

Alien plants have greater impact than habitat fragmentation on native insect flower visitation networks

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Abstract

Aim: Habitat fragmentation and alien species are among the leading causes of biodiversity loss. In an attempt to reduce the impact of forestry on natural systems, networks of natural corridors and patches of natural habitat are often maintained within the afforested matrix, yet these can be subject to degradation by invasion of non-native species. Both habitat fragmentation and alien invasive species disrupt the complex interaction networks typical of native communities. This study examines whether an invasive plant and/or the fragmented nature of the forestry landscape influences natural flower visitation networks (FVNs), flower–visitor abundance and richness or flower/visitor species composition.

Location: The species rich and diverse grasslands in the KwaZulu-Natal Midlands, South Africa is under threat from transformation, particularly by commercial forestry plantations, restricting much of the remaining untransformed grasslands into remnant grassland patches (RGPs). Remaining patches are under additional threat from the invasive *Rubus cuneifolius* Pursh (bramble). Sites were established in RGPs and in a nearby protected area (PA), with and without brambles present for both areas.

Results: Flower abundance and flower area of native plant species were greater within RGP than in PA, but only in the absence of *R. cuneifolius*. Flower–visitor assemblages differed between invaded and uninvaded sites and also differed between PA and RGP sites. Both areas lost specialist flower–visitor species in the presence of brambles. Network modularity was greatly reduced by the presence of bramble, indicating a reduction in complexity and organization. The structure of FVNs was otherwise unaffected by presence of bramble or being located in RGPs or the PA.

Main conclusions: The RGPs contribute to regional biodiversity conservation through additional compositional diversity and intact FVNs. *Rubus cuneifolius* reduces ecological complexity of both RGPs and PAs, however, and its removal must be prioritized to conserve FVNs.

KEYWORDS

ecological networks, flower network analyses, food web, insect conservation, landscape ecology, pollination

1 | INTRODUCTION

Global timber needs have driven a rapid expansion of commercial forestry, threatening biodiversity (Brokerhoff, Jactel, Parrotta, Quine, & Sayer, 2008; Rouget, Richardson, Cowling, Lloyd, & Lombard, 2003). To ameliorate fragmentation of natural vegetation caused by forestry, commercial timber production companies may maintain remnant habitat patches within the plantation matrix. Remnant patches in these landscapes are characterized by strips or patches of remnant habitat, which connect protected areas (PA) and other natural areas to each other within the transformed landscapes (Gurrutxaga & Lozano, 2010; Samways, Bazelet, & Pryke, 2010). These corridors and patches form landscape ecological networks intended to minimize the effects of fragmentation (Jongman, 1995). Although having some positive effects, these remnant patches often contain impoverished faunas compared to larger areas (Weibull, Östman, & Granqvist, 2003). Isolation of patches leads to slower immigration by new species and slower repopulation after local extinctions (Simberloff, 1974). In addition, commercial forestry plantations may negatively affect processes such as pollination and flower visitation networks (FVNs) in these patches, with considerable economic and ecological consequences (Gallai, Salles, Settele, & Vaissière, 2009; Tschamtké, Klein, Krüss, Steffan-Dewenter, & Thies, 2005). In our study site, in the southern African grasslands of KwaZulu-Natal, afforestation is of particular concern, because biodiversity-rich areas largely overlap with areas most suitable for commercial timber plantations (Neke & du Plessis, 2004).

The problem of fragmentation is compounded by invasion of non-native ("alien") species. Invasion by alien plant species is one of the greatest threats to biodiversity and community structure worldwide (Mack et al., 2000). American bramble (*Rubus cuneifolius* Pursh) is one of the most problematic invasive plant species of grasslands in the KwaZulu-Natal highlands and midlands regions, South Africa, and is one of the top ten most prominent invaders of South African grasslands (Erasmus, 1984; Henderson, 2007). Environmental conditions in the area, and a lack of natural enemies and competitors, have enabled bramble to become a naturalized weed (Erasmus, 1984). Its encroachment can lead to communities more characteristic of woodlands, threatening specialist grassland taxa (Henderson, 2007). Bramble infests large areas with thorny, dense stands, and it spreads rapidly due to its efficient reproductive system (Erasmus, 1984). Bramble responds to disturbance with a period of rapid and prolific growth, making it expensive, time-consuming and difficult to control (Henderson, 2007).

Despite bramble's detrimental and widespread effects in areas in which it has become naturalized, very little information is available on its effects on native biodiversity and ecological processes within production landscapes. Because it forms thick stands, it outcompetes adult native plants, preventing them from producing seed through shading effects. Bramble has been shown to be unfavourable for grassland birds (Lipsey & Hockey, 2010; Reynolds & Symes, 2013) and so disrupts the ecological processes mediated by these birds. Disruption of mutualisms by invasive species like bramble can see the extinction of ecological interactions like pollination (Valiente-Banuet et al., 2015) and seed dispersal. This, in turn, causes local extinctions,

placing species that are already threatened by commercial forestry under even greater pressure, and potentially on the pathway to extinction (Downey & Richardson, 2016).

Interactions between organisms form networks, the structure of which influences the resilience and robustness of the ecosystems that they occupy (Dunne, Williams, & Martinez, 2002a; Thébault & Fontaine, 2010). Anthropogenic disturbance results not only in habitat loss and fragmentation, which pose serious threats to conservation (Ewers & Didham, 2006; Filgueiras, Iannuzzi, & Leal, 2011), but also affects the structure of interaction networks. This has consequences for ecosystem processes, such as pollination and seed dispersal (Aizen, Morales, & Morales, 2008; Lopezariza-Mikel, Hayes, Whalley, & Memmott, 2007; Memmott et al., 2007; Thompson, 1994). Furthermore, even if biodiversity loss is not detected, disturbance may cause network properties to change, influencing ecological processes (Kehinde & Samways, 2014; Laliberté & Tylianakis, 2010; Tylianakis, Tschamtké, & Lewis, 2007).

Plant species can support, attract or share pollinators (Real, 1983). In this way, interactions between plants can be facilitative (as species support the pollinators of other species) or competitive (if pollinators are attracted away). The presence of invasive species introduces new possibilities for facilitation or competition. If invasive species are more attractive to flower visitors than native species, reduced visitation can lead to reduced reproductive capacity of native plants (Brown, Mitchell, & Graham, 2002; Chittka & Schurkens, 2001). A good example of this is the invasive *Acacia saligna* in the Cape Floristic Region of South Africa, which attracts native honeybees to such an extent that there is concern that they might affect the pollination of nearby flowering plant species (Gibson, Pauw, & Richardson, 2013). Invasive species can have a diluting effect on the pollen of native species by flooding the ecosystem with their own pollen in large amounts (Larson, Royer, & Royer, 2006). Invasive species can also affect pollination indirectly by competing with native species for resources (Brooks, 2000; Traveset & Richardson, 2014). However, it is also possible for invasive species to facilitate the pollination of native species by attracting more flower visitors to the area (Morales & Traveset, 2009; Nel, 2015).

Understanding these interactions is crucial in the light of the global decline in pollinators, driven primarily by loss of natural habitat (Potts et al., 2010; Winfree, Aguilar, Vazquez, LeBuhn, & Aizen, 2009). The extent to which species loss affects ecosystems depends on the complexity of the ecosystem in question (Dunne, Williams, & Martinez, 2002b). Here we asked (1) is flower and flower-visitor diversity and network structure affected negatively by *R. cuneifolius* (bramble) invasion, (2) how does the local context affect biodiversity and flower-visitor networks (i.e., location of community in a remnant patch instead of a natural area); and (3) is there any interaction between these two factors. We expect to see fewer species in the smaller fragmented patches as smaller habitat areas are predicted to lower levels of biodiversity (Kohn & Walsh, 1994; Sabatino, Maceira, & Aizen, 2010; Simberloff, 1974) although this would be somewhat mitigated by connective nature of these patches (Samways & Pryke, 2016). Whereas areas invaded by the alien species are likely to have more connected networks (i.e., more generalist species) due to simplification

of the flower–visitor network (Aizen et al., 2008; Albrecht, Padrón, Bartomeus, & Traveset, 2014), this would be further complicated by some level of competition or facilitation due to the additional floral resources (Ferrero et al., 2013). The most dramatic effects are expected when fragmentation and the presence of the invasive species interact with each other.

2 | METHODS

2.1 | Site selection

This study was conducted in the Karkloof area of the KwaZulu-Natal Midlands, South Africa. In this summer-rainfall region, temperatures range between 2°C and 38.8°C, with a mean annual temperature of 14.1°C; elevation ranges from 1,400 to 1,800 m above sea level (Sandwith, 2002). This study was conducted at various sites in Gilboa Estate (29°25'S, 30°30'E), a 52.4 km² area that is covered by commercial timber blocks interdispersed with just over a third of which designated for conservation in the form of remnant patches of grassland, wetlands and natural forests (Jackelman, Wistebaar, Rouget, Germishuizen, & Summers, 2006; Lipsey & Hockey, 2010) (Figure 1). Adjacent to this plantation is the Mount Gilboa Private Nature Reserve, a PA that forms part of the Karkloof Nature Reserve. Both Gilboa Estate and Gilboa Private Nature Reserve grasslands are classified as Drakensberg Foothill Moist Grassland (Mucina & Rutherford, 2006). Gilboa's open patches consist largely of firebreaks, riparian zones, roads and areas below power lines, as is common for remnant patches. However, there is a large continuous patch of grassland on Gilboa, which is interconnected along with the rest of the RGP to Mount Gilboa Nature Reserve (Lipsey & Hockey, 2010).

2.2 | Sampling design and data collection

Within the commercial timber plantation region, we focused on four landscape contexts: (1) PA without bramble (PA.Absent), (2) RGP without bramble (RGP.Absent), (3) PAs invaded by *R. cuneifolius* (PA.Present) and (4) RGPs invaded by *R. cuneifolius* (RGP.Present). Ten sites (Figure 1) were chosen in each of the PA.Absent and RGP.Absent categories, and five each for PA.Present and RGP.Present. Fewer bramble-invaded sites were sampled due to difficulty in finding flowering bramble. All sites had a minimum distance of 300 m between sites of the same type in order to minimize the chances of sampling the same individual flower visitor, and RGP sites were chosen within RGPs that were between 50 and 200 m wide only, in order to standardize patch size (Figure 1).

Ten of the most frequently encountered native flower species were used in this study. These species were (in order of abundance) as follows: (1) *Helichrysum pallidum* DC (Boleba), (2) *Helichrysum cymosum* (L.) (Yellow-tipped straw-flower); (3) *Senecio bupleuroides* DC (Yellow Starwort); (4) *Senecio tamoides* DC (Canary Creeper); (5) *Acalypha peduncularis* E.Mey. ex Meisn (Brooms and Brushes); (6) *Pentanisia prunelloides* (Hochst.) (Wild Verbena); (7) *Eriosema squarrosus* (Thunb.); (8) *Senecio elegans* L. (Wild Cineraria); (9) *Lobelia flaccida* (C.Presl); (10) *Hypoxis hemerocallidea* Fisch., C.A.Mey. & Avé-Lall (African Potato).

At each site, a 2 × 2 m quadrat was established. These quadrats were placed to maximize the number of representative focal species. Within each quadrat, all focal plant species were counted and identified (as a measure of plant diversity). When *R. cuneifolius* was present at a site, quadrats were placed within 1 m of the bramble patch, while at bramble absent sites quadrats were laid out randomly. In addition, flower abundance (total number of flowers of all focal species for that

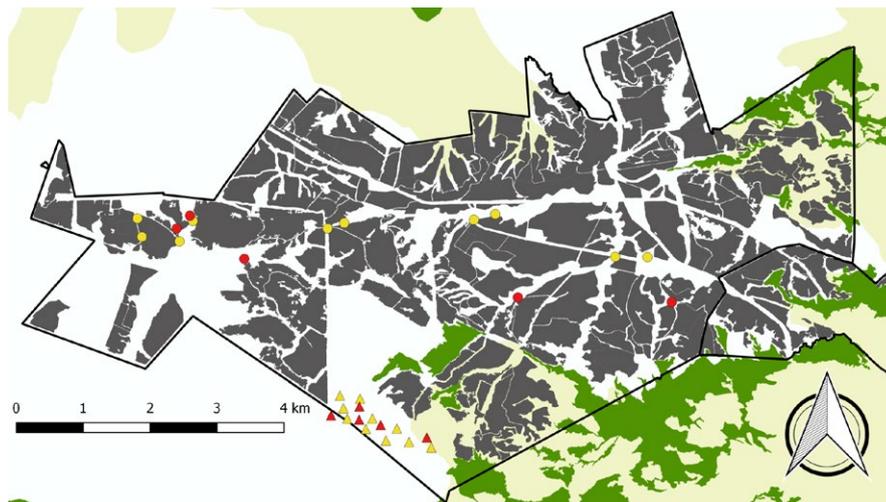


FIGURE 1 Study sites at the Mount Gilboa Nature Reserve and timber plantation in the KwaZulu–Natal Midlands where flower–visitor observations were performed on ten native plant species in protected areas and in remnant grassland patches within forestry areas, in areas infested by *Rubus cuneifolius* and those without it. PA.Absent—in protected areas without *R. cuneifolius* (yellow triangles); PA.Present—in protected areas with *R. cuneifolius* (red triangles); RGP.Absent—within remnant grassland patches (RGP) in forestry ecological networks without *R. cuneifolius* (yellow circles); RGP.Present—in RGPs with *R. cuneifolius* (red circles). Grey areas represent commercial forestry compartments, white areas represent Drakensberg Foothill Moist Grassland, yellow areas represent other grass types (Midlands Mistbelt Grassland and Mooi River Highlands Grassland), green areas represent Southern Mistbelt Forest as per Mucina and Rutherford (2006) classifications. [Colour figure can be viewed at wileyonlinelibrary.com]

plot) was also determined. For the purposes of this study, a “flower” is defined as a floral unit, including both flowers and pseudanthia (inflorescence of anything from a small cluster of flowers to hundreds or thousands of flowers grouped together to form a single flower-like structure (Eames, 1961)). To calculate the floral area (area per plot covered by focal flowers), each focal flower species had 10 individual flowers measured for floral cover giving a mean focal flower area per species (measured in cm²). Focal flower area per site was then calculated by multiplying the number of individual flowers to the mean focal flower area and then total floral area per sites was calculated by summing the focal flower areas per site.

2.3 | Flower–visitor observations

Observations were carried out three times at each site between the periods of 12 November and 11 December 2013, and 15 January and 14 February 2014, during bramble flowering. Each quadrat was set per visit to maximize focal flower–visit density. Two observers, standing at opposite corners of each quadrat, recorded all flower visitors to focal species for a period of 15 min. Flower visitors to these focal species were identified by sight, and if this was not possible, captured for later identification. Visits are defined as a flower visitor coming to rest on the flower. The reference specimens were pinned or preserved in alcohol and are stored at the Stellenbosch University Entomology Collection, Stellenbosch, South Africa. Surveys took place between 08:00 a.m. and 05:00 p.m., and only when cloud cover was below 50%, there was no rain, wind speed was below 10 m/s and temperature above 21°C. Wind speed and temperature were measured with a handheld anemometer (Testo 410-2).

Due to the low taxonomic resolution of insects in the area (few guides and experts to identify species), flower visitors were not identified to species level, but instead sorted into morphospecies as described in Gerlach, Samways, and Pryke (2013). With the morphospecies approach, a reference collection is created of all new species encountered, allowing a researcher to study compositional changes of flower visitors across a study. Morphospecies were allocated to higher taxonomic levels, usually to Order, with the exception of Apoidea (a superfamily within Hymenoptera) and Culicidae (a family within Diptera). This allowed Apoidea (bees) to be differentiated from wasps, due to their importance as pollinators. Mosquitoes (Culicidae) were separated from Diptera as mosquitoes are not known to be pollinators and might be skewing the Diptera results. Thus, morphospecies fell into the following groups: Hemiptera, Coleoptera, Diptera (excluding Culicidae), Culicidae, Lepidoptera, Hymenoptera (bees excluded) and Apoidea (all bee species encountered).

2.4 | Statistical analyses

We used generalized linear mixed models (GLMMs) to assess how flower abundance (the total number of flowers of all focal species), flower area (area of quadrat covered by flower), flower diversity (number of flowering focal plant species), number of flower visits (as a measure of abundance of interactions) and flower–visitor diversity

(number of visitor morphospecies) responded to site type (PA or RGP) and whether sites were invaded by bramble or not. GLMMs were calculated using the MASS package in R (Venables & Ripley, 2002), using the penalized quasi-likelihood estimation method and data fitted to a Poisson distribution (Bolker et al., 2009). Location (in RGP or PA) and presence of bramble were included as fixed variables. These data were tested for spatial autocorrelation using a semi-variogram. When a random, dummy variable was exponentially correlated to longitude and latitude, it improved the semi-variogram (Dormann et al., 2007). Exponentially correlated longitudinal and latitudinal data were used as the random variable to overcome spatial autocorrelation within the data. Forward selection was then used to determine the interaction between these factors.

To determine the similarity of flower–visitor assemblages between sites, a PERMANOVA was performed using the add-on package PERMANOVA+ in PRIMER 6 (PRIMER-E, 2008). As PERMANOVA is sensitive to heterogeneous dispersions (Anderson & Walsh, 2013), we balanced the design by randomly removing five sites from RGP. Absent and PA.Absent. Two abundance-based matrices were created, flower visitor and focal plant species. These matrices were square root transformed and a resemblance matrix constructed for each using the Bray–Curtis similarity index. For both models, PERMANOVAs and canonical analysis of principal coordinates (CAP) were calculated with location (RGP/PA) and bramble (present/absent) as fixed variables (Anderson, 2008; Anderson & Willis, 2003).

Using the Bipartite package in the R software (Dormann, Gruber, & Freund, 2008; R Development Core Team, 2007), FVNs were constructed for each site sampled. Webs were then constructed for each landscape context (PA.Absent, RGP.Absent, PA.Present and RGP.Present) with the focal flower species, the visitor morphospecies and visitor abundance. A graphical representation was then constructed with the *plotweb* function representing all 30 sites combined, and the morphospecies were placed into taxonomic groups for illustrative purposes only. Five FVNs were constructed, one representing all the interactions observed during data collection of the study and one for all of the interactions per landscape context. Using *group-level* statistics in the Bipartite package of the software R, the mean number of shared partners for the lower level (focal flower species) was calculated for the overall interaction network and for each site (Dormann, 2011). Using *network-level* statistics, connectance, weighted NODF (nestedness metric based on overlap and decreasing fill) and Shannon diversity of interactions were calculated for the overall FVN, each site type and each site. Weighted NODF was used as the measure of nestedness; it is a weighted nestedness index based on paired overlap in filled versus non-filled cells of matrices and decreasing marginal totals and is a more consistent measure of nestedness (Almeida-Neto, Guimarães, Guimarães, Loyola, & Ulrich, 2008; Wells, Feldhaar, & O'Hara, 2014). Modularity was calculated using the *computeModules* function for the overall FVN, as well as for each site (Dormann, 2011). Analyses at the network level are particularly useful for comparisons across different types of networks (Blüthgen, Menzel, & Blüthgen, 2006).

Generalized linear models were performed using a Gaussian distribution for each of mean number of shared partners of focal flower

species, connectance, weighted NODF, modularity and Shannon diversity of interactions as the response variable and location and bramble presence as explanatory variables. The models were built using the *lme4* package in R (Bates et al., 2011). Connectance and other network indices are strongly dependent on network size (Blüthgen et al., 2006). With the *multcomp* package, pairwise post hoc Tukey tests were performed for each network- or group-level index by site type (Hothorn, Bretz, & Westfall, 2008).

3 | RESULTS

3.1 | Diversity of flowers and flower visitors

We observed 131 flower–visitor species. RGP.Absent sites had the greatest floral abundance and this was significantly different to PA.Absent sites, which had the lowest flower abundance (Table 1, Figure 2). Flower abundance and flower area were significantly greater in the RGP than PA, with an interaction between location and bramble for flower area (Table 1; Figure 2). Neither flower diversity nor visitor diversity showed significant differences between the sites (Table 1).

Flower species assemblages were not significantly different in species composition for any site type (Table 1). When comparing the flower–visitor assemblages of all four site types, however, all differed significantly from each other (Table 1, Figure 3). Flower–visitor

TABLE 1 Differences in flower abundance, flower area, flower diversity, flower–visitor abundance and flower–visitor richness using a chi-squared statistic generated from generalized linear mixed models (GLMM using Poisson distribution dummy variable exponentially correlated to longitude and latitude as a random variable). Differences in flower and flower–visitor assemblages are reported as a pseudo- F using PERMANOVA, as well as the F -value from a flower visitation network as affected by bramble (present/absent) and location (RGP/PA) and their interaction (linear models)

Test	Location	Bramble	Location × Bramble
GLMM (χ^2)			
Flower abundance	2.92*	0.11	1.49
Flower area	2.66*	0.06	2.31*
Flower species richness	1.14	1.05	0.01
Flower–visitor abundance	0.25	0.27	0.83
Flower–visitor richness	0.27	0.53	0.83
PERMANOVA (pseudo- F)			
Focal flower assemblage	1.28	0.61	1.75
Flower–visitor assemblage	2.04*	1.66*	1.76*
Flower visitation network (F -value)			
Shared partners (flowers)	2.17	0.13	0.98
Connectance	1.40	0.72	0.17
Weighted NODF	1.55	1.25	0.94
Modularity	0.03	5.29*	0.85
Shannon diversity	0.60	0.00	0.42

* $p < .05$.

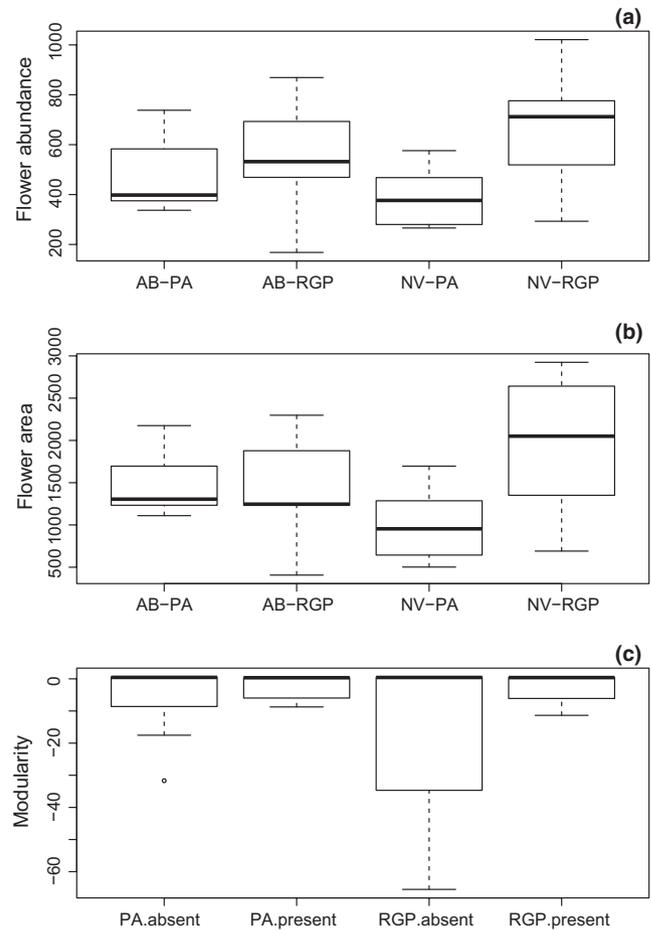


FIGURE 2 Boxplots showing the (a) average flower abundance, (b) average flower area and (c) modularity based on the location within the landscape (PA or RGP) and *Rubus cuneifolius* (absent or present), for the four site types: RGP.Absent—remnant grassland patches without bramble, PA.Present—PA invaded by bramble, RGP.Present—RGP invaded by bramble.

assemblages showed significant differences between sites with bramble present versus absent, between sites in RGPs and in PAs, as well as the interaction between these two effects (Table 1, Figure 3).

3.2 | Overall characteristics of FVNs

The overall FVN (Figure 4) was diverse, with 114 morphospecies taking part in 1,030 interactions over 30 sites. Coleoptera (47 morphospecies) were the most common flower visitors, participating in 41.6% of all interactions. Diptera (27 morphospecies) were observed in 29% of interactions, Hymenoptera (11 morphospecies) (excluding the superfamily Apoidea) took part in 8% of interactions, Apoidea (7 morphospecies) in 7.1% and Lepidoptera (7 morphospecies) participated in 6.7% of total interactions. Hemiptera (12 morphospecies) were observed in 5.5% of visits, and Culicidae (3 morphospecies) in 2.1% of visits. There were 15 634 focal flowers observed, of these, 42.1% were *H. pallidum*, 25.6% were *H. cymosum*, 12.2% were *S. bupleuroides*, and 10.2% were *S. tamoides*. The remaining focal flower species had less than 5% representation each.

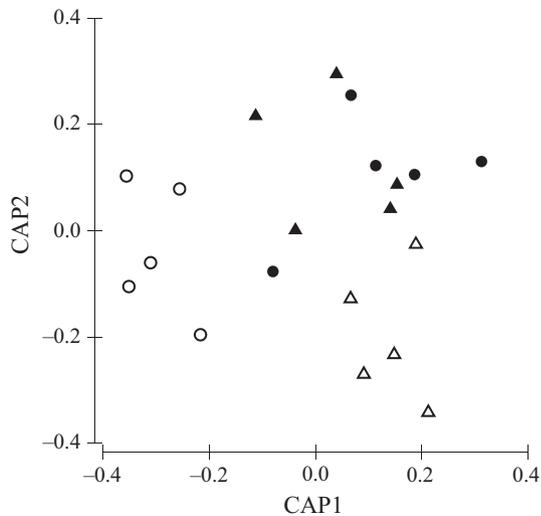


FIGURE 3 Canonical analysis of principal coordinates ordination of the flower-visitor assemblage for the site types: PA.Absent vegetation type, sites in the protected area and without *R. cuneifolius* (solid triangles); PA.Present, sites in the protected area that are invaded by bramble (open triangles); RGP.Absent, sites in the remnant grassland patches that are not invaded by bramble (solid circles), RGP.Present, sites in the remnant grassland patches that are invaded by alien *R. cuneifolius* (open circles)

Bees were positively associated with the presence of *R. cuneifolius* (Figure 5), with *Apis mellifera* making up 89.25% of the bees sampled and 96.39% of the *A. mellifera* visitations were recorded on bramble. Butterflies were most affected by invasion of *R. cuneifolius* within PAs, being the dominant flower visitors to *H. cymosum* in uninvaded sites,

but with flies being the dominant visitors to *H. cymosum* in invaded PAs (Figure 5). Butterflies are low in uninvaded RGP sites, but nearly disappear from RGPs when bramble is present (Figure 5). Invaded sites had significantly lower modularity than uninvaded areas (Table 1; Figure 2), but there was no significant difference in modularity of sites based on location (whether in PA or RGP) and there was no interactive effect between location and bramble (Table 1). No other index differed significantly between treatments (Table 1).

4 | DISCUSSION

The threats of habitat transformation and invasion by alien species can alter both biological pattern and process. Here, we found that although pattern was not always obviously impacted by these disturbances, process was. Plant species composition showed no significant alteration of community assemblage between habitat type or invasion status, but flower visitation did show significant differences. Interestingly, flower-visitor networks indices varied little between treatments, except for modularity, which was lower in invaded sites.

American bramble can have negative effects on local biodiversity within the areas it invades (van Wilgen, Reyers, Le Maitre, Richardson, & Schonegevel, 2008). Despite this, bramble had a negligible effect on flower diversity, floral surface area (as a measure of floral resource) and composition in study sites. However, flower-visitor assemblages differed significantly between sites in plantation forestry and the nearby PA, as well as those with bramble and without.

That invaded and uninvaded areas have similar floral community composition, but different flower-visitor communities may arise

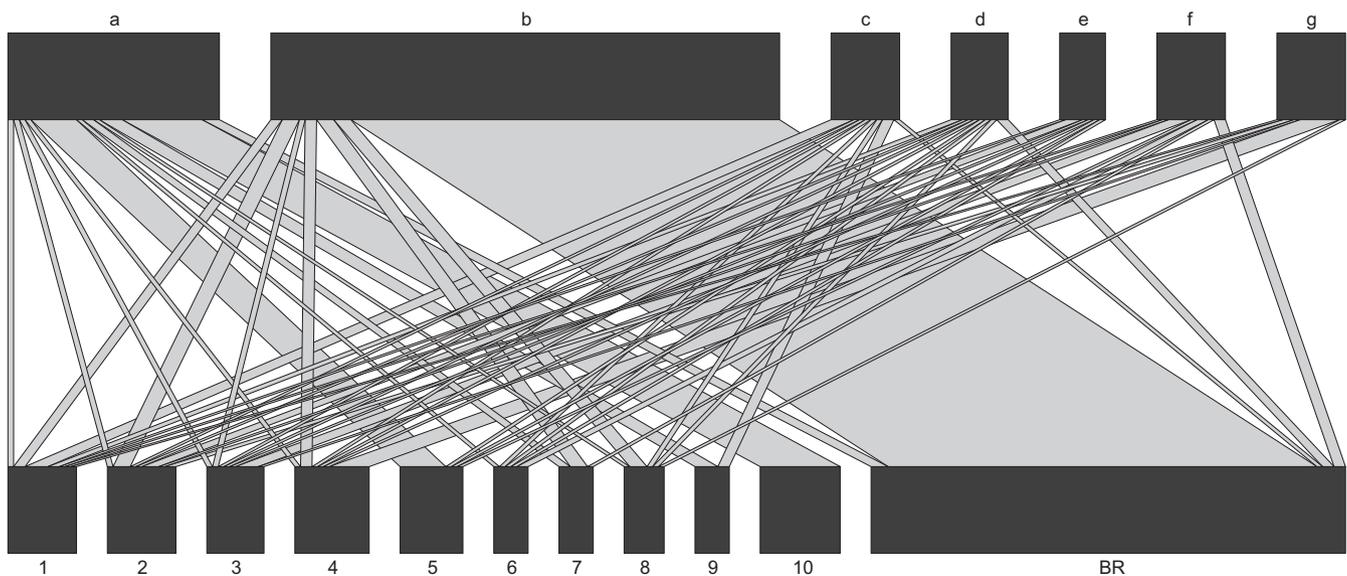


FIGURE 4 Flower visitation network showing the interaction between the focal plant species and their flower visitors, the networks were combined for all sites and morphospecies grouped for illustrative purposes. The width of the links is proportional to the number of interactions observed. The visitation morphospecies have been grouped into (a) Coleoptera; (b) bees/Apoidea; (c) wasps/Hymenoptera excl. bees; (d) Diptera; (e) Hemiptera; (f) Lepidoptera; and (g) Culicidae. (1) *Helichrysum pallidum*, (2) *Helichrysum cymosum*; (3) *Senecio bupleuroides*; (4) *Senecio tamoides*; (5) *Acalypha peduncularis*; (6) *Pentanisia prunelloides*; (7) *Eriosema squarrosus*; (8) *Senecio elegans*; (9) *Lobelia flaccida*; (10) *Hypoxis hemerocallidea*. BR, Bramble (*Rubus cuneifolius*)

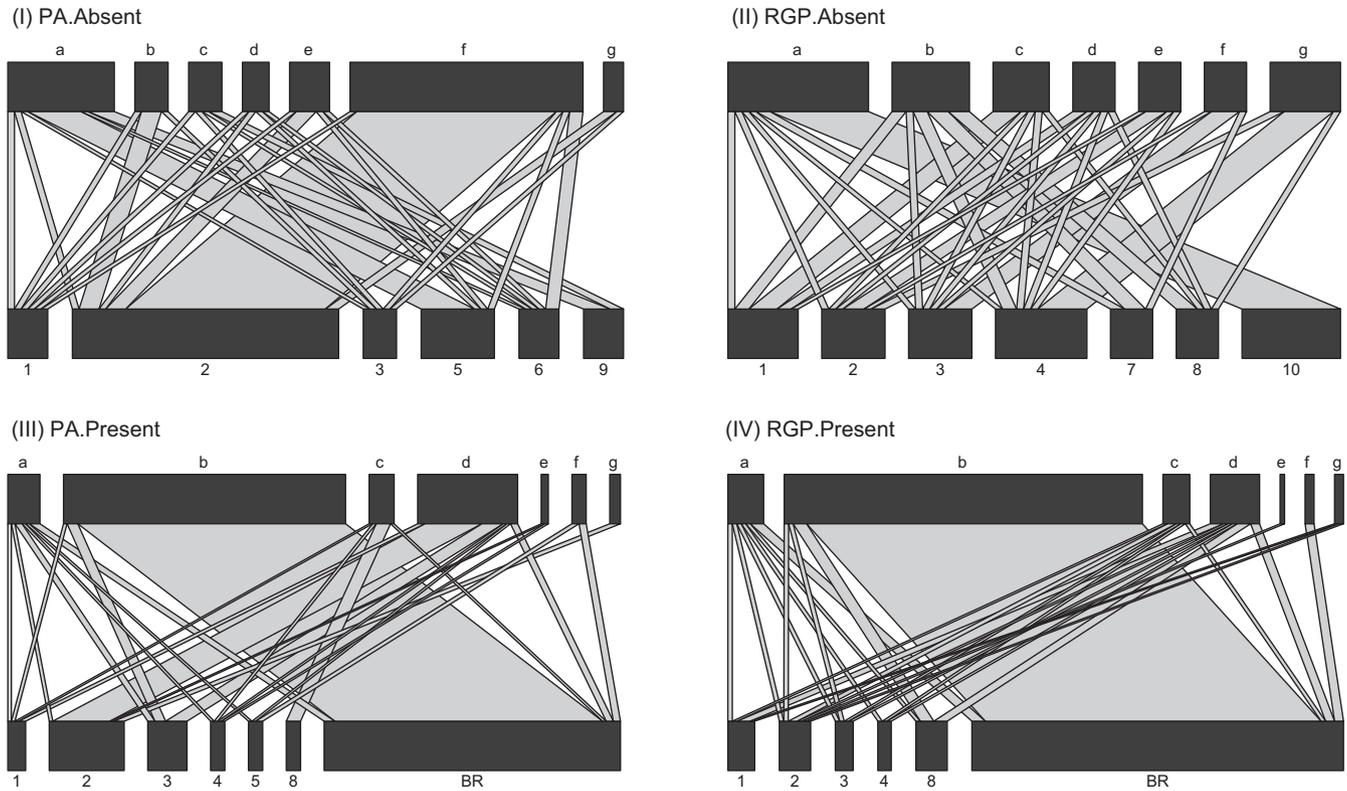


FIGURE 5 Flower-visitor interaction network structure in the site types, the networks were combined for all sites and morphospecies groups for illustrative purposes; (I) PA.Absent, (II) RGP.Absent, (III) PA.Present, and (IV) RGP.Present. The width of the links is proportional to the number of interactions observed. The flower-visitor morphospecies have been grouped in to (a) Coleoptera; (b) bees/Apoidea; (c) wasps/Hymenoptera excl. bees; (d) Diptera; (e) Hemiptera; (f) Lepidoptera; and (g) Culicidae. (1) *Helichrysum pallidum*, (2) *Helichrysum cymosum*; (3) *Senecio bupleuroides*; (4) *Senecio tamoides*; (5) *Acalypha peduncularis*; (6) *Pentania prunelloides*; (7) *Eriosema squarrosum*; (8) *Senecio elegans*; (9) *Lobelia flaccida*; (10) *Hypoxis hemerocallidea*. BR, Bramble (*Rubus cuneifolius*)

because most alien plant species arrive in areas without their natural pollinators but thrive in the presence of generalist pollinators, with very few documented cases of alien plants failing to reproduce due to the absence of pollinators (Richardson, Allsopp, D'Antonio, Milton, & Rejmánek, 2000). As generalist flower visitors are more likely to visit alien plant species than specialists, it follows that invaded areas should have more generalist flower-visiting species than specialists and therefore, a different species composition than uninvaded areas. Although flower species composition may not have changed markedly, the presence of alien species may be sufficient to elicit a response in the composition of the flower-visitor community. Future studies should investigate how the visitation patterns described in this study affect fruit formation and seed set of native plants in these altered environments. Indeed, changes in flower visitation might not necessary reflect changes in pollination services (Tur, Castro-Urgal, & Traveset, 2013). However, even if changes in pollinator diversity and composition might not affect average pollination services, they might also alter the stability of pollination in response to environmental changes (Brittain, Kremen, & Klein, 2013; Cariveau, Williams, Benjamin, & Winfree, 2013).

Flower visitation networks did not differ between locations or invasion in terms of mean number of shared partners for flower visitors and focal flower species, connectance, nestedness and Shannon diversity of interactions. This is similar to other studies that have shown that

the overall network can remain unaffected despite changes in species composition (Petanidou, Kallimanis, Tzanopoulos, Sgardelis, & Pantis, 2008). Modularity, however, showed significant differences between invaded and non-invaded sites. Modularity is a measure of network compartmentalization, that is, of whether interactions are more common within compartments than between compartments (Bahram, Harend, & Tedersoo, 2014). If an interaction network is very modular, it indicates that within the network, there are different groups of nodes performing different functions, and these groups have some degree of independence from one another (Guimerà & Amaral, 2005; Holme, Huss, & Jeong, 2002). The reduced modularity associated with invasion by *R. cuneifolius* therefore points to loss of independence between nodes, with concomitant loss of robustness, flexibility and stability of ecosystem processes (Guimerà, Sales-Pardo, & Amaral, 2004; Hartwell, Hopfield, Leibler, & Murray, 1999), potentially pollination in this case. These results therefore suggest that bramble-invaded sites will have a diminished ability to cope with disturbances, reducing the conservation value of the landscape and putting the biodiversity at risk.

Connectance and nestedness did not differ between locations or invasion status. Connectance measures the proportion of all possible interactions within a system that are realised (Gardner & Ashby, 1970). More complex communities that have many highly connected species will be more stable to outside influences than simple

communities with fewer highly connected species (Dunne et al., 2002b) and have increased stability (O'Gorman, Jacob, Jonsson, & Emmerson, 2010). Nestedness measures of unevenness of interactions, with highly-nested networks generally comprised of both generalists and specialists, where specialist species interact mostly with generalist species and not with other specialists (Bahram et al., 2014). Here, we found that grasslands maintain their FVN connectance and nestedness, even when invaded by bramble or fragmented by forestry.

Changes in species composition of flower visitors can yield some insights. Butterflies have long been used as ecological indicators of ecosystem health in many regions of the world as they are sensitive indicators of landscape change (Brown & Freitas, 2000; Oostermeijer & van Swaay, 1998; Thomas, 1991). Numerous studies have found that butterfly abundance and diversity declines when there is invasion by alien plant species (e.g., Florens, Mauremootoo, Fowler, Winder, & Baide, 2010; Skórka, Settele, & Woyciechowski, 2007). Butterflies had lower abundance within PAs invaded by bramble and were completely absent in RGP sites that had been invaded, suggesting that bramble has reduced habitat quality, particularly in fragmented patches. The absence of butterflies in RGP sites suggests that the combination of small patch size and alien plant invasion make these sites unable to support viable butterfly populations. The loss of butterflies likely has implications not only for the larval plants and species that butterflies visit but also for butterfly predators and parasitoids, so there are effects on both mutualistic and trophic networks. Interestingly, Diptera showed increased abundance in areas where butterflies had declined or disappeared. The increase in Diptera in the presence of exotic vegetation has been observed elsewhere (Breytenbach, 1986). These changes to flower–visitor communities means that certain plants will benefit over others, as pollinators vary in their efficiency for different plant species (Kevan & Baker, 1999). Bees, on the other hand, showed a major preference for brambles. The honeybee, *A. mellifera*, drove this response, which visited the brambles in over 95% of the *A. mellifera* visitations recorded here. There are few crops in the area, and the timber plantation is dominated by non-flowering *Pinus* spp. It seems likely that the *A. mellifera* observed here are wild bees that were making use of the additional food source provided by an invasive plant species. This interaction may be enabling bramble to flourish in this new environment and might lead to the impoverishment of local bee pollinated plant species (Gibson et al., 2013).

Previous studies in our study area have found that these 30- to 40-year-old RGP are sufficiently large, edge effects can be minimized, and if the patches can retain natural heterogeneity, then arthropod assemblages can be similar in composition to PAs (Pryke & Samways, 2012a, 2012b, 2015). This includes a study on pollinators (Bullock & Samways, 2005). Here, flower abundance and flower surface area were greatest in RGP sites and lowest in PA sites, seemingly indicating that commercial forestry plantations have a positive effect on these commonly found flower species. This could be due to higher other plants species levels in the PA sites or the 10 focal species are flowering more in the RGP sites. Although we found no significant effect of bramble on flower abundance or

surface area, our surveys included only the ten most common native flowering species. Thus, although there may be effects of fragmentation and invasion on rarer plant species, our study was not designed to detect those. Flower–visitor richness was also unaffected by bramble, location and the interactive effects between bramble and location. The results here indicates that these remnant areas are effective in mitigating the effects of land transformation and fragmentation, allowing most of the biodiversity within transformed landscapes to remain, although this might be an artefact of the study design excluding the rarest plants.

The results of this study show that RGP are a useful conservation tool within transformed landscapes, which would otherwise support very little native biodiversity. Uninvaded RGP and PAs had similar FVN indices, suggesting that flower–visitor networks are largely maintained in these well-connected patches. The largest impact remains the invasion of an alien flowering species, which disrupts the FVNs, reducing the conservation value of both PAs and RGP. When there is invasion by *R. cuneifolius* within RGP, these areas experience a loss of specialist flower–visitor species and subsequent replacement by more generalist species. A combination of factors involving the floral traits and plant architecture of brambles lead to different flower visitors and, thus, altered flower–visitor assemblages in invaded areas. Therefore, the removal of *R. cuneifolius* within RGP is crucial for their success in alleviating the effects of habitat transformation, specifically commercial forestry, on functionality of grasslands. As floral network indices for uninvaded patches here are better than those of invaded areas, the removal of *R. cuneifolius* should not have any negative effect on these networks (as suggested by Ferrero et al., 2013) and it should restore modularity and therefore bring about better resilience to the natural FVN. In this landscape, the removal of *R. cuneifolius* must be prioritised over fragmentation to ensure complex, robust and stable ecosystems which are resistant to outside disturbance in the face of a biodiversity crisis.

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DATA ACCESSIBILITY

The raw data files on species occurrences and environmental data are available from Fig Share: <https://doi.org/10.6084/m9.figshare.5346082>.

The raw data files on species occurrences and flower visitation are available from Fig Share: <https://doi.org/10.6084/m9.figshare.5346082>.

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BIOSKETCH

This work is the result of a collaboration between researchers from four different institutions on functional biodiversity in a changing world. This collaboration focuses on promoting ecosystem function in transformed landscapes, particularly agriculture and forestry.

Author contributions: S.H. was an MSc student supervised by J.P., F.R and C.S. S.H visited E.T. and F. van V. to analyse the interaction network structures. J.P., F.R., C.S. and S.H. conceptualized the project, S.H. did the fieldwork, S.H., E.T., J.P. and F. van V. helped with the data analyses. S.H. lead the writing of the manuscript, with contributions from all authors.