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Title:
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Date:
2017-08-01

Citation:
Kasel, S., Bennett, L. T., Aponte, C., Fedrigo, M. & Nitschke, C. R. (2017). Environmental heterogeneity promotes floristic turnover in temperate forests of south-eastern Australia more than dispersal limitation and disturbance. Landscape Ecology, 32 (8), pp.1613-1629. https://doi.org/10.1007/s10980-017-0526-7.

Persistent Link:
https://hdl.handle.net/11343/283086

Title: Environmental heterogeneity promotes floristic turnover in temperate forests of south-eastern Australia more than dispersal limitation and disturbance

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Date of the manuscript revision: 8 March 2017

Manuscript word count: 8940

Number of figures: 3

Number of tables: 3

Electronic Supplementary Material: 8 Appendices

Abstract

Context Australia's temperate forest landscapes encompass broad topographic and edaphic ranges, and are regularly disturbed by fire. Nonetheless, relative contributions of environmental heterogeneity, disturbance regimes, and dispersal limitations to plant species turnover remain poorly understood.

Objectives To evaluate the relative influences of deterministic (environmental, disturbance), and stochastic (spatial) processes on plant species turnover (β diversity) in natural forest landscapes, and how such influences vary among plant functional types and vegetation strata.

Methods We assessed the environment and species composition of 81 forest stands, representing a range of structures and fire histories across contiguous landscapes in south-eastern Australia, and examined the potential to explain β diversity using variance partitioning and distance decay analyses.

Results Explanatory variables accounted for 34–55% of β diversity of multiple plant functional types, with environmental heterogeneity explaining the greatest proportion (10–25%). Stand structural variables (e.g. leaf area index, height coeff. var.) accounted for 8–14% of β diversity in understorey life forms and 5% in canopy species, far greater than a single direct descriptor of disturbance history such as time-since-fire which explained just 2% of tree and shrub β diversity. β diversity increased with increasing geographic distance for all functional types. Dispersal limitation accounted for 5–11% of β diversity, and distance-decay rates varied among plant functional types.

Conclusions Landscape-scale conservation of forest biodiversity will require representation of a broad environmental range as well as metrics that fully capture site disturbance histories, including stand structural complexity as a potential proxy for fire regimes.

Keywords community assembly, niche, neutral theory, functional types, fire, stand structure, eucalypt, rainforest

Electronic supplementary material The online version of this article (doi:xx) contains supplementary material, which is available to authorized users.

Introduction

Understanding the processes that generate spatial and temporal changes in species composition is at the heart of community ecology. Fundamentally, plant species distributions are related to their environmental tolerances, intra- and inter-specific competition, reproduction, and dispersal capacities, although the relative importance of these processes is still debated (Chase and Myers 2011). Deterministic models or niche theory suggest that species turnover is a product of ecological and evolutionary differentiation among species, and non-random responses to the abiotic environment and to biotic interactions (Chase and Myers 2011). Alternatively, under stochastic models or neutral theory, all species are considered ecologically equal and species turnover is a product of dispersal limitation and demographic stochasticity (Hubbell 2001).

Beta-diversity (β) – the variation or turnover in species composition across space and/or time – is a common measure of ecological diversity, offering potential to examine the relative importance of stochastic and deterministic processes in community assembly (Anderson et al. 2011). In natural ecosystems, unravelling such processes is difficult due to niche-based distance-decay, which leads to a decrease in environmental similarity with increasing geographic distance (Nekola and White 1999). A full understanding of β diversity thus requires consideration of dispersal limitations in combination with environmental conditions and species differences (i.e. functional attributes) across multiple scales (Condit et al. 2002), using methods like variance partitioning to disentangle effects of deterministic and stochastic processes (Borcard et al. 1992; Chase and Myers 2011). Complementary analyses of distance decay provide insights into mechanisms of community assembly (Condit et al. 2002; Siefert et al. 2013; Liu et al. 2015); for example, distance decay is negatively related to the dispersal capacity of a species and has been shown to differ among plant functional groups (Nekola and White 1999; Liu et al. 2015).

Consideration of different plant functional groups provides insights on processes associated with plant community assembly that are not apparent when focussing on overall plant diversity (López-Martínez 2013; Siefert et al. 2013) since functional groups represent different strategies of resource partitioning, response to disturbance and capacity to colonise (Cornelissen et al. 2003). For example, plant dispersal limitations are related to seed size in that species with large seeds are less likely to be dispersed long distances (Hughes et al. 1994). Seed size in turn is correlated with plant height and life form in a range of floras (Leishman et al. 1995). In general: seed size increases up to a plant height of 10 m and then tends to decrease; woody plants have greater seed size than perennial herbs (Leishman et al. 1995); and seeds of spermatophytes are considerably heavier than spore producing pteridophytes (Adsersen 1995). Dispersal distance is also related to the dispersal vector's carrying capacity. Ants can carry seeds of myrmecochores an average distance of 2 m (Anderson and Morrison 1998), while airborne, wind-dispersed species can be dispersed 1000s of kilometres (Muñoz et al. 2004).

Environmental determinants of plant community composition are scale-dependent (Siefert et al. 2012). The distributions of major vegetation structural formations and associated canopy species are strongly associated with broad-scale climatic gradients (Beadle 1981). Turnover in floristic composition within vegetation types is, however, more frequently associated with finer-scale gradients in soil moisture and nutrient availability in both temperate (Beadle 1981; Hutchinson et al. 1999; Wills and Clarke 2008) and tropical forests (Jones et al. 2008, 2013). Canopy species influence these finer-scaled gradients in resource availability via structurally mediated effects on micro-climate and plant-soil feedbacks (Barbier et al. 2008). The strength and type of resource gradients shaping β diversity may also differ among understorey life forms (Wills and Clarke 2008; Bartels and Chen 2013; Liu et al. 2015). For example, relative to shrubs, herbs are more sensitive to moisture stress due to shallower root systems (Dodd et al. 1998), and are also more dependent on spatially variable and transient sun flecks (Chazdon and Peary 1991).

Disturbance is a primary driver in shaping forest species composition and structure, particularly in fire-prone temperate biomes (Fairman et al. 2016; Pulsford et al. 2016). In addition to direct effects on resource availability, changes in forest composition and structure reflect the intensity, frequency and extent of disturbance by fire (Lindenmayer et al. 2000, 2016; Pulsford et al. 2016). For example, Ashton (1981) reported development of a multi-layered ‘forest-in-forest’ structure during the transition of eucalypt-dominated wet forest to cool temperate rainforest in the long-term absence of fire. Fire severity effects are well reported for these wet forests, with high-severity fires leading to even-aged stands of the obligate-seeding canopy tree *Eucalyptus regnans*, and low- or moderate-severity fires leading to multi-aged stands containing biological legacies such as large trees (Pulsford et al. 2016). Recovery trajectories will therefore vary with fire severity, although changes in vegetation structure and diversity are broadly associated with increasing time-since-fire in these forest types (Lindenmayer et al. 2016). Studies in other forest types have similarly reported changes in forest structure with time-since-fire (Harper et al. 2005; Varga et al. 2005; Chen and Taylor 2012), indicating that measures of forest structure may prove an appropriate proxy for fire effects on forest composition.

While disturbance effects on temperate eucalypt forests are clearly evident in the canopy structure, it is the understorey vegetation that typically represents the largest component of diversity and provides insights on overstorey regeneration, site quality, ecosystem integrity, and conservation status (Hutchinson et al. 1999). The tall, wet forests of south-eastern Australia, for example, are typically characterised by a monospecific overstorey of eucalypt species that rely on fire for regeneration (Ashton 1981). During extended periods without fire, the structure and composition of these forests approaches that of the adjacent cool temperate rainforests (Ashton and Attiwill 1994). This forest transition represents a gradient in light availability associated with the two principal tree life forms – shallow light gradients associated with the open branching habit and vertical leaf orientation of the eucalypt trees, and dense shade under the broadleaved rainforest trees (Wright et al. 2006). Changes in the tree stratum are likely to lead to changes in the understorey due to reduced light availability, and changes to other resources including soil moisture and nutrient availability (Barbier et al. 2008).

We examined the relative importance of environmental and disturbance variables (representing deterministic processes) and spatial variables (representing stochastic processes such as dispersal limitation) in explaining the β diversity of temperate forests ranging from wet eucalypt forest to cool temperate rainforest in south-eastern Australia. We anticipate that the relative contributions of explanatory variables to β diversity will vary according to plant functional groups. Our specific hypotheses were: (i) Environmental determinants of β diversity will differ between vegetation strata and associated life forms. Specifically, canopy turnover will be driven by coarse-grained climatic gradients (Beadle 1981; Siefert et al. 2012) while understorey turnover will be driven by tree species effects on finer-grained environmental conditions such as soil moisture and nutrient availability (Barbier et al. 2008). (ii) Fire disturbance plays an important role in shaping the distribution of temperate forest species via effects on plant successional processes (Pulsford et al. 2016), and structurally, mediated effects on resource availability (Barbier et al. 2008). (iii) Spatial patterns of β diversity will reflect differences in dispersal ability. Specifically, animal-dispersed species with large seed will have a steeper rate of decay of species similarity with geographic distance than small-seeded ferns and wind-dispersed species. By disentangling factors influencing β diversity of Australia's temperate forests, we aimed to improve understanding of their landscape ecology, and to provide a stronger empirical basis for conserving their biodiversity.

Methods

Study area

The Central Highlands of Victoria span an area of ca. one million hectares in south-eastern Australia (Fig. 1). Annual rainfall ranges from 600 to 2000 mm, falling mainly in winter (June−August), with mean annual temperatures from 5.4 to 14.2 °C (1950–2000; Hijmans et al. 2005). The area encompasses elevations of 75 to 1600 m asl., characterised by moderate to steep slopes that support a diverse range of floristic communities primarily dry, damp and wet eucalypt forests (DNRE 1998). The underlying parent materials are predominantly sedimentary, volcanic and granitic rocks of Devonian origin, and associated soils are classified as dermosols, rudosols and tenosols (Isbell 2016).

Site selection and survey

Study sites were located within spatially contiguous landscapes, and represented stands of varying structure spanning a broad elevation gradient, and a range of topographic and edaphic conditions (Fig. 1, Electronic Supplementary Material (ESM) Appendix 1). There is a pronounced site-level trend of decreasing mean annual temperature (MAT) from the south (Powelltown, MAT 10.3 ºC; Mount Strickland 10.9 ºC), to the north-east, which is associated with higher elevations near Eildon (9.8 ºC) and Lake Mountain (9.1 ºC; Fig. 1). Three forest types were sampled, known locally as ‘Wet Forest’, ‘Cool Temperate Mixed Forest’ and ‘Cool Temperate Rainforest’ (Cheal 2010; Cameron 2011). Wet Forest and Cool Temperate Mixed Forest are considered seral stages because their structure and composition approach that of Cool Temperate Rainforest during extended periods without fire (Ashton and Attiwill 1994; Tng et al. 2012).

#Figure 1 here#

Wet Forest is defined by a tall overstorey to 30–80 m dominated by *Eucalyptus regnans*, above an understorey (20–40 m) of trees and tall broad-leaved shrubs (*Acacia spp*., *Pomaderris aspera*, *Cassinia trinerva*, *Zieria arborescens*, *Lomatia fraseri*). Cool Temperate Rainforest is described as closed forest to 40 m height, dominated in all strata by obligate rainforest species (e.g. *Nothofagus cunninghamii; Atherosperma moschatum*), with occasional emergent *Eucalyptus* trees, an understorey characterized by tree ferns *Cyathea australis* and *Dicksonia antarctica*, and a ground layer dominated by a diversity of ground ferns. Cool Temperate Mixed Forests (‘Ecotone’; Fedrigo et al. 2014) were located between the Wet Forest and Rainforest and were characterised by dominant *E. regnans* to 80 m height, with a sub-dominant canopy of both *Acacia spp*. (to 40 m) and *N. cunninghamii* (30 m). Mixed Forest lower strata included smaller understorey trees and shrubs (e.g. *Tasmannia lanceolata*) to 20 m height, with tree ferns and ground ferns dominating (as per above rainforest description) to about 10 m.

We sampled 81 sites involving four field campaigns from April 2011 to October 2014. The sites encompassed a range of environmental conditions of each forest type, and assessments involved a fixed-area plot of 20 × 20, 30 × 30, or 10 × 40 m^2 (ESM Appendix 2). Heterogeneity in sample plot area can influence estimates of species diversity and above-ground biomass (Lewis et al. 2009). However, both within forest types and across all sites, we found no correlation (Spearman’s rho) between plot area and either understorey species richness (ρ = -0.08–0.04, P >0.30) or total live basal area (ρ = -0.20–0.20, P >0.05). In addition, plot area did not make a significant (P >0.05) contribution to the turnover in plant community composition.

Vegetation sampling

In all three forest types, we defined understorey as up to 10 m height (the maximum height of the tree ferns). We assessed the cover-abundance of understorey vascular plants using the point intercept technique (ESM Appendix 2). On each occasion, the tallest understorey species intersected was recorded. At each site, species present but not intersected were given a score of 1. Our β diversity calculations were based on 151 understorey species, after removal of: (i) introduced species (n = 10); and (ii) annual plants (n = 6; 3 introduced) and seasonal species (orchids, n = 3) that could not be reliably assessed due to limited sampling times and transient above-ground presence. We used the richness and abundance of introduced species as explanatory variables in our analysis of plant community turnover to indicate potential competitive effects or proximity to physical disturbances like roads.

Live and dead trees, usually as canopy or understorey single-stemmed species and also tree ferns were assessed for species, diameter at breast height over bark (DBH, 1.3-m height), height, and mortality (live or dead; details in ESM Appendix 2).

Fire history and stand structure

Study sites were mostly located within the boundary of an extensive wildfire in 1939 (n = 57), with additional sites burnt by wildfires in 1983 (n = 7) or 2009 (n = 17). Sites were excluded if recently burnt by low-intensity planned fire (< 10 years), or if there were signs of logging in the past ca. 80 years. In addition to direct effects on resource availability, and in lieu of more direct measures of fire impact, we used canopy cover and stand structural complexity to represent disturbance history. We assumed that current community assemblage and structure was a consequence of the most recent fire rather than the complete fire history, an assumption considered appropriate for the study's timescale (Walker et al. 2010), and employed elsewhere (e.g. Chick et al. 2016). Thus, fire history was represented by a single variable, 'time-since-[last]-fire' with values 4 (2009 wildfire), 30 (1983), and 74 years (1939).

Shannon's index and coefficient of variation (CV) were used to quantify variability in stem-size as a measure of stand structural complexity (Staudhammer and Lemay 2001; Varga et al. 2005). Shannon's index was calculated as $H' = -\sum[p_i \ln(p_i)]$ where p_i is the basal area as a proportion of the total plot basal area of individuals in the ith DBH or height class

(Staudhammer and LeMay 2001). CV = SD/$\overline{x}$ × 100 where $\overline{x}$ is the plot mean DBH or mean height of all individual stems and SD the standard deviation. *H*' was calculated using 10, 20, 30 and 40 cm DBH bins and 4, 6, 8, 10, 12 m height bins. DBH and height bins responded similarly and only the 10 cm DBH and 4 m height bins are presented here (ESM Appendix 1).

Leaf area index (LAI, the single-sided leaf area per unit ground area) of each plot was estimated using hemispherical photography (ESM Appendix 2). Five to fifteen evenly spaced images per plot were captured during uniform overcast conditions using a Nikon D700 camera with a Nikkor 8 mm fisheye lens. All images were analysed from 0 to 60° zenith angles by one operator using the Gap Light Analyser software (GLA 2.0, Frazer et al. 1999).

Soil sampling and analysis

Soils were sampled from a random location within each quarter of each plot (4 sub-samples per depth per plot). After the removal of litter and gentle scraping to expose mineral soils, cores of known volume (349.7 cm^3) or a pogo corer were used to sample soils to 10 cm depth, and between 10 and 30 cm depth (ESM Appendix 2). Soil physicochemical characteristics were total C and N, electrical conductivity, pH, available N and P, exchangeable cations, loss on ignition, bulk density, and clay, silt and sand proportions (ESM Appendix 1).

Functional types

Functional types associated with resource partitioning and response to disturbance (life form; fire response) and the capacity to re-colonise (dispersal mode) were recorded for all species (Cornelissen et al. 2003). Life form classification followed Raunkiaer (1934), and classification of the hemicryptophyte growth form followed McIntyre et al. (1995). Dispersal mode classification was based on diaspore morphology (Cornelissen et al. 2003), with a 0.1 mg seed mass used to separate self-dispersed (‘mobile’; McIntyre et al. 1995) species from heavier seeded barochores. Categorical attributes by functional type were (ESM Appendix 3): life form (phanerophyte, chamaephyte, geophyte, flat or versatile rosette, erect rosette, partial-rosette, proto-hemicryptophyte, epiphyte); dispersal mode (endozoochory, epizoochory, anemochory, myrmecochory, barochory, mobile); and fire response (after Pausas et al. 2016: obligate seeders, hereafter ‘seeders’; obligate resprouters, ‘resprouters’; and facultative seeders, which involved just four species and was excluded from calculations of fire response β diversity).

β diversity

β diversity was calculated for both understorey and canopy species. Line-intercept data were used to calculate the β diversity of understorey species, whereas β diversity of canopy species was calculated using basal area. Values of β diversity range from 0, indicating identical composition and abundance, to 1, indicating complete turnover. Understorey β diversity per functional type was calculated as Bray-Curtis distance after Hellinger transformation, and as Sørensen distance (presence/absence transformation). Ferns were considered as a separate life form due to their dominance of the understorey, accounting for 26% of total abundance (ESM Appendix 3). Fern β diversity was also considered equivalent to β diversity of species with mobile seed (correlation of β diversity $\rho = 0.88$) as all ferns had mobile seed, and ferns represented 35 of 37 species with mobile seed. β diversity of canopy species (ESM Appendix 4) was based on the total basal area of all phanerophytes with stems ≥ 2 cm DBH. This approach allowed us to examine relationships among the understorey component and canopy species using the same set of sites, thus holding spatial configuration and environmental distance constant across all comparisons (Nekola and White 1999; Lenoir et al. 2012). We also calculated understorey phanerophyte β diversity based on basal area of stems ≥ 2 cm DBH, but ≤ 10 m height to assess effects of response variable selection (line-intercept v. basal area) on model outcomes (Jones et al. 2008).

Explanatory variables

Draftsman plots were used *a priori* to discard redundant environmental variables ($r \geq |0.7|$), and to avoid multi-collinearity (ESM Appendix 1). As necessary, environmental variables were $\log_{10}$ or power transformed after checks for normality and variance homogeneity using Ryan-Joiner and Levene's test (Minitab Inc. 2015 v. 17.2.1). Climatic, topographic and edaphic dissimilarities were calculated as Euclidean distances based on the included variables (ESM Appendix 1) after normalisation.

Our argument that forest structure could be used as a proxy for disturbance history was assessed using permutational multivariate analysis of variance (PERMANOVA) that tested for differences in the Euclidean distance matrix according to forest type and time-since-fire (PERMANOVA, Version 1.0.5, PRIMER-E Ltd., Plymouth, UK; Anderson et al. 2008). There were few significant differences in stand structural variables among forest types. Exceptions included LAI, which was significantly greater in Rainforest than Mixed or Wet forest, and height CV, which was significantly greater in Wet and Mixed forest than Rainforest (Table 1). There were however consistent and significant differences in structural variables with increasing time-since-fire, including increasing levels of structural complexity (H' and CV) and LAI (Table 1), which provided support for considering structural variables as disturbance variables.

#Table 1 here#

Distance-decay of β diversity and environmental variables

To test the spatial dependence of β diversities and spatial scale of autocorrelations with environmental variables (climatic, topographic, edaphic), we developed a spatial distance matrix by calculating the Euclidean distance of geographic coordinates among all site combinations. We used a RELATE test (as a Mantel test), using Pearson correlation coefficients to test for correlations with the spatial distance matrix, with correlation significance determined using 9999 permutations (PRIMER 7.0.10, PRIMER-E Ltd, Plymouth, UK; Clarke et al. 2014). We then used Mantel correlograms to examine the spatial autocorrelation significance by scale, using 20 distance classes, each with 162 sample pairs. Distance-decay plots, which show β diversity change with geographic distance, were used to describe spatial patterns of turnover (Nekola and White 1999). The strength of distance-decay of environmental gradients was assessed using a spatial structure index (SSI; Siefert et al. 2013), calculated as the percentage increase in dissimilarity from the smallest to the largest distance class. We also compared the intercepts, rate of distance-decay, and halving distance (Soininen et al. 2007) of β diversity among functional types using generalised linear models (Minitab Inc. 2015, v. 17.2.1) including interactions of functional types and distance (Jurasinski et al. 2009).

Spatial, environmental and disturbance determinants of β diversity

A non-parametric multivariate multiple regression analysis (DistLM; Anderson et al. 2008) was used to examine relationships of β diversity with explanatory variables representing ‘space’ (dispersal limitation), ‘environment’ (climate, soils, topography), and ‘disturbance’ (stand structure and time-since-fire; ESM Appendix 1). Spatial variables were represented by a matrix based on the latitude and longitude of each site containing the terms for a cubic trend surface polynomial ($x + y + x^2 + xy + y^2 + x^3 + x^2y + xy^2 + y^3$; Borcard et al. 1992).

Variance partitioning, which is based on partial redundancy analysis of multivariate response data (i.e. species composition), was then used to examine the relative importance of explanatory variables (spatial, environmental, and disturbance) in determining β diversity (Borcard et al. 1992). Following Blanchet et al. (2008), we used DistLM to partition variation in community composition using forward selection applied to the adjusted R^2 selection criterion (PERMANOVA, Version 1.0.5). Retained explanatory variables were used to partition variation in each response matrix into components representing pure (i.e. conditional), shared, and unexplained variation (Fig. 2). The sum of the pure and shared component of variation for each set of explanatory variables (i.e. spatial, environmental, disturbance) represents the marginal variation. The relative contributions of environmental and disturbance variables were determined via a second-tier conditional analysis, initially without structure and time-since-fire variables to determine their relative effects on explained β diversity (Fig. 2).

#Figure 2 here#

Results

Environmental dissimilarity with geographic distance

Climatic and edaphic dissimilarity increased consistently with increasing geographic distance indicating that environmental variation was spatially structured across all scales, although more weakly structured for edaphic (SSI 42%) than climatic variables (SSI 1095%; Fig. 3a, b). Mantel correlograms also indicated significant although decreasing levels of spatial autocorrelation of climatic and edaphic variables across all distance classes (Fig. 3a, b). In comparison, increases in topographic dissimilarity with geographic distance were minor (SSI = 24%; Fig. 3c).

#Figure 3 here#

Floristic diversity

Understorey species richness per site ranged from 8 to 37 species. No species was present at all 81 sites, and 47 species were limited to one site (ESM Appendices 3, 4). *Dicksonia antarctica* was the most abundant understorey species, accounting for 14% of all point-intercepts and present at 88% of study sites (ESM Appendix 3). *Eucalyptus regnans* dominated the basal area, and was present at 58 sites as a canopy species (ESM Appendix 4). Phanerophytes were the dominant life form (62 of 151 species), followed by erect rosettes (26) and proto-hemicryptophytes (24; ESM Appendix 3). The majority of species had seed with no apparent dispersal mechanism (46 species) or with mobile seed (37; Table 2), and resprouters were the most frequent fire-response type (92 species; ESM Appendix 3).

Distance decay of β diversity

Across all functional types β diversity was generally high (0.5–0.7) at the smallest distances and increased consistently, although weakly with increasing geographic distance (ESM Appendix 5). Nonetheless, Mantel correlograms indicated that β diversity of canopy species was not spatially structured (ESM Appendix 5l), and that myrmecochore β diversity was not spatially structured across distance classes > 10 km (ESM Appendix 5h). Intercepts of distance-decay relationships differed significantly among functional types (Table 2). For example, species with mobile seed (ferns) had a lower rate of species turnover over short distances (intercept 0.52) than other dispersal modes (intercepts 0.74–0.79) and a greater half distance, reflecting a slower rate of decay (Table 2). As indicated by intercepts and half distances, species turnover was also lower in anemochores than species with heavier seeds (myrmecochores, epi-endozoochores), in ferns than phanerophytes, in resprouters than seeders, and in canopy than understorey species (based on abundance; Table 2).

#Table 2 here#

Plant community turnover and variance partitioning

All models tested as part of the first- and second-tier variance partitioning (Fig. 2) were significant at $P \leq 0.05$. Model results were little affected by response variable selection as indicated by comparison of abundance data with presence/absence data for all understorey species and comparison of line-intercept and basal area abundance data for understorey phanerophytes (Table 3; ESM Appendices 6, 7). In addition, the abundance of introduced species did not contribute to β diversity of native species across all functional groups.

#Table 3 here#

Environment, space and disturbance all influenced β diversity across all functional types, accounting for 34–55% of β diversity (Table 3). Of the three sets of explanatory variables, environment consistently explained the greatest proportion of β diversity for all functional types (17–38%), with the exception of anemochores where disturbance variables were more important (21%; Table 3). The pure (conditional) environmental component accounted for a greater proportion of explained β diversity of canopy species than understorey phanerophytes and non-woody species (Table 3). Soil (particularly P, $[H^+]$, N, Mg^{2+}) and climate (particularly mean annual temperature) made the greatest contributions to the environmental component of β diversity across all functional types, with topography only making contributions to ferns and epi-endozoochores (ESM Appendix 6). For understorey species, soils accounted for one- to four-fold of β diversity explained by climate, whereas soils and climate were of roughly equal importance in explaining β diversity of canopy species (ESM Appendix 6). In addition, the proportion of pure variation explained by climate for canopy species was two- to four-fold that of the understorey species (ESM Appendix 6).

Variance partitioning models inclusive of disturbance variables increased the total explained β diversity across all functional types by 5–33% above models limited to spatial and environmental variables (ESM Appendix 8). The pure disturbance component was dominated by LAI and CV (height) and explained 3–14% of pure variation across all functional types (Table 3, ESM Appendix 6). The pure contribution by time-since-fire was less than 2% of β diversity and limited to phanerophytes, seeders and canopy species (ESM Appendix 6).

Space was responsible for a smaller component of β diversity of canopy species than all understorey species (8% vs. 20% respectively; Table 3). Among modes of dispersal, animal-dispersed species, barochores and species with mobile seed were influenced more by the spatial structure of sampling sites than wind-dispersed species (Table 3).

Discussion

Both niche (deterministic) and neutral (stochastic) processes explained β diversity in the temperate forests of south-eastern Australia. Distance-decay of β diversity was associated with spatial structuring of the environment, particularly climate and to a lesser degree, soils. Disturbance variables, here proxied by forest structure, also accounted for β diversity, although variance partitioning detected a pure spatial component in β diversity that was not related to environment or disturbance. This pure spatial component could be interpreted as evidence of neutral processes (i.e. dispersal limitation), although we cannot rule out contributions by unmeasured, spatially structured environmental variables (Anderson et al. 2011).

The pure environmental component consistently explained the largest component of β diversity, providing evidence that deterministic processes (i.e. environmental filtering) played a key role in species composition. This is consistent with previous findings (Cottenie 2005) that environment (reflecting habitat heterogeneity) exerted the dominant influence on species diversity but that space played an important role in capturing neutral dispersal processes. This apparently greater role of niche than neutral processes in β diversity of our temperate forests is in contrast to findings for tropical forests where higher species diversity and rarity makes stochastic processes unavoidable (Cottenie 2005). While differences in modelling approaches, environmental and response variable selection, and spatial grain and extent make meaningful comparisons among studies difficult (Jones et al. 2008), our findings support those of Gravel et al. (2006) and Kalyuzhny et al. (2015) that both niche and neutral processes influence species diversity and turnover.

Our models explained 50% of β diversity, which is comparable if not greater than that explained in many other studies of plant community assembly (see Murphy et al. 2015). Our unexplained component could be due to a number of factors including regional sampling effects (Chase and Myers 2011), demographic stochasticity or ecological drift (Cottenie 2005), past disturbances or undescribed events (Murphy et al. 2015), and unmeasured environmental and spatial variables (Jones et al. 2008). Overall, our findings indicate that environmental heterogeneity, dispersal limitation and disturbance together influence community turnover across our temperate forest landscapes. Nonetheless, the total explained β diversity and the relative importance of explanatory variables differed among functional types, particularly by dispersal mode, life form and vegetation strata.

Environmental determinants of β diversity differ between vegetation strata and within understorey life forms

Results were congruent with our first hypothesis in that climatic variables exerted a greater influence on β diversity of the canopy layer while localised edaphic conditions had a stronger influence on understorey β diversity. Among understorey life forms, climate also had a stronger independent effect relative to soils on β diversity of phanerophytes than of ferns. Stronger climatic controls on β diversity and richness of the overstorey relative to the understorey aligns with previous findings for both tropical (Jones et al. 2013) and temperate forests (Bartels and Chen 2013). Similarly, within forest understoreys, stronger independent effects of climate relative to soils have been reported for shrubs than for herbs (Bartels and Chen 2013; Liu et al. 2015).

Soil variables consistently accounted for ~25% of the explained β diversity of canopy species and understorey life forms. Available P, Mg, [H^+] and N were the strongest soil variables although the relative importance of variables differed among life forms, indicating that life forms were limited by different edaphic constraints, consistent with deterministic community assembly. For example, soil Mg is thought to have a role in the distribution of eucalypt species (Judd et al. 1996). Moreover, strong associations of canopy and understorey β diversity with available P is consistent with previous work across a gradient of eucalypt forest to cool-temperate rainforest that demonstrated available soil P depends on biological mineralisation of organic matter inputs from constituent species (Adams et al. 1989). Soil N effects on β diversity may be related to the distribution of *Acacia* spp. that fix N at high rates, particularly during their establishment phase, with high densities of *Acacia* spp. regeneration after fire known to return soil N mineralisation capacity of eucalypt forests to pre-disturbance levels within two years (Ashton and Attiwill 1994). This interpretation is supported by significant decreases in soil N availability with time-since-fire (PERMANOVA, $P = 0.05$), and by the contribution of time-since-fire to β diversity of phanerophytes and canopy species (discussed below).

Topography did not contribute to β diversity of understorey life forms or canopy species, with the notable exception of ferns. Here, associations with north-south slopes and potential direct incident radiation are consistent with the requirements of ferns for relatively cooler and wetter microclimates (Ashton and Bassett 1997). Moreover, tree fern distribution is increasingly limited to incised south-facing gullies as rainfall decreases (FPA 2012), and tree fern carbon has been linked with topographic gradients within the study area (Fedrigo et al. 2014).

Stand structure and time-since-fire increased total explained β diversity

That the total explained β diversity was improved by the inclusion of stand structural and time-since-fire variables is congruent with previous understanding of disturbance as a primary driver of temperate forest species composition and structure (Fairman et al. 2016; Pulsford et al. 2016). The presence or long-term absence of disturbance can modify stand environmental conditions including structurally mediated changes in light availability and associated micro-climates that variously affect different life forms (Barbier et al. 2008; Bartels and Chen 2013). For example, in the absence of disturbance, a decline in sub-canopy light conditions will favour shade-tolerant species, such as rainforest species, leading to changes in species composition and forest structure (Ashton and Attiwill 1994; Cameron 2011), including transitions of dominant understorey components from *Acacia* spp. to rainforest species along the gradient of Wet forest to Rainforest (Fedrigo et al. 2014). With increasing time-since-fire (100–350 years) a multi-layered structure develops, characterised as cool-temperate mixed forest (Ashton 1981; Cameron 2011; Fedrigo et al. 2014). Over extended periods (>350 years) without fire, canopy and understorey species are replaced by characteristic rainforest species (Ashton and Attiwill 1994) and might include emergent eucalypts (Tng et al. 2012). The relatively greater response of anemochores and seeders to stand structure and time-since-fire is consistent with these well-documented successional processes. Fires, particularly stand replacing fires, are typically followed by a prolific colonisation of 'fireweeds', including *Senecio* spp. and *Dryopa dives* (Ashton 1981). In addition, early seral shrubs like *Cassinia aculeata*, *Olearia argophylla* and *Pomaderris aspera* variously increase or decrease with time-since-fire depending on their shade-tolerance and competitive ability (Ashton 1981).

Our measures of stand structural complexity (*H'*, CV) largely captured the aforementioned stand structural dynamics, and in particular, the decline in understorey light availability with increasing time-since-fire, and with transition from Wet forest to Rainforest. The significantly greater height CV in eucalypt forests relative to Rainforest also reflected the variable intensity of wildfire, in that not all were stand replacing. This was clearly demonstrated in the diameter class distribution of eucalypts at the 2009 wildfire sites, which supported live trees across a range of diameters from 40 to 140 cm DBH, as well as some older, larger individuals of >200 cm DBH (data not shown). Studies in other forest types have similarly reported changes in stand structural complexity with time-since-fire (e.g. Harper et al. 2005). Nonetheless, Varga et al. (2005) demonstrated that differences in stand structural complexity between pure and mixed conifer stands varied with age, and Chen and Taylor (2012) also reported variable time-since-fire effects related to soil nutrient availability.

We assumed that measures of canopy cover and structure would more closely reflect disturbance history than limited coarse fire history variables like time-since-fire, and this was shown to be the case. Moreover, the generally strong correlations between time-since-fire and stand structural metrics (r = 0.31–0.67; e.g. LAI r = 0.48, CV height r = 0.67) were in support of our initial assumption that stand structural dynamics would reflect the most recent fire. We cannot however rule out that limited sampling of the 1983 and 2009 wildfire sites, and the coarse resolution of disturbance history data, might have caused us to underestimate the explanatory importance of fire on β diversity (Henderson and Keith 2002; Murphy et al. 2015).

Distance-decay of β diversity reflected dispersal distance

Our hypothesis that distance-decay rates of β diversity would be inversely related to dispersal distance was in part supported. Lower intercepts and greater half distances indicated limited distance-decay for species with more readily dispersed propagules, particularly mobile and wind-dispersed seed, relative to species with ant and vertebrate-dispersed seed and barochorous seed. Similarly, ferns with mobile seed, had a lower intercept and greater half distance than phanerophytes; and non-woody species had a lower intercept than phanerophytes. This was consistent with previous understanding that ferns and fern allies with light and effectively dispersed diaspores have lower β diversity distance-decay than seed-bearing plants with heavier and less-readily dispersed diaspores (Nekola and White 1999; Lenoir et al. 2012). Long-distance dispersal offers advantages to species, such as avoidance of conspecific competition, while propagules of dispersal-limited species may benefit from favourable environmental conditions close to the parent plant (Karst et al. 2005).

Contrary to our hypothesis, distance decay of epi-endozoochores was greater than that of myrmecochores, and similar to (rather than less than) that of barochores. This disconnect could be related to long-distance dispersal by non-standard seed dispersers (Higgins et al. 2003). For example, myrmecochores and barochores can be dispersed large distances by vertebrates including deer (Vellend et al. 2003), which are common and known to feed on several myrmecochorous species in our study area (Parker 2009). This apparent discrepancy could also be due to stronger clumping of seed deposition of vertebrate and ant-dispersed species relative to barochorous species (van Breugel et al. 2007). Another explanation relates to the highly variable dispersal distance among vertebrate-dispersed species that will depend on fruit traits, the mobility, body size, diet and home range of the dispersal agent, and the availability of alternate food sources (Muller-Landau et al. 2008).

The disconnect between dispersal distance and distance decay might also be due to a ‘storage effect’, which is regarded as a stabilisation mechanism that allows species to persist over time during unfavourable conditions but increase in abundance under favourable conditions (Kalyuzhny et al. 2015). The storage effect can therefore manifest as a neutral process versus a niche process and confound tests of their respective importance (Alder et al. 2007). Similarly, resprouting provides a pathway for community assembly based on vegetation *in situ* at the time of disturbance and disconnects species composition from seed availability (López-Martínez et al. 2013). In this way resprouting may help explain why species with relatively small dispersal distances were common in our forests, representing a key regenerative strategy in these fire-prone landscapes (Clarke et al. 2015).

Conclusions and implications for conservation

Our results show that both niche and neutral processes contribute to β diversity in these temperate forests. Distance decay of β diversity reflected dispersal distance, particularly at smaller distances. However, environmental heterogeneity was consistently more important than dispersal limitation regardless of plant functional type although the relative importance of constituent environmental predictors (soils, climate, topography) differed between vegetation strata and within understorey life forms. Our results also demonstrate that consideration of disturbance-mediated effects increased our capacity to explain β diversity and that stand structural variables were more important in explaining β diversity than a single descriptor of disturbance history like time-since-fire.

Consistent with work elsewhere (DiStefano et al. 2013; Chick et al. 2016), these findings suggest forest biodiversity conservation measures that are based on broad-scale classification systems such as developmental stages and single fire history variables like time-since-fire (e.g. Cheal, 2010; Burrows and McCaw 2013) will not necessarily capture the full suite of factors influencing biodiversity. DiStefano et al. (2013), for example, recognised that time-since-fire represented just one component of the disturbance regime influencing landscape-level biodiversity of eucalypt woodlands, and that additional factors, like fire severity, were worthy of consideration in conservation management units. In the absence of detailed disturbance data, we suggest that stand structural variables offer potential as a proxy of disturbance history that, together with representative measures of environmental heterogeneity, would provide a strong basis for supporting landscape-scale conservation decisions.

Acknowledgements

This research was undertaken with approval by the Victorian Department of Environment, Land, Water and Planning (DELWP) under research permit numbers 10006440, 10006691 and 10007105. The work was funded by the Victorian DELWP iFER (Integrated Forest Ecosystem Research) program as well as the CSIRO Sustainable Agriculture Flagship program. We would like to thank those who contributed to data collection and processing, including B. Smith, J. Najera, D. Lockwood and L. Parker. We thank two anonymous reviewers for comments that improved the manuscript.

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Table 1 Significance of differences in stand structure of canopy species (>10 m height) from covariate PERMANOVA tests of effects of forest type (main factor) and time-since-fire (as covariate, TSF (covar.)) and subsequent PERMANOVA test of effect of time-since-fire (main factor). Forest type: CTR, cool temperate rainforest (*n* = 24); MF, mixed forest (*n* = 14); WF, wet forest (*n* = 43). Time-since-fire: 4 years, 2009 wildfire (*n* = 17); 30 years, 1983 wildfire (*n* = 7); 74 years, 1939 wildfire (*n* = 57). Values are means with 95% confidence intervals in brackets.

	Forest type (main factor), time-since-fire (covariate)						Time-since-fire (main factor)				
	Test	Pesudo -*F*	*P* Value	CTR	MF	WF	Pseudo -*F*	*P* Value	4 years	30 years	74 years
Basal Area	Forest Type	1.9	0.159	49.0	60.3	60.2	4.9	0.0114	31.4^{a}	66.3^{ab}	64.6^{b}
(m^2 ha^{-1})	TSF (covar.)	7.9	0.007	(33.2, 67,7)	(37.8, 88.0)	(46.8, 75.4)			(17.6, 48.9)	(35.6, 106.3)	(53.0, 77.4)
Stem density	Forest Type	0.6	0.5544	381	243	230	21.6	0.0001	34.8^{a}	511.2^{b}	396.0^{b}
(stems ha^{-1})	TSF (covar.)	28.3	0.0001	(217, 623)	(104, 490)	(144, 351)			(12.2, 79.7)	(227.8, 1001.8)	(298.3, 516.0)
LAI	Forest Type	13.3	0.0001	3.2^{a}	2.1^{b}	2.0^{b}	16.7	0.0001	1.3^{a}	2.8^{b}	2.6^{b}
	TSF (covar.)	31.2	0.0001	(2.8, 3.5)	(1.6, 2.5)	(1.8, 2.3)			(0.95, 1.74)	(2.14, 3.37)	(2.41, 2.84)
H' Stems ha^{-1}	Forest Type	0.2	0.8026	1.09	1.16	0.97	12.3	0.0003	0.53^{a}	0.75^{a}	1.22^{b}
(DBH)	TSF (covar.)	24.3	0.0001	(0.84, 1.33)	(0.84, 1.48)	(0.79, 1.15)			(0.28, 0.79)	(0.36, 1.15)	(1.08, 1.36)
H' Stems ha^{-1}	Forest Type	1.6	0.2139	1.05	1.32	0.95	21.6	0.0001	0.38^{a}	0.72^{a}	1.28^{b}
(height)	TSF (covar.)	44.4	0.0001	(0.80, 1.31)	(0.98, 1.66)	(0.76, 1.14)			(0.13, 0.63)	(0.33, 1.11)	(1.15, 1.42)
H' BA (DBH)	Forest Type	0.9	0.4013	1.16	1.05	0.79	10.0	0.0002	0.45^{a}	0.72^{ab}	1.12^{b}
	TSF (covar.)	20.1	0.0001	(0.92 1.41)	(0.72, 1.37)	(0.61, 0.98)			(0.18, 0.72)	(0.29, 1.14)	(0.97, 1.27)
H' BA (height)	Forest Type	0.6	0.5211	1.03	1.06	0.71	14.5	0.0001	0.31^{a}	0.58^{a}	1.07^{b}
	TSF (covar.)	29.0	0.0001	(0.79, 1.27)	(0.74, 1.37)	(0.53, 0.89)			(0.05, 0.56)	(0.18, 0.98)	(0.93, 1.21)
CV (Height)	Forest Type	7.7	0.0009	0.36^{a}	0.51^{b}	0.41^{b}	35.8	0.0001	0.09^{a}	0.39^{b}	0.51^{b}
	TSF (covar.)	76.5	0.0001	(0.27, 0.46)	(0.38, 0.64)	(0.33, 0.48)			(0.01, 0.18)	(0.26, 0.53)	(0.46, 0.56)
CV (DBH)	Forest Type	0.2	0.8246	0.71	0.75	0.59	31.0	0.0001	0.17^{a}	0.74^{b}	0.78^{b}
	TSF (covar.)	47.6	0.0001	(0.56, 0.86)	(0.55, 0.95)	(0.47, 0.70)			(0.03, 0.31)	(0.53, 0.96)	(0.71, 0.86)
Multivariate	Forest Type	2.3	0.0221	a	b	b	17.8	0.0001	a	b	c
PERMANOVA	TSF (covar.)	32.1	0.0001								

PERMANOVA tested for differences in the Euclidean distance matrix according to forest type and time-since-fire (9999 permutations). Significant ($P \leq 0.05$) pairwise comparisons are indicated by means followed by different superscripts. Transformations (to meet assumptions of normality) prior to analysis: basal area ^0.5, stem density ^0.25. Presented values for basal area and stem density are back transformed. Multivariate PERMANOVA tested for the multivariate significance of differences across all the stand structure variables. Significant ($P \leq 0.05$) pairwise comparisons are indicated by different letters.

Abbreviations: LAI, leaf area index; *H'* (Shannon's index); DBH (diameter at breast height); BA (basal area); CV (coefficient of variation); CI (confidence interval)

All variables were measured at >10 m height except for LAI that was measured at 1.3 m height.

Table 2 The intercept and slope of generalised linear models (GLM) of β diversity (Bray-Curtis dissimilarity) against ln-transformed distance (km) (see ESM Appendix 5). All GLMs were significant at $P < 0.0001$.

					Half Distance[B]		P-Values[C]	
Functional Type	n[A]	Intercept	Slope	R^2 (%)	ln (km)	(km)	Intercept	Slope
Dispersal Mode							<0.0001	<0.0001
Mobile seed	35	0.521	0.043	5.92	5.61	274		
Barochores	46	0.742	0.038	5.78	3.39	30		
Anemochores	22	0.745	0.026	2.16	4.86	130		
Myrmecochores	18	0.794	0.025	1.89	4.06	58		
Epi-endozoochores	26	0.755	0.038	6.04	3.23	25		
Life Form (ferns v. phanerophytes)							<0.0001	0.083
Ferns	35	0.521	0.043	5.92	5.61	274		
Phanerophytes	62	0.669	0.036	6.72	4.60	99		
Life Form (non-woody v. phanerophytes)							<0.0001	0.026
Non-woody species	91	0.634	0.044	8.89	4.19	66		
Phanerophytes	62	0.669	0.036	6.72	4.60	99		
Fire Response							<0.0001	0.081
Seeders	46	0.769	0.034	4.83	3.44	31		
Resprouters	92	0.622	0.040	8.81	4.77	118		
Vegetation Strata							<0.0001	<0.0001
All understorey species (abundance)	153	0.656	0.039	9.97	4.36	78		
All understorey species (P/A)	153	0.578	0.046	12.82	4.64	103		
Canopy species	42	0.606	0.020	0.91	10.01	22251		

[A] The number of species in each functional type.

[B] The half distance is the distance (on the ln scale, and back-transformed) that halves the similarity from its initial value and thus considers both the initial similarity and rate of decay

[C] P-values indicate significance of differences in the intercept and slope of the GLMs within each functional type. For life form, comparisons were limited to independent functional types (ferns v. phanerophytes; non-woody v. phanerophytes) given ferns were a sub-set of the non-woody life form. For vegetation strata comparisons were limited to understorey (abundance) v. canopy; and understorey (P/A) v. canopy. The *P-Values* were consistent among these two comparisons.

Table 3 Variance partitioning results for the marginal and conditional components of variation for spatial (Sp), environmental (Env), and disturbance (Disturb) variables to β diversity. Values are percentages of variation in β diversity explained by the data.

	Marginal			Pure (conditional)							Total
Functional Type	Sp	Env	Disturb	Sp	Env	Disturb	Sp & Disturb	Sp & Env	Env & Disturb	Sp & Env & Disturb	
Dispersal Mode											
Mobile seed	18	39	11	9	25	8	0	9	3	2	53
Barochores	23	28	16	11	14	9	1	9	4	2	49
Anemochores	9	17	21	6	10	14	1	2	5	1	38
Myrmecochores	14	27	8	7	18	5	0	5	2	2	39
Epi-Endozoochores	19	25	5	7	12	3	0	10	1	2	34
Life Form											
Ferns	18	39	11	9	25	8	0	9	3	2	53
Non-woody species	22	35	15	6	17	10	0	13	2	4	51
Phanerophytes	18	32	21	6	17	12	2	8	5	2	52
Phanerophytes[A]	10	22	10	7	19	11	0	3	0	0	39
Fire Response											
Seeders	18	26	17	7	14	9	1	6	3	4	44
Resprouters	20	35	16	5	17	9	1	12	4	1	50
Vegetation Strata											
All understorey species (abundance)	20	38	20	6	20	11	1	9	5	4	55
All understorey species (P/A)	24	32	19	6	12	11	1	14	4	3	50
Canopy species	8	31	13	7	25	10	0	3	5	0	47

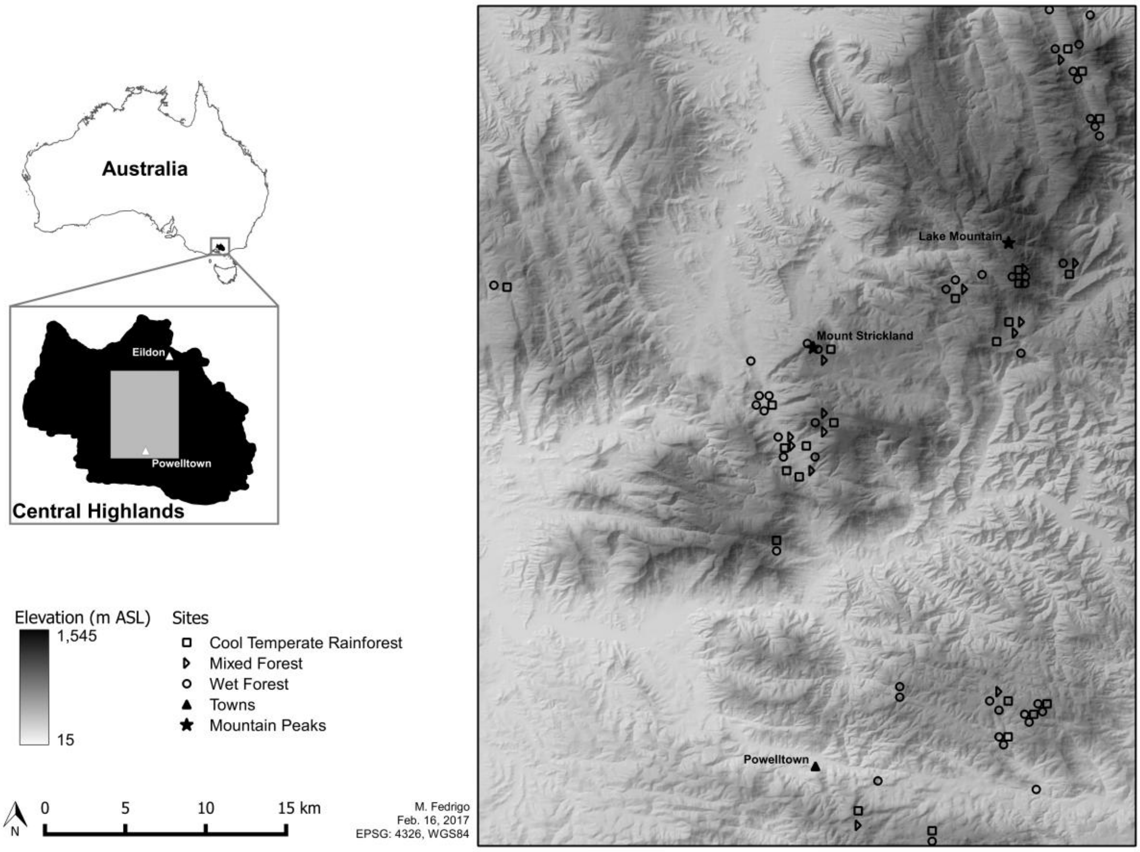
[A] Understorey phanerophytes based on basal area of stems ≤ 10 m height

Figure headers

Fig. 1 Map of study sites within the Central Highlands region of south-eastern Australia. Overlapping site symbols have been separated for clarity. The number of sites sampled within each wildfire year (2009, 1983, 1939) were: Cool Temperate Rainforest (2, 1, 21); Mixed Forest (2, 0, 12); Wet Forest (13, 6, 24).

Fig. 2 Fractions for the initial two-way and subsequent three-way variance partitioning of the variable sets (spatial, (Sp); environmental (E); disturbance (D)). The relative contributions of component environmental (climate 'C', soil 'S', topography 'T') and disturbance (stand structure, time-since-fire 'TSF') variables were subsequently determined via a second-tier conditional analysis as indicated by the arrows. The sum of the pure and shared component of variation for each set of explanatory variables (i.e. spatial, environmental, disturbance) represents the marginal variation.

Fig. 3 Distance decay plots showing increases in environmental dissimilarity (left axis, principal component score, PC) with increasing geographic distance for a) climate; b) soil; and c) topography. Circles represent mean dissimilarity (with lower and upper quartile range), and triangles represent associated Mantel correlograms for the 20 distance classes (each representing 162 sample pairs). Positive Mantel r indicates spatial autocorrelation among sites, with filled symbols indicating significant Mantel's r ($P \leq 0.05$) per distance class. SSI is the spatial structure index, and r and P summarise RELATE test results. Lines and equations represent best-fit regressions.


Australia
Eildon
Powelltown
Central Highlands
Lake Mountain
Mount Strickland
Powelltown
Elevation (m ASL)
1,545
15
Sites
□ Cool Temperate Rainforest
▷ Mixed Forest
○ Wet Forest
▲ Towns
★ Mountain Peaks
N
0
5
10
15 km
M. Fedrigo
Feb. 16, 2017
EPSG: 4326, WGS84

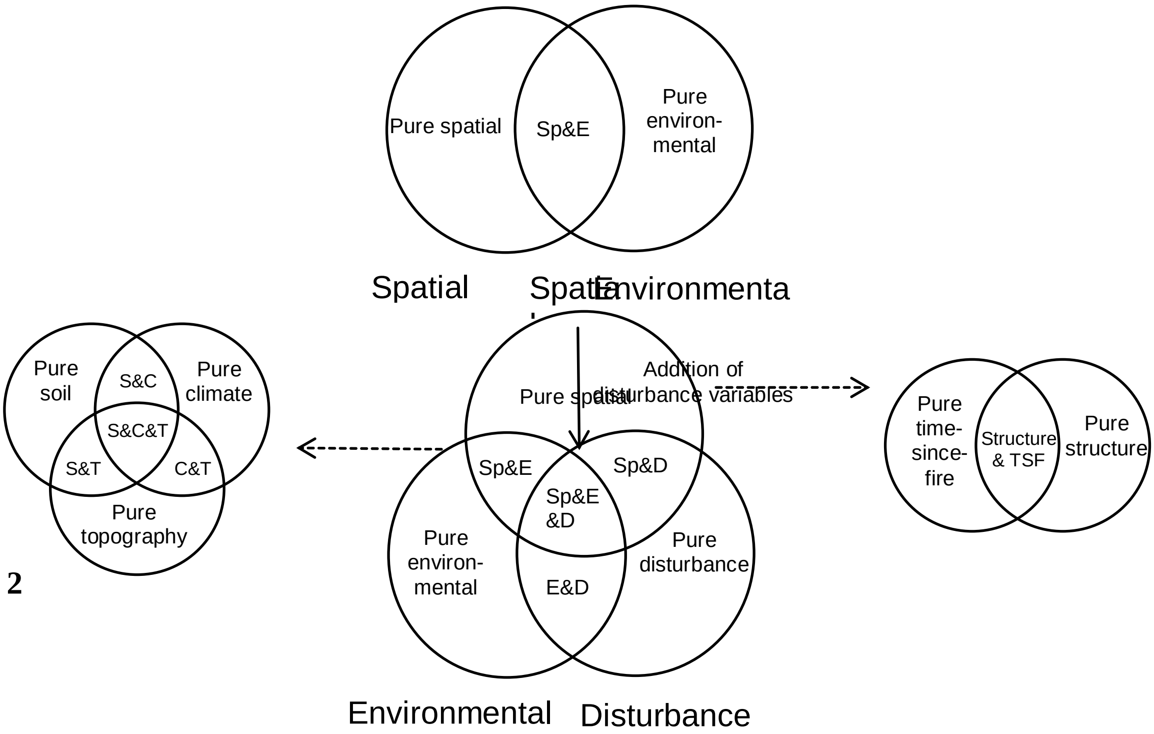
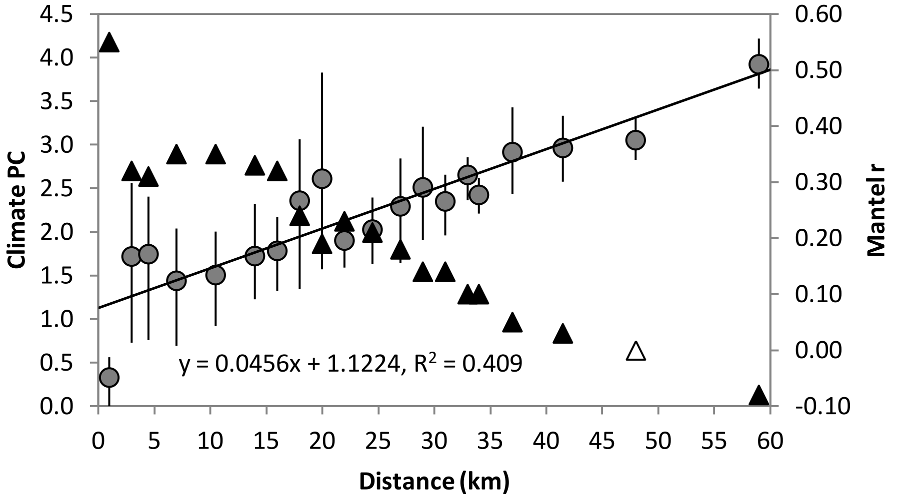
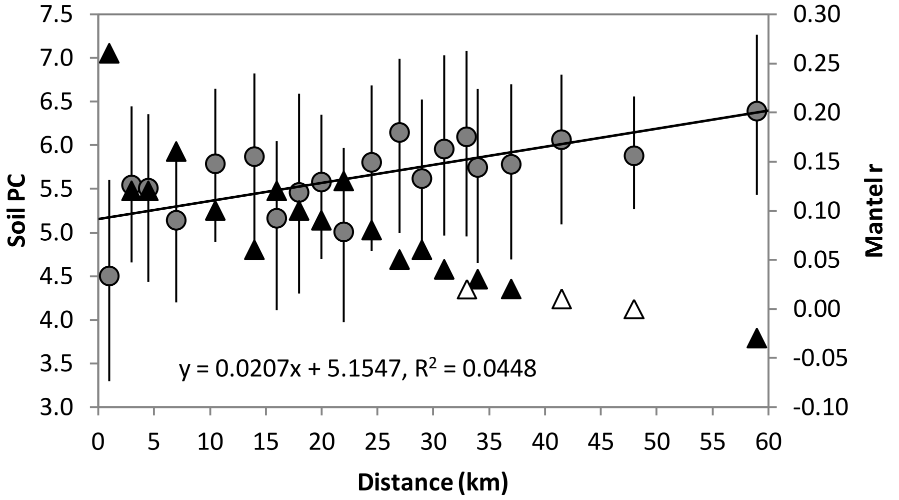

Pure spatial
Sp&E
Pure environ-mental
Spatial
Spatial
Environmenta
Pure soil
S&C
Pure climate
S&C&T
S&T
C&T
Pure topography
Pure spatial
Addition of disturbance variables
Sp&E
Sp&D
Sp&E &D
Pure environ-mental
E&D
Pure disturbance
Environmental
Disturbance
Pure time-since-fire
Structure & TSF
Pure structure

Fig. 2

(a) Climate, $r = 0.64$, $P = 0.0001$; SSI = 1095 %



(b) Soil, $r = 0.21$, $P = 0.0001$; SSI = 42 %



(c) Topography, $r = 0.13$, $P = 0.0002$; SSI = 24 %

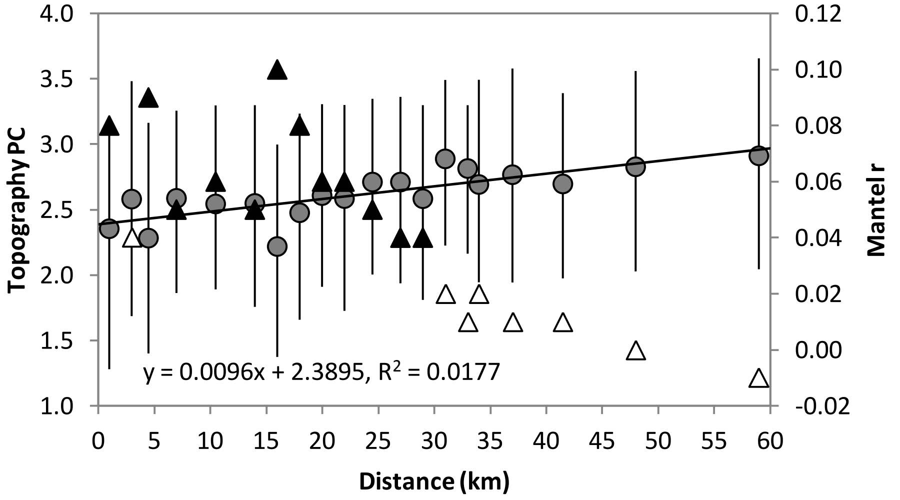


Fig. 3

Appendix 1 Spatial, environmental and structural variables across temperate forests in the Central Highlands region. Bolded variables are uncorrelated ($r < |0.7|$) and were used in the DistLM analysis (see Table 3); non-bolded variables were excluded from the DistLM analysis due to strong correlation ($r > |0.7|$) with a bolded variable (as listed in the final column, including the direction of correlation).

Variable	Mean	Minimum	Maximum	Correlation^{I}
Spatial				
Longitude (x, º)	145.82	145.51	145.94	
Latitude (y, º)	-37.62	-37.91	-37.33	
Climate^{A}				
Elevation (m above sea level)	826	302	1375	- bio1
Annual mean temperature (bio1; °C)	10.2	7.3	12.5	
Mean diurnal range (mean of monthly (maximum temperature – minimum temperature)) (bio2; °C)	10.1	9.3	11.1	+ bio1
Isothermality (bio2/bio7*100) (bio3; %)	4.4	4.2	4.9	+ bio1
Temperature seasonality (std dev * 100) (bio4; °C)	426.3	383.7	459.6	
Maximum temperature of warmest month (bio5; °C)	23.4	20.7	25.9	+ bio1
Minimum temperature of coldest month (bio6; °C)	1.0	-1.3	2.6	+ bio1
Temperature annual range (bio5 – bio6) (bio7; °C)	22.4	21.5	23.3	
Mean temperature of wettest quarter (bio8; °C)	5.1	1.7	8.2	+ bio1
Mean temperature of driest quarter (bio9; °C)	15.7	13.1	17.8	+ bio1
Mean temperature of warmest quarter (bio10; °C)	15.7	13.1	17.8	+ bio1
Mean temperature of coldest quarter (bio11; °C)	4.7	1.7	7.5	+ bio1
Annual precipitation (bio12; mm)	1697	1263	1957	- bio1
Precipitation of wettest month (bio13; mm)	211	141	246	- bio1
Precipitation of driest month (bio14; mm)	62	47	72	- bio7
Precipitation seasonality (CV) (bio15; %)	33	24	41	+ bio4
Precipitation of wettest quarter (bio16; mm)	593	403	692	- bio1
Precipitation of driest quarter (bio17; mm)	229	188	265	- bio7
Precipitation of warmest quarter (bio18; mm)	229	188	265	- bio7
Precipitation of coldest quarter (bio19; mm)	586	376	692	- bio1
Annual heat moisture index (bio1+10)/(bio12/1000)	12.1	8.8	17.8	+ bio1
Topography				
Slope (°)	12.13	0.57	36.00	
North-south aspect^{B}	-0.12	-1.00	1.00	
East-west aspect^{B}	-0.03	-1.00	1.00	+ HLI
Heat load index^{C} **(HLI)**	0.74	0.10	1.27	
PDIR^{D} **(MJ cm**$^{-2}$ **yr**$^{-1}$**)**	0.71	0.12	1.10	
Soil^{D} *(0–10 cm)*				
Nitrogen (%)	0.79	0.26	1.29	+ N$_{30}$
Carbon (%)	15.66	5.58	31.49	
C/N	19.90	16.08	26.38	
Electrical Conductivity (EC, µS cm^{-1}**)**	165.82	54.66	338.50	
pH	4.45	3.64	5.68	
NO_3^--N (mg kg^{-1}**)**	7.02	0.05	44.39	
NH_4^+-N (mg kg^{-1}**)**	14.46	0.54	88.91	

Variable	Mean	Minimum	Maximum	Correlation[I]
Available P (mg kg^{-1})	5.71	0.20	28.57	
Ca^{2+} (cmol p^{+} kg^{-1})	1.97	0.35	5.85	+ Mg$^{2+}_{30}$
K^{+} (cmol p^{+} kg^{-1})	0.57	0.16	1.08	
Mg^{2+} (cmol p^{+} kg^{-1})	1.08	0.26	2.65	+ Mg$^{2+}_{30}$
Na^{+} (cmol p^{+} kg^{-1})	0.14	0.06	0.39	
Loss on Ignition (%)	24.77	7.94	42.92	+ N$_{30}$
Bulk Density (g cm^{-3})	0.38	0.22	0.72	- C$_{10}$
Clay (%)	26.8	9.0	49.8	
Silt (%)	46.3	22.2	65.3	
Sand (%)	26.9	7.7	52.9	- Silt$_{10}$
Soil (10–30 cm)				
Nitrogen (%)	0.54	0.12	1.04	
Carbon (%)	10.20	2.85	19.76	+ N$_{30}$
C/N	19.24	14.76	27.73	+ C/N$_{10}$
Electrical Conductivity (EC, µS cm^{-1})	70.58	38.00	143.20	
pH	4.68	4.11	5.55	+ pH$_{10}$
NO$_3^{-}$-N (mg kg^{-1})	3.06	0.05	21.65	+ NO$_3^{-}$-N$_{10}$
NH$_4^{+}$-N (mg kg^{-1})	6.71	0.19	56.44	+ NH$_4^{+}$-N$_{10}$
Available P (mg kg^{-1})	1.90	0.00	18.24	+ P$_{10}$
Ca^{2+} (cmol p^{+} kg^{-1})	0.50	0.05	2.27	+ Mg$^{2+}_{30}$
K^{+} (cmol p^{+} kg^{-1})	0.30	0.04	0.66	+ K$^{+}_{10}$
Mg^{2+} (cmol p^{+} kg^{-1})	0.35	0.11	1.25	
Na^{+} (cmol p^{+} kg^{-1})	0.08	0.01	0.19	
Loss on Ignition (%)	16.86	4.77	33.05	+ N$_{30}$
Bulk Density (g cm^{-3})	0.57	0.40	1.01	- N$_{30}$
Clay (%)	29.8	8.1	53.3	+ Clay$_{10}$
Silt (%)	44.1	22.0	65.5	+ Silt$_{10}$
Sand (%)	26.2	6.3	56.9	- Silt$_{10}$
Stand Structure[EFG]				
Leaf area index	2.37	0.42	4.83	
H' Stems ha^{-1} (10 cm DBH bins, unitless)	1.04	0.00	2.13	+ H' BA (height)
H' Stems ha^{-1} (4 m height bins, unitless)	1.04	0.00	2.15	+ H' BA (height)
H' Basal Area (10 cm DBH bins, unitless)	0.95	0.00	2.15	+ H' BA (height)
H' Basal Area (4 m height bins, unitless)	0.87	0.00	2.30	
Coefficient of Variation (DBH, %)	68	0	166	+ CV (height)
Coefficient of Variation (Height, %)	43	0	93	
Basal Area (m^{2} ha^{-1})	83.5	0.00	189.6	
Density (stems ha^{-1})	452	25	2395	
Introduced species				
Richness introduced species	0.4	0.0	4.0	+, Abun intro
Total abundance introduced species	0.02	0.00	0.48	
Time-since-fire [H] ***(Years)***	56	4	74	

[A] Climate variables, are 926.1 m in resolution (30 arc seconds, Hijmans et al., 2005) for the present range from 1950–2000

[B] Separated into north–south and east–west layers (Beers et al., 1966)

[C] Calculated using Hyperniche (Version 2.2; McCune and Mefford, 2009), PDIR, Potential Direct Incident Radiation

[D] Soil pH and Electrical conductivity 'EC' in 1:5 soil/ solution (Rayment and Higginson, 1992); soil total C and N via LECO CHN analyser (LECO Corporation, USA); loss on ignition via combustion at 375ºC for 2.5 hours; exchangeable cations in 1M ammonium acetate (Raymond and Lyons, 2010) determined by Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-AES; Vista Pro Axial, Varian, Australia); bulk density corrected for the volume of stones using a specific density of 2.65 g cm^{-3} (Post and Kwon, 2000); NH$_4^{+}$–N and NO$_3^{-}$–N in 1 M

KCl extracts, concentrations determined colorimetrically (Bran and Luebbe, 1993, 1994); Available P, fluoride-extractable Bray 1 (Rayment and Higginson, 1992); Clay, Silt, Sand using the hydrometer method (DSNR, 2002).

[E] All variables calculated for >10 m height except for leaf area index measured at 1.3 m height

[F] Shannon's Index (*H*') calculated using 10 cm DBH and 4 m height bins

[G] Stand structural variables were limited to LAI because basal area, stem density, and allied measures of stand structural complexity were confounded with the calculation of β diversity of canopy species (see methods)

[H] Number of years since last fire (1939 wildfire = 74, 1983 wildfire = 30, 2009 wildfire = 4)

[I] Subscripts indicate the depth of the associated soil variable (10, 0–10 cm, 30, 10–30 cm)

Appendix 2 Site survey and sampling strategies conducted across the four (1–4) sampling campaigns

	1[B]	2[B]	3	4
Forest type [A,B]	WF (*n* = 6), MF (*n* = 6), CTR (*n* = 6)	WF (*n* = 25), MF (*n* = 6), CTR (*n* = 12)	WF (*n* = 9), CTR (*n* = 1)	WF (*n* = 3), MF (*n* = 2), CTR (*n* = 5)
Site dimensions	30 m × 30 m (0.09 ha plot size adjusted for slope)	20 m × 20 m (~0.04 ha)	20 m × 20 m (~0.04 ha)	10 m × 40 m (~0.04 ha, shortest side parallel to slope)
Soil sampling (one sample collected from each quarter per plot)	349.7 cm^3 (6.5 cm diameter) corer; 0–10 cm, 10–20 cm, 20–30 cm depths	Pogo corer; 0–10 cm, 10–30 cm depths.	Pogo corer; 0–10 cm, 10–30 cm depths.	349.7 cm^3 (6.5 cm diameter) corer; 0–10 cm, 10–30 cm depths
Soil bulk density	Measured using 349.7 cm^3 corer	Modelled (see Fedrigo et al., 2014)	Measured using 349.7 cm^3 corer	Measured using 349.7 cm^3 corer
Soil analysis (total C, N)	Results based on the mean concentration of 4 samples per site	Results based on one composite sample per site	Results based on the mean concentration of 4 samples per site	Results based on the mean concentration of 4 samples per site
Soil analysis (all other variables)	Results based on one composite sample per site	Results based on one composite sample per site	Results based on the mean concentration of 4 samples per site	Results based on one composite sample per site
Understorey vegetation survey	20 m × 20 m plot, point intercept every 1 m on transects located every 2 m (total 210 points)	20 m × 20 m plot, point intercept every 1 m on transects located every 2 m (total 210 points)	20 m × 20 m plot, point intercept every 1 m on transects located every 2 m (total 210 points)	10 m × 40 m plot, point intercept every 1 m on transects located every 2 m (total 205 points)
Vegetation Structure	All trees ≥10 cm measured for DBH and height, counts and also average height within 2<10 cm DBH class	Counts and representative trees measured for DBH and height for 2<10, 10<20 and 20<30 cm DBH classes. Larger trees were counted in DBH classes adapted to the size distribution of that plot.	Counts and representative trees measured for DBH and height for 2<10, 10<20 and 20<30 cm DBH classes. Larger trees were counted in DBH classes adapted to the size distribution of that plot.	All trees ≥20 cm measured, counts and also maximum and minimum height within 2<10 and 10<20 cm DBH classes
Leaf Area Index (at 1.5 m height)	Mean of 5 hemispherical photos per sites (one photo located within each quarter and one photo in the centre)	Mean of 5 hemispherical photos per sites (one photo located within each quarter and one photo in the centre)	Mean of 5 hemispherical photos per sites (one photo located within each quarter and one photo in the centre)	Mean of 15 hemispherical photos per site (photos at 10 m intervals: 0, 10, 20, 30, 40 m along 3 transects 0, 5, 10 m)
Date: Soil sampling	October to December 2012	October to December 2012	April to November 2011	March to June 2014
Date: Vegetation structure	October to December 2012	October to December 2012	September to December 2013	March to June 2014
Date: Understorey vegetation	September to December 2013	September to December 2013	September to December 2013	October 2014

[A] WF, wet forest; MF, cool temperate mixed forest; CTR, cool temperate rainforest.

[B] See Fedrigo et al. (2014) for further details

DBH, Diameter at Breast Height (1.3 m) Over Bark

Appendix 3 Plants recorded as 'understorey' species across the Central Highlands, by functional types (dispersal mode, fire response and life form). Abundance is the relative proportion (%) of hits across all study sites using the line-intercept technique (see Appendix 2). Frequency is the number of sites that included a species (from a total of 81 sites). We obtained functional type values from the literature (see Meers et al. 2010), publically available databases (DEWLP 2014; NSW National Parks and Wildlife Service 2002), and field observations. Nomenclature follows Walsh and Stajsic (2007).

Family	**Species**	**Dispersal mode**[B]	**Fire Response**[C]	**Life form**[D]	**Abun-dance**	**Freq-uency**
ALSEUOSMIACEAE	*Wittsteinia vacciniacea*	end	R	C	0.017	3
APIACEAE	*Hydrocotyle geraniifolia*	bar	S	HE	0.006	1
	Hydrocotyle hirta	bar	R	HE	0.100	17
	Hydrocotyle algida	bar	R	HE	0.030	5
APOCYNACEAE	*Parsonsia brownii*	ane	SR	P	0.094	15
ARALIACEAE	*Polyscias sambucifolia subsp. 1*	end	R	P	1.101	21
	Polyscias sambucifolia subsp. 1/3 intermediate	end	R	P	0.059	4
	Polyscias sambucifolia subsp. 3	end	R	P	0.611	16
ASPLENIACEAE[A]	*Asplenium bulbiferum subsp. gracillimum*	mob	S	HE	0.053	9
	Asplenium flabellifolium	mob	R	HE	0.006	1
ASTERACEAE	*Bedfordia arborescens*	ane	R	P	0.311	3
	Coronidium scorpioides s.s	ane	R	HP	0.006	1
	Lagenophora montana	bar	R	HF	0.006	1
	Lagenophora stipitata	bar	R	HF	0.012	2
	Olearia argophylla	ane	R	P	0.532	15
	Olearia lirata	ane	S	P	0.121	8
	Ozothamnus secundiflorus	ane	R	P	0.006	1
	Ozothamnus thyrsoideus	ane	R	P	0.006	1
	Senecio velleioides	ane	S	C	0.117	7
	Taraxacum sp.	ane	R	HF	0.012	2
	Cassinia aculeata	ane	S	P	0.680	26
	Cassinia trinerva	ane	S	P	0.335	10
	Leptinella filicula	ane	R	HF	0.035	5
	Olearia megalophylla	ane	R	P	0.006	1
	Olearia phlogopappa subsp. continentalis	ane	R	P	0.509	33
	Senecio linearifolius	ane	S	C	0.017	3
	Senecio linearifolius var latifolius	ane	S	C	0.094	5
ATHYRIACEAE[A]	*Diplazium australe*	mob	R	C	0.012	1
BIGNONIACEAE	*Pandorea pandorana*	ane	SR	P	0.023	4
BLECHNACEAE[A]	*Blechnum cartilagineum*	mob	R	C	0.017	2
	Blechnum chambersii	mob	R	C	0.023	4
	Blechnum fluviatile	mob	R	C	0.017	3
	Blechnum nudum	mob	R	C	0.688	21
	Blechnum patersonii	mob	R	C	0.006	1
	Blechnum penna-marina subsp. alpina	mob	R	C	0.017	1

Family	**Species**	**Dispersal mode**[B]	**Fire Response**[C]	**Life form**[D]	**Abun-dance**	**Freq-uency**
	Blechnum wattsii	mob	R	C	3.484	53
CAPRIFOLIACEAE	*Sambucus gaudichaudiana*	end	R	P	0.083	14
CARYOPHYLLACEAE	*Stellaria flaccida*	bar	S	HPr	0.233	22
CONVOLVULACEAE	*Dichondra repens*	bar	R	HF	0.006	1
CYATHEACEAE[A]	*Cyathea australis*	mob	R	P	2.554	27
CYPERACEAE	*Carex appressa*	bar	R	HE	0.017	2
	Carex sp.	bar	R	HE	0.030	5
	Gahnia sieberiana	end	R	HE	0.006	1
	Gahnia sp.	end	R	HE	0.023	3
	Isolepis sp.	mob		HE	0.070	3
	Lepidosperma elatius	myr	R	HE	0.136	11
	Lepidosperma lateral var majus	myr	R	HE	0.006	1
	Uncinia sp.	bar	S	HE	0.006	1
DENNSTAEDTIACEAE[A]	*Histiopteris incisa*	mob	R	HPr	0.284	28
	Hypolepis amaurorachis	mob	R	HPr	0.017	2
	Hypolepis glandulifera	mob	R	HPr	0.012	2
	Hypolepis muelleri	mob	R	HPr	0.012	2
	Hypolepis rugosula	mob	R	HPr	0.006	1
	Pteridium esculentum	mob	R	G	1.098	25
DICKSONIACEAE[A]	*Dicksonia antarctica*	mob	R	P	13.598	71
DRYOPTERIDACEAE[A]	*Polystichum proliferum*	mob	R	HE	3.386	60
	Rumohra adiantiformis	mob		EPI	0.012	2
EPACRIDACEAE	*Leucopogon gelidus*	end	R	P	0.012	2
FABACEAE	*Daviesia laxiflora*	bar	R	P	0.012	2
	Goodia lotifolia var. pubescens	myr	S	P	0.006	1
	Indigofera australis	bar	R	P	0.006	1
	Platylobium reflexum	myr	R	P	0.090	1
	Platylobium sp.	myr	R	P	0.147	4
	Pultenaea muelleri	myr	S	P	0.691	7
FAGACEAE	*Nothofagus cunninghamii*	ane	R	P	3.843	29
GERANIACEAE	*Geranium homeanum*	bar	R	HPr	0.128	21
GLEICHENIACEAE[A]	*Sticherus lobatus*	mob	R	HPr	0.019	1
	Sticherus urceolatus	mob	R	HPr	0.006	1
GOODENIACEAE	*Goodenia ovata*	myr	S	P	0.088	3
GRAMMITIDACEAE[A]	*Notogrammitis angustifolia subsp. nothofageti*	mob		EPI	0.006	1
	Notogrammitis billardieri	mob	S	EPI	0.136	22
HALORAGACEAE	*Gonocarpus humilis*	bar	S	HPr	0.012	2
	Gonocarpus montanus	bar	R	HPr	0.006	1
	Gonocarpus tetragynus	bar	R	HPr	0.006	1
HYMENOPHYLLACEAE[A]	*Crepidomanes venosum*	mob	S	EPI	0.053	9
	Hymenophyllum australe	mob	S	EPI	0.030	5
	Hymenophyllum cupressiforme	mob	S	EPI	0.053	9
	Hymenophyllum flabellatum	mob	S	EPI	0.048	8
	Hymenophyllum peltatum	mob	S	EPI	0.006	1
	Hymenophyllum rarum	mob	S	EPI	0.019	3
IRIDACEAE	*Libertia pulchella*	bar		HE	0.030	3

Family	**Species**	**Dispersal mode**[B]	**Fire Response**[C]	**Life form**[D]	**Abun-dance**	**Freq-uency**
JUNCACEAE	*Juncus pauciflorus*	mob	R	HE	0.006	1
LAMIACEAE	*Mentha laxiflora*	bar		HPr	0.052	8
	Prostanthera lasianthos var. lasianthos	bar	S	P	1.017	19
	Prostanthera melissifolia	bar	S	P	0.149	3
LILIACEAE	*Astelia australiana*	end	R	HE	0.006	1
	Dianella tasmanica	end	R	HE	0.377	23
MIMOSACEAE	*Acacia dealbata*	myr	R	P	6.283	39
	Acacia frigescens	myr	S	P	5.268	22
	Acacia melanoxylon	myr	R	P	1.783	13
	Acacia obliquinervia	myr	S	P	0.952	6
	Acacia verticillata	myr	S	P	0.017	2
MONIMIACEAE	*Atherosperma moschatum*	ane	R	P	2.815	18
	Hedycarya angustifolia	end	R	P	0.463	22
MYRTACEAE	*Eucalyptus delegatensis*	bar	S	P	0.264	7
	Eucalyptus nitens	bar	R	P	0.053	2
	Eucalyptus pauciflora	bar	R	P	0.012	1
	Eucalyptus regnans	bar	S	P	0.670	10
	Leptospermum grandifolium	bar	R	P	1.799	10
OLEACEAE	*Notelaea ligustrina*	end	R	P	0.299	14
ONAGRACEAE	*Epilobium sp.*	ane	S	HPr	0.006	1
OSMUNDACEAE	*Todea barbara*	mob	S	P	0.006	1
OXALIDACEAE	*Oxalis exilis*	bar	R	G	0.058	9
	Oxalis exilis / perennans	bar	R	G	0.064	10
	Oxalis magellanica	bar	R	G	0.006	1
PITTOSPORACEAE	*Billardiera macrantha*	end	R	P	0.052	9
	Billardiera mutabilis	end	R	P	0.012	2
	Pittosporum bicolor	end	SR	P	0.267	24
POACEAE	*Deyeuxia sp.*	bar	R	HE	0.006	1
	Dryopoa dives	bar	S	HE	0.335	16
	Microlaena stipoides var. stipoides	epi	R	HF	0.023	4
	Poa ensiformis	bar	R	HE	1.328	28
	Poa sieberiana var. sieberiana	bar	R	HE	0.006	1
	Poa tenera	bar	R	HE	0.011	1
	Rytidosperma sp	epi	R	HE	0.012	2
	Tetrarrhena juncea	bar	R	HPr	4.347	43
POLYPODIACEAE[A]	*Microsorum pustulatum*	mob	S	EPI	0.077	13
PROTEACEAE	*Lomatia fraseri*	ane	R	P	0.588	19
	Persoonia arborea	end	SR	P	0.368	10
PSILOTACEAE[A]	*Tmesipteris obliqua*	mob	S	EPI	0.012	2
	Tmespteris ovata	mob	S	EPI	0.006	1
PTERIDACEAE[A]	*Pteris tremula*	mob	S	HPr	0.006	1
RANUNCULACEAE	*Clematis aristata*	ane	R	P	0.259	43
	Ranunculus sp.	epi		HP	0.006	1
RHAMNACEAE	*Pomaderris aspera*	myr	S	P	4.030	19
	Spyridium parvifolium	myr	R	P	0.006	1

Family	**Species**	**Dispersal mode**[B]	**Fire Response**[C]	**Life form**[D]	**Abun-dance**	**Freq-uency**
ROSACEAE	*Rubus parvifolius*	end	R	P	0.075	10
	Acaena novae-zelandiae	epi	R	C	0.105	16
RUBIACEAE	*Coprosma hirtella*	end	R	P	0.100	17
	Coprosma nitida	end	S	P	0.006	1
	Coprosma quadrifida	end	R	P	0.389	22
	Nertera granadensis	end	R	HE	0.006	1
	Asperula polymera	bar	R	HPr	0.070	11
	Asperula scoparia subsp. scoparia	bar	R	HPr	0.006	1
	Galium binifolium subsp. binifolium	bar	S	HPr	0.006	1
	Galium leiocarpum	bar	S	HPr	0.006	1
	Galium sp.	bar	S	HPr	0.053	8
	Leptostigma breviflorum	end		HPr	0.047	8
RUTACEAE	*Correa lawrenceana var. latrobeana*	bar	S	P	4.073	33
	Leionema bilobum subsp. serrulatum	myr	S	P	0.041	1
	Philotheca myoporoides subsp. myoporoides	bar	S	P	0.106	1
	Zieria arborescens subsp. arborescens	bar	S	P	1.159	17
SANTALACEAE	*Exocarpos cupressiformis*	end	R	P	0.070	1
SCROPHULARIACEAE	*Derwentia derwentiana subsp. derwentiana*	bar	R	C	0.012	2
THYMELAEACEAE	*Pimelea axiflora subsp. axiflora*	myr	S	P	0.188	13
	Pimelea ligustrina subsp. ligustrina	bar	R	P	0.006	1
URTICACEAE	*Australina pusilla subsp. muelleri*	bar		HPr	0.111	18
	Urtica incisa	bar	R	HPr	0.053	8
VIOLACEAE	*Viola hederacea s. l.*	myr	R	HF	0.158	25
WINTERACEAE	*Tasmannia lanceolata*	end	S	P	0.230	27
XANTHORRHOEACEAE	*Lomandra longifolia subsp. exilis*	myr	R	HE	0.006	1
Introduced species						
ASTERACEAE	*Cirsium vulgare*	ane/epi	R	T	0.012	2
	Conyza bonariensis	ane	S	T	0.006	1
	Hypochaeris radicata	ane	R	HF	0.012	2
	Leontodon taraxacoides subsp. taraxacoides	ane		HF	0.006	1
ONAGRACEAE	*Leycesteria formosa*	end		P	0.012	2
POACEAE	*Anthoxanthum odoratum*	epi	R	HE	0.083	1
ROSACEAE	*Rubus anglocandicans*	end	R	P	0.047	8
	Rubus fruticosis spp agg	end	R	P	0.012	2
	Rubus polyanthemus	end	R	P	1.546	13
SCROPHULARIACEAE	*Digitalis purpurea*			T	0.011	1

[A] Ferns

[B] ane: anemochory (pappus, coma, samara or similar attachment); bar: barochory (no apparent seed dispersal mechanism); end: endozoochory (fleshy fruit); epi: epizoochory (barbs, hooks, burrs or awns enabling adhesion to animal fur); mob: mobile (barochores with seed mass < 0.1 mg); myr: myrmecochory (eliosome attached to seed to attract ants).

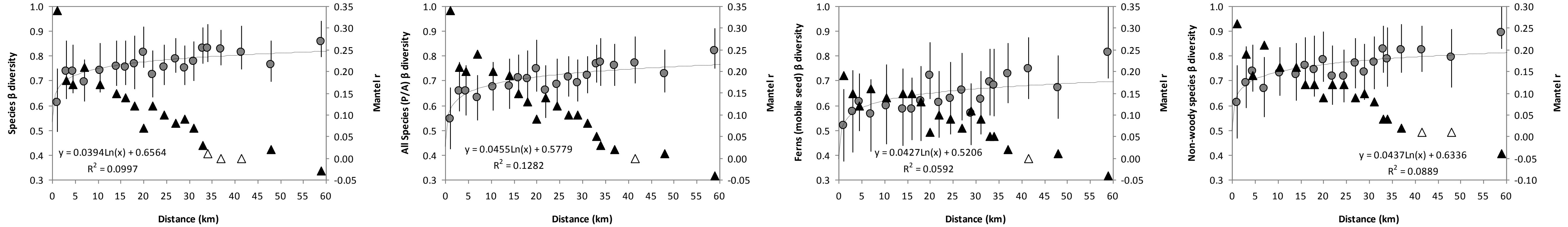
[C] R; obligate resprouter (plants that rely on resprouting to regenerate after fire); S: obligate seeder (plants that do not resprout and rely on seeding to regenerate after fire), RS, facultative seeders (plants that are able to resprout and to germinate seeds after fire)

[D] C: chamaephyte (plants whose branch system remains below 0.5 m, or plants that die back to below that height, i.e. dwarf shrubs); EPI: epiphyte (a plant that has no roots in the soil and grows upon another plant or object merely for physical support); G: geophyte (plants with seasonal reduction to below ground storage organ); HE: erect rosette (all leaves radical, leaves always erect); HF: flat or versatile rosette (all leaves radical, leaves flat or erect depending on conditions); HP: partial-rosette (radical and cauline leaves present, largest leaves on lower stem); HPr: proto-hemicryptophyte (all leaves cauline, largest leaves towards the middle of stem); P: phanerophyte (trees and shrubs taller than 0.5 m).

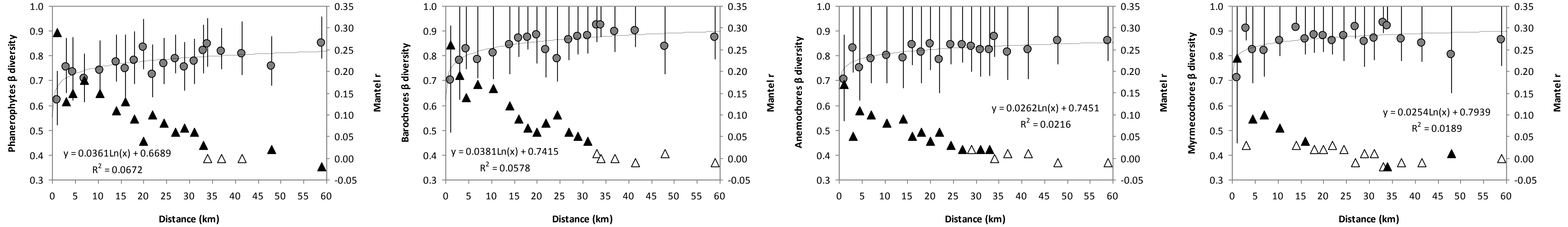
Appendix 4 Plants recorded as 'canopy' species across the Central Highlands by total and proportional basal area, and frequency (the number of sites that included a species from total of 81 sites).

Species	Total Basal Area (m^2 ha^{-1})	Proportion (%)	Frequency
Acacia dealbata	164.6	2.285	39
Acacia frigescens	56.0	0.777	9
Acacia melanoxylon	143.8	1.995	26
Acacia obliquinervia	0.03	0.001	1
Acacia verticillata	0.6	0.008	2
Atherosperma moschatum	66.1	0.918	19
Bedfordia arborescens	2.6	0.037	3
Cassinia aculeata	0.7	0.010	5
Cassinia spp.	0.8	0.012	2
Cassinia trinerva	3.7	0.052	3
Coprosma quadrifida	3.9	0.054	5
Correa lawrenceana var. latrobeana	33.9	0.471	21
Cyathea australis	181.9	2.525	25
Dicksonia antarctica	1363.0	18.915	62
Eucalyptus cypellocarpa	1.5	0.021	2
Eucalyptus delegatensis	624.4	8.665	12
Eucalyptus globulus subsp. bicostata	2.1	0.029	1
Eucalyptus nitens	19.6	0.273	2
Eucalyptus obliqua	1.1	0.015	1
Eucalyptus regnans	3322.6	46.108	58
Eucalyptus viminalis subsp. viminalis	83.0	1.152	2
Hedycarya angustifolia	5.9	0.082	8
Leptospermum grandifolium	44.5	0.617	10
Leucopogon gelidus	1.4	0.020	1
Lomatia fraseri	6.8	0.095	13
Notelaea ligustrina	0.1	0.001	1
Nothofagus cunninghamii	921.4	12.786	35
Olearia argophylla	15.5	0.215	13
Olearia lirata	1.1	0.016	5
Olearia phlogopappa subsp. continentalis	8.5	0.119	8
Persoonia arborea	0.9	0.013	4
Pimelea axiflora subsp. axiflora	0.3	0.004	1
Pittosporum bicolor	9.4	0.130	20
Polyscias sambucifolia	18.1	0.252	20
Pomaderris aspera	82.2	1.141	18
Prostanthera lasianthos var. lasianthos	3.4	0.047	3
Tasmannia lanceolata	1.9	0.027	13
Zieria arborescens subsp. arborescens	8.4	0.117	9

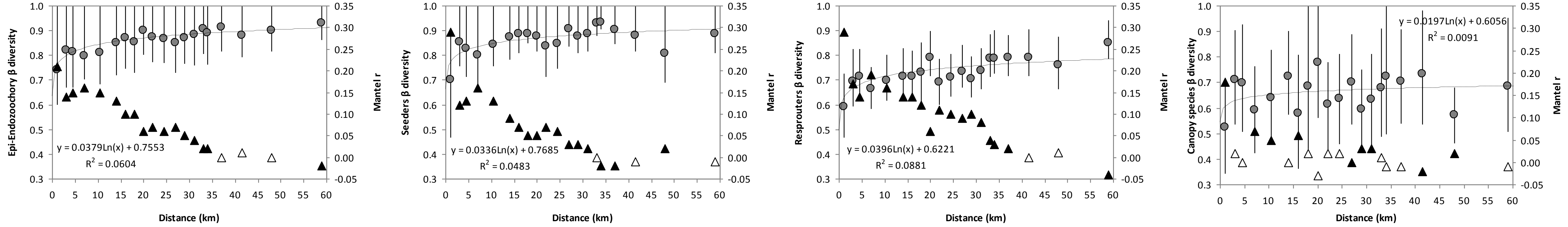
(a) All understorey species (abund.), *r* = 0.32, *P* = 0.0001 (b) All understorey species (P/A), *r* = 0.36, *P* = 0.0001 (c) Ferns (mobile seed), *r* = 0.24, *P* = 0.0001 (d) Non-woody species, *r* = 0.30, *P* = 0.0001



(e) Phanerophytes, *r* = 0.26, *P* = 0.0001 (f) Barochores, *r* = 0.24, *P* = 0.0001 (g) Anemochores, *r* = 0.15, *P* = 0.0001 (h) Myrmecochores, *r* = 0.14, *P* = 0.0001



(i) Epi-endozoochoores, *r* = 0.25, *P* = 0.0001 (j) Seeders, *r* = 0.22, *P* = 0.0001 (k) Resprouters, *r* = 0.30, *P* = 0.0001 (l) Canopy species, *r* = 0.10, *P* = 0.0016



Appendix 5 Distance decay plots showing the increase in β diversity with increasing geographic distance: all understorey species (a, b); life form (c, d, e); dispersal mode (c, f, g, h, i); fire response (j, k); canopy species (l). Circles represent the mean dissimilarity and bars represent the lower and upper quartile range. Best-fit regression curves and equations are provided. The triangles represent the associated Mantel correlograms for the 20 distance classes (each representing 162 sample pairs). A significant Mantel's *r* ($P \leq 0.05$) for a distance class is indicated by a filled symbol. Positive correlations indicate positive spatial autocorrelation among sites. Results of the RELATE test (*r*, *P* values) that examined overall significance of correlation with the spatial distance matrix are provided.

Appendix 6 Variance explained by examined variables (ESM Appendix 1) retained after forward selection in the DistLM analysis of β diversity of temperate forests in the Central Highlands. Values are the pure (conditional) contribution of each of the examined variables. Variables not included in any of the final models were removed from the table. Bold values represent the two variables that made the greatest contribution to explained variance per plant functional type.

	Dispersal Mode					Life Form				Fire Response		Vegetation Strata		
Set / Variable	Mobile seed	Baro-chores	Anemo-chores	Myrme-cochores	Epi-Endo-zoochores	Ferns	Non-woody species	Phanero-phytes	Phanero-phytes^{D}	Seeders	Re-sprouters	All understorey species (abund)	All understorey species (P/A)	Canopy species^{E}
Spatial														
x (longitude)		1.9		2.0	2.7		1.5	0.7		0.8	0.6	1.3	0.7	
y (latitude)	1.7	**2.9**	3.0	1.6	**3.3**	1.7	2.3	2.2	2.3	2.5	2.0	1.5	1.7	
x^2	1.7	2.3				1.7				0.9			1.2	
xy														2.9
y^2	**5.6**	2.5				**5.6**			**4.9**					2.4
x^3							1.8	0.8			0.9	1.1		
xy^2				2.4	1.4		1.2	1.4		1.5	0.9	1.4	1.3	
y^3		2.8	2.5											
Environmental: Climate														
bio1	3.6	1.7	**3.7**	2.6	3.2	3.6	1.7	2.4	2.1	2.6	2.3	2.6	2.7	**10.4**
bio4				2.1				2.4	2.2		2.1	1.7	1.9	
bio7		1.6			2.7		1.6					1.8		
Environmental: Topography														
Slope														
North-South aspect	2.8					2.8								
HLI					1.9									
PDIR	2.8					2.8								
Environmental: Soil														
Carbon (0–10 cm)	2.6					2.6			1.8	2.1				
C/N (0–10 cm)^{A}			2.2	**2.9**				1.3			1.5	1.2		
EC (0–10 cm)					1.8									
$[H^+]$ (0–10 cm)^{B}		2.2	2.3	**3.7**			2.0	**2.7**		**3.9**	1.6	1.6	**2.8**	3.3
P (0–10 cm)^{A}	3.5		1.9	2.4		3.5	2.3	2.4	**5.4**	2.0	**2.5**	**2.7**		**6.3**
K^+ (0–10 cm)								2.0				1.6		
Na^+ (0–10 cm)^{B}	2.1					2.1		2.4	2.3		1.9	1.5		
Clay (0–10 cm)		1.6												2.2
N (10–30 cm)	1.9	**2.8**			**3.5**	1.9	2.4	2.0	2.2	2.7	1.4	1.5	2.7	2.8
Mg^{2+} (10–30 cm)^{A}	3.7	1.5				3.7	**3.4**				1.4	1.4		
Na^+ (10–30 cm)^{B}				2.2			2.0			2.6			1.5	
Disturbance: Structure														
LAI	**5.3**	2.6	**8.5**	2.1	2.7	**5.3**	**7.4**	2.4	2.9	**3.5**	**5.6**	**5.4**	**5.8**	5.3
Stems ha$^{-1\ B}$		1.6		2.1				2.0	2.5		1.7	1.5		NA
H' BA (height)		2.1	1.8					1.1			1.8	1.9	2.3	NA
CV (Height)^{C}	2.1	2.2	1.7			2.1	2.1	**2.5**		2.2		1.5	1.8	NA
Disturbance: Time-since-fire								1.9	3.6	1.8				1.6
TOTAL	53.3		37.7			53.3	50.9	51.9	39.2	43.8	50.1	55.2	49.6	47.4

Transformations: ^{A} $\log_{10}$; ^{B} ^0.25; ^{C} ^0.5; NA, Not assessed. P/A, Presence/Absence data.

^{D} Understorey phanerophytes based on basal area of stems ≤ 10 m height

^{E} Stand structural variables were limited to LAI as basal area, stem density, and allied measures of stand structural complexity were confounded with the calculation of β diversity of canopy species (see methods)

Appendix 7 Variance partitioning results for the relative contribution of the pure (conditional) component of environmental (soil; climate, C; topography, T) and disturbance (structure, Str; time-since-fire, TSF) variables to β diversity as determined via a second-tier conditional analysis (as depicted in Figure 2). Values are percentages of variation explained by the data.

	Environmental							Disturbance		
Functional Type	Pure Soil	Pure C	Pure T	Soil & C	Soil & T	T & C	T & C & Soil	Pure Str	Pure TSF	Str & TSF
Dispersal Mode										
Mobile seed	15	4	5	1	0	0	0	8		
Barochores	8	5		0				9		
Anemochores	6	4		0				14		
Myrmecochores	10	5		3				5		
Epi- endozoochores	4	5	2	1	0	0	0	3		
Life Form										
Ferns	15	4	5	1	0	0	0	8		
non-woody species	12	5		0				10		
Phanerophytes	12	4		1				8	2	2
Phanerophytes[A]	12	6		4				5	4	2
Fire Response										
Seeders	11	3		0				6	2	2
Resprouters	11	4		1				9		
Vegetation Strata										
All understorey species (abundance)	13	6		1				11		
All understorey species (P/A)	6	5		0				11		
Canopy species	14	10		1				5	2	3

[A] Understorey phanerophytes based on basal area of stems ≤ 10 m height

Appendix 8 Variance partitioning results for the relative contribution of the pure (conditional) and shared component of spatial (Sp) and environmental (Env) variables to β diversity exclusive of any disturbance variables (see Figure 2). Relative differences in the contribution of spatial and environmental variables and total explained variation in models inclusive of disturbance variables (see Table 3) are provided. Values are percentages of variation explained by the data.

	Variance Explained (%) – models exclusive of disturbance variables				Relative change (%) following inclusion of disturbance variables			
Functional Type	Sp	Env	Sp & Env	Total	Sp	Env	Sp & Env	Total
Dispersal Mode								
Mobile seed	7	32	11	50	36	-23	-17	8
Barochores	11	21	13	45	2	-36	-29	11
Anemochores	7	20	2	29	-26	-50	-4	31
Myrmecochores	7	23	7	37	1	-19	-22	5
Epi-endozoochores	6	13	12	31	6	-6	-15	9
Life Form								
Ferns	7	32	11	50	36	-23	-17	8
Non-woody species	10	22	12	44	-38	-23	8	16
Phanerophytes	4	27	7	39	43	-38	5	33
Phanerophytes[A]	8	22	2	32	-11	-14	42	24
Fire Response								
Seeders	8	19	10	37	-9	-27	-42	20
Resprouters	6	28	14	48	-6	-40	-15	5
Vegetation Strata								
All understorey species (abundance)	7	28	13	48	-7	-30	-28	15
All understorey species (P/A)	6	22	17	46	-9	-48	-22	9
Canopy Species	6	32	2	39	22	-22	70	20

[A] Understorey phanerophytes based on basal area of stems ≤ 10 m height

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