

Rates of species turnover across elevation vary with vertical stratum in rainforest ant assemblages

Leahy, Lily; Scheffers, Brett R.; Andersen, Alan N.; Williams, Stephen E.

Published in:
Ecography

DOI:
[10.1111/ecog.06972](https://doi.org/10.1111/ecog.06972)

Published: 01/05/2024

Document Version
E-pub ahead of print

[Link to publication](#)

Citation for published version (APA):

Leahy, L., Scheffers, B. R., Andersen, A. N., & Williams, S. E. (2024). Rates of species turnover across elevation vary with vertical stratum in rainforest ant assemblages. *Ecography*, 2024(5), 1-12. Article e06972. <https://doi.org/10.1111/ecog.06972>

General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal

Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

ECOGRAPHY

Research article

Rates of species turnover across elevation vary with vertical stratum in rainforest ant assemblages

Lily Leahy¹✉^{1,4}, Brett R. Scheffers², Alan N. Andersen³ and Stephen E. Williams⁴

¹Department of Environment and Genetics, La Trobe University, Melbourne, Vic, Australia

²Department of Wildlife Ecology and Conservation, University of Florida, Gainesville, FL, USA

³Research Institute for the Environment and Livelihoods, Charles Darwin University, Palmerston, NT Australia

⁴Centre for Tropical Environmental and Sustainability Science, College of Science and Engineering, James Cook University, Townsville, Qld, Australia

Correspondence: Lily Leahy (l.leahy@latrobe.edu.au)

Ecography

2024: e06972

doi: [10.1111/ecog.06972](https://doi.org/10.1111/ecog.06972)

Subject Editor: Tim Bonebrake

Editor-in-Chief: Miguel Araújo

Accepted 23 November 2023



Climatic variation at local scales can influence both exposure and sensitivity of organisms and thereby scale up to influence population persistence and community composition across broader geographic extents. Tropical forest canopies are more climatically dynamic than the understorey. Consequently, the niche space of forest canopies has higher overlap in thermal conditions along elevation gradients, which imposes less of a climatic barrier to arboreal species than their ground-dwelling counterparts. We use ant communities of the Australian Wet Tropics to test the prediction that ground communities should have higher rates of species turnover over elevation compared to arboreal communities. We sampled ground and arboreal ants along elevation gradients at a bioregional scale that includes four mountain sub-regions. We assessed community composition at three spatial resolutions (regional, elevation, vertical) and then calculated beta diversity (species turnover) over elevation for ground and arboreal communities using null modelling procedures to compare different sized species pools. Vertical niche affinity was a strong contributor to overall biogeographic patterns; indicated by a strong interaction between vertical niche and elevation in beta diversity models. On average, the ground community exhibited a pronounced elevational distance–decay pattern while the arboreal community showed no pattern. Mean species turnover was 36% higher in ground than arboreal communities. Our findings suggest that the vertical niche has a pronounced effect on biogeographic patterns which has important implications for understanding the role of local scale climate conditions in shaping communities and for potential responses to future climate change.

Keywords: ants, arboreal, biogeography, canopy, climate change, community composition, distance–decay, microgeography, verticality



www.ecography.org

© 2024 The Authors. Ecography published by John Wiley & Sons Ltd on behalf of Nordic Society Oikos

This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

Introduction

A key goal of ecology is to predict how environmental variation influences different processes across multiple spatial and temporal scales (Buckley and Kingsolver 2021, Halpern et al. 2023). Thermal variation can have profound impacts across different biological levels, from individual physiology through species distributions to patterns of community composition (Huey and Hertz 1984, Gilchrist 1995, Holt et al. 2004, Nadeau et al. 2017, Oliveira et al. 2020). Exposure to thermal variation strongly depends on the integration of different spatiotemporal scales; a lizard shuttling between shade and sun is experiencing short-term climatic variation at the local scale (Huey 1991), but its annual exposure to variability will strongly depend on its home range across habitat, elevation, and even latitude. How climate variability integrates from local to landscape scales to influence species distributions and community composition remains an understudied topic in macroecology.

Janzen's seasonality hypothesis (1967) links biological levels and climatic scales into a simple framework. Janzen (1967) observed that for thermally stable environments such as the tropics, there is little thermal overlap between different elevational bands, whereas in thermally variable environments such as the highly seasonal temperate zone there is a large degree of thermal overlap. This implies that tropical species are adapted to a narrower range of temperatures and consequently have more restricted elevational distributions compared to temperate species (Gilchrist 1995, Ghalambor et al. 2006, Sheldon et al. 2018). This should result in a higher rate of species turnover (beta diversity) across tropical mountains relative to temperate mountains (Fagan et al. 2006, Jankowski et al. 2009, Archibald et al. 2013, Zagmajster et al. 2014).

Although Janzen's seasonality hypothesis compared differences in seasonality (climatic variation) across latitude, the same framework can be applied at smaller geographic (micro-geographic) scales (Sheldon et al. 2018). In forests, the vertical structure of a tree creates a strong temperature and humidity gradient (Scheffers et al. 2013, Bujan et al. 2016, Spicer et al. 2017, Law et al. 2020, Leahy et al. 2021a, Xing et al. 2022). Even at just three metres above the ground, daytime temperatures can be up to 5°C (average of 2°C) higher than on the forest floor (Leahy et al. 2021a). Importantly, in the context of Janzen's hypothesis, daily temperature variance increases with vertical height: Leahy et al. (2021a) reported air temperature variance averaged four times higher in the canopy, while canopy surface temperatures can be up to eight fold more variable than understorey surface temperatures (Kaspari et al. 2015). Higher thermal variation in any given habitat should lead to greater thermal overlap across elevation (Janzen 1967, Klings and Scheffers 2021).

The consistent pattern of thermal variance across vertical gradients laid the ground work for a large scale study which measured thermal overlap in ground and canopy temperature profiles across elevation bands (Scheffers and Williams 2018). Overlap in daily temperatures between lowland and highland

environments was significantly higher for canopy environments compared to ground environments (Scheffers et al. 2017). In subsequent global analysis including 29 mountains spanning 6 continents, Klings and Scheffers (2021) found that for each 1 m increase of vertical height there was a consistent increase in thermal overlap between lowland and upland environments; the highest overlap occurring between lowland and upland canopy habitats. This work added a new dimension to Janzen's original hypothesis and provided climatic evidence to support the suggestion that arboreal species (analogous here to Janzen's temperate species) should face less climatic barriers to moving over mountain passes than their counterparts from stable environments on the forest floor (analogous to Janzen's tropical species).

Building support for this hypothesis, ground ant species have narrower thermal tolerance ranges compared to arboreal ant species (Baudier et al. 2015, Kaspari et al. 2015, Leahy et al. 2021b). Moreover, Leahy et al. (2021a) demonstrated a positive relationship between ant vertical distributions (ground to arboreal), exposure to thermal variation, and elevation range size. These examples have focused on the role of microgeography in driving individual species distributions across meso- and macro-scale gradients but the consequences for the geographic arrangement of whole communities have been largely ignored (Fagan et al. 2006). We predict that if the occupants of a climatically variable microhabitat can persist and thrive at multiple climatic-elevational bands, this should lead to lower rates of species turnover across elevation for that assemblage.

In this study, we investigate micro- to macro-geographical processes in shaping community patterns across mountains using the study system of rainforest ants in the Australian Wet Tropics bioregion. Vertical gradients in mean temperature and temperature variance have been well-documented in this study system (Leahy et al. 2021a), as has thermal overlap in ground and canopy temperature profiles across elevation bands (Scheffers and Williams 2018). Ants are ideal organisms for the study of biogeographic patterns as they are highly speciose (Kass et al. 2022) and widely distributed across both vertical and elevation gradients (Sanders et al. 2007, Bishop et al. 2014, Longino et al. 2019, Leahy et al. 2020, Vasconcelos et al. 2023). In addition to experiencing different microclimates, ground and arboreal ants also occupy different habitat templates with distinct nesting and food resources (Yanoviak and Kaspari 2000).

Here, our first aim is to assess community composition at the three spatial scales of verticality (microscale – ground to canopy), elevation (mesoscale) and region (macroscale – among four mountain ranges) to explore how these dimensions contribute to community patterns across the bioregion. Our second aim is to extend Janzen's seasonality hypothesis to a multiscale framework and test our prediction that ground communities will exhibit higher species turnover between different elevations compared with arboreal ant communities (Fagan et al. 2006, Davison and Chiba 2008, Oliveira and Scheffers 2019, Antoniazzi et al. 2020). We predict an elevational distance–decay in species turnover across elevation for

the ground community. In contrast, we predict little or no relationship between species turnover and elevational distance in arboreal communities.

Material and methods

Study sites and sampling

Our study was conducted across the Australian Wet Tropics (AWT) bioregion, Queensland (Williams et al. 1995, 2010). Elevational gradients were sampled in four mountain ranges (referred to here as sub-regions; Williams et al. 1995) that

represent four of six main sub-regions within the AWT, running from north to south: Mt Finnegan, Mt Windsor, Mt Carbine, and Atherton Range (Fig. 1). The number of elevation sites (15 sites) sampled for each sub-region varied depending on the availability of rainforest habitat: Finnegan (200, 500, 700 m a.s.l.), Windsor (900, 1100, 1300 m a.s.l.), Carbine (100, 600, 1000, 1200 m a.s.l.) and Atherton (200, 400, 600, 800, 1000 m a.s.l.) (geographical and elevational distance: Supporting information). Rainfall in the AWT is seasonal with 75–90% of the 2000–8000 mm per year falling during the wet season from November to April.

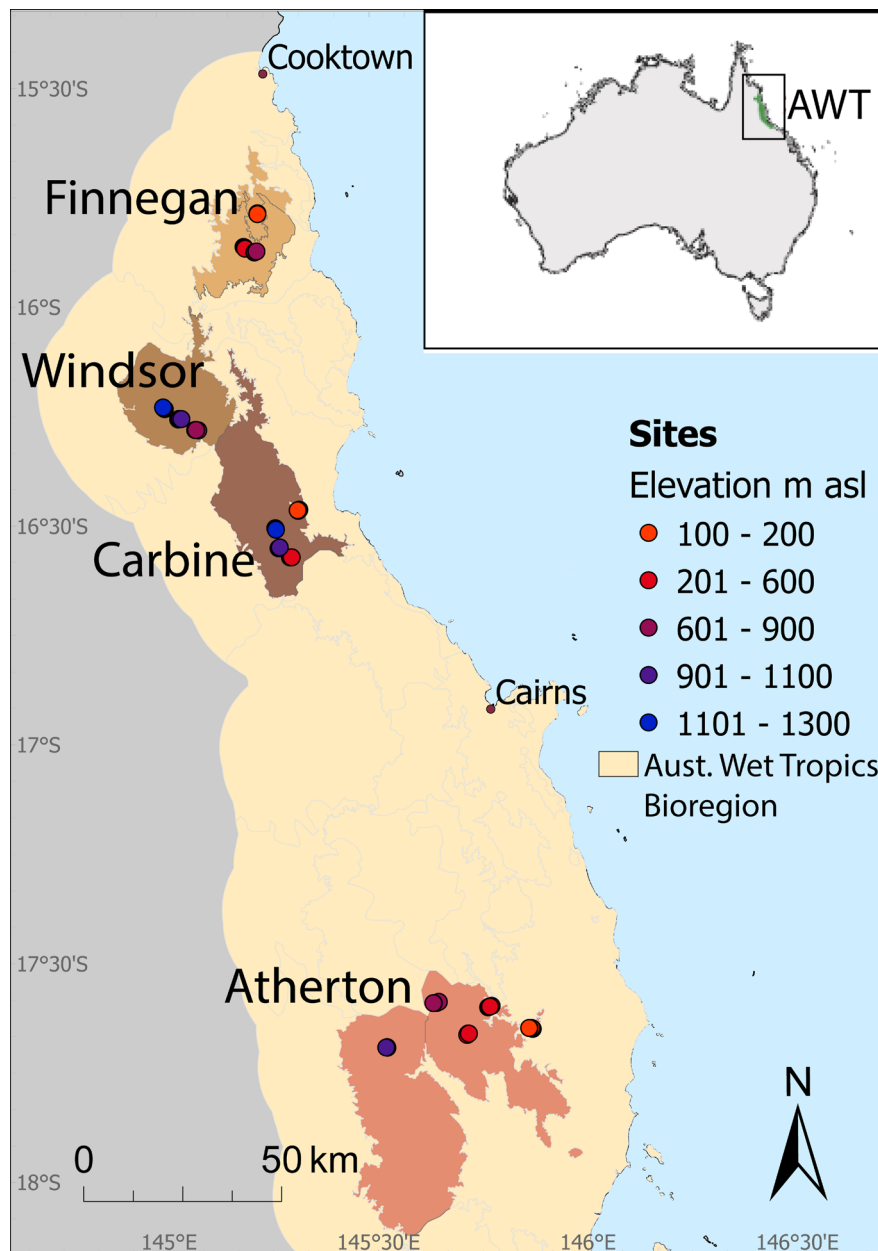


Figure 1. Map of the Australian Wet Tropics bioregion (AWT) showing ant survey locations for four mountain subregions. Elevation binned into five colours as indicated in legend, see text for exact elevation of each survey site for each subregion.

Thermal data has been previously published for two of the four sub-regions sampled here demonstrating the relationship between vertical height, climatic variation, and the degree of thermal overlap across elevation in the Australian Wet Tropics study system (Scheffers et al. 2017, Scheffers and Williams 2018, Klinges and Scheffers 2021, Leahy et al. 2021a). At the Atherton sub-region, Leahy et al. (2021a) deployed temperature loggers at each elevation site. The median temperature variance was 3.13°C on the ground compared to 12.90°C in the high canopy (24 m vertical height) over the period of sensor deployment (Leahy et al. 2021a). Scheffers et al. (2017) recorded temperature profiles of ground and canopy habitats at the Carbine sub-region to determine the degree of thermal overlap between lowland (100 and 400 m a.s.l.) and upland (1000 m a.s.l.) study sites (Scheffers et al. 2017). Canopy habitats overlapped in their temperature profile to a greater degree compared to ground habitats (Scheffers et al. 2017). Ground habitats are therefore less thermally variable and more thermally segregated across elevation compared to canopy habitats (Scheffers and Williams 2018, Klinges and Scheffers 2021).

To sample for ants, we utilised the same sampling methodology (baiting) in ground and arboreal habitats, thereby facilitating a direct comparison of beta diversity for each community across the same geographic extent (Antoniazzi et al. 2020). At each elevation site per sub-region, we sampled an average of four trees per site, at six sites five trees were sampled (see Leahy et al. 2021a for further details). Trees were sampled using tuna-baited traps comprised of plastic vials (1 cm in diameter, 5 cm in length) attached to the tree. At each tree, five bait traps were set on the ground and every three metres above ground level up to the maximum accessible height of the tree. Survey height ranged from 15–27 m, depending on the height of the tree and accessibility (see Leahy et al. 2021a for further details). There was no specific pattern in tree height across elevation for our sites (Leahy et al. 2021a). Traps were set in the morning and collected 2–3 h later. The canopy was accessed using the single-rope climbing technique. At each site, sampled trees were at least 50 m apart and were chosen based on size and climbing accessibility. Finnegan, Windsor and Carbine Uplands were surveyed from October–December 2012 and Atherton Uplands surveyed from December–February of 2017–2018. Ants were sorted to species and where possible named. Unnamed species were given codes following Nowrouzi et al. (2016). Voucher specimens were deposited in the CSIRO TERC collection in Darwin, Australia.

Analysis

Species composition across sub-region, elevation, and vertical gradients

We first investigated the relative contributions of sub-regional, elevational, and vertical gradients as drivers of variation in species composition. We applied a multivariate analysis and used a PERMANOVA model with vertical height (0–27 m), elevation, and sub-region as fixed factors

and 999 permutations. In this specific analysis the ‘sites’ are the concatenation of sub-region, elevation, and vertical height (every three metres) with 101 species collected across the region (pooling across individual tree plots). As we had an unbalanced design due to the different elevational extents of each sub-region, we tested the marginal effects of each factor rather than using sequentially added terms (McArdle and Anderson 2001). We created a dissimilarity matrix using a species-by-site table with species abundances calculated as the proportion of trees occupied at each site and the Bray–Curtis dissimilarity index. We evaluated multivariate dispersion (Supporting information) and used the percentage of explained variance (partial R^2) to compare effect sizes between the three factors. Community composition was then visualised with an ordination plot following non-metric multidimensional scaling with $k=3$ dimensions and 999 permutations. All analyses were implemented using the statistical software package R (www.r-project.org) using the ‘vegan’ ver. 2.5 package (Oksanen et al. 2013). The correlation of sub-region, elevation, and vertical height, with NMDS axes was visualised with boxplots. To ease visualisation in these boxplots, the ground and arboreal strata were classed as categorical with 0 m = ground, and 3–27 m = arboreal on the x-axis.

Species composition across vertical strata

Next, we investigated whether the ant community is partitioned into distinct vertical strata at the local scale. The purpose of this analytical step was to precede the downstream analysis of beta diversity across elevation and provide an evidential basis for categorically assigning communities to distinct ground and arboreal assemblages. We pooled all data from each sub-region, elevation site, and individual tree plots and constructed a species-site matrix with species presence-absence and each 3 m in vertical height (sampling points) as sites. We then performed an ordination using non-metric multidimensional scaling using the jaccard dissimilarity index (appropriate for presence-absence), and $k=2$ dimensions with 999 permutations and plotted the results to visualise whether there was separation between ground and arboreal vertical habitats.

Assigning species as ground and arboreal assemblages

To compare species turnover for ground and arboreal communities across elevation, we assigned species to each vertical community – either ground (0 m) or arboreal (≥ 3 m) – if their frequency of occurrence in samples exceeded 90% in their respective vertical habitat (Supporting information). This procedure resulted in 36 species in the ground assemblage and 65 species in the arboreal assemblage across the study region.

Species turnover

We use beta diversity as a powerful tool for quantifying species turnover (Fitzpatrick et al. 2013, Socolar et al. 2016). Beta diversity patterns in ant communities have been assessed for ground or arboreal communities separately along elevation (Longino and Colwell 2011, Bishop et al. 2015,

Nowrouzi et al. 2016, Plowman et al. 2020) and latitude (Majer et al. 2001), but as far as we are aware ours is the first study that explicitly compares them. For ground and arboreal communities respectively, we calculated beta diversity metrics through pairwise comparisons between each set of elevation sites within each sub-region separately. Note, we did not compare elevation sites among sub-regions (e.g. Atherton elevation sites were only contrasted within Atherton). We pooled individual tree surveys together to create a ground and arboreal 'assemblage' for each elevation site and compared that with all other elevation sites within that sub-region (e.g. Atherton 200 m versus Atherton 800 m and so on). We used species presence-absence data and calculated beta diversity metrics using *beta.pair* function of package 'BETAPART' ver. 1.5.2 in R (Baselga and Orme 2012). We extracted the species turnover (β_{sim}) metric, which calculates compositional change due to species replacement across sites (Baselga 2010) resulting in 22 β_{sim} values for ground and arboreal respectively. We then calculated the mean β_{sim} value for ground and arboreal communities and compared them using Wilcoxon rank sum tests.

Elevational distance-decay

Based on climatic data analysis from Klinges and Scheffers (2021) extension of Janzen's seasonality hypothesis, thermal variation at microgeographic scales can drive climate overlap on mountains. As such, we would expect species turnover to be a function of the interaction between vertical niche (ground or arboreal) and elevational distance. Specifically, the intercept and slope of the relationship between community turnover and elevational distance should be higher and stronger for the ground than arboreal community. Within each sub-region, elevational distance was calculated as the difference between pairwise sites, for example, 200 m in elevational distance could be 400–200 m a.s.l. and so on. We first plotted elevational distance against species turnover values for each sub-region separately and found patterns among sub-regions were highly similar (Supporting information). In early model exploration, including sub-region as a random effect did not account for any additional variance (compared using Akaike information criteria (AIC), Supporting information). Therefore, sub-region was removed as a random variable in the subsequent model. Using generalised linear models (GLM) we modelled the response variable (β_{sim} – species turnover) as a function of vertical niche, elevational distance, and their interaction using a Beta family distribution and *logit-link* function using package 'glmmTMB' (Brooks et al. 2017). Models with 'elevational distance' and the \log_{10} of 'elevational distance' were compared using AIC. The model \log_{10} of 'elevational distance' performed better (Supporting information). Model diagnostics were checked using the package 'DHARMA' (Hartig 2021).

Monte Carlo simulation

For the generalised linear models, the response variable was not independent (because beta diversity values are obtained from pairwise comparisons of site-species compositions),

violating the assumptions of the model. We therefore obtained adjusted pseudo p-values to test the significance of each coefficient by constructing a custom Monte Carlo simulation using a mantel-test approach (Supporting information).

Null modelling of beta diversity

Due to the implicit relationship between regional (gamma), local (alpha) and beta diversity, it can be problematic to compare beta diversity for different sized regional species pools (Chase and Myers 2011, Kraft et al. 2011). In our study, we are comparing beta diversity of two assemblages based on their habitat niches, but the same issues apply owing to differences in the size of the species pools for ground and arboreal communities. We used a null modelling procedure to establish whether differences in species turnover across elevation for ground and arboreal communities still held after accounting for the potential influence of the size of each community species pool (Chase and Myers 2011). To do so, we randomised species occurrences across sites and explored whether the relationship between species turnover and distance deviated from what we would expect given a random assortment of species across sites. For elevational distance, a null distribution of species turnover values was generated using a 1000 random community assemblage matrices using the 'c0' algorithm (using *null.model* and *simulate* in package 'vegan'). This algorithm is appropriate for testing null expectations of species turnover patterns as it randomly shuffles species occurrence across sites, maintaining individual species frequencies across sites but randomises site species richness (Jonsson 2001). Standardised effect sizes were calculated using the observed species turnover values and the mean and SD of the 1000 null assemblages as follows:

$$SES = \frac{\text{Observed} - \text{Mean}(\text{null})}{\text{SD}(\text{null})}$$

SES values less than 0 are smaller than expected by random chance, while values greater than 0 are larger than expected by random chance. We were interested in the magnitude of departure from random expectation and how that changed over elevational distance. Models were constructed as above for observed species turnover. However, the response variable was gaussian (normal distribution) and therefore we used ordinary least squares (OLS) regression models. It was not necessary to obtain pseudo p-values for the null models (as above for the Monte Carlo simulation) because the underlying beta diversity values were already randomised.

Results

Species composition

A total of 11 770 individual ants from 101 species from 30 genera were collected at the 60 trees across the 15 elevation sites and four sub-regions. We found that substantially more variation in species composition was explained by

elevation (28%) than either sub-region (9%) or verticality (7%) (Supporting information). Sub-regions were delineated in the nMDS plot, particularly the most southern site, Atherton, while there was less differentiation in species composition between the more northerly sub-regions of Carbine and Windsor (Fig. 2). Each nMDS axis correlated well with one of the climatic gradient axes (Supporting information). Both sub-region and elevation showed a systematic trend with NMDS axes 1 and 2 because different sub-regions contain different elevational extents (Supporting information). Arboreal and ground communities separated clearly along NMDS axis 3 (Supporting information).

Vertical strata

Pooling all data from each sub-region, elevation site, and individual tree plots, we found clear vertical partitioning between ground (0 m) and arboreal (3–27 m) habitats (Fig. 3). This indicates that the arboreal assemblage becomes compositionally distinct from the ground at three metres in height. This supports our decision to reduce vertical strata into a categorical assignment of ground (0 m) and arboreal (3–27 m) assemblages for the subsequent beta diversity analysis.

Patterns of beta diversity over elevation

We found higher rates of species turnover with elevation for ground communities compared to arboreal communities. Mean species turnover rates (comparing all pairwise values) across elevation were 36% higher for the ground compared with the arboreal communities (mean $\beta_{sim} = 0.771 \pm 0.07$ SE vs 0.564 ± 0.03 SE; Wilcoxon: $W = 114.5$, $p = 0.003$; Fig. 4).

Species turnover in the arboreal community showed no relationship with elevational distance (Fig. 5), whereas the ground community showed a strong positive and logarithmic relationship, a classic distance–decay pattern. This pattern was consistent across the four mountain sub-regions (Supporting information). This was evidenced by a significant interaction between elevational distance and vertical niche (pseudo p -value = 0.034, Table 1). This trend persisted in standardised null models (interaction: p -value = 0.06, Table 1) and so our results were unlikely to be due to different sized species pools (Fig. 6). Species composition on the ground was more similar than expected by chance up to 300 m but tended to be less similar than expected by chance at larger elevational distances between samples (Fig. 6).

Discussion

Our study explores how climatic variation at the microscale can influence macroecological patterns of species diversity and turnover. We investigated community composition of ant species at three spatial scales (verticality, elevation, and region) and found elevation to be the strongest driver of compositional patterns. We then tested the interaction between vertical niche affinity and elevational distance on rates of species turnover over elevation. In line with our predictions based on the change in climatic variation along the vertical thermal gradient, ground communities had far higher rates of species turnover across elevation compared to arboreal communities (Fig. 4). This result was consistent among the four mountain ranges we studied (Supporting information),

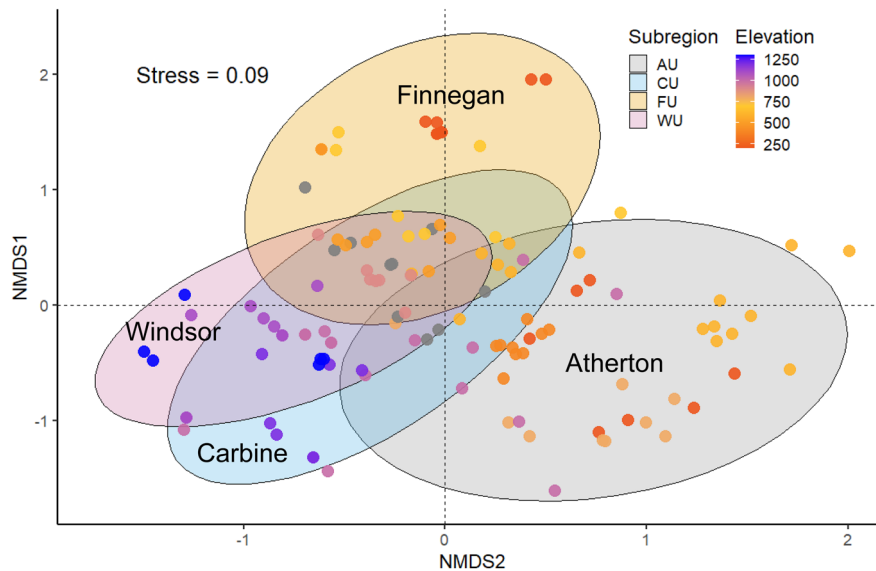


Figure 2. Ant species composition (101 species) at vertical height, elevation, and sub-region from vertical tree surveys at 15 elevation sites at four mountain sub-regions in the Australian Wet Tropics bioregion. Ordination of sites represented through a NMDS with Bray–Curtis dissimilarity for species frequency of occurrence. Points are sites (sub-region, elevation, vertical height), coloured by elevation and ellipses show species groupings for each sub-region, vertical height is not indicated by symbols or colours in this model to allow easier interpretation of elevation and regional patterns. AU = Atherton Uplands, CU = Carbine Uplands, FU = Finnegan Uplands, WU = Windsor Uplands, elevation is m a.s.l.

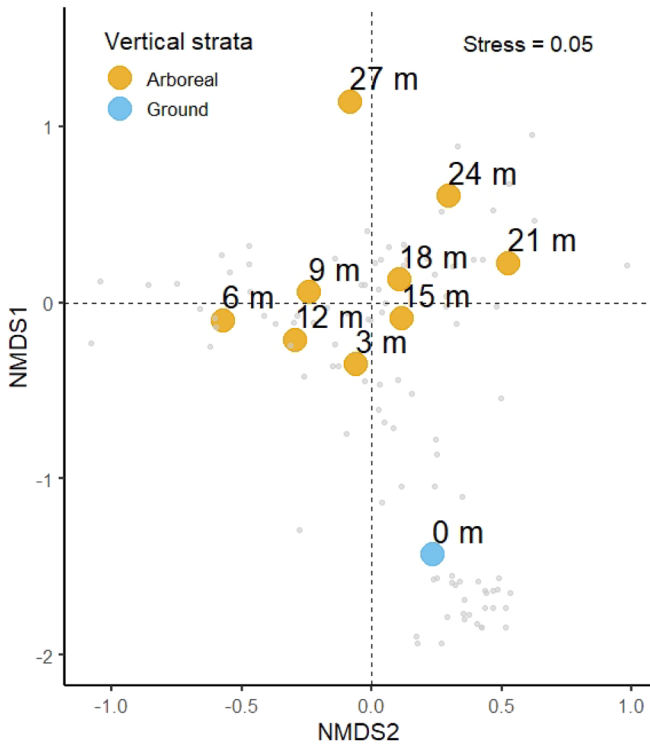


Figure 3. Ant species composition (101 species) along vertical height for surveys pooled together from 60 trees sampled at 15 elevation sites along four sub-regions in the Australian Wet Tropics bioregion. Ordination of sites calculated with a NMSD with Jaccard dissimilarity based off species presence-absence at each height. Individual species represented by grey points.

suggesting that this is a widespread pattern for ants of the Australian Wet Tropics.

Assessment of compositional patterns for the entire ant community (arboreal and ground) at three spatial scales of sub-region, elevation, and verticality, revealed a dominating influence of elevational gradients on community patterns. Elevation explained 3 to 4 times as much variation in community composition than mountain sub-region identity or local scale vertical gradients (Supporting information), a pattern consistent with other studies of tropical ant faunas (Brühl et al. 1999, Sanders et al. 2007, Burwell and Nakamura 2015, Longino and Branstetter 2019). As distinguished in the NMSD plot (Fig. 2), Windsor and Carbine sub-regions were similar in composition, compared to the more distinct ant faunas of Finnegan and Atherton, the most northerly and southerly sites (map in Fig. 1). This is likely due to historic and contemporary climatic conditions (Schneider and Moritz 1999, Moritz et al. 2009) and geographic distance (Perillo et al. 2021). This specific sub-regional pattern is also consistent with prior studies of ants (Nowrouzi et al. 2016, Leahy et al. 2020), birds, and small mammals in the Australian Wet Tropics (Williams and Pearson 1997, Williams et al. 2002).

We found a strong disjuncture in species composition between the ground and just three metres above the ground,

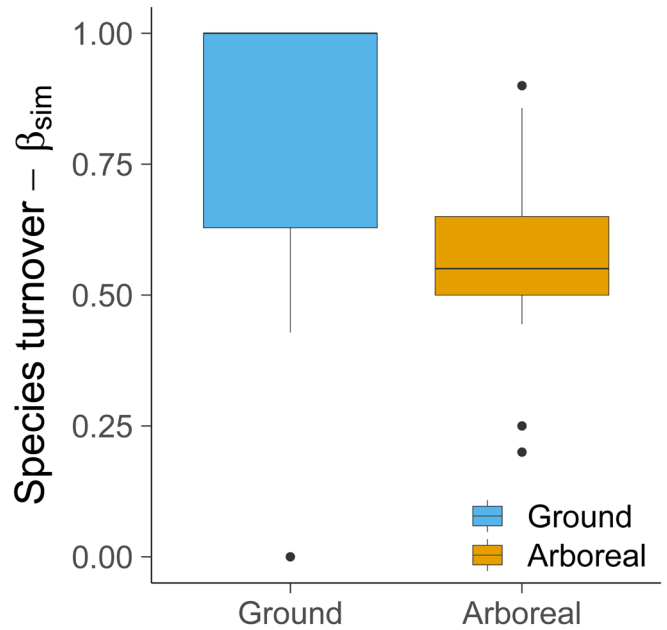


Figure 4. Mean species turnover (β_{sim} component of beta diversity) for pairwise site comparisons between elevation sites of four mountain range sub-regions. Showing the distribution of beta diversity values for ground and arboreal communities. On the y-axis, 0 represents low turnover and 1 represents high turnover. Boxplots show median (central band), 25th and 75th percentiles (bottom and top of boxes) and 1.5 times the interquartile range above or below the 25th and 75th percentiles (whiskers) and points show outliers above or below this.

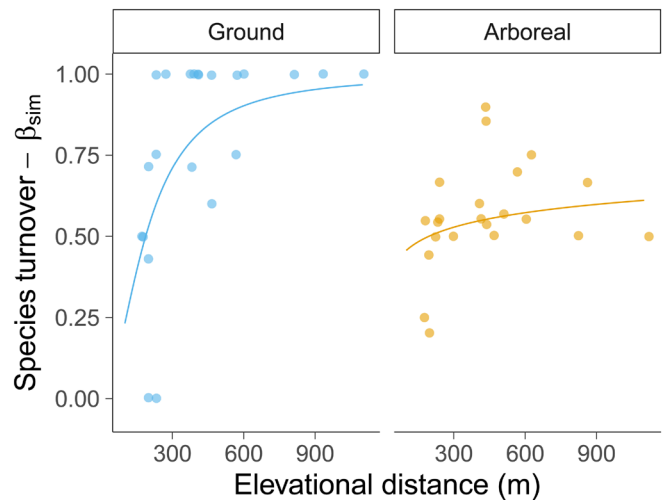


Figure 5. Observed ant species turnover with increasing elevational distance in the Australian Wet Tropics for ground and arboreal ant communities. Showing species turnover component of beta diversity (β_{sim}). Points are pairwise comparisons of species composition between elevation sites within each mountain range pooled from four mountain sub-regions. Lines are model fits from models presented in Table 1. On the y-axis, 0 represents low turnover and 1 represents high turnover.

Table 1. Model summaries for the relationship between species turnover as a function of elevational distance and vertical habitat and their interaction. Observed turnover (β_{sim} – generalised linear model) and standardised turnover (SES β_{sim} – linear model) models shown. Variation explained by model indicated by pseudo R^2 for observed model and adjusted R^2 for standardised model. Note, coefficient estimates and SEs for the observed β_{sim} models are on the logit scale.

Models	GLM		LM – SES		
	– Observed β_{sim}		β_{sim}		
Pseudo/ adjusted R^2	0.48		0.19		
	Coef. \pm SE	Pseudo p-value	Coef. \pm SE	p-value	
Estimates					
Vertical habitat – Ground	1.14 \pm 0.35	0.999	0.35 \pm 0.33	0.294	
\log_{10} (elev. distance)	0.14 \pm 0.25	0.002	0.16 \pm 0.24	0.507	
Vertical: \log_{10} (elev. distance)	0.9 \pm 0.34	0.034	0.65 \pm 0.34	0.061	

indicating a strong ecological delineation in just a few meters of vertical space (Beaulieu et al. 2010, Basham et al. 2019). Interestingly, sub-region and verticality explained similar, albeit low, variance in community composition. This underscores that local scale niche partitioning may be as an important as biogeographic processes occurring at the scale of mountain ranges in determining community structure across the bioregion.

Having established elevation as an important driver of community composition, we then utilised the interaction between micro- and meso-climatic gradients to extend Janzen’s classical hypothesis (Janzen 1967) in a novel

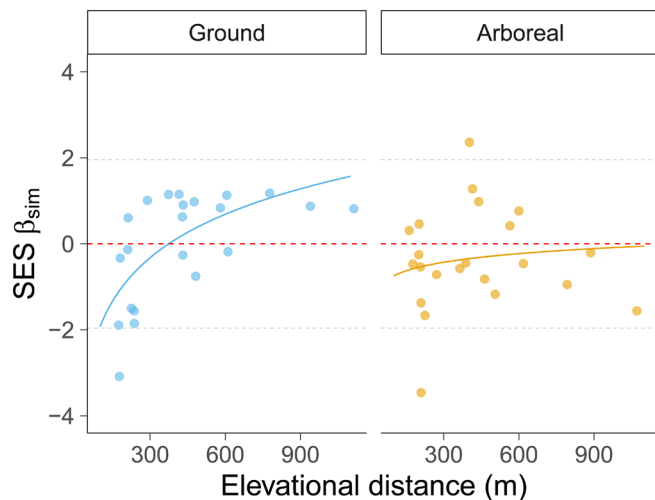


Figure 6. Standardised null models of ant species turnover with increasing elevational distance pooled from four mountain sub-regions in the Australian Wet Tropics. Showing species turnover component of beta diversity (β_{sim}). Points are as for Fig. 5. Lines are model fits from models presented in Table 1. Red dotted lines at 0 indicate random expectation, where points below the line indicate less than expected by random chance and above the line indicate more than expected by random chance. The grey dotted lines indicate significance threshold ($\alpha=0.05$) of ± 1.96 SES.

direction. Scheffers and Williams (2018) downscaled conception of Janzen’s seasonality hypothesis proposed that ground and arboreal communities experience different thermal variability, which should result in differences in thermal overlap and diverging patterns of turnover across elevation (Jankowski et al. 2009, Scheffers and Williams 2018, Klinges and Scheffers 2021). In support of this hypothesis, we found that the relationship between elevational distance and species turnover strongly depended on the vertical niche. The ground community showed a classic distance–decay pattern whereby species composition was similar between short distances but became rapidly dissimilar with increasing elevational distance, whereas there was no relationship between arboreal species turnover and elevational distance.

Our null modelling approach showed that the difference in beta diversity across elevation was not simply explained by random chance effects due to differences in the size of the ground and arboreal community (Qian et al. 2013, Stegen et al. 2013, Bishop et al. 2015, Xu et al. 2015, Ashton et al. 2016). We note that the effect of species richness on rates of stochastic turnover would likely be most pronounced within the arboreal community, which was approximately twice as speciose as that of the ground (65 versus 36 species). However, we found that the arboreal community had lower rates of species turnover than the ground community with a similar pattern in our null models.

High elevational turnover in ground ants has been reported in several other studies (Brühl et al. 1999, Bishop et al. 2015, Nowrouzi et al. 2016, Perillo et al. 2021) but elevational turnover has rarely been investigated for arboreal communities (Plowman et al. 2020). In line with our results, Plowman et al. (2020) found relatively low dissimilarity in arboreal communities from low to mid-elevations (200 versus 900 m a.s.l.) but very high dissimilarity between mid and high (900 versus 1800 m a.s.l.) elevations in a Papua New Guinean rainforest (ground communities were not compared within that study). We note that 1800 m a.s.l. is a high maximum elevation and is likely to be dramatically colder than the maximum elevations studied here (1300 m a.s.l.), which could explain the more distinct arboreal montane community in that study (Plowman et al. 2020).

The vertical niche determines both the exposure (Leahy et al. 2021a) and tolerance (Kaspari et al. 2015, 2016) of species to climatic variability. This in turn will influence species turnover through its effect on a suite of traits ranging from thermal physiology to morphology (Law et al. 2020, Mena et al. 2020, Sosiak and Barden 2021). Arboreal and canopy ants of tropical rainforests have broader tolerance ranges than ground-restricted ants (Kaspari et al. 2015, Bujan et al. 2020, Leahy et al. 2021b). A broader thermal tolerance range should allow species to adapt to thermal variation at local scales and achieve broader geographical distributions (Brown 1984, Slatyer et al. 2013, Leahy et al. 2021a). In addition, thermal overlap is higher for arboreal than ground habitats across elevation (Klinges and Scheffers 2021). In theory, newly dispersing young queens from arboreal habitats should 1) be more likely to find climatically suitable sites along the

elevation gradient, and 2) produce workers with thermal traits suited to foraging in a greater range of climatic conditions, together ensuring the persistence of that colony/population and acting to reduce beta diversity amongst elevation sites. This is consistent with our finding of an elevational distance–decay relationship in ground ants but not arboreal ants.

In addition to climate, variation in nesting and food resources might also influence patterns of species turnover across elevation. At local scales, for example, differences in the stability of food and nesting resources results in contrasting temporal turnover patterns between leaf litter (high temporal turnover) and canopy (low temporal turnover) communities (McGlynn 2012, Neves et al. 2021). We found low elevational turnover for arboreal assemblages suggesting either that resources (e.g. epiphytes, trophobiont insects) do not vary markedly with elevation, or that arboreal ants are flexible with their resource use. Plowman et al. (2020), for example, found arboreal ants exhibited intraspecific shifts towards smaller, more insulated nests, and smaller colony sizes with increasing elevation. The higher elevational turnover in ground communities is unlikely to be explained by variation in nesting sites given that variation in litter depth and soil variables have little effect on species turnover compared to climatic variables in the region (Nowrouzi et al. 2019). The elevational patterns that we have described are therefore more likely to be driven by climate than by resources.

An alternative hypothesis could be that an arboreality (tree-living) syndrome (Scheffers et al. 2013, 2017, Sosiak and Barden 2021) in ants is associated with longer dispersal distance, thereby setting species up to colonise further distances along the elevation gradient. In rainforests, the workers of arboreal ants are, on average, larger than the workers of ground ant species (Kaspari et al. 2015), and may therefore have larger bodied queens with greater reserves for achieving long distance dispersal (Helms Iv 2018, Hakala et al. 2019). An exciting direction could be to use genetic techniques (Suni and Gordon 2010) to test the alternative hypothesis that arboreality is associated with distinct dispersal strategies thereby contributing to biodiversity patterns across landscapes.

Conclusion

Our study gives important insight into the role of the vertical niche in driving compositional change and provides evidence of niche-contingent rates of species turnover over elevation. This provide conceptual support to further explore and advance research across multiple scales of biogeography to better understand range shift responses under climate change. On average, ground-based species might find it more difficult to shift ranges upwards in elevation in response to rising temperatures than their arboreal counterparts; this hypothesis awaits testing. Additionally, high species turnover in the ground community is likely to increase the chances of encountering novel interspecific interactions as species move upwards in elevation. Such differential responses of ground

versus arboreal species to climate change create diverse possibilities for the formation of novel communities in the vertical realm of tropical ecosystems.

Acknowledgements – We thank and acknowledge the traditional owners of the eastern Kuku Yalanji, western Yalanji, Mamu, and Jirrbal people on whose lands this work was conducted. Field research conducted under permit WITK15811415 issued by the Queensland Government of Australia. We also thank Donald McKnight for assistance with statistical analysis.

Funding – We thank our funders: Sloan Research Fellowship (BRS), The Explorer's Club (LL), Wet Tropics Management Authority (LL), Skyrail Rainforest Foundation (LL), Holsworth Wildlife Research Endowment – Equity Trustees Charitable Foundation (LL). LL was supported by a RTPS PhD scholarship from the Australian Government.

Author contributions

Lily Leahy: Conceptualization (equal); Data curation (equal); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (equal); Project administration (equal); Resources (equal); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal).

Brett R. Scheffers: Conceptualization (equal); Data curation (equal); Formal analysis (supporting); Funding acquisition (equal); Investigation (supporting); Methodology (equal); Project administration (equal); Resources (equal); Supervision (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

Alan N. Andersen: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Project administration (supporting); Resources (supporting); Supervision (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

Stephen E. Williams: Conceptualization (equal); Data curation (supporting); Formal analysis (supporting); Funding acquisition (supporting); Investigation (supporting); Methodology (supporting); Project administration (supporting); Resources (equal); Supervision (equal); Visualization (supporting); Writing – original draft (supporting); Writing – review and editing (equal).

Transparent peer review

The peer review history for this article is available at <https://publons.com/publon/10.1111/ecog.06972>.

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.59zw3r2fn> (Leahy et al. 2023).

Supporting information

The Supporting information associated with this article is available with the online version.

References

- Antoniazzi, R., Viana-Junior, A. B., Pelayo-Martínez, J., Ortiz-Lozada, L., Neves, F. S., Leponce, M. and Dáttilo, W. 2020. Distance–decay patterns differ between canopy and ground ant assemblages in a tropical rainforest. – *J. Trop. Ecol.* 36: 234–242.
- Archibald, S. B., Greenwood, D. R. and Mathewes, R. W. 2013. Seasonality, montane beta diversity, and Eocene insects: testing Janzen’s dispersal hypothesis in an equable world. – *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 371: 1–8.
- Ashton, L. A., Nakamura, A., Basset, Y., Burwell, C. J., Cao, M., Eastwood, R., Odell, E., de Oliveira, E. G., Hurley, K., Katabuchi, M., Maunsell, S., McBroom, J., Schmidl, J., Sun, Z., Tang, Y., Whitaker, T., Laidlaw, M. J., McDonald, W. J. F. and Kitching, R. L. 2016. Vertical stratification of moths across elevation and latitude. – *J. Biogeogr.* 43: 59–69.
- Baselga, A. 2010. Partitioning the turnover and nestedness components of beta diversity. – *Global Ecol. Biogeogr.* 19: 134–143.
- Baselga, A. and Orme, C. D. L. 2012. betapart: an R package for the study of beta diversity. – *Methods Ecol. Evol.* 3: 808–812.
- Basham, E. W., Seidl, C. M., Andriamahohatra, L. R., Oliveira, B. F. and Scheffers, B. R. 2019. Distance–decay differs among vertical strata in a tropical rainforest. – *J. Anim. Ecol.* 88: 114–124.
- Baudier, K. M., Mudd, A. E., Erickson, S. C. and O’donnell, S. 2015. Microhabitat and body size effects on heat tolerance: implications for responses to climate change (army ants: Formicidae, Ecitoninae). – *J. Anim. Ecol.* 84: 1322–1330.
- Beaulieu, F., Walter, D. E., Proctor, H. C. and Kitching, R. L. 2010. The canopy starts at 0.5 m: predatory mites (Acari: Mesostigmata) differ between rain forest floor soil and suspended soil at any height. – *Biotropica* 42: 704–709.
- Bishop, T. R., Robertson, M. P., van Rensburg, B. J. and Parr, C. L. 2014. Elevation–diversity patterns through space and time: ant communities of the Maloti-Drakensberg mountains of Southern Africa. – *J. Biogeogr.* 41: 2256–2268.
- Bishop, T. R., Robertson, M. P., van Rensburg, B. J. and Parr, C. L. 2015. Contrasting species and functional beta diversity in montane ant assemblages. – *J. Biogeogr.* 42: 1776–1786.
- Brooks, M. E., Kristensen, K., Van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M. and Bolker, B. M. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. – *R J.* 9: 378–400.
- Brown, J. H. 1984. On the relationship between abundance and distribution of species. – *Am. Nat.* 124: 255–279.
- Brühl, C. A., Mohamed, M. and Linsenmair, K. E. 1999. Altitudinal distribution of leaf litter ants along a transect in primary forests on Mount Kinabalu, Sabah, Malaysia. – *J. Trop. Ecol.* 15: 265–277.
- Buckley, L. B. and Kingsolver, J. G. 2021. Evolution of thermal sensitivity in changing and variable climates. – *Annu. Rev. Ecol. Syst.* 52: 563–586.
- Bujan, J., Yanoviak, S. P. and Kaspari, M. 2016. Desiccation resistance in tropical insects: causes and mechanisms underlying variability in a Panama ant community. – *Ecol. Evol.* 6: 6282–6291.
- Bujan, J., Roeder, K. A., de Beurs, K., Weiser, M. D. and Kaspari, M. 2020. Thermal diversity of North American ant communities: cold tolerance but not heat tolerance tracks ecosystem temperature. – *Global Ecol. Biogeogr.* 29: 1486–1494.
- Burwell, C. J. and Nakamura, A. 2015. Can changes in ant diversity along elevational gradients in tropical and subtropical Australian rainforests be used to detect a signal of past lowland biotic attrition? – *Austral Ecol.* 41: 209–218.
- Chase, J. M. and Myers, J. A. 2011. Disentangling the importance of ecological niches from stochastic processes across scales. – *Phil. Trans. R. Soc. B* 366: 2351–2363.
- Davison, A. and Chiba, S. 2008. Contrasting response to Pleistocene climate change by ground-living and arboreal *Mandarina* snails from the oceanic Hahajima archipelago. – *Phil. Trans. R. Soc. B* 363: 3391–3400.
- Fagan, L. L., Didham, R. K., Winchester, N. N., Behan-Pelletier, V., Clayton, M., Lindquist, E. and Ring, R. A. 2006. An experimental assessment of biodiversity and species turnover in terrestrial vs canopy leaf litter. – *Oecologia* 147: 335–347.
- Fitzpatrick, M. C., Sanders, N. J., Normand, S., Svenning, J. C., Ferrier, S., Gove, A. D. and Dunn, R. R. 2013. Environmental and historical imprints on beta diversity: insights from variation in rates of species turnover along gradients. – *Proc. R. Soc. B* 280: 20131201.
- Ghalambor, C. K., Huey, R. B., Martin, P. R., Tewksbury, J. J. and Wang, G. 2006. Are mountain passes higher in the tropics? Janzen’s hypothesis revisited. – *Integr. Comp. Biol.* 46: 5–17.
- Gilchrist, G. W. 1995. Specialists and generalists in changing environments. I. Fitness landscapes of thermal sensitivity. – *Am. Nat.* 146: 252–270.
- Hakala, S. M., Seppä, P. and Helanterä, H. 2019. Evolution of dispersal in ants (Hymenoptera: Formicidae): a review on the dispersal strategies of sessile superorganisms. – *Myrmecol. News* 29: 35–55.
- Halpern, B. S. et al. 2023. Priorities for synthesis research in ecology and environmental science. – *Ecosphere* 14: e4342.
- Hartig, F. 2021. DHARMA: residual diagnostics for hierarchical (multi-level/mixed) regression models. <https://CRAN.R-project.org/package=DHARMA> ver. 0.4.1.
- Helms Iv, J. A. 2018. The flight ecology of ants (Hymenoptera: Formicidae). – *Myrmecol. News* 26: 19–30.
- Holt, R. D., Barfield, M. and Gomulkiewicz, R. 2004. Temporal variation can facilitate niche evolution in harsh sink environments. – *Am. Nat.* 164: 187–200.
- Huey, R. B. 1991. Physiological consequences of habitat selection. – *Am. Nat.* 137: S91–S115.
- Huey, R. B. and Hertz, P. E. 1984. Is a jack-of-all temperatures a master of none? – *Evolution* 38: 441–444.
- Jankowski, J. E., Ciecka, A. L., Meyer, N. Y. and Rabenold, K. N. 2009. Beta diversity along environmental gradients: implications of habitat specialization in tropical montane landscapes. – *J. Anim. Ecol.* 78: 315–327.
- Janzen, D. H. 1967. Why mountain passes are higher in the tropics. – *Am. Nat.* 101: 233–249.
- Jonsson, B. G. 2001. A null model for randomization tests of nestedness in species assemblages. – *Oecologia* 127: 309–313.
- Kaspari, M., Clay, N. A., Lucas, J., Yanoviak, S. P. and Kay, A. 2015. Thermal adaptation generates a diversity of thermal limits in a rainforest ant community. – *Global Change Biol.* 21: 1092–1102.
- Kaspari, M., Clay, N. A., Lucas, J., Revzen, S., Kay, A. and Yanoviak, S. P. 2016. Thermal adaptation and phosphorus shape thermal performance in an assemblage of rainforest ants. – *Ecology* 97: 1038–1047.
- Kass, J. M. et al. 2022. The global distribution of known and undiscovered ant biodiversity. – *Sci. Adv.* 8: eabp9908.

- Klinges, D. H. and Scheffers, B. R. 2021. Microgeography, not just latitude, drives climate overlap on mountains from tropical to polar ecosystems. – *Am. Nat.* 197: 75–92.
- Kraft, N. J., Comita, L. S., Chase, J. M., Sanders, N. J., Swenson, N. G., Crist, T. O., Stegen, J. C., Vellend, M., Boyle, B., Anderson, M. J., Cornell, H. V., Davies, K. F., Freestone, A. L., Inouye, B. D., Harrison, S. P. and Myers, J. A. 2011. Disentangling the drivers of β diversity along latitudinal and elevational gradients. – *Science* 333: 1755–1758.
- Law, S. J., Bishop, T. R., Eggleton, P., Griffiths, H., Ashton, L. and Parr, C. 2020. Darker ants dominate the canopy: testing macroecological hypotheses for patterns in colour along a microclimatic gradient. – *J. Anim. Ecol.* 89: 347–359.
- Leahy, L., Scheffers, B. R., Williams, S. E. and Andersen, A. N. 2020. Diversity and distribution of the dominant ant genus *Anonychomyrma* (Hymenoptera: Formicidae) in the Australian Wet Tropics. – *Diversity* 12: 474.
- Leahy, L., Scheffers, B. R., Andersen, A. N., Hirsch, B. T. and Williams, S. E. 2021a. Vertical niche and elevation range size in tropical ants: implications for climate resilience. – *Divers. Distrib.* 27: 485–496.
- Leahy, L., Scheffers, B. R., Williams, S. E. and Andersen, A. N. 2021b. Arboreality drives heat tolerance while elevation drives cold tolerance in rainforest ants. – *Ecology* 103: e03549.
- Leahy, L., Scheffers, B. R., Andersen, A. N. and Williams, S. E. 2023. Data from: Rates of species turnover across elevation vary with vertical stratum in rainforest ant assemblages. – *Dryad Digital Repository*, <https://doi.org/10.5061/dryad.59zw3r2fn>.
- Longino, J. T. and Colwell, R. K. 2011. Density compensation, species composition, and richness of ants on a Neotropical elevational gradient. – *Ecosphere* 2: 1–20.
- Longino, J. T. and Branstetter, M. G. 2019. The truncated bell: an enigmatic but pervasive elevational diversity pattern in Middle American ants. – *Ecography* 42: 272–283.
- Longino, J. T., Branstetter, M. G. and Ward, P. S. 2019. Ant diversity patterns across tropical elevation gradients: effects of sampling method and subcommunity. – *Ecosphere* 10: e02798.
- Majer, J. D., Kitching, R. L., Heterick, B. E., Hurley, K. and Brennan, K. E. C. 2001. North–south patterns within arboreal ant assemblages from rain forests in Eastern Australia. – *Biotropica* 33: 643–661.
- McArdle, B. H. and Anderson, M. J. 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. – *Ecology* 82: 290–297.
- McGlynn, T. P. 2012. The ecology of nest movement in social insects. – *Annu. Rev. Entomol.* 57: 291–308.
- Mena, S., Kozak, K. M., Cárdenas, R. E. and Checa, M. F. 2020. Forest stratification shapes allometry and flight morphology of tropical butterflies. – *Proc. R. Soc. B* 287: 20201071.
- Moritz, C., Hoskin, C. J., MacKenzie, J. B., Phillips, B. L., Tonione, M., Silva, N., VanDerWal, J., Williams, S. E. and Graham, C. H. 2009. Identification and dynamics of a cryptic suture zone in tropical rainforest. – *Proc. R. Soc. B* 276: 1235–1244.
- Nadeau, C. P., Urban, M. C. and Bridle, J. R. 2017. Climates past, present, and yet-to-come shape climate change vulnerabilities. – *Trends Ecol. Evol.* 32: 786–800.
- Neves, F. S., Antoniazzi, R., Camarota, F., Pacelhe, F. T. and Powell, S. 2021. Spatiotemporal dynamics of the ant community in a dry forest differ by vertical strata but not by successional stage. – *Biotropica* 53: 372–383.
- Nowrouzi, S., Andersen, A. N., Macfadyen, S., Staunton, K. M., VanDerWal, J. and Robson, S. K. A. 2016. Ant diversity and distribution along elevation gradients in the Australian Wet Tropics: the importance of seasonal moisture stability. – *PLoS One* 11: e0153420.
- Nowrouzi, S., Bush, A., Harwood, T., Staunton, K. M., Robson, S. K. A. and Andersen, A. N. 2019. Incorporating habitat suitability into community projections: ant responses to climate change in the Australian Wet Tropics. – *Divers. Distrib.* 25: 1273–1288.
- Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O’hara, R., Simpson, G. L., Solymos, P., Stevens, M. H. H. and Wagner, H. 2013. Package ‘vegan’. – *Community Ecology Package*, <https://CRAN.R-project.org/package=vegan.ver.2.64>.
- Oliveira, B. F. and Scheffers, B. R. 2019. Vertical stratification influences global patterns of biodiversity. – *Ecography* 42: 249–249.
- Oliveira, B. F., Flenniken, J. M., Guralnick, R. P., Williams, S. E. and Scheffers, B. R. 2020. Historical environmental stability drives discordant niche filling dynamics across phylogenetic scales. – *J. Biogeogr.* 47: 807–816.
- Perillo, L. N., Castro, F. S. d., Solar, R. and Neves, F. d. S. 2021. Disentangling the effects of latitudinal and elevational gradients on bee, wasp, and ant diversity in an ancient Neotropical mountain range. – *J. Biogeogr.* 48: 1564–1578.
- Plowman, N. S., Mottl, O., Novotny, V., Idigel, C., Philip, F. J., Rimandai, M. and Klimes, P. 2020. Nest microhabitats and tree size mediate shifts in ant community structure across elevation in tropical rainforest canopies. – *Ecography* 43: 431–442.
- Qian, H., Chen, S., Mao, L. and Ouyang, Z. 2013. Drivers of β -diversity along latitudinal gradients revisited. – *Global Ecol. Biogeogr.* 22: 659–670.
- Sanders, N. J., Lessard, J. P., Fitzpatrick, M. C. and Dunn, R. R. 2007. Temperature, but not productivity or geometry, predicts elevational diversity gradients in ants across spatial grains. – *Global Ecol. Biogeogr.* 16: 640–649.
- Scheffers, B. R. and Williams, S. E. 2018. Tropical mountain passes are out of reach – but not for arboreal species. – *Front. Ecol. Environ.* 16: 101–108.
- Scheffers, B. R., Phillips, B. L., Laurance, W. F., Sodhi, N. S., Diesmos, A. and Williams, S. E. 2013. Increasing arboreality with altitude: a novel biogeographic dimension. – *Proc. R. Soc. B* 280: 20131581.
- Scheffers, B. R., Shoo, L., Phillips, B., Macdonald, S. L., Anderson, A., VanDerWal, J., Storlie, C., Gourret, A. and Williams, S. E. 2017. Vertical (arboreality) and horizontal (dispersal) movement increase the resilience of vertebrates to climatic instability. – *Global Ecol. Biogeogr.* 26: 787–798.
- Schneider, C. and Moritz, C. 1999. Rainforest refugia and Australia’s Wet Tropics. – *Proc. R. Soc. B* 266: 191–196.
- Sheldon, K. S., Huey, R. B., Kaspari, M. and Sanders, N. J. 2018. Fifty years of mountain passes: a perspective on Dan Janzen’s classic article. – *Am. Nat.* 191: 553–565.
- Slatyer, R. A., Hirst, M. and Sexton, J. P. 2013. Niche breadth predicts geographical range size: a general ecological pattern. – *Ecol. Lett.* 16: 1104–1114.
- Socolar, J. B., Gilroy, J. J., Kunin, W. E. and Edwards, D. P. 2016. How should beta-diversity inform biodiversity conservation? – *Trends Ecol. Evol.* 31: 67–80.
- Sosiak, C. E. and Barden, P. 2021. Multidimensional trait morphology predicts ecology across ant lineages. – *Funct. Ecol.* 35: 139–152.

- Spicer, M. E., Stark, A. Y., Adams, B. J., Kneale, R., Kaspari, M. and Yanoviak, S. P. 2017. Thermal constraints on foraging of tropical canopy ants. – *Oecologia* 183: 1007–1017.
- Stegen, J. C., Freestone, A. L., Crist, T. O., Anderson, M. J., Chase, J. M., Comita, L. S., Cornell, H. V., Davies, K. F., Harrison, S. P., Hurlbert, A. H., Inouye, B. D., Kraft, N. J. B., Myers, J. A., Sanders, N. J., Swenson, N. G. and Vellend, M. 2013. Stochastic and deterministic drivers of spatial and temporal turnover in breeding bird communities. – *Global Ecol. Biogeogr.* 22: 202–212.
- Suni, S. S. and Gordon, D. M. 2010. Fine-scale genetic structure and dispersal distance in the harvester ant *Pogonomyrmex barbatus*. – *Heredity* 104: 168–173.
- Vasconcelos, H. L., Neves, K. C. and Andersen, A. N. 2023. Vertical stratification of ant assemblages varies along a latitudinal gradient in Brazilian savanna. – *J. Biogeogr.* 50: 1331–1340.
- Williams, S. E. and Pearson, R. G. 1997. Historical rainforest contractions, localized extinctions and patterns of vertebrate endemism in the rainforests of Australia's Wet Tropics. – *Proc. R. Soc. B* 264: 709–716.
- Williams, S. E., Pearson, R. G. and Walsh, P. J. 1995. Distributions and biodiversity of the terrestrial vertebrates of Australia's Wet Tropics: a review of current knowledge. – *Pac. Conserv. Biol.* 2: 327–362.
- Williams, S. E., Marsh, H. and Winter, J. 2002. Spatial scale, species diversity, and habitat structure: small mammals in Australian tropical rainforest. – *Ecology* 83: 1317–1329.
- Williams, S. E., Shoo, L. P., Henriod, R. and Pearson, R. G. 2010. Elevational gradients in species abundance, assemblage structure and energy use of rainforest birds in the Australian Wet Tropics bioregion. – *Austral Ecol.* 35: 650–664.
- Xing, S., Hood, A. S. C., Dial, R. J. and Fayle, T. M. 2022. Species turnover in ant assemblages is greater horizontally than vertically in the world's tallest tropical forest. – *Ecol. Evol.* 12: e9158.
- Xu, W., Chen, G., Liu, C. and Ma, K. 2015. Latitudinal differences in species abundance distributions, rather than spatial aggregation, explain beta-diversity along latitudinal gradients. – *Global Ecol. Biogeogr.* 24: 1170–1180.
- Yanoviak, S. P. and Kaspari, M. 2000. Community structure and the habitat templet: ants in the tropical forest canopy and litter. – *Oikos* 89: 259–266.
- Zagmajster, M., Eme, D., Fišer, C., Galassi, D., Marmonier, P., Stoch, F., Cornu, J. F. and Malard, F. 2014. Geographic variation in range size and beta diversity of groundwater crustaceans: insights from habitats with low thermal seasonality. – *Global Ecol. Biogeogr.* 23: 1135–1145.