

Do habitat fragmentation and fire influence variation of plant species composition, structure and diversity within three regional ecosystems on the Sunshine Coast, Queensland, Australia?

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Abstract. Habitat fragmentation is considered to be one of the greatest threats to biodiversity. Species richness is predicted to decrease with decreasing patch size and increasing isolation, and this has been shown in some ecosystems. However, few studies have specifically investigated the effects of fragmentation on specific vegetation types, or compared different vegetation types within the same region. In this study, we assessed the influence of habitat fragmentation and time since fire on the floristic composition, structure and diversity of three ecosystems with varying fire proneness within the Sunshine Coast region. This study found that the tall-open forest ecosystem (RE 12.9-10.14) had higher overall species richness within fixed sample areas used for this study than did either open forest (RE 12.5.3) or gallery rainforest (RE 12.3.1), because it was composed of species typical of each of these ecosystem types. Open forest species richness was found mostly in the lower stratum, whereas gallery rainforest diversity was found in the upper stratum. Species richness decreased with increasing isolation in the open forest ecosystem where seeds are mostly abiotically dispersed. However, this study did not find strong evidence for reduced species richness within smaller patches in any ecosystem type studied; instead, finding species richness decreased with increasing patch size in the open forest ecosystem. Overall, across ecosystems, time since fire affected vegetation structure, but in fire-prone ecosystems, time since fire was not a determinant of species richness within the sites studied.

Additional keywords: diversity, functional groups, fire, isolation, open forest, patch size, rainforest.

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Introduction

Habitat fragmentation is considered to be one of the greatest threats to biodiversity on a global scale, converting connected forests into a mosaic of patches, of varying size and isolation (Fahrig 2003; Ewers and Didham 2006; Alados *et al.* 2009; Archibald *et al.* 2011; Laurance *et al.* 2011; Parsons and Gosper 2011; Rodriguez-Loinaz *et al.* 2012). The species–area relationship (SAR) hypothesises that smaller patches have a less heterogeneous environment, supporting fewer species (Gleason 1922, 1925; Williams 1943; MacArthur and Wilson 1967; Connor and McCoy 1979). Recent studies by Godefroid and Koedam (2003), Cagnolo *et al.* (2006), Aparicio *et al.* (2008), Brown and Boutin (2009), Gonzalez *et al.* (2010) and Laurance *et al.* (2011) have supported this relationship. Smaller, and therefore more isolated, patches are predicted to support smaller, genetically similar species populations that are vulnerable to localised extinction from disease, population decline and altered microclimatic conditions (Connor and McCoy 1979; Baldwin and Bradfield 2007; Shapcott *et al.* 2009).

Isolation occurs both spatially (distance between patches of the same type) and temporally (how long the patches have been

separated) (Collard *et al.* 2011). Isolation can impede the dispersal of seed and pollen both abiotically and biotically, therefore reducing emigration and immigration between communities (White *et al.* 2004; Cramer *et al.* 2007; Alados *et al.* 2009). Isolated patches, irrespective of patch size are therefore still vulnerable to population decline and, therefore, localised to extinctions (Baldwin and Bradfield 2007; Shapcott *et al.* 2009). This is important with respect to keystone species, because a significant alteration of structure and therefore microclimate can lead to altered disturbance regimes (e.g. fire) at the patch level, leaving other species vulnerable to further population declines and/or extinctions (Alados *et al.* 2009; Parsons and Gosper 2011; Knox and Clarke 2012).

Fire is responsible for shaping the structure, composition and diversity of many Australian plant communities (Bradstock and Myerscough 1981; Russell-Smith *et al.* 2004; Scott *et al.* 2012). Increased fire frequency can decrease species richness by removing or reducing the fecundity of obligate seeder species (Knox and Morrison 2005; Fisher *et al.* 2009). High-frequency fire regimes have also been shown to increase fine fuel loads such as grasses, in turn further increasing the frequency of fire

(Hoffmann *et al.* 2012; Scott *et al.* 2012). Conversely, an absence of fire can cause understorey strata to develop to a stage where fine fuels are scarce and the probability of fire is decreased (Close *et al.* 2011; Scott *et al.* 2012; Williams *et al.* 2012). Habitat fragmentation can alter the frequency and intensity of fire regimes (Driscoll *et al.* 2010). Alterations in patch size have been shown to alter fire regimes with respect to how a fire behaves and the probability of fire reoccurring in small patches (Ross *et al.* 2002; Parsons and Gosper 2011).

Many studies investigating the effects of fragmentation have employed broad vegetation classification systems that include varying geologies and vegetation types (Cagnolo *et al.* 2006; Alados *et al.* 2009). This may weaken the results because different ecosystems may respond differently to fragmentation, fire and other anthropogenic disturbances. By comparing vegetation structure and composition within defined communities, variation can be attributed to exogenous pressures rather than variation in environmental qualities (Adams *et al.* 2011; Collard *et al.* 2011). Sampling effects may also affect comparability of results and most field assessments of diversity are based on subsampling within fixed plots. Management and conservation decisions for vegetation communities in Queensland are largely based on regional ecosystem (RE) mapping (Wilson *et al.* 2002; Carter *et al.* 2009). This mapping was developed by the Queensland Herbarium and is at a scale of ~1 : 100000 (Wilson *et al.* 2002). Compared with other Australian states, and other countries globally, this mapping is specific, differentiating among different bioregions, geologies, community structures and compositions (Sattler and Williams 1999; Wilson *et al.* 2002; Fensham 2008). Therefore, this detailed mapping provides the opportunity to study fragmentation within specific ecosystems.

The Sunshine Coast is located in the subtropics of the eastern coast of Australia (Fig. 1). As a result of variation in climate, geology and topography, the Sunshine Coast has high biodiversity, supporting a wide range of different ecosystem types, such as coastal heath (Brownlie *et al.* 2009), rainforests (Moran *et al.* 2009; Shapcott *et al.* 2009) and a variety of dry and wet eucalypt communities (Callaghan *et al.* 2011). As a result of urban development over the past 40 years, the landscape of this area is heavily fragmented (Brownlie *et al.* 2009; Carter *et al.* 2009; Moran *et al.* 2009). Fragmentation of these important ecosystems has been identified as having a major impact on both fauna and flora of the area (Moran *et al.* 2009; Shapcott *et al.* 2009; Callaghan *et al.* 2011). Therefore, investigation into the impact of habitat fragmentation and its effects on biodiversity is important, particularly because urban development is expected to increase rapidly into the future (Carter *et al.* 2009).

The study specifically aimed to compare and contrast the species composition, structure and diversity among three different ecosystems and assess the influence of habitat fragmentation on fire-prone and non-fire-prone communities within the Sunshine Coast. We predicted that study sites located within larger, more connected patches would have higher floristic diversity because they would be less disturbed, therefore maintaining a more stable vegetation structure and composition than smaller, isolated patches. Furthermore, the influence of isolation on floristic composition was investigated

with respect to dispersal mechanisms. We aimed to reduce statistical noise in the study by consistency in sample size, replication and vegetation type.

Materials and methods

Ecosystem selection

The study expanded on the vegetation component of a wider biodiversity assessment undertaken on the Sunshine Coast; thus, some components of vegetation and site selection were determined as part of this wider study and expanded on for this study. Three REs were selected for comparison on the basis of perceived differences in structural complexity and frequency of fire and were identified as of significance for fauna within the wider study (Specht 1970; Knox and Clarke 2012; Queensland Herbarium 2012). RE 12.5.3 is an open forest of *Eucalyptus racemosa* (Specht 1970; Eyre 2006; Queensland Herbarium 2012). This ecosystem is a typical fire-prone community, with fires every 5–10 years maintaining an open canopy with a grassy to shrubby understorey (Parsons and Gosper 2011; Queensland Herbarium 2012). Once common on the sandy-loam soils of the Sunshine Coast, the RE is now listed as *Endangered* in Queensland (*Vegetation Management (VM) Act* 1999). RE 12.9-10.14 is a tall-open forest dominated by *E. pilularis* on sedimentary rocks (Specht 1970; Queensland Herbarium 2012). Fires have been estimated to typically occur every 10–20 years, and without fire, a rainforest understorey can develop (Queensland Herbarium 2012). The third ecosystem, RE 12.3.1, is characterised by an absence of fire and is gallery rainforest occurring on alluvial substrates (Queensland Herbarium 2012). This ecosystem is listed as *Endangered* in Queensland (VM Act) and, as a lowland subtropical rainforest, it is listed as *Critically Endangered* federally (*Environmental Protection and Biodiversity Conservation (EPBC) Act* 1999).

Site selection

The most current version of the Regional Ecosystem Mapping (v6.1) was used to identify the distribution of the three study REs (State of Queensland – Department of Natural Resources and Mines 2012a) in ArcMap 10 (ESRI 2011). Ten sites per vegetation type (RE) were selected to represent their distribution within the Sunshine Coast local government area (SCLGA). These sites were also selected to represent their range of varying patch sizes and degrees of isolation (Fig. 1). Sites were selected with a minimum patch width of 100 m, to allow surveying to occur more than 50 m from the edge of the patch to reduce impact of edge effects (Gosper *et al.* 2010). Gallery rainforest was associated with watercourses; therefore, sites were selected to avoid connectivity between study areas by allowing only one site per watercourse or drainage system. Logistical constraints, including access, and permitting also determined site selection within these parameters.

Isolation and patch area

To test the species–area relationship (SAR), the area of RE patch (A_{RE}) and total area of remnant/high-value regrowth within a 1 km radius of the sample site (A_{TOTAL}) was measured in ArcMap 10 (ESRI 2011). Patches were manually

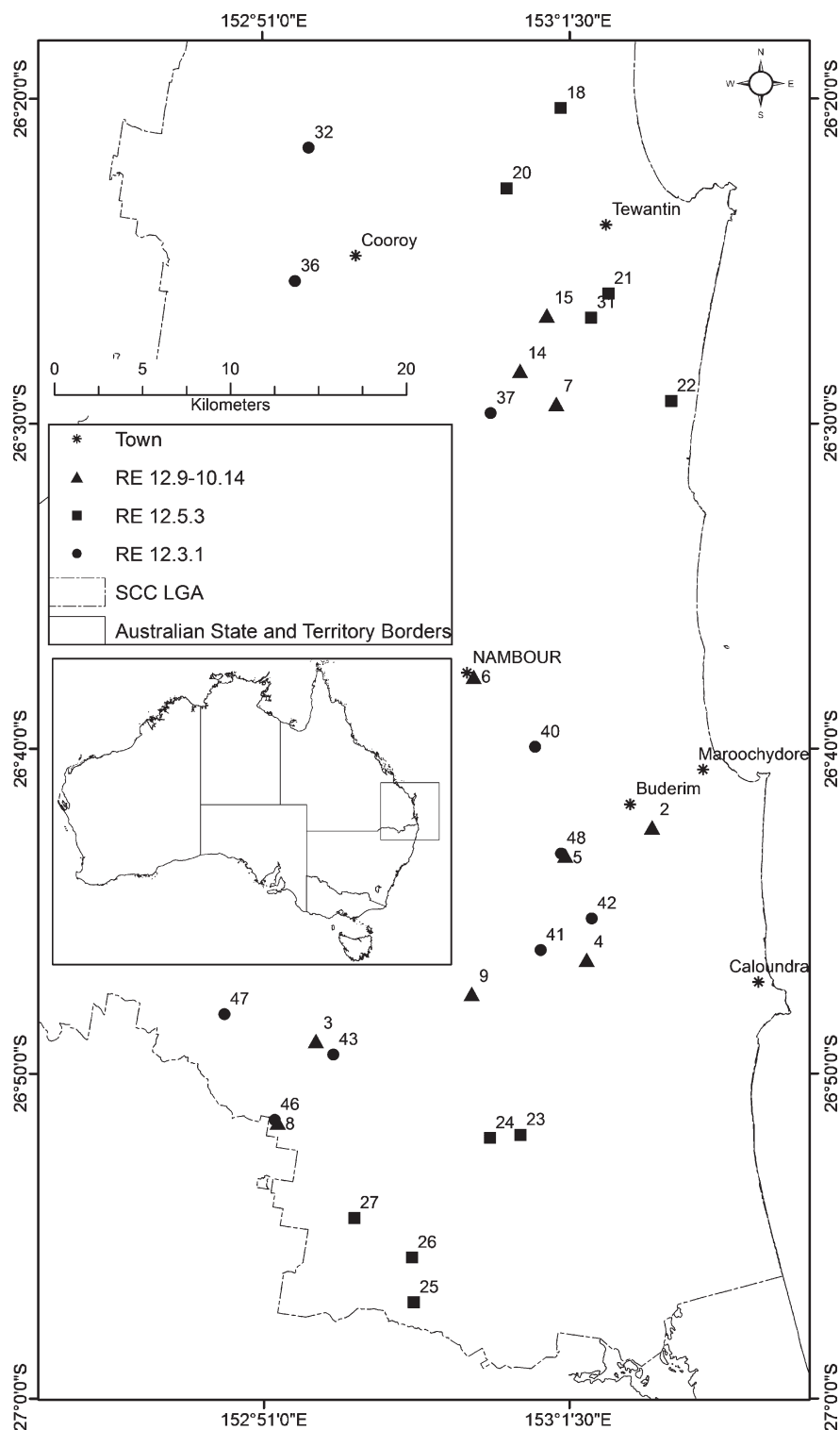


Fig. 1. Location of study sites on the Sunshine Coast, Queensland, Australia. Symbols indicate regional ecosystem type, as follows: RE 12.5.3 open forest (■), RE 12.9-10.14 tall-open forest (▲) and RE 12.3.1 gallery rainforest (●). Boundary is the Sunshine Coast local government area (SCLGA).

delineated, with 'spurs' of less than 50 m width being removed. Patch area was calculated by drawing a rectangle over the patch, estimating the proportion of the rectangle taken up by the patch and then multiplying that proportion by the area of the rectangle.

Isolation from patches of same RE type (ISO) was measured by calculating the average distance to the nearest five patches of same RE type (Broadhurst and Young 2006). In addition, to quantify the fragmentation of the surrounding landscape, a score was

calculated using the following three components: patch size, connectivity and context, consistent with the methodology developed for Queensland Biocondition assessments (Eyre *et al.* 2011). This methodology relates to vegetation deemed to be 'high-value' by the VM Act. Therefore, in addition to the Regional Ecosystem Mapping v6.1, the High-value Regrowth Vegetation v2.1 layer was also used to calculate patch size (A_{TOTAL}), connectivity and context (State of Queensland – Department of Natural Resources and Mines 2012b). Patch size was calculated as the total area of high-value vegetation within which the study site was located (A_{TOTAL} ; Eyre *et al.* 2011). The connectivity component scores the level of linkage a patch has to surrounding patches (Eyre *et al.* 2011). Context is the amount of high-value vegetation within a 500 m radius of the study site (Eyre *et al.* 2011). The sum of these three components formed the landscape score (LS), which is a score out of 20 (Eyre *et al.* 2011).

Vegetation sampling

A vegetation-survey methodology consistent with Neldner *et al.* (2005) was used at each site to enable the data to be added to the Queensland Herbarium CORVEG database. Vegetation sampling was performed within the interior of the patch more than 50 m from the edge (Gosper *et al.* 2011). In extremely thin, linear gallery rainforest patches, this was often unachievable because of the presence of waterways and six sites were surveyed less than 50 m inside the patch. The location of plots was undertaken to be as consistent as possible within each vegetation type and sampled along rather than across creek lines. At each site, species richness and composition were determined within a 50 m by 100 m plot (or an equivalent area in thin, linear patches), which was systematically surveyed (Neldner *et al.* 2005). This methodology recorded species presence only and, thus, did not enable other diversity indices to be calculated. Herbarium vouchers were made and lodged with the University of the Sunshine Coast Herbarium. Specimens were named according to the Census of Queensland Flora (Bostock and Holland 2010). Identification was confirmed by local botanists or the Queensland Herbarium.

Community structure was sampled in a 10 × 50 m belt transect, located within the 50 × 100 m plot consistent with Neldner *et al.* (2005) and Eyre *et al.* (2011). Community structure was classified by identifying the strata; emergent (E), canopy (T1), subcanopy (T2), shrub layer (S1) and/or ground layer (G) present (Neldner *et al.* 2005). For each stratum (excluding the ground layer), the following variables were recorded: minimum, median and maximum stratum height was estimated in metres with a clinometer and measuring tape, following standard methods (Neldner *et al.* 2005). The number of stems within each stratum was counted, where practical, in the belt transect (Austin 1978; Neldner *et al.* 2005). However, if the density of stems was too high to count accurately, counting was performed within a subsampled 50 × 5 m or 50 × 2 m belt transect. Total percentage crown cover was calculated through the 50 m transect by using the line intercept method (Greig-Smith 1964; Neldner *et al.* 2005).

The ground layer was sampled within a 1 m² quadrat at five points along the 50 m transect, with the mean of these values

used to represent that site. Minimum, median and maximum heights (cm) of the ground layer were recorded. Percentage cover of grasses, forbs and non-grass species, woody plant seedlings and shrubs, litter, bare rock and cryptogams were also recorded consistent with the methods of Neldner *et al.* (2005) and Eyre *et al.* (2011).

All species recorded were later grouped for analyses by taxonomy (genus and family), life form (large trees >20 m, small-medium trees <20 m, shrubs <6 m, ferns, forbs and herbs, and grasses, vines and epiphytes), species origin (native or exotic to Australia; Bostock and Holland 2010) and dispersal mechanism (abiotic or biotic; Cagnolo *et al.* 2006; Campetella *et al.* 2011; Pekin *et al.* 2012). To identify the contribution each group of species made to their respective functional grouping, each sample site was standardised by dividing the number of species in that grouping by the total species richness of the site (Figueroa *et al.* 2011; Pekin *et al.* 2012). Thirteen species were not able to be identified because of time constraints and were not included in functional grouping analysis; however, they were used in estimates of species richness.

Fire history

All available fire-history data for each site were obtained from Queensland Parks and Wildlife Service (QPWS), Sunshine Coast Council (SCC) and local Rural Fire Brigades (RFB), but was often limited. The time-since-fire (TSF) data were the most consistently available data; however, these data were not uniformly accurate across sites; therefore, each site was classified as exposed to fire (1) 0–4 years ago, (2) 5–10 years ago, (3) >10 years ago or (4) not on record. We attempted to select sample sites that covered the range of fire histories of the vegetation types.

Statistical analysis

Multivariate analyses were used to compare sites within and among ecosystem types. Multivariate distance matrices, using Euclidian distance, were calculated for life form, species origin and dispersal mechanism in PRIMER v6.1.5 (Clarke and Gorley 2006). The values of species richness of each vegetation type were standardised for each sample before the Euclidian distance matrix was generated. Community structure variables were standardised by the maximum, before generating a Euclidian distance matrix of multivariate structure. A Bray–Curtis dissimilarity matrix of species presence and absence at each site was constructed for each of the three ecosystems and across all sites in PRIMER v6.1.5 (Clarke and Gorley 2006). Non-metric multidimensional scaling (NMDS) analysis was performed on each matrix, using a repetition value of 9999 to test for clustering of sites within and among ecosystem types according to these different attributes on a two- and three-dimensional plane, using PRIMER v6.1.5, (Clarke and Gorley 2006). It was detected from the preliminary assessment of community structure and composition in addition to MDS outputs of species composition that sites grouped according to community structure. To test this relationship, paired distance matrices of multivariate species composition and community structure were compared with a Mantel test, using the

RELATE analysis with 9999 random permutations in PRIMER v6.1.5 (Clarke and Gorley 2006).

The three ecosystem types were tested for significant differences in their fragmentation, structure and species diversity, and composition variables were measured using ANOVA or Kruskal–Wallis tests, followed by Duncan's *post hoc* test in SPSS Statistics v19 (IBM 2010). Within ecosystem types, Spearman's rank correlations were used to test whether RE patch size (A_{RE}) and or isolation were significantly correlated with taxonomic- and functional-grouping species richness and community structure variables, to assess the influence of patch size and isolation on structural complexity and diversity in SPSS Statistics v19 (IBM 2010). Accurate fire-history data were available for the open forest system and the effect of time-since-fire (TSF) and community composition and community structure variables was tested using Spearman's rank correlation in SPSS Statistics v19 (IBM 2010). To avoid a Type 1 error, a Bonferroni correction was applied to results tables (Townend 2002). Spearman's rank coefficients that were rejected after the Bonferroni correction, but had a strong bivariate relationship (i.e. $r_s \geq 0.5$ or $r_s \leq -0.5$), were accepted.

Results

Comparisons among vegetation types

In total, 473 species of flora from 108 families were recorded across the 30 sites, with 38 of these being exotic species (Table 1). In contrast to expectations, the tall-open forest

ecosystem recorded higher species richness (275) than did open forest (230) or gallery rainforest (198) sites (Table 1). The open forest and gallery rainforest sites had distinctly different species composition. In open forest and gallery rainforest communities, 100 and 98 species were exclusive to these ecosystems, respectively (Table 1). In contrast, the tall-open forest ecosystem had only two species (*Denhamia celastroides* and *Xanthorrhoea macronema*) that were unique to this ecosystem.

Of the 460 species positively identified, 64 were large trees, 97 species were small–medium trees, 106 were shrubs, 107 species were ferns, forbs or herbs, 31 were species of grass and 67 species were vines or epiphytes (Table 1). Large trees (25.79%; $F=37.674$, $P<0.05$) and small–medium trees (24.16%; $F=8.019$, $P<0.05$) were significantly more dominant life forms in the gallery rainforest system (Table 2). In contrast, forbs, ferns and herbs (31.33%; $F=37.349$, $P<0.05$) and grasses (9.85%; $F=20.785$, $P<0.05$) were the dominant life forms in the fire-prone open forest system, in comparison to the tall-open forest and gallery rainforest (Table 2). However, their abundance and diversity were not significantly ($P>0.05$) correlated with differences in canopy cover. The open forest sites had a vegetation structure different from that in the other two vegetation communities (Fig. 2). The open forest sites had significantly lower canopy height than did tall-open forest and gallery rainforest (18.701 m; $F=5.069$, $P<0.05$, Table 2). The tall-open forest and gallery rainforest sites were not significantly ($P<0.05$) different for most structure variables measured and clustered together (Fig. 2). However, the gallery rainforest had a

Table 1. Comparison of habitat fragmentation (ISO, A_{RE} , A_{TOTAL} and LS) and species richness among three regional ecosystems on the Sunshine Coast, Queensland

Means within a row followed by the same letter are not significantly different from each other (Duncan's *post hoc* analysis, $P=0.05$). F -statistics given in parentheses are significant after Bonferroni correction for multiple comparisons. * $P<0.05$, ** $P<0.01$ or *** $P<0.001$ (ANOVA)

Measure	Open forest	Tall-open forest	Gallery rainforest	F -statistic	Total
Fragmentation					
ISO	823.52a	812.90a	2394.28b	(18.861***)	
A_{RE}	36.79	47.21	9.49	2.649	
A_{TOTAL}	164.85	117.75	111.78	1.117	
LS	15.30	12.60	12.70	1.350	
Diversity					
Total species richness	230	275	198	n.a.	473
Mean species richness	59.00a	75.10b	54.80a	7.884**	
No. of exclusive spp.	100	2	98	n.a.	
Mean family richness	28.60a	41.50b	32.80a	(11.636***)	
Native	55.00a	70.80b	55.00a	(8.703***)	422
Exotic	4.00	4.10	0.80	1.673	38
Life form					
Large tree	4.90a	13.40b	14.30b	(22.742***)	64
Small–medium tree	9.20a	16.10b	13.60b	5.938**	97
Shrub	13.70	14.20	11.30	1.510	106
Forb, fern and herb	18.30b	15.10b	6.10a	(29.529***)	107
Grasses	6.20b	3.90b	0.20a	(11.344***)	31
Vines and epiphyte	6.80	11.50	10.30	3.271	67
Dispersal					
Abiotic	46.10c	15.70b	46.10a	(39.827***)	272
Biotic	12.90a	36.20b	38.90b	(21.442***)	188

Table 2. Comparison of structure and composition among three regional ecosystems on the Sunshine Coast, Queensland

Means within rows followed by the same letter are not significantly different from each other (Duncan's *post hoc* analysis of subsets, $P=0.05$). *F*-statistics given in parentheses are significant after Bonferroni correction for multiple comparisons. * $P<0.05$, ** $P<0.01$ or *** $P<0.001$ (ANOVA)

Measure	Open forest	Tall-open forest	Gallery rainforest	<i>F</i> -statistic
Life form				
Large trees	8.01a	18.23b	25.79c	(37.674***)
Small-medium trees	15.56a	21.45b	24.16b	(8.019**)
Shrubs	24.18	19.29	20.38	1.494
Forb, fern and herbs	31.33c	20.76b	11.27a	(37.349***)
Grasses	9.85c	5.09b	0.40a	(20.785***)
Vines and epiphytes	11.04a	15.16ab	17.98b	4.815*
Dispersal				
Biotic	20.73a	47.68b	70.26c	(72.925***)
Canopy layer (T_1)				
Median height (m)	18.701a	27.609b	26.073b	5.069*
Crown cover (%)	64.820	80.820	82.540	2.444
Density (stems ha^{-1})	250.00	260.00	450.00	2.328
Ground layer (G)				
Median height (m)	38.26b	38.57b	18.68a	4.918*
Species richness (n)	6b	5b	3a	7.548**
Vegetative cover (%)	57.28b	55.14b	17.12a	(18.565***)
Native grasses (%)	29.26b	10.66a	0.40a	(10.103***)
Forbes and non-grasses (%)	15.88a	38.16b	4.22a	(9.846***)
Seedlings and shrubs (%)	12.14	6.32	12.59	1.755
Litter cover (%)	40.84a	40.56a	62.20b	3.807*
Bare ground (%)	2.08a	1.50a	20.20b	7.535**

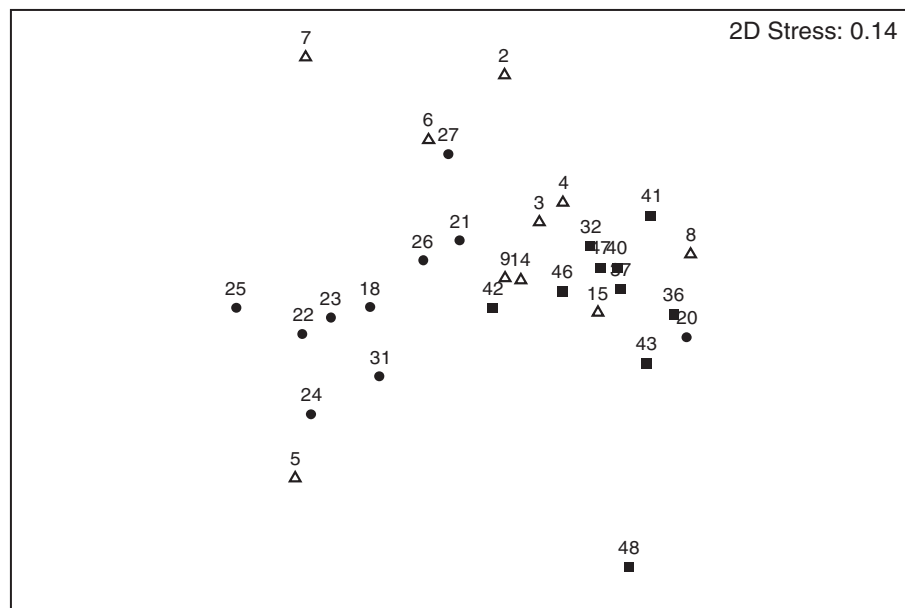


Fig. 2. Non-metric multidimensional scaling (NMDS) of community structure across all 30 sites on the Sunshine Coast, Queensland, showing clustering of open forest sites away from other ecosystems. Numbers denote sites. Ecosystems denoted by symbols, as follows: open forest (●), tall-open forest (△) and gallery rainforest (■).

significantly lower ground strata vegetation cover and a higher litter cover than did the other two vegetation types where vegetation cover in the ground layer was greater than 50% (Table 2).

However, species composition was distinctly different for each vegetation type (Fig. 3). The sclerophyll communities, open forest and tall-open forest were more similar in species composition. Two gallery rainforest sites (41 and 43) exhibited

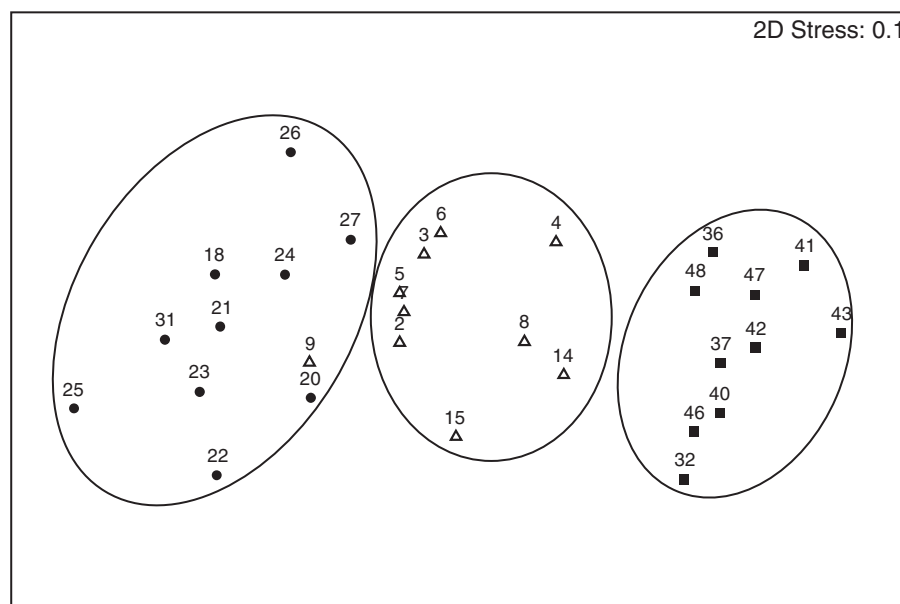


Fig. 3. Non-metric multidimensional scaling (NMDS) of species composition across all 30 sites, showing clear clustering of vegetation types in 2D. Numbers denote sites. Ecosystems denoted by symbols, as follows: open forest (●), tall-open forest (△) and gallery rainforest (■) and encircled.

species composition and structural patterns that suggested they were at a later successional stage because their canopies were composed of late-successional species, such as *Ficus macrophylla*, *Elaeocarpus grandis* and *Castenospermum australe*. In contrast, canopies of the other sites were dominated by secondary rainforest species such as *Neolitsea dealbata* or sclerophyll species *Lophostemon confertus*, *Syncarpia glomifera* or *Eucalyptus grandis*. The majority of species sampled utilised abiotic dispersal mechanisms (272 species), with 188 species bearing fleshy fruits (Table 1). The proportion of biotically dispersed species per site in gallery rainforest was significantly higher than that in the open forest and tall-open forest communities ($F=72.925$, $P<0.05$; Table 2). There was a weak yet significant relationship between species composition and community structure across the study sites ($r_s=0.295$, $P<0.05$; Table 3).

Fragmentation

The three ecosystems did not differ significantly in size of RE patches and remnant areas; however, gallery rainforest sites were significantly more isolated than were the sites of the other two ecosystems studied (Table 1). In contrast to expectations, open forest total species richness and native species richness were significantly ($P<0.05$) negatively correlated with the total area of the patch (A_{TOTAL} ; $r_s=-0.872$; $r_s=-0.839$), but were not correlated with RE patch area (A_{RE} ; Table 4). Species richness was not significantly ($P>0.05$) correlated with RE patch or total patch area in the tall-open forest or gallery rainforest (Table 4). The percentage of rainforest shrubs was negatively correlated with increasing isolation (Table 4). In the open forest ecosystem, native species richness was negatively correlated with isolation ($r_s=-0.685$; Table 4).

Table 3. Results of tests for correlations among species composition, life-form composition, dispersal-type similarity matrices and the multivariate community-structure similarity matrix

Strength of relationships is indicated by Spearman's rank correlation coefficient (r_s). Coefficients enclosed by parentheses remain significant after Bonferroni correction for multiple comparisons, where $P^c=0.00227$. * $P<0.05$, ** $P<0.01$ or *** $P<0.001$

Measure	Community structure
All ecosystems	
Species composition	(0.295***)
Life form	(0.319***)
Dispersal mechanism	(0.337***)
Open forest	
Species composition	0.126
Life form	0.486*
Dispersal mechanism	-0.070
Gallery rainforest	
Species composition	-0.025
Life form	0.107
Dispersal mechanism	-0.067

The structure of any of the vegetation communities was not generally correlated with patch size or isolation. However, the dominance of different strata in the open forest and gallery rainforest ecosystems was related to habitat fragmentation variables. The percentage of forbs was positively correlated with increasing isolation ($r_s=0.632$), landscape scores ($r_s=0.647$) and total remnant patch area in the open forest system ($r_s=0.726$; Table 4). However, the percentage of shrubs ($r_s=-0.809$) and small-medium tree species ($r_s=-0.697$) decreased as gallery rainforest patches became more isolated (Table 4). This study found that small-medium

Table 4. Summary of Spearman's correlation analyses among habitat fragmentation (ISO, A_{RE} , A_{TOTAL} and LS), total and native species richness and percentage composition of life form (large trees, small-medium trees, shrubs, forbs, ferns and herbs, grasses and vines and epiphytes), and abiotically and biotically dispersed species in each regional ecosystem (RE)

Spearman's rank correlation coefficient (r_s) is given. * $P < 0.05$, ** $P < 0.01$ or *** $P < 0.001$

Measure	Isolation (m)	RE patch area (ha)	Total patch area (ha)	Landscape score
Open forest				
Total species richness	-0.498	-0.261	-0.872**	-0.745*
Native species richness	-0.685*	-0.273	-0.839**	-0.716*
Large tree species (%)	-0.103	-0.309	-0.261	-0.263
Small-medium tree species (%)	-0.523	0.304	-0.046	0.294
Shrub species (%)	0.285	-0.030	0.377	0.404
Fern, sedges and herb species (%)	0.632*	0.249	0.726*	0.647*
Grass species (%)	0.042	-0.042	-0.571	-0.661*
Abiotic (%)	0.648*	0.285	0.590	0.373
Biotic (%)	-0.527	-0.297	-0.553	-0.336
Tall-open forest				
Total species richness	-0.103	0.080	0.098	-0.172
Native species richness	-0.055	0.190	0.190	-0.135
Large tree species (%)	0.030	0.166	0.067	0.400
Small-medium tree species (%)	0.418	0.301	0.141	0.714*
Shrub species (%)	-0.115	0.411	-0.257	-0.246
Fern, sedges and herb species (%)	-0.115	-0.190	-0.098	-0.369
Grass species (%)	0.333	0.117	0.489	0.185
Abiotic (%)	-0.127	0.018	-0.177	-0.197
Biotic (%)	0.127	-0.018	0.177	0.197
Gallery rainforest				
Total species richness	0.127	-0.055	0.426	0.455
Native species richness	0.127	-0.055	0.426	0.455
Large tree species (%)	0.419	0.116	-0.607	-0.543
Small-medium tree species (%)	-0.697*	0.590	-0.164	-0.234
Shrub species (%)	-0.809**	-0.055	0.070	0.043
Fern, sedges and herb species (%)	-0.479	-0.140	-0.067	-0.062
Grass species (%)	0.510	-0.399	-0.156	-0.022
Abiotic (%)	-0.333	-0.061	0.085	0.080
Biotic (%)	0.600	0.255	0.006	-0.043

tree species contributed more to species richness in tall-open forest sites with higher landscape scores ($r_s = 0.714$). The percentage of abiotically dispersed species in open forest sites increased with greater isolation ($r_s = 0.648$). In contrast, the percentage of biotically dispersed species increased with increasing isolation ($r_s = 0.600$) in gallery rainforest (Table 4).

Time since fire

Open forest sites had been burnt either within the past 4 years (Class 1) or between 5 and 10 years ago (Class 2). Tall-open forest sites were mostly burnt more than 10 years ago (Class 3) or had no fire records (Class 4). No gallery rainforest sites had any recorded fire events (Class 4). Tall-open forest sites sampled less than 14 years following fire (Sites 2, 3, 5, 6, 7 and 9) were more similar to open forest sites (Fig. 2). Within the fire-prone open forest ecosystem, there was no significant correlation between time since fire and species richness, whereas the percentage of biotic dispersed species increased with time since fire ($r_s = 0.798$; Table 5). The canopy and understorey of the open forest system developed in the absence of fire, with canopy cover ($r_s = 0.724$) and shrub height ($r_s = 0.805$) being positively correlated and

Table 5. Summary of Spearman's rank correlation analysis between time since fire (TSF), habitat fragmentation (ISO and A_{RE}) and vegetation structure variables of median height, stem density and crown cover data for T₁ and S layers, in addition to bare ground, in open forest sites on the Sunshine Coast, Queensland

All variables have a sample size (n) of 10, with the exception of time since fire ($n = 8$). Strength of relationships was tested using Spearman's rank correlation; the coefficient (r_s) is given. * $P < 0.05$, ** $P < 0.01$ or *** $P < 0.001$

Measure	TSF (years)	ISO (m)	A_{RE} (ha)
Canopy layer (T₁)			
Median height (m)	0.295	-0.067	0.164
Crown cover (%)	0.724*	-0.733*	-0.733*
Density (stems ha ⁻¹)	0.235	-0.433	-0.280
Shrub layer (S)			
Median height (m)	0.805*	-0.300	-0.200
Crown cover (%)	-0.235	0.524	-0.452
Ground layer (G)			
Bare ground (%)	-0.889**	0.317	0.459
Dispersal			
Biotic	0.798*	-0.527	-0.336

bare ground negatively correlated with time since fire ($r_s = -0.889$; Table 5).

Discussion

Rainforest ecosystems are known for their high diversity of species (Janzen 1970; Connell 1971; Hubbell 1979; Denslow 1987). Rainforests generally have a diverse upper stratum, with a closed canopy maintaining a sparse understorey (Janzen 1970; Connell 1971; Hubbell 1979, 1980; Mangan *et al.* 2010). The species richness of the studied gallery rainforest community was highest in the tree layers. Conversely, open forest sites had low tree diversity and higher diversity in the grass and herbaceous layers. However, the gallery rainforest community did not have the highest species richness of the ecosystems in this study, but was still comparable with the open forest in terms of total species richness. Le Brocq (1998) also found that diversity of the tree layer was a poor indicator of total species richness across various different ecosystems; particularly in open forests and closed forests (i.e. rainforests). The tall-open forest in this study had overall highest diversity and did not possess the distinctive partitioning of species to different layers that we observed in the open forest and gallery rainforest systems. Instead, the tall-open forest was composed of species found in both the open forest and gallery rainforest ecosystems.

In contrast to the tall-open forest community, the open forest is more fire prone because of higher cover of herbaceous and grass species, as shown by this study (Queensland Herbarium 2012). Increased time since fire was significantly correlated with changing vegetation structure, particularly with increased shrub-layer height, in the open forest community. Other studies have found the understorey (shrub and subcanopy) of sclerophyll systems to become structurally complex in the prolonged intervals between fire events (Russell-Smith *et al.* 2004; Close *et al.* 2011; Parsons and Gosper 2011; Gosper *et al.* 2012; Scott *et al.* 2012). Lewis *et al.* (2012) reported that understorey fire-prone species were replaced by rainforest species when fire intervals were increased in a long-term experimental plot located within the same tall-open forest community as was studied here. There were obvious differences in composition between recently burnt and long-unburnt sites within this study. Recently burnt tall-open forest sites had species composition similar to that of the fire-prone open forest system. Conversely, long-unburnt tall-open forest sites possessed many fire-intolerant species that they shared with the rainforest ecosystem. This is likely to have implications for wet sclerophyll forests in the metropolitan south-eastern Queensland area into the future, because prescribed burns are a key management tool utilised to maintain community structure and composition (Kuenzi *et al.* 2008; Knox and Clarke 2012; Scott *et al.* 2012).

The species–area relationship predicts that larger patches will support higher species diversity of plants and animals (Gleason 1922, 1925; Williams 1943; MacArthur and Wilson 1967; Connor and McCoy 1979). Several recent studies have provided empirical evidence to support its theoretical predictions in relation to assessing the influence of altered patch size, caused by habitat fragmentation, on vascular plant diversity (Cagnolo *et al.* 2006; Aparicio *et al.* 2008; Brown and Boutin 2009;

Gonzalez *et al.* 2010; Laurance *et al.* 2011). Laurance *et al.* (2011) reported that species richness of many different taxa decreased in smaller patches in the Amazonian rainforest. It was expected that patch size would affect species richness at rainforest sites more than at sclerophyll sites because rainforest sites are less resilient to disturbance which is often amplified in fragmented landscapes (Laurance *et al.* 2011). However, although species richness was weakly correlated with total patch area in the open forest, we found no significant relationship between species richness and RE patch or total patch area in the gallery rainforest or tall-open forest ecosystems. Conversely, the results of this study were more consistent with Ross *et al.* (2002) and Rodriguez-Loinaz *et al.* (2012) who found larger habitat patches to support fewer species than did smaller fragments, with species richness being significantly negatively correlated with an increasing total patch size in the open forest ecosystem of this study.

Ross *et al.* (2002) also worked in coastal, fire-prone open forests on the central coast of New South Wales and found lower species richness with increased time since fire in fragmented and unfragmented patches, with the relationship being more pronounced on patches of 5–25 ha. Although no direct relationship was established between increased time since fire and a decline in species richness by this study, a negative relationship between species richness and landscape context and connectivity was detected. This may involve interplay between habitat fragmentation and altered disturbance regimes. Parsons and Gosper (2011) studied the relationship between patch area and fire regime in fire-prone ecosystems of Western Australia, concluding that large patches (100–500 ha) maintain fire regimes by allowing higher proportions of the patch to be burnt. Therefore, larger patches of fire-prone vegetation may be less species rich because small patches may have a more heterogeneous environment as a result of components of the patch being at varying stages of succession following a fire.

Patch area and connectivity to the surrounding landscape have been shown to influence the composition of species with different dispersal mechanisms (Aparicio *et al.* 2008; Alados *et al.* 2009; Brown and Boutin 2009; Alofs and Fowler 2010; Jesus *et al.* 2012). In this study, the open and tall-open forest ecosystems had mostly abiotically dispersed fruits, whereas gallery rainforest contained species with mostly fleshy biotically dispersed fruits. Jesus *et al.* (2012) found wind-dispersed seeds to decrease in quantity in larger, more connected patches. Consistent with this, our study found species richness to be negatively correlated with increasing isolation in the open forest ecosystem. Isolation was expected to negatively affect dispersal in gallery rainforest sites as a result of biotic dispersal being impeded (White *et al.* 2004; Cramer *et al.* 2007; Aparicio *et al.* 2008; Moran *et al.* 2009). Cramer *et al.* (2007) found that large-seeded species are dispersed shorter distances than are small-seeded species in fragmented patches, hypothesising that their result was due to an absence of large mammalian frugivores in these patches. Moran *et al.* (2009) found frugivore species richness and abundance to decline with increasing fragmentation in their study of rainforest patches in the Sunshine Coast hinterland. We found that the rainforest patches were more isolated than were the other two vegetation types studied and were composed

largely of frugivore-dispersed species. However, we did not find that species richness of gallery rainforest sites declined with increasing isolation, or with decreasing patch size. This may have been due to the riparian nature of this system allowing species to employ hydrochory as a key dispersal mechanism (Jansson *et al.* 2005).

Conclusions

This study found that tall-open forest sites had a higher overall species richness within fixed sample areas used for the study than did either open forest or gallery rainforest because it was composed of species typical of both of these ecosystem types. Open forest species richness was found mostly in the lower strata, whereas gallery rainforest diversity was found in the tree layers. Species richness negatively correlated with increasing isolation in the open forest ecosystem where seeds are mostly being dispersed abiotically. However, this study did not find strong evidence for reduced species richness with decreasing RE or total patch size in any ecosystem type studied when using a consistent survey size and found that species richness decreased with increasing patch size in the open forest ecosystem. Time since fire affected vegetation structure in fire-prone ecosystems but was not a determinant of species richness within the sites studied.

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