RESEARCH ARTICLE

Journal of Vegetation Science ⬥ IAVS

Effects of fragmentation on the plant functional composition and diversity of remnant woodlands in a young and rapidly expanding city

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Abstract

Questions: How do plant functional trait abundance and diversity in urban remnants of a rapidly urbanizing city change with fragmentation? Is there a delayed functional response to fragmentation?

Location: Thirty remnant *Banksia* woodlands, Perth, Australia.

Methods: We used GLMM to examine the effects of remnant age and area, and their interaction, on the relative abundance and functional diversity (FD) of five plant functional traits: growth form, pollination, seed dispersal, nutrient acquisition and regeneration strategies. We then used fourth-corner analysis to examine the influence of a wider set of fragmentation-related factors on trait abundances.

Results: The functional composition and diversity of *Banksia* woodlands changed with remnant age, particularly in the smaller remnants. Plants more prone to decline with remnant age were the growth form shrubs, root-clustered trees, herbaceous obligate seeders and understorey species that are insect-pollinated, have seeds dispersal internally by animals and have arbuscular or ericoid mycorrhizas. In contrast, plants more prone to persist were growth forms trees, sedges and rushes, ectomycorrhizal trees, herbaceous resprouters, wind-pollinated and root-clustered understorey species. FD increased with remnant age in the growth forms and overstorey, but declined among the herbaceous and shrub pollination and nutrient acquisition traits.

Conclusions: Functional traits that consistently signalled the plant community response to fragmentation were growth form, pollination and dispersal. This functional response was largely delayed, suggesting a "functional extinction debt", which will lead to a further decline of plants with vulnerable trait states in the future, especially in the small- and medium-sized remnants. Our study illustrates the vulnerability of small remnants to changes in community assembly and ecosystem function due to fragmentation. Furthermore, it exemplifies how a functional trait approach is valuable to understand the impacts of urbanization on remnant plant communities, before local extinctions may occur. Finally, the study shows how cities' fragmentation history and biogeographic settings provide an important context influencing plant functional responses to urbanization-related processes.

1 | INTRODUCTION

In the next four decades the world population is forecast to increase from 7.3 to 9.8 billion, a growth that will occur primarily in cities (United Nations 2014). This population increase and consequent urban expansion have major negative implications for biodiversity. Urbanization is a leading driver of habitat loss and fragmentation of native vegetation into small and isolated urban remnants (Hahs et al., 2009; Williams et al., 2009). These remnants can be relatively intact, yet undergo a slow process of change in response to fragmentation and anthropogenic disturbances (e.g., Williams, Morgan, McDonnell, & McCarthy, 2005; Ramalho, Laliberté, Poot, & Hobbs, 2014). Understanding this change is crucial to inform land-use planning and conservation management on how to minimize urbanization impacts on ecosystems and safeguard their long-term conservation capacity.

A functional trait-based approach has been recognized as a valuable framework to forecast the response of plant communities to environmental change (Lavorel & Garnier, 2002; Mouillot, Graham, Villéger, Mason, & Bellwood, 2012), and several studies have used it to understand changes in urban remnant vegetation (e.g., Williams et al., 2005; Vallet, Daniel, Beaujouan, Rozé, & Pavoine, 2010). However, despite the key underlying assumption that plant communities are the result of a hierarchical set of environmental factors that filter which species and traits, from a regionally available pool, can persist locally (Williams et al., 2009), these environmental factors are seldom explicitly considered. Instead, aggregated urbanization measures (e.g., density of roads) have been predominantly used (McDonnell & Hahs, 2008). Not considering individual factors might lead ecologists to conclude that particular functional traits are not responsive to urbanization, whereas they may in fact be influenced by unmeasured urbanization-related factors. It might also explain why comparative studies often show high variation in trait responses across different cities (e.g., Duncan et al., 2011). To further advance current understanding of the effects of urbanization on remnant functional ecology it is important to focus on specific urbanization-related factors and the mechanisms through which they filter plant communities (Williams, Hahs, & Vesk, 2015; Aronson et al., 2016).

Urban floras are affected by four main environmental filters – habitat transformation, fragmentation, urban environmental conditions and human preferences (Williams et al., 2009). Yet, in relatively young cities where urbanization is an important fragmentation driver (i.e., cities where extensive landscape transformation occurred after the 1800s and has been mostly associated with urban development; see Hahs et al., 2009), this is likely a major filter shaping remnant vegetation. Fragmentation reduces both the size and connectivity of remnants, influencing plant communities in two main ways, each involving a different set of environmental filters and plant traits. First, fragmentation affects the colonization–extinction dynamics of the plant species and the biotic agents that they rely on for seed dispersal and pollination (Aguilar, Ashworth, Galetto, & Aizen, 2006; Damschen et al., 2008). Second, fragmentation has an indirect effect via alteration of the disturbance regimes and local environmental conditions (Hobbs & Yates, 2003). In this case, traits related to resource acquisition and regeneration are likely to be predominantly affected (Lavorel & Garnier, 2002). For instance, increased soil fertility (e.g., due to run-off from surrounding paved areas or atmospheric deposition) might alter competitive hierarchies between species with different nutrient acquisition strategies (Lambers, Brundrett, Raven, & Hopper, 2010). Furthermore, increased fire frequency, which in mediterranean-type ecosystems is associated with the process of urbanization (Syphard, Radeloff, Hawbaker, & Stewart, 2009), might shift the relative abundance of resprouters and obligate seeders (Pausas, Bradstock, Keith, Jon, & The, 2004). Finally, fragmentation may also lead to trait convergence and thus reduced functional diversity (FD), as the species that remain through the environmental filtering process share trait values necessary for their survival under fragmented conditions (Sonnier, Jamoneau, & Decocq, 2014).

We examined the effects of fragmentation on the abundance and diversity of five plant functional traits in 30 remnant *Banksia* woodlands located in Perth, which is situated in the south-western Australian global biodiversity hotspot (Hopper & Gioia, 2004). The plant traits considered were growth form, pollination syndrome, seed dispersal, nutrient acquisition and regeneration strategies. These traits were selected because they influence plant responses to fragmentation (Kolb & Diekmann, 2005; Williams et al., 2005; Aguilar et al., 2006; Knapp, Kuhn, Stolle, & Klotz, 2010; Schleicher, Biedermann, & Kleyer, 2011). A previous study of these *Banksia* woodlands (Ramalho et al., 2014) showed a delayed response to fragmentation that was consistent with a species extinction debt (Kuussaari et al., 2009). Hence, we hypothesized that: (1) remnant age and its interactive effect with remnant area are important factors explaining the abundance and diversity of the selected traits; (2) historical remnant area is more relevant to explain plant trait abundances than current remnant area; (3) different trajectories of landscape change might also influence plant trait composition (Foster et al., 2003); (4) lower remnant area might lead to a decline in plant species that depend on biotic agents for pollination and seed dispersal (Aguilar et al., 2006; Damschen et al., 2008); (5) higher soil fertility might shift the competitive hierarchies between species with different nutrient acquisition strategies to the detriment of those best adapted to nutrient-impoverished soils (Lambers et al., 2010); and (6) higher fire frequency might favour

resprouters over obligate seeders (Bell, 2001). Our study sheds light on the key processes affecting the assembly of *Banksia* woodlands, which are federally listed as a threatened ecological community. Furthermore, our study contributes valuable knowledge for future reviews and meta-analyses of urbanization effects, providing patterns from a plant community and biogeographic settings that have not been extensively studied, and where urbanization is occurring incredibly fast.

2 | METHODS

2.1 | Study area and study sites

Our study was conducted in remnant *Banksia* woodlands of the Perth Metropolitan Area, Australia (31°57′18.64″S, 115°51′30.37″E; WGS84). Perth is a sprawling city with a population of two million that is estimated to reach 3.2 million by 2030 (Australian Bureau of Statistics 2015). The city was founded in 1829, and since the 1960s urbanization has been the main driver of *Banksia* woodland fragmentation. Remnants persist in a few large conservation and Crown Land areas on the current city boundaries, in small and isolated urban reserves, roadside verges and rural private properties. These woodlands have an open canopy dominated by *Banksia attenuata* R.Br. and *Banksia menziesii* R.Br., and other less abundant tree species including *Eucalyptus marginata* Sm. and *Allocasuarina fraseriana* (Miq.) L.A.S.Johnson. The species-rich understorey is dominated by sclerophyllous shrubs from the families Proteaceae, Myrtaceae and Fabaceae, and perennial herbaceous plants from the families Restionaceae, Cyperaceae and Haemodoraceae. Most non-native species are herbaceous and originate from the Mediterranean Basin and South African Cape Region (Dodd & Griffin, 1989).

We sampled 30 *Banksia* woodlands (study sites) located within a radius of 30 km from the city centre (Appendix S1). Remnant selection was based on a stratified sampling design considering three classes of remnant size (1–5 ha, 5–50 ha, >50 ha) and four classes of time since urbanization (urbanized by 1965, 1985, 2006, still in a rural matrix). Three remnants belonging to each size and time since urbanization class were randomly selected. From the potential sample of 36 remnants, only 30 were selected because there were fewer than three remnants available in some classes. In particular, no remnants urbanized by 1965 and >50 ha were available. Three, five and seven plots were randomly located in each remnant with 1–5 ha, 5–50 ha and >50 ha, respectively. A total of 130 plots were surveyed. Plots were composed of nested circular areas where different variables were estimated. These circular areas consisted of two concentric circles of 11.0-m and 5.5-m radius, plus three circles of 1.5-m radius located in the north, south and randomly selected east or west inner sides of the 5.5-m circle (see plot configuration in Appendix S2). All plots were located at least 25 m from the remnant edge, 5 m from main tracks and had not been burned in the previous 5 years (Ramalho et al., 2014).

2.2 | Vegetation survey

We surveyed remnant vegetation in the spring and early summer of 2008 and 2009. Within each plot, all vascular plants were recorded and their relative abundances visually estimated using 13 classes of cover (+; <1%; 1%; 1%–4%; 5%–9%; 10%–14%; 15%–19%; 20%–24%; 25%–34%; 35%–49%; 50%–74%, 75%–89%, 90%–100%). Woody and herbaceous species were recorded in the 5.5-m and 1.5-m radius circles, respectively. Mean percentage cover per species per plot was calculated by taking the mean of each cover class (a value of 0.1 and 0.5 was attributed to the classes of ″+″ and ″<1%″, respectively). In the case of herbaceous species, data obtained in the three 1.5-m radius circles were averaged at the plot level.

2.3 | Environmental variables

2.3.1 | Landscape fragmentation dynamics

We estimated current remnant area (2006) using a 2006 vectorial remnant vegetation map provided by the Western Australian Department of Planning, and historical remnant area (1965) through photo-interpretation of 1965 aerial photographs. Remnant age (in years) was assessed through observation of aerial photos, Landsat imagery and historical maps, and was estimated using three criteria. First, if a remnant was created through a single clearing event, then the year of that clearing was considered the date of fragmentation. Second, if a remnant was gradually reduced in size over time through different clearing events, then the year in which the remnant was cleared to a size no greater than twice the current one was considered the date of fragmentation. We used this criterion to identify the clearing event that was mostly responsible for the spatial configuration of the remnant at the time of the survey. Third, remnants isolated for 45 years or more were given an age of 45 years, given the scarcity of older records available. Finally, we classified remnants into three classes of landscape fragmentation trajectory: (1) urban remnants historically fragmented for agricultural development (trajectory rural–urban), (2) urban remnants fragmented for urban development (trajectory woodland–urban) and (3) remnants still located in a rural matrix (trajectory rural–rural).

2.3.2 | Local environmental conditions and disturbance regimes

We estimated fire frequency in the past 30 years for each plot through observation of aerial photos, Landsat imagery and records of land management agencies. Furthermore, we assessed intensity of recreation-induced trampling within the 11-m radius sampling plot using a semi-qualitative index that was calculated using two questions: (1) are there diffuse, narrow, vegetated ″goat″ tracks? (2) are there narrow cleared tracks? These questions were scored from zero to five in ascending order of significance in the plot (0 = absent; 1 = very low; 2 = low; 3 = intermediate; 4 = high; 5 = very high). A final composite variable was calculated

by summing the two scores and dividing by ten, the total maximum value. To assess soil fertility, we randomly collected surface soil samples (0–10-cm depth) in the 5.5-m radius sampling circle, using a 3.5-cm diameter auger, bulked together, and sent to CSBP Soil and Plant Analysis Laboratories (Perth) for soil chemical analyses [Colwell P, extractable S, Colwell K, Walkley Black percentage organic C, NO_3, NH_4 and pH (in H_2O)]. Then, we conducted a PCA of these soil properties (Appendix S3). The first PCA axis represented a gradient of soil fertility (36.4% of variation explained) and was used as such in the data analyses. Ecosystem management is likely to influence the functional trait composition of the study remnants. However, we were not able to obtain consistent information about it across all the study sites; therefore, it could not be considered.

Environmental variables were not strongly correlated (|0.01| < Pearson correlation coefficient < |0.52|), with the exception of the negative relationships between "historical remnant area" and (1) "trajectory rural–urban" (ANOVA, $r = -.81$, $F = 56.75$, $p < .0001$) and (2) "remnant age" (Pearson correlation coefficient = -0.71). These relationships are likely because in areas that were settled first and where vegetation was cleared longer ago, the predominant fragmentation driver was agricultural development. By 1965, most of these areas were urbanized and the remnant vegetation left was reduced to small patches (older remnants).

2.4 | Plant functional traits

We collected functional trait data (Appendix S4) for all vascular plant species with an estimated cover >5% in at least one of the sampling plots (102 out of 292 sampled species) and all those with an estimated cover between 2% and 4% occurring in >25% of the sampling sites (total of 124 species; Appendix S5). Definition of these thresholds was based on careful observation of the species abundance data, and aimed to focus the functional analysis on the species that more significantly contributed to plant cover at plot and landscape level. Only traits states (classes within each functional trait) with average relative abundance ≥5% were considered for data analysis (Appendix S4). Trait information was assembled from several sources, including literature on regional flora, biological databases, expert knowledge and unpublished field data collected and observed in the study area (Appendix S6). In the few cases (<5%) where trait information was not available at the species level, information at the genus and family level was used. Multiple categorical classifications were allowed.

2.5 | Data analysis

We used GLMMs with Gaussian distribution (Zuur, Ieno, Walker, Saveliev, & Smith, 2009) to examine the effect of remnant age and area, and their interaction, on the relative abundance and FD of the selected traits. The relative abundance of each trait state was calculated as the relative abundance of species bearing each trait state at plot level (i.e., community-weighted mean; Garnier et al., 2004). FD for each trait and the overall plant community was

calculated using the Rao's quadratic entropy (Rao Q; Rao, 1982). Community-weighted mean and RaoQ describe the mean and the dispersion of functional traits within a given species assemblage, respectively (Ricotta & Moretti, 2011). In the GLMMs, remnant was used as a random effect, and remnant age, current area and their interaction term, as fixed effects. Predictors were centred on their means so that coefficients could be interpreted as the amount of change in the response variable following a unit change in the predictor, holding other predictors constant at their mean values (Aiken & West, 1991).

We used the fourth-corner method (Dray & Legendre, 2008) to assess how all environmental factors affected the relative abundance of each trait state. This method quantifies the relationship between three separate matrices: a species abundance per site matrix (L), an environmental variable per site matrix (R) and a species trait matrix (Q). The significance of the correlation between variables is determined by permutation testing (999 permutations), followed by adjustment of the resulting p-values using Holm's procedure for multiple testing (Holm, 1979). The permutation model can vary depending on the ecological model, and in this study we chose the permutation model 1, which assumes that species distributions are primarily determined by environmental conditions, and permutes each row (species) of matrix L independently (Dray & Legendre, 2008).

We used scatterplots to depict the relationship between the relative abundance/FD of each trait and remnant age, for the three classes of remnant area used in the survey design (1–5 ha, 5–50 ha, >50 ha). The significance of these relationships was tested using linear regression. We conducted the GLMMs and fourth-corner method with all species together for the growth forms' analysis, and then separately for the overstorey and understorey, shrubs and herbaceous layers, given the different life history of these groups and potentially different relevant environmental filters. Data analysis was conducted in the R Environment (v 3.3.2, R Foundation for Statistical Computing, Vienna, AT). Plant trait relative abundances and FD were calculated using the package FD (Laliberté & Legendre, 2010). GLMMs and fourth-corner analysis were conducted using the packages lme4 (Bates, Maechler, & Bolker, 2011) and ade4 (Dray & Dufour, 2007), respectively.

3 | RESULTS

3.1 | Changes in plant trait abundances

The relative abundance of several plant trait states was lower in the older and historically small remnants (Tables 1, 2, Fig. 1). These included growth form shrubs, root-clustered trees and understorey plants that are insect-pollinated, have seeds dispersal internally by animals, and have arbuscular or ericoid mycorrhizas. In contrast, other trait states reached higher relative abundances in those remnants. These included growth forms trees, sedges and rushes, ectomycorrhizal trees, wind-pollinated and root-clustered understorey plants. The older remnants also had higher abundances of

TABLE 1 Results of the GLMM. These models tested the interactive effect of remnant age and current remnant area on (I) the relative abundance and (II) functional diversity of the selected plant functional traits

	Remnant age (years)	Current remnant area (ha)	Remnant age x area
(I) Trait relative abundances			
Growth form			
Shrub	−0.0054**	n.s.	0.0114***
Tree	n.s.	n.s.	−0.0080***
Sedge and rush	0.0032***	0.03612*	n.s.
Overstorey			
Nutrient uptake strategy			
Root cluster	−0.0067*	n.s.	n.s.
Ectomycorrhizal	0.0073**	n.s.	n.s.
Understorey			
Pollination syndrome			
Insect pollination	−0.0051**	n.s.	n.s.
Wind pollination	0.0034*	n.s.	n.s.
Seed dispersal			
Unassisted dispersal	n.s.	0.0526*	n.s.
Wind dispersal	−0.0026*	−0.0556*	n.s.
Internal animal transport	−0.0020**	n.s.	n.s.
Nutrient uptake strategy			
Arbuscular mycorrhizal	−0.0035*	n.s.	n.s.
Root cluster	0.0075***	n.s.	n.s.
Ectomycorrhizal	n.s.	n.s.	0.0039*
Ericoid mycorrhizal	−0.0020**	n.s.	n.s.
(II) Functional diversity			
Growth form	n.s.	n.s.	−0.0082*
Overstorey			
All traits	n.s.	n.s.	−0.0015*
Pollination syndrome	n.s.	n.s.	−0.1122*
Nutrient uptake strategy	n.s.	n.s.	−0.0813*

Only trait states with average relative abundance ≥5% and with significant relationships with the fixed factors are shown. Standardized β and *p*-values are provided (n.s., not significant; *p < .05; **p < .01; ***p < .001).

herbaceous resprouters than obligate seeders (Appendices S7, S8). The GLMMs further indicated an interactive effect between remnant age and area on three trait states: the decline of shrubs relative abundance with time since isolation was more accentuated in the smaller remnants, whereas only in these remnants was a greater abundance of trees and lower abundance of ectomycorrhizal understorey species observed (Table 1).

The relative abundance of growth form herbs, and understorey plants that are bird-pollinated, have unassisted or wind seed dispersal did not change with remnant age, but was influenced by remnant area (Table 2). Historically small remnants had more herbs and less understorey bird-pollinated plants. The latter were also less abundant in currently small remnants, which in addition, had less understorey plants with dispersal-unassisted seeds (84% of the understorey) and more with wind-dispersed seeds.

The landscape fragmentation trajectory was related to shifts in some trait state abundances. Growth form shrubs and understorey plants with all nutrient acquisition strategies but root clusters and ericoid mycorrhizas were more abundant in remnants directly fragmented for urbanization. Conversely, growth forms trees, sedges and rushes were less abundant in those remnants. Moreover, rural remnants had more grasses and root-clustered trees, and less ectomycorrhizal trees, N-fixing and root-clustered understorey plants (Table 2).

Abundance of root-clustered trees was negatively related with soil fertility, whereas the opposite pattern was found for mycorrhizal trees. However, such a pattern was not observed in the understorey. Additionally, no significant effects of fire frequency were observed on the relative abundance of resprouters and obligate seeders, even when these two vegetation layers were analysed separately (Appendix S8).

3.2 | Changes in plant FD

The FD of growth forms increased slightly with remnant age in the small remnants. The same pattern was observed in the overstorey, including within the pollination and nutrient acquisition traits (Table 1, Fig. 2). Significant patterns in the understorey were only observed when shrubs and herbaceous layers were analysed separately (Appendix S8). The FD of the herbaceous layer declined slightly with remnant age. A similar pattern was observed in the pollination and nutrient acquisition traits of the shrub layer, but only in the small remnants.

4 | DISCUSSION

Our study suggests a time-lagged functional response to fragmentation in remnant *Banksia* woodlands. Indeed, changes in the relative abundance of most plant traits, and to a lesser extent in FD, were explained by remnant age, and were more rapid in smaller remnants and among herbaceous plants. These patterns consistently suggest a delayed plant response to fragmentation (Piqueray et al., 2011; Saar, Takkis, Pärtel, & Helm, 2012), and are in accordance with Ramalho et al. (2014), who observed a similar time-lagged pattern in the plant species diversity of the same woodlands. Importantly, the results indicate that further decline in the abundance of plants with more vulnerable trait states (i.e., growth form shrubs, root-clustered trees, herbaceous obligate seeders and understorey species that are insect-pollinated, have seeds dispersal internally by animals and

TABLE 2 Summary of the fourth-corner analysis

	Landscape fragmentation dynamics						Disturbance regimes and environmental conditions		
	Remnant age (years)	Historical remnant area (ha)	Current remnant area (ha)	Trajectory rural–urban	Trajectory woodland–urban	Trajectory rural–rural	Fire frequency	Trampling	Soil fertility
Growth form									
Shrub	–**	+**		–**	+**		+**	–*	–**
Tree	+*	–**		+**	–**		–**		+**
Sedge and rush	+**	–**		+**	–*				
Herb		–*							
Grass						+**	–*		
Overstorey									
Nutrient acquisition strategy									
Root cluster	–**	+**		–**		+*		–**	–*
Ectomycorrhizal	+**	–**		+**		–*		+**	+*
Understorey									
Pollination syndrome									
Insect pollination	–**	+**		–**					
Wind pollination	+*	–**		+*					
Bird pollination		+*	+*				+*	–*	–*
Seed dispersal									
Unassisted dispersal			+*				+*		
Wind dispersal			–*	–*					
Internal animal transport	–**	+*						–*	–**
Nutrient acquisition strategy									
Arbuscular mycorrhizal	–*	+**		–**	+*				
Root cluster	+**	–**		+**		–**	+**	+*	+*
N-fixing					+**	–**			+*
Ectomycorrhizal				–*	+**				
Ericoid mycorrhizal	–**	+**						–*	–**

Significant relationships between each functional trait state and the environmental factors in the 30 remnant *Banksia* woodlands are shown. Positive relationships are indicated with a positive (+) sign and negative relationships are indicated with a negative (–) sign. Only trait states with average relative abundance ≥5% and with significant relationships with the environmental factors are represented (p-values: * p < .05; ** p < .01).
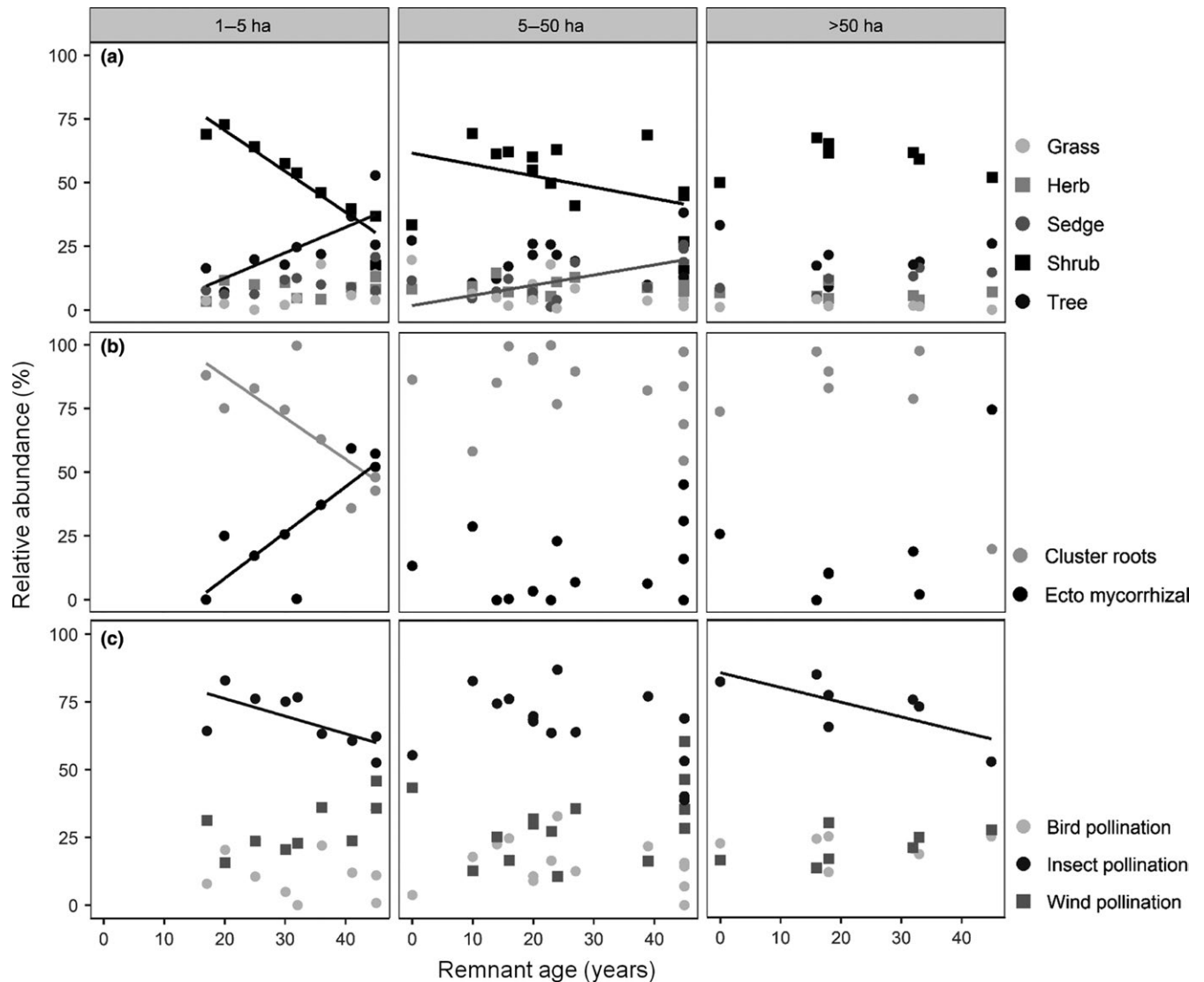
FIGURE 1 Relationship between plant trait relative abundances and remnant age. Scatterplots of the relationship between trait relative abundances and remnant age, for the three classes of current remnant area used in the survey design (1–5 ha, 5–50 ha, >50 ha): (a) growth forms, (b) nutrient acquisition strategies in the overstorey plant community and (c) pollination syndrome in the understorey plant community. Lines represent significant relationships (*p* < .05)

have arbuscular or ericoid mycorrhizas) can be expected in the future, especially in the smaller remnants.

4.1 | Functional responses to remnant age, remnant area and landscape fragmentation trajectory

Shifts in (sub)-dominant growth forms with remnant age provide insights into how the structure and composition of *Banksia* woodlands change in the urbanizing landscape. First, the dense shrub layer that is characteristic of these woodlands steadily declined in the smaller remnants, from an average relative abundance of 70% in recently isolated remnants to 30% in remnants that have been isolated for ~50 years. This rapid decline suggests the impact of multiple synergistic factors, including edge effects, visitor-induced trampling, disruption of the fire regimes and plant diseases (Kemper, Cowling,

& Richardson, 1999; Moxham & Turner, 2011). Second, the higher relative abundance of trees in the smaller remnants may result from a greater soil resource availability in these remnants (Ramalho et al., 2014), possibly due to run-off from surrounding paved and fertilized areas (Kaye, Groffman, Grimm, Baker, & Pouyat, 2006). Third, the increased relative abundance of sedges and rushes may be due to the predominance in this group of tough leaves, clonality and the associated ability to form large, dense mats. These traits are recognized as being associated with local persistence and better competitive ability under increasing disturbance (Piqueray et al., 2011; Saar et al., 2012).

The synergistic effects of fragmentation in the smaller remnants, including the observed decline in shrub abundance, are likely to increase the availability of niches (see Ricotta & Moretti, 2011), which are taken by disturbance-tolerant native and non-native species,
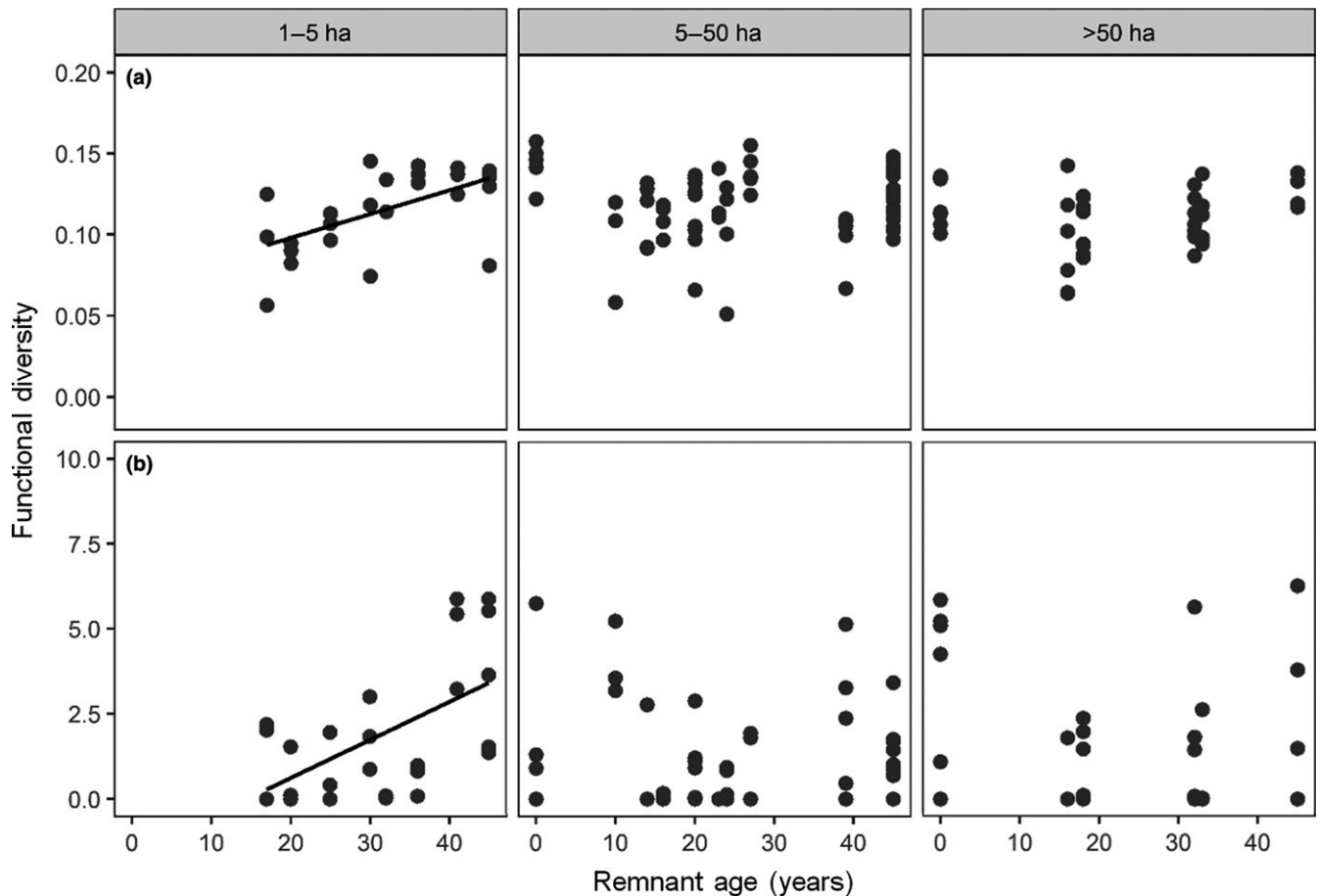
FIGURE 2 Relationship between functional diversity and remnant age. Scatterplots of the relationship between FD (RaoQ) and remnant age, for the three classes of current remnant area used in the survey design (1–5 ha, 5–50 ha, >50 ha): (a) growth forms and (b) nutrient acquisition strategy of the overstorey. Lines represent significant relationships ($p < .05$)

mostly grasses and herbs. This may explain the observed increased FD of growth forms with remnant age. Similar patterns of increased FD with fragmentation have been observed by Wu, Liu, and Qian (2013). Despite this, and contrary to other studies (e.g., Moxham & Turner, 2011), we did not observe significant shifts in the dominance of grasses and herbs with remnant age or area, which may be due to a confounding effect played by weed management practices undertaken across most urban reserves. In the rural remnants, though, lower weed management efforts and greater proximity to farmland may explain their higher abundance of grasses.

The overstorey of the older *Banksia* woodlands had a higher FD (only the smaller remnants) and higher dominance of ectomycorrhizal trees (including the wind-pollinated *A. fraseriana*) to the detriment of root-clustered *Banksia* trees, when compared to recently isolated remnants of the same size. Similar changes have been observed in a repeat survey (60-year interval) undertaken in one of the oldest and largest remnants in Perth (Crosti, Dixon, Ladd, & Yates, 2007), and may be due to several factors negatively affecting *Banksia* species. First, both *B. attenuata* and *B. menziesii* are relatively sensitive to drought and fluctuations in the water table (Canham, Froend, & Stock, 2009). Decreasing groundwater levels, due to extraction for public metropolitan supply and on-going

drying climate (Commander & Hauck, 2005), have caused regional-scale *Banksia* mortality (e.g., Groom, Froend, & Mattiske, 2000). Second, both *Banksia* species are sensitive to *Phytophthora cinnamomi*, a plant pathogen that is associated with disturbance and has renowned negative impacts on *Banksia* woodlands (Shearer & Dillon, 1996). Third, increased fire frequency may lower seed production and hamper recruitment in *B. attenuata* (Enright, Marsula, Lamont, & Wissel, 1998).

Shifts in the abundance of different pollination modes in the understorey were consistent with other studies, showing that fragmentation has a more negative effect on insect pollination than other pollination types (Kolb & Diekmann, 2005; Aguilar et al., 2006; Winfree, Aguilar, Vázquez, LeBuhn, & Aizen, 2009). Reduction of remnant size limits dispersal of insect pollinators, leading to a reduction in pollinator visits, and consequently to pollen limitation (Winfree et al., 2009). The fact that historical rather than current remnant area was associated with the decline of insect-pollinated plants suggests a delayed response to pollen limitation (Rusterholz & Baur, 2010). Yet, other factors may also contribute to the decline of insect-pollinated plants in urban landscapes (Harrison & Winfree, 2015). For example, soil disturbance may lead to the decline of ground-nesting insect pollinators (Cane, Minckley, Kervin,

Roulston, & Williams, 2006). Furthermore, remnants in more heavily urbanized areas are more likely to suffer pollen limitation than those in less urbanized and rural areas (Pauw, 2007), where there is higher availability of floral resources (Harrison & Winfree, 2015). The higher availability of mature trees and relatively larger and more diverse gardens in Perth's older suburbs compared to the younger suburbs, may in fact explain why we did not observe a decline of bird-pollinated plants in the older remnants. These floral resources are important for urban-tolerant nectarivorous birds, whose ability to persist in the urban landscape (Davis, Gole, & Roberts, 2013) may buffer the decline in pollination services provided by urban-sensitive birds. Finally, the higher abundance of wind-pollinated plants in the older remnants is consistent with other studies (e.g., Knapp et al., 2010), although other patterns have also been observed (see Williams et al., 2015).

The majority of the understorey native plants in *Banksia* woodlands lack specialized seed dispersal mechanisms, and seeds tend to stay within a short distance of the mother plant (Hopper, 2009). The predominance of this trait is tied to the natural history of south-western Australia, where the absence of major disturbance events during the evolution of the flora, such as glaciations and volcanism, did not lead to the widespread development of specialized seed dispersal mechanisms (Hopper & Gioia, 2004; Hopper, 2009), as occurred elsewhere (e.g., Williams et al., 2005; Thompson & McCarthy, 2008; Knapp et al., 2010). The lower relative abundance of plants with unassisted seed dispersal in currently small remnants may be due to their invasion by non-native (largely wind-dispersed) species. Moreover, the lower relative abundance of plants with animal-dispersed seeds in the older and historically small remnants likely indicates a delayed response to the decline of their seed dispersal agents because of habitat loss and limited immigration (Damschen et al., 2008).

Finally, the observed decline of FD with remnant age in the herbaceous and shrub plant communities may indicate that fragmentation leads over time to functional convergence (Grime, 2006) within these different layers. Patterns of FD decline with fragmentation have also been observed by Sonnier et al. (2014).

4.2 | Functional responses to increased soil fertility and altered fire regimes

The response of nutrient acquisition and regeneration traits to soil fertility and fire frequency, respectively, did not follow our predictions. We expected increased soil fertility to shift the competitive hierarchies between species with different nutrient acquisition strategies to the detriment of those best adapted to impoverished soils and which can suffer from P toxicity, i.e., non-mycorrhizal root-clustered species (Lambers et al., 2010). While this pattern was observed in the *Banksia* woodland canopy, we only expected it in the smaller and older remnants, where larger soil P levels were detected (Ramalho et al., 2014). Patterns were also inconsistent in the understorey, where root-clustered plants reached higher relative abundance in the older and more fertile remnants. Similarly,

whilst we expected higher fire frequency to favour resprouters over obligate seeders (Bell, 2001), such patterns were not observed. Plant traits are often acted upon by multiple stressors, which may or may not act in the same direction. Inconsistent patterns or no significant responses, as we observed here, are likely to occur when stressors act in different directions (Williams et al., 2015).

4.3 | Broader implications

Our study illustrates the vulnerability of small remnants to changes in community assembly and ecosystem function due to fragmentation. From a practical perspective, this points to the need for: (1) careful consideration of remnant sizes during planning processes, and (2) intervention efforts (e.g., through reserve design and ecosystem management) that minimize fragmentation effects.

Our study also illustrates how a functional trait approach using abundance-weighted metrics can provide insight into the impacts of urbanization-related processes before local extinctions occur. Such an approach offers the potential for advanced warning, helping to predict which species will be affected first and most (Mouillot et al., 2012). Therefore, it can be used to help guide the selection of plant species for ecological restoration. Applying a functional trait approach in ecological restoration poses a major and yet still unanswered question. Should restoration efforts counteract the disturbance-based trait filtering by using a larger proportion of species with vulnerable trait states, or should they use plants that can successfully and in the long term cope with the changing environmental conditions (e.g., Shackelford et al., 2013)?

Finally, our study offers an example of how cities' fragmentation history and biogeographic settings provide an important context influencing plant functional responses to urbanization-related processes (Duncan et al., 2011; Williams et al., 2015; Palma et al., 2016). First, in cities with a recent development history and expanding into native vegetation (e.g., Perth, Melbourne, Adelaide, Cape Town, Los Angeles, San Francisco), remnant plant communities are likely to be strongly affected by fragmentation. However, as seen here, these effects may be time-lagged and only noticeable in the older and smaller remnants. In contrast, in cities with a long human occupation (e.g., most European cities), urban remnants may have already lost significant biodiversity (Hahs et al., 2009), and plant functions, such as seed dispersal, may even depend on human activities and/or domestic animals (Thompson & McCarthy, 2008). Second, in the ancient and nutrient-impoverished landscapes of south-western Australia, the predominant lack of specialized seed dispersal mechanisms, large dependence on insects and birds for pollination, and high susceptibility to invasion are traits that are intimately shaped by the region's biogeography (Hopper & Gioia, 2004). Younger, often disturbed and more fertile landscapes (e.g., Northern hemisphere) are characterized by different environmental evolutionary pressures, and therefore provide a different background context to plant traits–urban environment relationships (Hopper & Gioia, 2004; Hopper, 2009). Hence, explicitly considering cities' transformation

history, biogeographic settings and habitat characteristics is fundamental to understand plant functional responses to urbanization-related processes at the city and multi-city level.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Appendix S1 Map of the study area

Appendix S2 Configuration of the sampling plot

Appendix S3 Principal Components Analysis of soil nutrient data

Appendix S4 Plant functional traits and trait states analysed

Appendix S5 List of plant species selected for functional trait analysis

Appendix S6 Bibliographic references used for functional trait characterization of selected species

Appendix S7 Results of the GLMM for the shrub and herbaceous plants

Appendix S8 Summary of the fourth corner-analysis for the shrub and herbaceous plants