl 2015; Stewart, Austin & Bourne 1993). Similarly, only two studies (Russell & Downs 2012; Trimble & van Aarde 2014) considered amphibians, despite their potential vulnerability to the impacts of alien plants on water resources (Le Maitre et al. 2015).

Context dependencies

It is well recognised that the impacts of alien plants on fauna are context-dependent and are shaped by a variety of factors, including the abundance and distribution of the IAP, the time since its introduction and the invasion history (e.g. rate of spread and lag times), the spatial extent of the study area, the degree of contrast of the alien plant form and function to the native vegetation, the ecosystem type and climatic conditions (e.g. seasonality) and the habitat preference of the animal species assessed (Kumschick et al. 2015; Maron & Marler 2008; Pyšek et al. 2012; Schirmel et al. 2016; Vilà et al. 2011). Little knowledge of these factors and the extent to which they may interact makes the prediction of impacts of invasive alien vegetation on native animal diversity a difficult task. Furthermore, these variables are essential for incorporating moderators in meta-analyses that seek to explore the direction of effects of alien plants on community metrics and avoid spurious results. These difficulties were encountered in our synthesis in various ways. The 42 studies differed in alien vegetation abundance, ranging from mildly invaded sites (e.g. Robertson et al. 2011) to plantations of alien plants (e.g. Pryke & Samways 2009) but, in general, little information was provided about the extent of the invasion, the study site size and its landscape context (e.g. degree of fragmentation and edge effects), and the invasion history, with a few notable exceptions (e.g. Liu, Janion & Chown 2012; Mgobozi, Somers & Dippenaar-Schoeman 2008). In some cases, or regions, the lack of long-term vegetation surveys or a poor knowledge of the alien plant (e.g. site of origin and genetic lineage; Thompson et al. 2014) may explain the lack of such detailed accounts.

Our synthesis also showed that opposite effects of alien plants on the same taxonomic group are found and generally depend on the animal group investigated, the type of IAP and the occurrence of other environmental stresses (cattle and habitat alteration). For example, alien plants can have decreasing (Samways & Grant 2006), neutral (Kinvig & Samways 2000; Samways & Sharratt 2010) or increasing (Kietzka, Pryke & Samways 2015) effects on dragonfly species diversity. Kietzka et al. (2015) suggested that the invasive American bramble (*Rubus cuneifolius*) provided additional perching sites and protection from predators to dragonflies, but where the alien plant stands were very dense, the negative effects outweighed the positive. The direction of the impact is also influenced by the behaviour and physiological requirements of the species or groups investigated. For example, shade specialists such as some Odonata species can benefit from increased shade (Samways & Grant 2006), whereas basking species are negatively affected by closed canopies that can result from plant invasions. Similarly, herbivore arthropods were generally more affected than detritivores (e.g. van der Colff et al. 2015). Finally, novel or very dissimilar alien plant forms to those of native plants species are likely to impact local communities most (Martin & Murray 2011), and although some comparisons involving alien plants with similar growth form to the native vegetation found no differences in native species abundance or richness (e.g. Olckers & Hulley 1989; van der Colff et al. 2015; van der Merwe, Dippenaar-Schoeman & Scholtz 1996), this was not always the case (Pryke & Samways 2009; Ratsirarson et al. 2002).

Study approaches

This review further revealed that most studies examining the impacts of alien plants on ectothermic animals employed the same methodological approach, comparing invaded and non-invaded sites. A very small proportion of studies included a gradient of alien plant abundance (e.g. Schreuder & Clusella-Trullas in press; Robertson et al. 2011) or incorporated comparisons with restored sites that had been cleared from alien plants (e.g. Maoela et al. 2016) or among sites with different times since invasion (e.g. Mgobozi et al. 2008). Although all of these approaches have their strengths and caveats (Hulme et al. 2013; Kueffer, Pyšek & Richardson 2013), progress in the understanding of impacts of alien plants on animal diversity requires a multifaceted approach (Kumschick et al. 2015). For example, comparisons of invaded and uninvaded plots can be confounded by differences that are inherent to each site (altitude, topography and soil properties) and require increased replication to boost the power of the analyses by incorporating variation originating from each site’s characteristics. It is often particularly difficult to find uninvaded reference sites because baseline data (prior to the invasion) are not available. Despite South Africa having a national-scale government-funded project to clear alien plants, the Working for Water Programme, relatively few studies have incorporated removal of aliens as part of their study design or assessed how rapidly fauna assemblages reflect pre-invasion reference sites.

Species abundance, richness and composition results provided useful data to compare key animal community changes between invaded and uninvaded habitats (albeit with the known problems associated with, e.g., comparison of species richness; Gotelli & Colwell 2001). However, this review also illustrated that in some cases, these metrics were insufficient to obtain an adequate understanding of the change detected or lack thereof. For example, Magoba & Samways (2012) showed that adult dragonfly species richness was not hampered by riparian alien vegetation, but assemblages changed drastically in sites cleared of IAPs. Although some generalist, widespread species (e.g. spiders and hymenopterans) can thrive in invaded areas, rare, endemic or sensitive species often disappear from alien-infested sites (e.g. Stewart & Samways 1998). These findings illustrate that additional metrics such as beta-diversity, species evenness, measures of commonness and rarity and functional richness (e.g. Magurran & McGill 2011) should be incorporated in assessments of impacts of alien vegetation on animal communities in South Africa.

Overall, these metrics alone give little insight into the mechanisms underpinning community changes. Less than 13% of the studies reviewed here incorporated an experimental approach for testing for mechanisms. These are essential for describing processes underpinning patterns, distinguishing direct and indirect effects of alien plants on ecosystems (Hulme et al. 2013) and, ultimately, enabling predictions of invasion outcomes in the context of future distributions of alien plants in South Africa (Rouget et al. 2004) and in the face of other environmental alterations and climate change. The ability to forecast impacts of IAPs and develop management strategies will rest on knowing these mechanisms.

Conclusion

The current state of knowledge of the impacts of IAPs on resident ectothermic animal species in South Africa relies heavily on a few key studies, with distinct biases in geographic locations and taxonomic groups. In cases where detailed information is available, it is nevertheless clear that there are pronounced negative impacts of IAPs on terrestrial animal (ectotherm) species diversity. The mechanisms underlying these impacts are unclear, but here we highlight a few key abiotic and biotic processes that could be examined in future, especially if microenvironments determine key behaviours and life-cycle timing that lead to changes in population abundance. Such an integrated approach to the question of IAPs and their impact on native animal species diversity would be of direct value to monitoring and conservation efforts, such as alien plant removal and control programmes. At present, it is wholly unclear whether the removal of IAPs will be sufficient to allow recovery of native ectotherm biodiversity.

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Competing interests

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Author(s) contributions

Both S.C.-T. and R.A.G. contributed equally to the article.

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Appendix 1

Literature review search terms

TABLE 1-A1: Search terms used in the literature review on the ISI Web of Science.

Issue	Search terms
Location	"South Africa*"
Invasive plants	((invas* OR alien* OR non$nativ* OR exotic* OR introduced OR non$indigenous OR naturali?ed OR plantation*) AND (plant* OR vegetat* OR tree* OR shrub* OR grass* OR forest* OR forb* OR herb* OR vine* OR *weed*)) OR (invaded AND (habitat* OR site* OR plot*))
Reptiles	reptil* OR squamata OR snake* OR python* OR boa* OR cobra* OR mamba* OR viper* OR adder* OR colubrid* OR elapid* OR lizard* OR gecko* OR skink* OR chameleon * OR agama* OR monitor* OR lacertid* OR amphisbaenid* OR cordylid* OR testudine* OR chenolian* OR turtle* OR tortoise* OR terrapin* OR crocodylia OR crocodil*
Amphibians	amphibian* OR frog* OR anura* OR tadpole*
Terrestrial invertebrates	invertebrate* OR platyhelminthe* OR *worm* OR nematod* OR nematomorph* OR nemertea* OR acanthocephalan* OR annelid* OR oligochaet* OR leech* OR mollus* OR gastropod* OR snail* OR slug* OR tardigrad* OR onychophora* OR arthropod* OR crustacea* OR *lice OR "terrestrial crab*" OR amphipod* OR isopod* OR myriapod* OR centipede* OR millipede* OR chilopod* OR diplopod* OR chelicerat* OR Araneae OR arachnid* OR spider* OR Acari OR acarin* OR mite* OR tick* OR opiliones OR harvestm?n OR scorpion* OR hexapod* OR insect* OR apterygot* OR odonat* OR dragonfl* OR damselfl* OR orthoptera* OR grasshopper* OR cricket* OR isoptera* OR termite* OR mantodea* OR mantis* OR mantid* OR blattodea* OR cockroach* OR embioptera* OR webspinner* OR phasmid* OR phasmatodea* OR hemiptera* OR *bug* OR cicada* OR aphid* OR *hopper* OR thysanoptera* OR thrip* OR psocoptera* OR coleoptera* OR beetle* OR lepidoptera* OR butterfl* OR moth* OR diptera* OR *flies OR *fly OR mosquito* OR flea* OR hymenoptera* OR wasp* OR ant OR ants OR bee OR bees OR neuroptera* OR lacewing* OR antilon* OR pollinat*
Effect on diversity	((population* OR communit* OR assemblage* OR species) AND (abundan* OR richness OR ((population* OR communit* OR assemblage* OR species) AND (abundan* OR richness OR diversity OR composition OR evenness OR dominance OR equitability OR structure OR poor* OR impoverish*)) OR ((functional OR *genetic) AND diversity)
Effect mechanism	(habitat* NEAR/3 (quality OR structure OR heterogeneity)) OR shad* OR thermal* OR hydrolog* OR micro$site* OR micro$climate* OsR micro$habitat* OR refuge* OR prey* OR activity OR thermo$regulat* OR behavio$r* OR bask* OR predat* OR competit* OR herbivo$r* OR resource* OR nutrient* OR fire* OR soil* OR sediment* OR locomoti* OR host* OR reproducti* OR toxic* OR poison* OR hybrid* OR disease* OR parasit*

A first search combined terms for location, invasive plants, reptiles, amphibians and terrestrial invertebrates, and effects on diversity, whereas a second search replaced the terms for effects with terms for mechanisms.

Search 1: Effect on diversity (358 records)

TOPIC = "South Africa*" AND (((invas* OR alien* OR non$nativ* OR exotic* OR introduced OR non$indigenous OR naturali?ed OR plantation*) AND (plant* OR vegetat* OR tree* OR shrub* OR grass* OR forest* OR forb* OR herb* OR vine* OR *weed*)) OR (invaded AND (habitat* OR site* OR plot*))) AND ((reptil* OR squamata OR snake* OR python* OR boa* OR cobra* OR mamba* OR viper* OR adder* OR colubrid* OR elapid* OR lizard* OR gecko* OR skink* OR chameleon * OR agama* OR monitor* OR lacertid* OR amphisbaenid* OR cordylid* OR testudine* OR chenolian* OR turtle* OR tortoise* OR terrapin* OR crocodylia OR crocodil*) OR (amphibian* OR frog* OR anura* OR tadpole*) OR (invertebrate* OR platyhelminthe* OR *worm* OR nematod* OR nematomorph* OR nemertea* OR acanthocephalan* OR annelid* OR oligochaet* OR leech* OR mollus* OR gastropod* OR snail* OR slug* OR tardigrad* OR onychophora* OR arthropod* OR crustacea* OR *lice OR "terrestrial crab*" OR amphipod* OR isopod* OR myriapod* OR centipede* OR millipede* OR chilopod* OR diplopod* OR chelicerat* OR Araneae OR arachnid* OR spider* OR Acari OR acarin* OR mite* OR tick* OR opiliones OR harvestm?n OR scorpion* OR hexapod* OR insect* OR apterygot* OR odonat* OR dragonfl* OR damselfl* OR orthoptera* OR grasshopper* OR cricket* OR isoptera* OR termite* OR mantodea* OR mantis* OR mantid* OR blattodea* OR cockroach* OR embioptera* OR webspinner* OR phasmid* OR phasmatodea* OR hemiptera* OR *bug* OR cicada* OR aphid* OR *hopper* OR thysanoptera* OR thrip* OR psocoptera* OR coleoptera* OR beetle* OR lepidoptera* OR butterfl* OR moth* OR diptera* OR *flies OR *fly OR mosquito* OR flea* OR hymenoptera* OR wasp* OR ant OR ants OR bee OR bees OR neuroptera* OR lacewing* OR antilon* OR pollinat*)) AND (((population* OR communit* OR assemblage* OR species) AND (abundan* OR richness OR diversity OR composition OR evenness OR dominance OR equitability OR structure OR poor* OR impoverish*)) OR ((functional OR *genetic) AND diversity))

Refined by: DOCUMENT TYPES: (ARTICLE OR REVIEW OR BOOK CHAPTER)

Timespan: All years.

Search 2: Effect mechanisms (702 records)

TOPIC = "South Africa*" AND (((invas* OR alien* OR non$nativ* OR exotic* OR introduced OR non$indigenous OR naturali?ed OR plantation*) AND (plant* OR vegetat* OR tree* OR shrub* OR grass* OR forest* OR forb* OR herb* OR vine* OR *weed*)) OR (invaded AND (habitat* OR site* OR plot*))) AND ((reptil* OR squamata OR snake* OR python* OR boa* OR cobra* OR mamba* OR viper* OR adder* OR colubrid* OR elapid* OR lizard* OR gecko* OR skink* OR chameleon * OR agama* OR monitor* OR lacertid* OR amphisbaenid* OR cordylid* OR testudine* OR chenolian* OR turtle* OR tortoise* OR terrapin* OR crocodylia OR crocodil*) OR (amphibian* OR frog* OR anura* OR tadpole*) OR (invertebrate* OR platyhelminthe* OR *worm* OR nematod* OR nematomorph* OR nemertea* OR acanthocephalan* OR annelid* OR oligochaet* OR leech* OR mollus* OR gastropod* OR snail* OR slug* OR tardigrad* OR onychophora* OR arthropod* OR crustacea* OR *lice OR "terrestrial crab*" OR amphipod* OR isopod* OR myriapod* OR centipede* OR millipede* OR chilopod* OR diplopod* OR chelicerat* OR Araneae OR arachnid* OR spider* OR Acari OR acarin* OR mite* OR tick* OR opiliones OR harvestm?n OR scorpion* OR hexapod* OR insect* OR apterygot* OR odonat* OR dragonfl* OR damselfl* OR orthoptera* OR grasshopper* OR cricket* OR isoptera* OR termite* OR mantodea* OR mantis* OR mantid* OR blattodea* OR cockroach* OR embioptera* OR webspinner* OR phasmid* OR phasmatodea* OR hemiptera* OR *bug* OR cicada* OR aphid* OR *hopper* OR thysanoptera* OR thrip* OR psocoptera* OR coleoptera* OR beetle* OR lepidoptera* OR butterfl* OR moth* OR diptera* OR *flies OR *fly OR mosquito* OR flea* OR hymenoptera* OR wasp* OR ant OR ants OR bee OR bees OR neuroptera* OR lacewing* OR antilon* OR pollinat*)) AND ((habitat* NEAR/3 (quality OR structure OR heterogeneity)) OR shad* OR thermal* OR hydrolog* OR micro$site* OR micro$climate* OsR micro$habitat* OR refuge* OR prey* OR activity OR thermo$regulat* OR behavio$r* OR bask* OR predat* OR competit* OR herbivo$r* OR resource* OR nutrient* OR fire* OR soil* OR sediment* OR locomoti* OR host* OR reproducti* OR toxic* OR poison* OR hybrid* OR disease* OR parasit*)

Refined by: DOCUMENT TYPES: (ARTICLE OR REVIEW OR BOOK CHAPTER)

Timespan: All years.

Appendix 2 starts on the next page →

Appendix 2

Studies reviewed

Search 1: Effects on diversity

Botzat, A., Fischer, L. & Farwig, N., 2013, 'Forest-fragment quality rather than matrix habitat shapes herbivory on tree recruits in South Africa', *Journal of Tropical Ecology*, 29(02), 111–122. https://doi.org/10.1017/S0266467413000102

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