Received: 1 October 2024 | Accepted: 17 March 2025

DOI: 10.1111/icad.12824

ORIGINAL ARTICLE

Insect Conservation and Diversity

Royal Entomological Society

Scolytine beetle diversity along an altitudinal gradient in Papua New Guinea

Yiyi Dong[1] | Sierra Shepherd[1] | Nigel E. Stork[2] | Andrew J. Johnson[1] | Sarah M. Smith[1,3] | Carl Wardhaugh[4] | Maurice Leponce[5,6] | Martin Mogia[7] | Vojtech Novotny[8] | Jiri Hulcr[1]

[1]School of Forest, Fisheries, and Geomatics Sciences, University of Florida, Gainesville, Florida, USA

[2]Griffith School of Environment and Science, Griffith University, Nathan Campus, Brisbane, Queensland, Australia

[3]Department of Entomology, Michigan State University, East Lansing, Michigan, USA

[4]Scion (New Zealand Forest Research Institute), Rotorua, New Zealand

[5]Royal Belgian Institute of Natural Sciences, Brussels, Belgium

[6]Université Libre de Bruxelles, Brussels, Belgium

[7]New Guinea Binatang Research Center, Madang, Papua New Guinea

[8]Biology Center of the Czech Academy of Sciences, Institute of Entomology and Faculty of Science, University of South Bohemia, Ceske Budejovice, Czech Republic

Correspondence

Jiri Hulcr, School of Forest, Fisheries, and Geomatics Sciences, University of Florida, Gainesville, FL 32603, USA.

Email: hulcr@ufl.edu

Funding information

National Science Foundation; USDA Forest Service; Praemium Academiae award from the Czech Academy of Sciences; Prince Albert II of Monaco Foundation; Stavros Niarchos Foundation; Total Foundation; Fondation d'entreprise EDF; Fonds Pacifique; Spiecapag; Entrepose Contracting; New-Caledonia Government; Reef Foundation; FNRS (Belgium); Belgian National Lottery

Editor: Yves Basset and **Associate Editor:** Michał Filipiak

Abstract

1. Tropical elevation gradients support highly diverse assemblages, but competing hypotheses suggest either peak species richness in lowland rainforests or at mid-elevations. We investigated scolytine beetles—phloem, ambrosia and seed-feeding beetles—along a tropical elevational gradient in Papua New Guinea.
2. Highly standardised sampling from 200 to 3700 m above sea level (asl) identified areas of highest and lowest species richness, abundance and other biodiversity variables.
3. Using passive flight intercept traps at eight elevations from 200 to 3500 m asl, we collected over 9600 specimens representing 215 species. Despite extensive sampling, species accumulation curves suggest that diversity was not fully exhausted.
4. Scolytine species richness followed a unimodal distribution, peaking between 700 and 1200 m asl, supporting prior findings of highest diversity at low-to-mid elevations.
5. Alternative models, such as a monotonous decrease from lowlands to higher elevations and a mid-elevation maximum, showed lesser fit to our data. Abundance is greatest at the lowest sites, driven by a few extremely abundant species. The turnover rate—beta diversity between elevation steps—is greatest between the highest elevations.
6. Among dominant tribes—Dryocoetini, Xyleborini and Cryphalini—species richness peaked between 700 and 2200 m asl. Taxon-specific analyses revealed distinct patterns: *Euwallacea* spp. abundance uniformly declined with elevation, while other genera were driven by dominant species at different elevations. *Coccotrypes* and phloem-feeding *Cryphalus* have undergone evolutionary radiations in New Guinea, with many species still undescribed. Species not yet known to science are most likely to be found at lower and middle elevations, where overall diversity is highest.

KEYWORDS

bark beetles, elevational gradients, mid-domain effect, Papua New Guinea, Scolytinae, species diversity

---

Yiyi Dong and Sierra Shepherd are joint first authors.

INTRODUCTION

A key aim in ecology is identifying the factors that determine species distribution. One factor that impacts species diversity across broad scales is elevation. It presents a gradient of abiotic conditions and ecotones, resulting in high vegetation turnover and high species richness (Mayor et al., 2017). The distribution of species along elevation gradients may be driven by macroecological scenarios independent of environmental parameters, but it may also follow variables such as temperature and humidity (McCain & Grytnes, 2010). These patterns are important with respect to climate change, as changes in precipitation, temperature and seasonal variation are expected to shift species distribution across montane ecosystems and threaten alpine zones in certain areas of the world (Griffiths et al., 2021; White et al., 2021). Investigation of elevational gradients is therefore informative, as measuring diversity along them can provide a baseline to assess how community structures will change over time as temperatures increase.

Beta diversity, which describes the turnover of community composition across different habitats or spatial units (Baselga, 2010; Harrington et al., 2016; Koleff et al., 2003; Legendre et al., 2005), serves as a valuable metric for exploring elevational gradients. Beta diversity provides a proxy for ecosystem complexity, enables comparisons between studies and provides baseline information for the response of communities to environmental changes.

Previous research on the effects of elevation on species richness and turnover yielded varied results. Most studies on elevational gradients determine either greatest species richness at mid-elevations with a unimodal hump-shaped curve (Lomolino, 2001; Zhang et al., 2016) or a monotonic decline in richness with elevation (Brehm & Fiedler, 2003; Corcos et al., 2018; Gaston, 2007; Le Cesne et al., 2015; McCain, 2007; Rahbek, 2005; Yombai et al., 2021). Others have documented multimodal species richness patterns across elevations (Colinet et al., 2016). Factors such as temperature, precipitation, biotic interactions and individual species biology influence whether diversity along an elevational gradient follows any one of these distributions (Cirimwami et al., 2019; McCain, 2007; Neves et al., 2020). In addition, local species diversity may be partly the result of neutral, macroecological mechanisms independent of natural history. For example, the mid-domain theory predicts greater diversity in the middle of a gradient simply due to the overlap of species ranges (Colwell et al., 2004). The opposite, a uniform decrease in species richness, may be predicted by the fact that the area of land at each elevation generally decreases with altitude, supporting fewer species. On the other hand, higher elevations may support higher diversity because of the more complex higher-elevation topography providing more habitats. To distinguish among these hypotheses, studies of richness and turnover patterns for biologically distinct groups remain key.

Bark and ambrosia beetles (Coleoptera: Curculionidae: Scolytinae) are abundant, diverse and ubiquitous in tropical forests worldwide (Knížek & Beaver, 2004). The literature typically treats them as two ecological guilds—true bark beetles feeding on the phloem of dead trees and ambrosia beetles which colonise the tree xylem and use symbiotic fungi. In reality, scolytine beetles display a much greater diversity of ecologies, particularly in the tropics, including feeding on seeds, twigs, xylem without fungi and even herbaceous vegetation (Atkinson & Equihua, 1986; Kirkendall et al., 2015). We use the term scolytine beetles for all scolytine weevils throughout the text. Although the literature on bark and ambrosia beetles often includes Platypodinae (Col., Curculionidae), these are an independent subfamily of weevils, different morphologically and genetically from scolytine ambrosia beetles, and they have not been included in this study.

The feature that sets scolytines apart from other wood boring beetles, and from most weevil clades, is that the adult life stage also spends a substantial amount of time within the host tissue, facilitating colonisation and larval development (Biedermann & Taborsky, 2011). This contributes to their capacity for rapid population response to substrate availability, and the subsequent large abundances in the world's forests. Adults spend a relatively short time outside of the host during a dispersal flight to a new host. The contrast between the widely varied host use and the uniform requirement of a dispersal flight in all of these beetles has implications for sampling. Collecting from host plants or via traps baited with specific lures results in large specimen counts but leads to sampling biases (Gaylord et al., 2006; Gusmão et al., 2020; Johnson et al., 2016). Passive methods such as flight traps are slower, but are comparatively unbiased and capture a more representative subsample of the local scolytine fauna (Bussler et al., 2011; Dole et al., 2021; Hulcr, Beaver, et al., 2008; Hulcr, Novotny, et al., 2008).

Scolytine beetles have been studied for their alpha and beta diversity, but their elevational stratification has not been studied comprehensively. The few studies that exist are limited in scale and yielded conflicting conclusions. Some report a distinct decrease in diversity with altitude but an increase in beta diversity. In other words, lower elevations seem to contain a larger but more homogeneous diversity of species, and changes in community composition become more pronounced as elevation increases (Luo et al., 2022; Marathe et al., 2021; Rubin-Aguirre et al., 2015). In contrast, scolytine beetles in the more homogeneous conifer-dominated forests in northern latitudes appear to be equally diverse at different elevations, as long as their hosts are available (Chinellato et al., 2014; Williams et al., 2008). These studies are however not directly comparable, as they differ in their sampling methodology, and most employed guild-specific lures. A comprehensive assessment of a bark beetle altitudinal gradient using an unbiased sampling is still lacking.

In terms of vertical stratification within a single forest, some species fly close to the ground while smaller numbers prefer the canopy (Maeto & Fukuyama, 2003; Stork & Grimbacher, 2006). In terms of horizontal beta diversity—across distance but not elevation—existing studies suggest that bark beetles are unevenly distributed within small scales, largely as a result of the patchy availability of hosts (Hulcr, Beaver, et al., 2008; Hulcr, Novotny, et al., 2008; Peltonen et al., 1998), but as with other insects, they display remarkably little turnover over large geographic distances when environmental factors and altitude are excluded (Hulcr, Beaver, et al., 2008; Hulcr, Novotny, et al., 2008; Novotny et al., 2007).

The two environmental parameters that are most likely to influence temperate scolytine beetle elevational gradients are host availability and temperature, with the latter influencing development and dispersal (Jones et al., 2019; Williams et al., 2008). It is unclear, however, whether tropical beetles will follow patterns seen in temperate regions. Most studies focused on temperature gradients in the northern genera *Ips* or *Dendroctonus*, which are rare or absent in tropical regions. Similarly unresolved is the effect of host availability and host diversity. A logical extension of the decrease of plant diversity from sea level to mountain peaks in the tropics would suggest that scolytine beetle diversity will follow the same pattern; however, most tropical beetle species have relatively low host specificity (Beaver, 1979; Hulcr, Beaver, et al., 2008; Hulcr, Novotny, et al., 2008; Luo et al., 2022; Novotny et al., 2010).

Scolytine beetles are frequently studied because of the economic damage some species cause. In natural, non-anthropogenic ecosystems, less than 1% of documented scolytine beetle species cause noticeable tree death (Ranger, 2016). However, with the introductions of invasive species, and environmental stress and density of trees, especially in managed plantations, scolytine beetles of all ecological types can become pests (Ge et al., 2018; Lira-Noriega et al., 2018; Stouthamer et al., 2017). Similarly, many native and formerly harmless feeders on stressed or dying trees are now erupting into outbreaks due to the increasing environmental stress on their hosts (Hulcr & Skelton, 2023). This increasing environmental and economic impact of scolytine beetles is another reason why studies on tropical species are more urgent than ever. Detailed studies in native regions are useful for predicting and preventing future invasions (Grégoire et al., 2023; Hulcr et al., 2017; Mech et al., 2019), particularly as the homogenization of the global beetle and tree communities continues.

This study aims to examine the following questions: (1) how do species richness and abundance of scolytine beetles change with elevation: do they continually decrease with elevation, or peak at middle elevation? (2) What are the distributions of several specific, important genera? As species within a genus tend to have a similar ecology, we can also test whether ecologically specialised groups, such as fungus-feeding ambrosia beetles or seed-feeding scolytines, peak in diversity and abundance at specific local environments. (3) How does beta diversity change with elevation? In particular, does fauna change faster, slower or equally fast between elevational steps in lowland rainforests compared with the mountains? And lastly, (4) Are undescribed species equally likely to be found at all elevations, or are some elevations better documented than others? The sampling was carried out in Papua New Guinea (PNG), which is an ideal location for studying the spatial distribution of insects and the drivers of ecology and diversification: its environment is little disturbed, unique and species-rich.

MATERIALS AND METHODS

Study site

New Guinea is a tropical island in the Pacific. With 68% of its plants being endemic and a total of 13,634 plant species, the island boasts the highest floristic diversity and is the third largest canopied rainforest by landmass in the world (Barrows et al., 2009; Camara-Leret et al., 2020).

The specimens for this study were collected along an elevational gradient on Mount Wilhelm, Madang province, Papua New Guinea. Mount Wilhelm has its highest peak at 4509 m above sea level (asl), with an annual rainfall of 4660 mm at lower elevations to 3000 mm at higher elevations, and climate characterised by cycles of wet, dry and transitional seasons (Hnatiuk et al., 1976; Sam & Koane, 2014). The mean temperature of the different elevations at the sampling sites during 2010–2011 ranged from 27.4°C at 200 m asl to 8.6°C at 3700 m asl (Leponce et al., 2016). The entire transect of our study area on Mount Wilhelm spanned roughly 40 km. The forest types and elevations throughout the gradient are described in Table 1.

Sampling methods

Traps were placed at eight different elevations along Mount Wilhelm rainforest elevation gradient, starting at 200 m asl and ending at 3700 m asl, with 500 m asl elevation between each site. The site description and sampling methods are provided in Leponce et al. (2016). Each trap was designated with a five-digit 'P-number', spanning from P0001 to P5789. The P-number represents a unique collecting event from a certain trap on a certain date after 2 days of exposure. A total of 20 traps were set per elevation, resulting in 160 collection events at each elevation, except for 3200 m asl, which had 162 collection events. In total, 1282 such trapping events were conducted and included in this analysis. Trap inspections occurred from October 16 to December 2 of 2012, with data from traps 200–1700 m asl collected 9 days after the rest.

Besides flight interception traps (FITs), the umbrella project also included other sampling methods such as Malaise traps, Steiner traps and beating of vegetation (Leponce et al., 2016, 2020). Since only FITs collect scolytine beetles routinely and in substantive numbers, only specimens from those were included in this analysis. Malaise and other traps collected occasional specimens of scolytinae, but not in the numbers that would warrant inclusion in the analyses. Twenty FITs were placed 50 m apart or more at each elevation. The construction of each FIT consisted of a black mesh net (120 cm × 200 cm) stretching between two sticks with three large aluminium baking trays (65 cm × 45 cm) placed at the base, whose contents included a solution of water, salt and liquid detergent to catch any fallen insects. A full description of FITs can be found in Leponce et al. (2016). Holes were drilled at the top of the trays to prevent overflow during heavy rains, and plastic roofing over each trap protected them from adverse weather conditions. Care was taken to place these traps on flat ground.

All samples were initially processed at the New Guinea Binatang Research Center with the help of 63 field participants, both local trained research assistants and international scientists and students. Beetles from FITs were collected by pouring the trap's contents into a 13-oz Whirl-pak© plastic bag filled with ethanol. Traps at every

TABLE 1 Characteristics of diversity in different elevations.

Elevation (m asl)	TIN	TNUS	Genus count	Species count	SC (*n*)	SC (2*n*)	Forest types	Chao1	USC	SJ
200	2915	44	26	78	0.9904	0.995	Mixed lowland forest	115.8 ± 19.44	43	0.60
700	997	68	28	109	0.9659	0.9822	Mixed lowland forest	155.75 ± 21.87	59	0.73
1200	1837	83	23	102	0.9886	0.9973	Mixed lowland forest	115.13 ± 7.59	62	0.69
1700	2021	47	21	67	0.9876	0.994	Lower montane forest	97.00 ± 16.15	42	0.61
2200	1672	24	14	35	0.9952	0.9971	Mid-montane forest	44.33 ± 8.85	22	0.55
2700	130	7	8	13	0.9693	0.9815	Mid-montane forest	16.00 ± 4.14	7	0.20
3200	53	5	6	10	0.8686	0.9018	Upper montane forest	20.50 ± 10.47	5	0.07
3700	4	2	2	2	1	1	Sub-alpine forest	2.00 ± 0.35	2	0.30

Note: Characteristics of forest types at each elevation (200–3700 m asl), contained in our study site, as described in Johns (1982), are outlined. These designations were made based on overall vegetation cover at each of the eight elevations studied. A comprehensive table of values discussed in this paper is presented. The species count column contains the actual species observations collected from traps. The Chao1 values were the non-parametric estimator used to estimate the total number of species in our samples. TIN represents total individual number. TNUS represents total individual number of unclassified species. Unclassified species count (USC) was the number of species that we were unable to name to species. SC (*n*) and SC (2*n*) represent sample coverage estimates, where *n* is the observed total individual number, and 2*n* refers to twice the observed total individual number. SJ represents the standardised Jaccard turnover index, reflecting the dissimilarity in bark beetle composition among elevations. It is calculated based on coverage ($q = 0$, species richness) for collection events at each trap within each elevation.

elevation were checked on an alternating 2-day cycle, with 10 of the 20 traps being checked each day.

Identification of scolytine beetles

Scolytinae were separated from the remaining insects at the Binatang Research Center, led by C.W. Specimens were point-mounted and sorted by N.E.S. Further sorting and taxonomic identifications were carried out by N.E.S., J.H, A.J.J and S.M.S. Many morphospecies were designated by morphological characters, but could not be determined to a taxonomic name. For the ecological analysis here, both described species and designated morphospecies are referred to as 'species'. Identification, location, trap, collecting event number and each corresponding specimen were recorded from the pinned specimens into a spreadsheet. Beetle identifications across different locations and traps were standardised by employing four taxonomists, and using consistent identification guides for difficult taxa (Hulcr, unpublished). In cases of undescribed species, individuals were classified as distinct morphospecies (e.g., sp. 1, sp. 2) rather than grouping all undescribed species as a single 'sp.' category. The dataset was then transformed into a species-by-trap matrix of counts. For morphotype groups with unclear morphological characters or species boundaries, elevation was used as a method of reciprocal illumination of hypothetical species identity, and in multiple cases, distinct character combinations were found corresponding to certain elevations. Species were identified either by comparison with authors' existing collections, of keys in the literature or online (Hulcr & Cognato, 2013; Smith et al., 2020) and the remaining mysteries were compared with types in the NHMW in Vienna, USNM in Washington, DC, and HNHM in Budapest. All voucher samples in this study were preserved at the University of Florida Forest Entomology Collection.

Sampling exhaustiveness estimates and sampling evenness

The degree of completeness of species sampling at each elevation was tested by species accumulation curves (Colwell & Coddington, 1994; Ugland et al., 2003). Site-level samples (160 in total) were randomised by one hundred permutations. Species accumulation curves were also generated for each elevation (Figure 1b).

Sampling effort was even between the traps along the elevational gradient; therefore, abundances did not need to be standardised. Species richness is modelled using rarefaction and/or accumulation curves. All samples were included in the analyses, including those which included zero scolytine beetles.

Community diversity and changes along the gradient

The community of scolytine beetles completely changes from the lowest to the highest elevation. To test whether this change was nonrandom, we employed permutational multivariate analysis of variance (PERMANOVA) with 999 permutations of the Bray–Curtis dissimilarity matrix with Hellinger-transformed species abundances.

Besides raw numbers of species (Figure 1), we express diversity at different elevations by two commonly used indices that combine species richness as well as abundance (Morris et al., 2014). Hill numbers (species richness, Shannon diversity, Simpson diversity and coverage-based standardised Jaccard dissimilarity) were used because they provide a balanced representation of diversity and facilitate comparison by accounting for incomplete coverage, while beetle abundances in our samples were highly uneven due to a few extremely abundant species (Chao et al., 2023; Chao, Chiu, et al., 2014; Chao, Gotelli, et al., 2014; Kim et al., 2017). Chao1 is a robust diversity index that also enabled us to extrapolate our observations towards a total

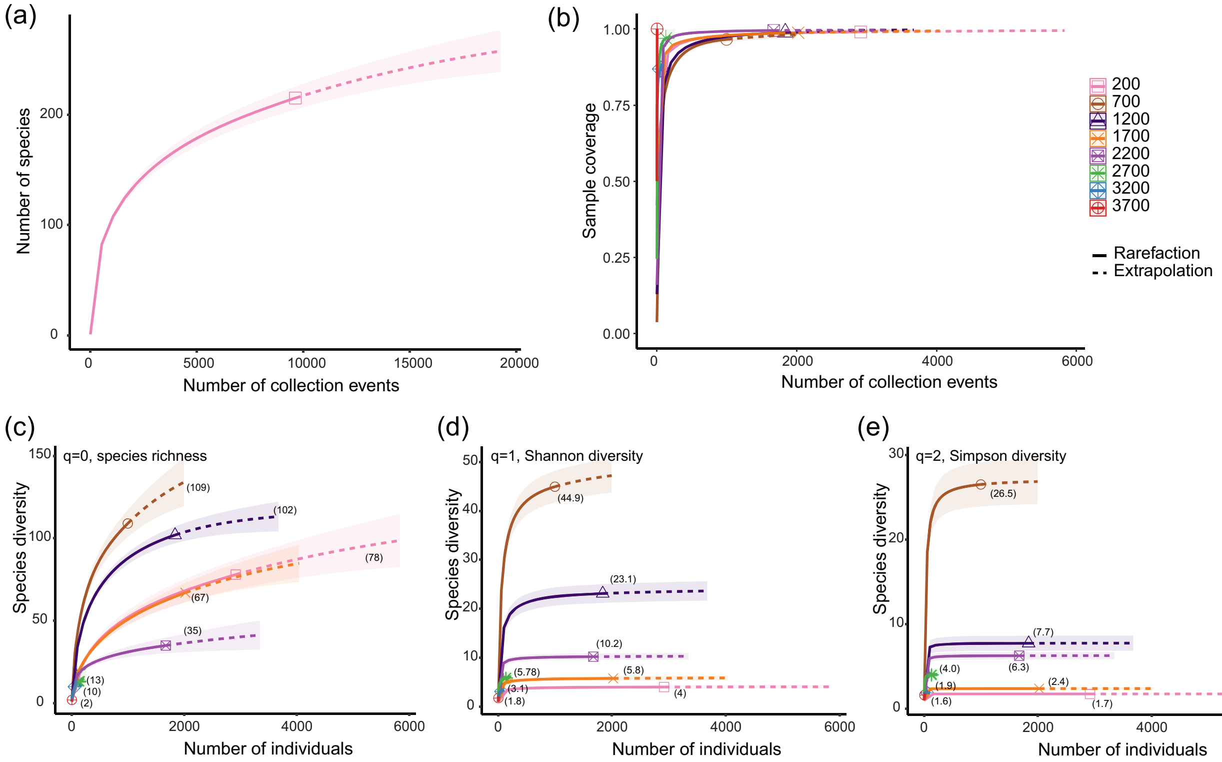

FIGURE 1 (a) Species accumulation curve for entire transect. (b) Plot of sample coverage at different elevations as a function of the number of collection events. All rarefactions and extrapolations are based on Hill numbers with $q = 0$, which corresponds to species richness. The light shaded areas represent the 95% confidence intervals. Rarefaction and extrapolation curves with 95% confidence intervals for (c) species richness, (d) Shannon diversity and (e) Simpson diversity. The values in parentheses within each panel indicate the corresponding observed diversity indices.

local diversity, as it accounts also for unobserved or rare species (Chao, 1984; Chao & Jost, 2012).

The changes in scolytine beetle communities across elevations were assessed using species replacement (turnover) and species loss (nestedness), calculated with the beta.pair function from the betapart package (Baselga & Orme, 2012). To determine the most likely relationship between elevation and dependent variables (the number of species, Chao1 index, species replacement in community (turnover), and undescribed species count), we used generalised additive models (GAMs), which provide flexible, smooth relationships between predictors and response variables. To avoid overfitting and ensure sufficient support for the smooth term, we limited the degrees of freedom to $k = 6$ (less than the number of unique elevation values). Smoothing parameters were selected using Restricted Maximum Likelihood. The GAMs were fitted using the mgcv package in R: $Y = \beta_0 + f(\text{Elevation}, k = 6) + \epsilon$; in this model, Y is the dependent variable; $f(\text{Elevation}, K = 6)$ is the smooth spline function of elevation with a limited degrees of freedom ($k = 6$). For comparison, we also fit linear and cubic regression models: (1) Simple linear regression: $Y = \beta_0 + \beta_1 \cdot \text{Elevation} + \epsilon$; (2) Cubic regression: $Y = \beta_0 + \beta_1 \cdot \text{Elevation} + \beta_2 \cdot \text{Elevation}^2 + \beta_3 \cdot \text{Elevation}^3 + \epsilon$. In these models, Y is a dependent variable, including number of species, or mean value of Chao1 index, or a community turnover (species replacement), or the count of unclassified species, at that elevation. The simple linear model assumes a straightforward linear relationship between elevation and the dependent variables. The cubic model includes a cubic term of elevation to capture potential unimodal distributions of species, such as in the scenario of peak diversity in middle elevations. The best-fitting model was determined using the Akaike information criterion (AIC).

To examine the effect of the elevation on the turnover rate of the scolytine beetle community, we calculated the dissimilarity of community between adjacent pairwise elevations using the Jaccard dissimilarity index, based on presence-absence matrices of beetles at different elevations, as proposed by Baselga (2010). This pairwise dissimilarity was calculated between each elevation level and its immediate neighbour and the lowest elevation (200 m asl). An additional, intuitive illustration of the species turnover was provided as the rate of Jaccard dissimilarity.

Diversity and elevational distribution of specific tribes and genera

The top three scolytine beetle tribes (Dryocoetini, Xyleborini and Cryphalini) and the most abundant genera (*Coccotrypes* in Dryocoetini, *Cryphalus*, the only genus in Cryphalini, and *Cyclorhipidion* and *Euwallacea* in Xyleborini) were further analysed individually.

The genus *Coccotrypes* is exceptional in that many species develop in non-phloem tissues—such as fruits, nuts, ferns, woody pods, leaf stalks or seeds—and may potentially display different diversity patterns than the more typical phloem-feeding scolytine beetles (Browne, 1961; Dong et al., 2024; Jordal et al., 2002). The degree to which seed-feeding scolytine diversity may be influenced by the host taxon remains one of the gaps in tropical forest entomology. While recent studies have provided insights into seed-feeding insect diversity and trophic interactions in tropical rainforests (Basset et al., 2018; Gripenberg et al., 2019), these studies primarily focus on broad community-level patterns and host specificity across multiple insect groups. The specificity of seed-feeding scolytine beetles, particularly *Coccotrypes*, remains underexplored. In tropical entomology literature, seed-feeding guilds are not always distinguished among spermatophages, granivores and fruit chewers (Novotny & Basset, 2005), and some *Coccotrypes* may fit more than one definition (Atkinson & Martínez, 1985).

Cryphalus is an example of an abundant and speciose phloem-feeding scolytine beetle group, which has experienced radiation in Oceania, and especially in New Guinea (Johnson et al., 2020). It is therefore interesting to test whether diversity is dispersed across different elevations, suggesting that elevation may have contributed to the radiation, or whether most of the diversity is sympatric, in low elevations. *Cyclorhipidion* and *Euwallacea* are ambrosia beetles that feed on symbiotic fungi inoculated in the wood of a wide range of tree species, and whose diversity is therefore unlikely to be a response to host tree diversity. Separating the effect of elevation on their species distribution may contribute to our understanding of the diversification process in the absence of host specificity. In addition, *Euwallacea* is a genus containing tropical, subtropical and even temperate ambrosial species, of which several are capable of attacking living trees (Wang et al., 2021). Exploring the distribution of *Euwallacea* spp. in different elevations is interesting because of this unique relationship with host trees, but also because this genus contains several emerging invasive ambrosia species spreading around the world.

With respect to ambrosia beetles, previous tropical entomology literature may classify them into different guilds, namely xylemycetophages or xylophages (Novotny & Basset, 2005). The feeding substrate is different between these two guilds, however (symbiotic fungus vs. wood, respectively), and the host specificity differs dramatically (xylomycetophages display high specificity to the fungus, and near-complete polyphagy with respect to host taxonomy; Hulcr et al., 2007), while true xylophages vary (Tavakilian et al., 1997). Therefore, the diversity distribution of the true scolytine xylomycetophages, which form the bulk of tropical ambrosia beetles, is expected to be limited by host taxa to a lesser degree than typical herbivorous insects.

Analysis of undescribed or unidentified species

To explore whether elevations differed in the degree to which scolytine beetle diversity is documented by taxonomic names, the number of putatively undescribed species (morphotypes for which we were not able to determine the species) was counted across elevations. The proportion of undescribed species at each elevation was modelled using a binomial generalised linear model. The model was fit using the glm() function in R (R Core Team, 2013), with the binomial family and a logit link function. The performance of linear regression was assessed using the AIC. The statistical significance of the elevation predictor was evaluated using z-tests, and 95% confidence intervals were estimated for the coefficients.

RESULTS

The sampling collected 9629 individuals derived from 215 unique species or morphotypes belonging to 34 genera of Scolytinae (Table 1). A complete list of species and genera can be found in Table S1. The most abundant species in our sample was *Coccotrypes myristicae*, with 2867 specimens, followed by *Cryphalus* sp. 5403 with 1595 specimens. In total, 60 species (27.9%) were singletons. Of the 160 traps, 137 yielded scolytine beetles, leaving only 23 trap sites with zero scolytine beetles throughout the timespan of this study. The genera *Coccotrypes*, *Cryphalus*, *Debus* and *Eidophelus* were the most species-rich, while *Coccotrypes*, *Cryphalus* and *Cyclorhipidion* were the most abundant.

The species accumulation curve for the entire dataset did not plateau, suggesting that additional unsampled species likely exist in this region (Figure 1). Using extrapolation through the Hill numbers and Chao1 index, we estimated that the total number of scolytine beetle species in the Mount Wilhelm transect may be 296 (observed 215 species).

Species richness and abundance

The highest species count was recorded between 700 and 1200 m asl (Table 1, Figure 2a, Figure S1). The sample coverages ranged from 0.87 at 3200 m asl to 1.00 at 3700 m asl, indicating near-complete species detection at the highest elevation. The Hill numbers calculated at a standardised sample coverage of 0.9 revealed a similar pattern, with a distinct peak at 700 m asl, suggesting that species diversity is highest at this elevation. Therefore, we report that rather than being highest at the lowest elevation, scolytine beetle diversity conforms to a unimodal diversity distribution, with the peak at lower- to mid-elevation. Diversity decreased both towards the lowest site (at 200 m asl) and even more towards higher elevations. The sub-alpine forest at 3700 m asl, the maximum elevation from which we sampled, had the lowest species richness with just 2 species documented. When broken down by site counts, 700 m asl had the greatest variability in species collected among the traps.

The greatest abundance of scolytine beetles—2915 specimens—was collected at the lowest elevation, 200 m asl (Table 1, Figure 1). Abundance was, however, highly influenced by a few extremely common species and followed a different trend than richness, with a notable dip in specimen count at 700 m asl, followed by an increase in count at 1200 and 1700 m asl.

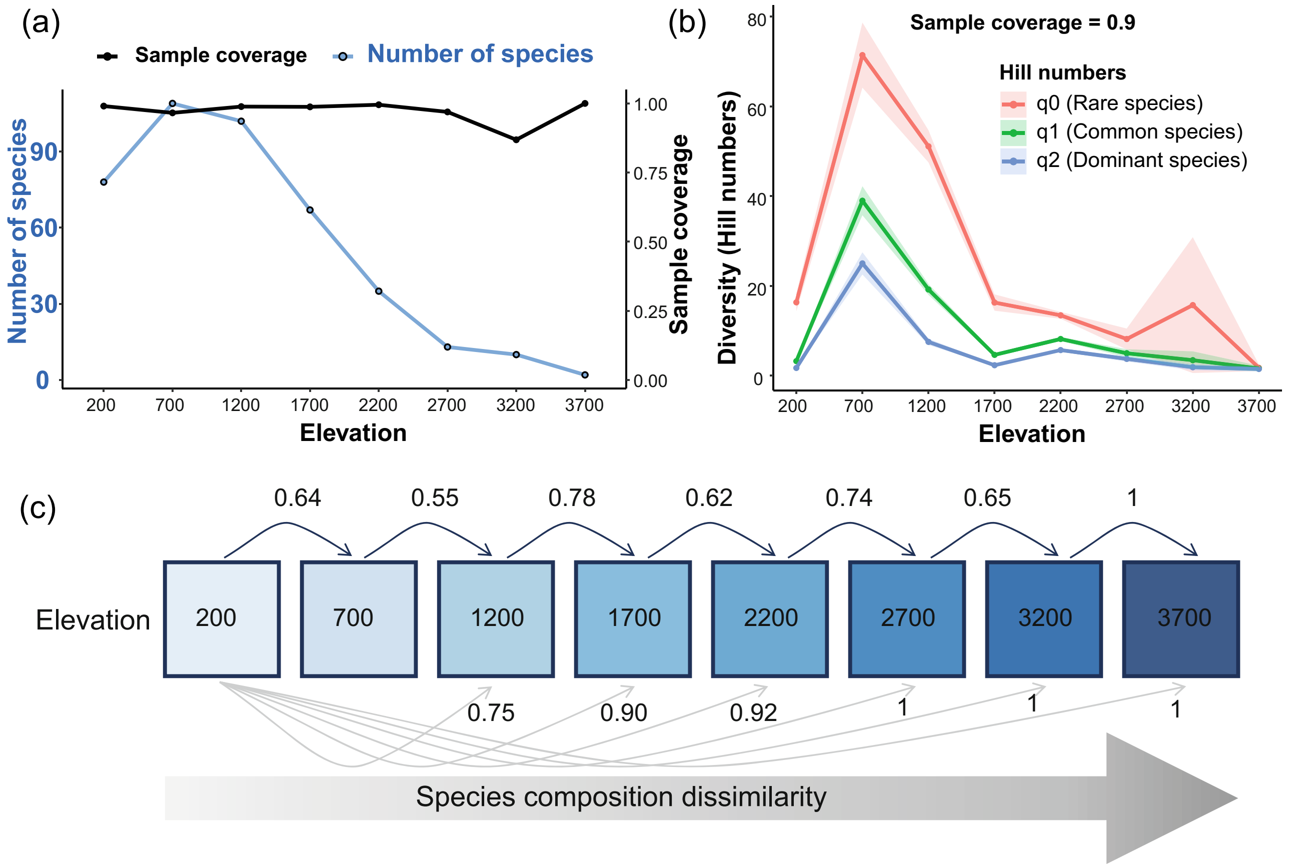

FIGURE 2 Changes of (a) the number of species and sample coverage. (b) diversity (Hill numbers) at a standardised sample coverage of 0.9 across elevation gradients. (c) Species composition dissimilarity in scolytine beetle community along the elevation gradient. The numbers ranging from 0.55 to 1 represent the Jaccard pair-wise dissimilarity. The closer the value is to 1, the more dissimilar the two elevations of scolytine beetle species collected from traps.

Taking both species count and abundance into account by the two diversity indices, the highest scolytine beetle diversity is indeed estimated at 700 m asl with 109 observed species (Shannon diversity: 44.9, Simpson diversity: 26.5), with the local species number estimated at 161 spp. by Chao1. The lowest was at 3700 m asl, where the total estimated number of species by Chao1 is 2, equal to the observed 2 species we actually observed, and Shannon diversity being 1.8 (Simpson diversity: 1.6) (Figure 1, Table 1).

Species turnover

PERMANOVA analysis revealed that elevation had a statistically significant effect on the composition of scolytine beetles (Pseudo $F = 44.694$, $df = 7$, $p = 0.001$). The cubic and GAM models yielded very similar AIC values; both are unimodal and show similar progression of species diversity: highest at lower-mid elevation, decreasing slightly towards sea level and decreasing substantially towards the subalpine zone. The cubic model was chosen for our interpretation of the biological pattern due to its parsimony and greater ease of biological interpretation. All tested variables—number of species, Chao1 index, species turnover, and the number of unclassified species—show similar significantly non-linear relationships with elevation (Table 2). The Chao1 index, number of species and unclassified species count exhibited peak diversity at elevations of approximately 700–1200 m asl.

The turnover rate and beta diversity index of scolytine beetle communities were significantly positively correlated with elevation, with species composition turnover peaking at the highest elevation (Figures 2c and 3a,b). Conversely, the nestedness of scolytine beetle communities significantly declined with elevation (Figure 3c). However, when analysing stepwise diversity, including stepwise beta diversity, stepwise turnover and stepwise nestedness between adjacent elevation gradients, no significant correlation was found between any variable and elevation (Figure 3d–f). Scolytine communities thus appear to reflect the faster rate of environmental change and host tree community change among higher elevations.

Unknown species distribution

The distribution of the undescribed species recorded at various elevations exhibited a non-linear pattern (Tables 1 and 2). The count of unknown species showed bell changes with increasing elevation,

TABLE 2 Summary of comparison between the linear, cubic models and generalised additive models (GAMs).

Dependent variables	Model	*F*-statistic	Adjusted-R^2	*p*-Value	AIC
Number of species	Linear	*F*(1, 6) = 27.81	0.7930	0.0019**	73.85
	Cubic	*F*(4.855, 2.145) = 376.9	0.9571	0.00264**	41.39
	GAMs	*F*(4.865, 2.135) = 370.6	0.996	0.00274**	41.57
Chao1 index	Linear	*F*(1, 6) = 38.53	0.8428	0.0008***	76.33
	Cubic	*F*(3.094, 3.906) = 22.67	0.922	0.00545**	72.76
	GAMs	*F*(3.338, 3.662) = 22.3	0.926	0.00533**	71.01
Species replacement (turnover)	Linear	*F*(1, 6) = 17.59	0.7032	0.0057**	−0.31
	Cubic	*F*(3.69, 3.31) = 51.61	0.969	0.00421***	−16.62
	GAMs	*F*(3.577, 3.423) = 50.51	0.968	0.00436**	−17.47
Unclassified species count	Linear	*F*(1, 6) = 21.79	0.7481	0.003438**	66.51
	Cubic	*F*(4.742, 2.258) = 211.2	0.993	0.00471***	37.37
	GAMs	*F*(4.657, 2.343) = 271	0.995	0.00367***	35.24

Note: Species replacement (turnover) refers to the pairwise turnover components from lowest elevation (200 m asl) to other elevations. The star symbols in the *p*-value column denote significance level: *<0.05; **<0.01; ***<0.001.
Abbreviation: AIC, Akaike information criterion.

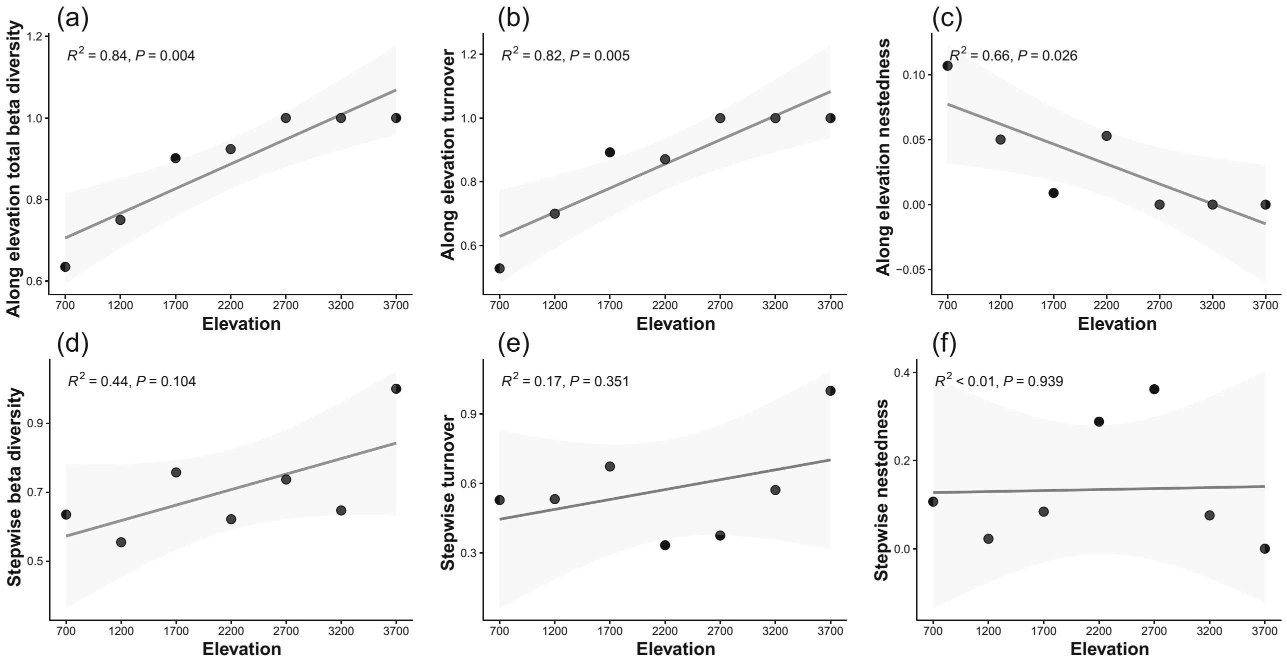

FIGURE 3 The relationships between elevational gradients and community beta diversity index, species replacement (turnover), and species loss (nestedness) are shown in (a), (b) and (c), respectively, from the lowest elevation (200 m asl) to higher elevations. (d), (e) and (f) demonstrate the correlation of stepwise diversity, including beta diversity, turnover and nestedness, between each elevation and its immediately adjacent higher elevation. Stepwise beta diversity, turnover and nestedness were calculated by comparing each elevation with its next higher adjacent elevation.

peaking at 1200 m asl with 62 species, followed by 59 species at 700 m asl. The model did not detect a significant relationship between elevation and the proportion of undescribed species ($z = 0.964$, $p = 0.335$, AIC = 37.18). The predicted proportion of undescribed species showed a slightly upward but insignificant trend across the elevation gradient (from 55% at the lowest elevation to 66% at the highest elevation) suggesting that undescribed species are likely to be found at any elevation (Figure S2).

Tribe and genus distribution

Three scolytine tribes dominated the sample: Dryocoetini, Xyleborini and Cryphalini (Figure 4). All three have strongly skewed species-abundance ratios, but their abundances peaked at different elevations. Dryocoetini and Xyleborini together form a paraphyletic clade (Johnson et al., 2018), and as such represent a single large evolutionary radiation of tropical bark and ambrosia beetles, unparalleled

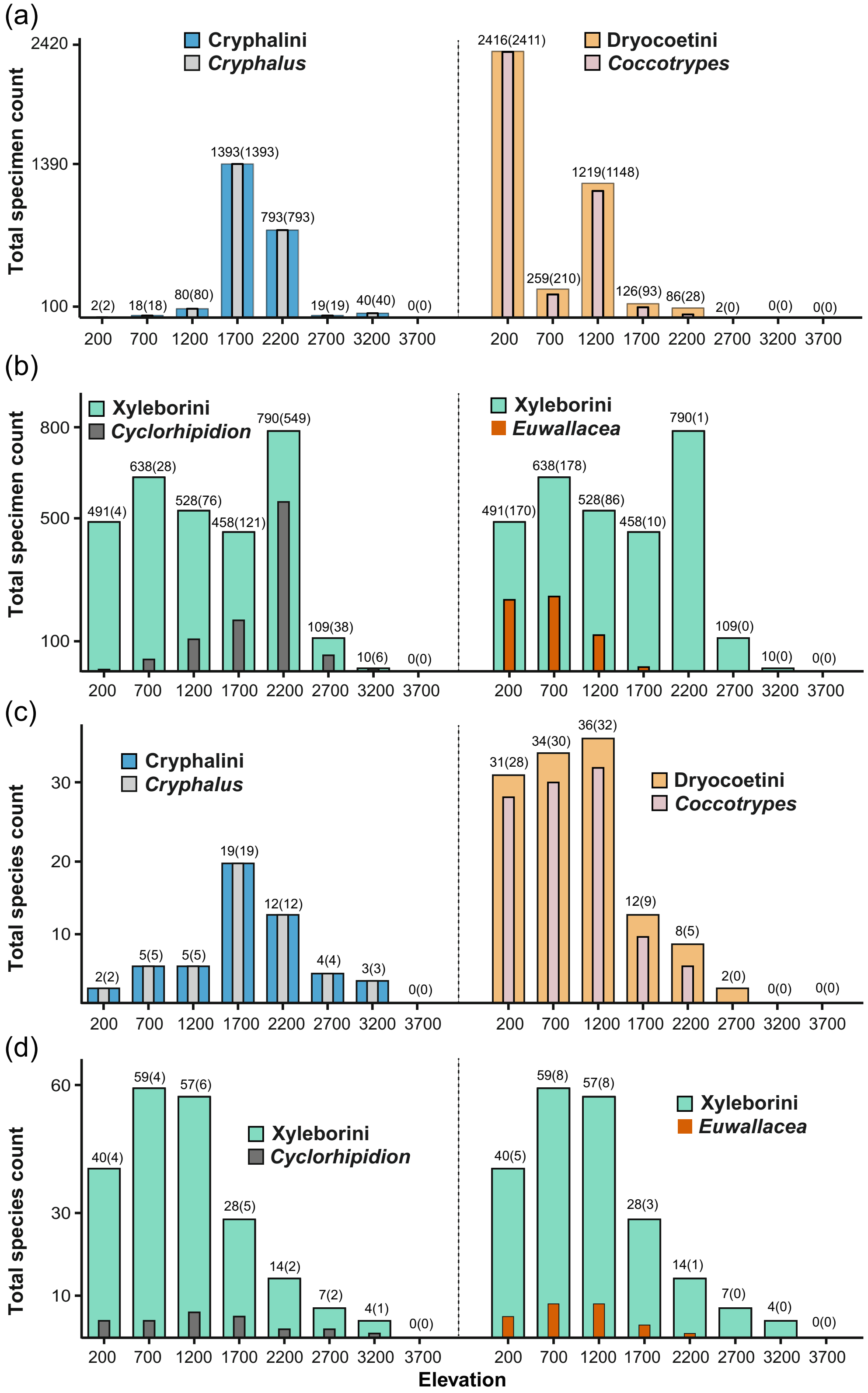

FIGURE 4 The abundances (a, b) and species count (c, d) of the top three tribes and genera were recorded at each elevation level. The number shows the total number of specimens or the total species count for each tribe, and the numbers in parentheses represent the total number of specimens or the total species count for each genus. Cryphalini only contains one genus, *Cryphalus*.

among other groups. Xyleborini appears to follow the general trend of highest diversity at around 700 m, followed by a steady decline, with the exception of an abundance peak at 2200 m. This abundance spike is driven by a pair of endemic, nearly identical species, *Cyclorhipidion spurlinum* and what appears to be a sister, undescribed species *Cyclorhipidion* sp. n. 'shagreened', both most abundant at the 2200 m location. Another important xyleborine genus, *Euwallacea*, was uniformly distributed between 200 and 1200 m asl. The genus was represented by 11 species, most of them identifiable to species. Notable are the four individuals tentatively identified as *Euwallacea fornicatus*. This is a Palearctic complex of species, some of which are globally invasive, tree-killing pests. It is not known which of the cryptic species these PNG individuals belong to.

Dryocoetini as a tribe are also difficult to evaluate, as the overall abundance is driven by a few species of a single genus *Coccotrypes*; one species is hyper-abundant at the lowest elevation of 200 m asl, and another one at 1200 m asl. The genus *Coccotrypes* is represented by 58 species and 3890 specimens in our sample, making it the most abundant as well as species-rich of all New Guinean scolytine beetle genera.

Cryphalini, represented by the single genus *Cryphalus* with 29 species and 2345 specimens, was very abundant at mid-elevations and decreased in both directions, towards lowlands and highlands. Like other tribes, Cryphalini have a skewed species-abundance rank, with the three most common species representing 75% of all individuals. Tribes other than Xyleborini, Dryocoetini and Cryphalini are represented by lower diversities and abundances. The Scolytoplatypodini and Hyorrhynchini were each only represented by single species, *Scolytoplatypus eutomoides* and *Sueus insulanus* respectively. Ernoporini and Trypophloeini are both represented by a single genus with 4 species. Hylesinini is dominated by the genus *Ficicis* in terms of abundance. Phloeosinini yielded only three specimens, two *Hyledius* spp. and one *Phloeosinus* sp.

Species counts across these specific genera (*Cryphalus*, *Coccotrypes*, *Cyclorhipidion* and *Euwallacea*) followed a unimodal distribution, with the highest species count occurring at mid-elevations ranging from 700 to 2200 m asl., and lower species counts at both lower and higher elevations. *Cryphalus* had the most abundant species count (19 species) at 1700 m asl, while *Coccotrypes*, *Cyclorhipidion* and *Euwallacea* had their highest species count at 1200 m asl, with 32 species, 6 species and 8 species, respectively. A peak in the species count of *Euwallacea* was also found at 700 m asl.

DISCUSSION

Species richness of scolytine beetles along an elevational gradient in Papua New Guinea appears to follow a unimodal curve, with a peak at low to mid-elevations and decreasing richness towards higher elevations. This trend aligns with patterns observed in other arthropods, for example, alpine moths (Beck et al., 2010) and ants in southern Africa (Bishop et al., 2014). This unimodal distribution may be attributed to several factors, including higher temperatures at lower elevations, which support greater species richness in most taxa, including the host trees on which most bark beetles depend (Bishop et al., 2014). Additionally, vegetation structure—such as increased tree density and canopy cover at lower elevations—creates more complex habitats that can sustain higher biodiversity (Dolson & Kharouba, 2024). Alternative models observed in other organisms fit our data less well. For example, birds, butterflies and bats showed a monotonous decrease from lowlands to higher elevations (Sam et al., 2019; Sivault et al., 2023), while ferns and frogs are most diverse in the middle of the rainforest elevation gradient (Colwell et al., 2016; Dahl et al., 2024).

We recorded a total of 215 species, the majority of the total species richness estimated by the Chao1 index, and each elevation had a high sample coverage (0.87–1). That not all species have been intercepted is also supported by the fact that existing taxonomic lists from the region include species not sampled here (Hulcr & Cognato, 2013). However, the proportion of singletons in our dataset (Supplementary data) was modest compared with other surveys of megadiverse regions (Dole et al., 2021).

What explains the unimodal, skewed diversity gradient of scolytine beetles? The most consistent abiotic factor that changes with elevation is temperature (Hodkinson, 2005), but how and if this variable affects bark beetle diversity directly is unclear. A more likely influence, also correlated with elevation, is the diversity and abundance of host substrates—trees, twigs, lianas, seeds, etc. Host plants show a relatively minor influence on the diversity structure of the fungus-feeding ambrosia beetles, given their low host specificity (Beaver, 1979; Hulcr et al., 2007). In the more host-specific phloem- and seed-feeders, however, host plant availability may be the single most important factor influencing their distribution and diversity, enabling their presence. This is consistent with our records of taxa where host preferences are known. For example, the observed abundance of the genus *Cyclorhipidion* in higher elevations is likely aligned with the distribution of Fagaceae. *Cyclorhipidion* species have a preference for Fagaceae, a family primarily found in middle- to high-elevation regions in the tropics (Ash, 1987). Similarly, the most abundant genera *Cryphalus* and *Coccotrypes*—specialised phloem-feeders and seed-feeders, respectively—show a diversity distribution that is different from the trends in the overall dataset, dominated by the diversity of host-generalist ambrosia beetles. Without comprehensive data on flora composition throughout the studied transect, however, drawing conclusions about the effect of plant diversity on the whole beetle assemblage would be speculative. In addition, other factors for which no data are available—such as species biology and interactions, niche availability, and precipitation—might have also affected abundance and richness values.

The abundance of a species does not correlate with scientific knowledge about the species. The most common scolytine beetle in Papuan forests—*C. myristicae*—has not been properly studied in the Papuan region. Little is known about the ecology of this species, despite its great abundance and its vast geographic distribution from Sri Lanka to Samoa. Browne (1961) reported on its biology in Malaysia and suggested that it is a polyphagous seed-feeder recorded from multiple plant families. It was reported to feed on nutmeg in Java by the author who described the species (Roepke, 1919), and then on unspecified fruits and nuts in Malaysia (Beaver & Browne, 1978); after that, no additional feeding records are known, and none from New Guinea. It is not even clear whether the New Guinean population is the same species as the very distant populations in mainland Asia. Of the 58 species or morphospecies of *Coccotrypes* in our sample, 42 did not match specimens in the collections that we visited.

Similarly, little is known about the second most abundant genus, *Cryphalus*. The most common bark beetle morphotype in our sample was *Cryphalus* sp. 5403. Despite its abundance, it appears to be an undescribed species, and nothing is known about its biology. On the other hand, nearly all morphotypes of the tribe Xyleborini, which have been studied by multiple authors recently, were assigned to species using keys and the literature.

The relationship between species richness and abundance is not uniform across elevations. At 200 m asl elevation, a single species, *C. myristicae*, accounts for 75.5% of total specimens (2201 out of 2915), driving the highly uneven community structure. Similarly, at 2700 m asl elevation, a few species dominate the community of only 13 species. These trends are not unusual, and previous studies have shown that dominant species alter abundance curves (Corcos et al., 2018; Meng et al., 2022).

Phylogenetic diversity may be a more reliable and reproducible measure of species diversity than categorical classification by morphology alone, mostly because of its explicit accounting for evolutionary non-independence of species (Chao, Chiu, et al., 2014; Chao, Gotelli, et al., 2014; Miller et al., 2018). This is not to suggest, however, that morphological classification is inadequate. Several recent studies on scolytine species complexes have shown that what allows species lineages discovery and delineation is a combination of careful morphological assessment with a phylogenetic backbone (Smith et al., 2019; Stouthamer et al., 2017). Even in the haplo-diploid Xyleborini and Dryocoetini, morphology tends to correlate with phylogenetic clades (LeMay et al., 2024). There are some groups, however, namely the hyperdiverse *Coccotrypes* and Trypophloeini, in which current morphological assessment is preliminary, and future diversity studies will require a molecular phylogenetic component. Fortunately, most specimens collected in this study spent very little time in the collection liquid and appear to be in good condition; therefore, in the next iteration of this study, DNA extraction, sequencing and phylogenetic analysis can be attempted.

In climate change studies, temperature is typically the primary driver of range and abundance shifts, including in herbivorous insects (Bale et al., 2002). Recent studies continue to support this notion for many insect taxa (Hill et al., 2021). Most scolytines are not strictly herbivorous and instead rely on dead wood or stressed trees. Consequently, the changing climate will likely influence their populations in a less predictable way, mainly via dead wood availability. Indirect climate impacts, such as increased storm frequency and intensity, drought-induced tree mortality and forest management practices, are likely to play a critical role in shaping their future communities. Papua New Guinea, like most tropical island environments, could see increases in temperatures and extreme weather events at an even faster rate than other regions of the globe (Fleishman, 2022). Its biodiversity is characterised by species inhabiting unique niches that face a greater threat of loss under warming (Bazzaz, 1998; Dorey et al., 2020). Instances of previously inhospitable climates becoming suitable for bark beetles as temperatures warm have already been evidenced in temperate regions, including for tree-killing species (Garrick et al., 2021; Logan et al., 2010), and a similar trend could be seen in Papua New Guinea. Additional threats to the biodiversity of Papua New Guinea—such as logging, anthropogenic fire and invasive species—have the potential to shift faunal communities out of their current range (White et al., 2021). With the significance of temperature changes in montane ecosystems and the impact of human encroachment, this could result in dramatic changes in elevational distributions of species, or their removal from optimal niches.

AUTHOR CONTRIBUTIONS

Yiyi Dong: Data curation; formal analysis; visualization; writing – original draft; writing – review and editing. **Sierra Shepherd:** Data curation; resources; writing – original draft. **Nigel E. Stork:** Data curation; investigation; writing – review and editing. **Andrew J. Johnson:** Data curation; resources; writing – review and editing. **Sarah M. Smith:** Data curation; resources; writing – review and editing. **Carl Wardhaugh:** Data curation; resources; writing – review and editing. **Maurice Leponce:** Data curation; resources; writing – review and editing. **Martin Mogia:** Data curation; resources; writing – review and editing. **Vojtech Novotny:** Data curation; resources; writing – review and editing. **Jiri Hulcr:** Conceptualization; data curation; resources; writing – original draft; writing – review and editing.

ACKNOWLEDGEMENTS

A massive collaborative effort was conducted in 2012 to gather data on flora and fauna distributions in Papua New Guinea. We thank all participants of this project, detailed in Leponce et al. (2016). This field work was conducted in the framework of ‘Our Planet Reviewed Papua-New-Guinea 2012-2013’ set up by Pro-Natura International, the National Museum of Natural History (MNHN, France), the Institut de Recherche pour le Développement (IRD, France) in partnership with the Royal Belgian Institute of Natural Sciences, the New Guinea Binatang Research Center, the University of Papua New Guinea, and the Divine Word University of Madang and with core funding of Prince Albert II of Monaco Foundation, the Stavros Niarchos Foundation, the Total Foundation, the Fondation d’entreprise EDF, the Fonds Pacifique, Spiecapag, Entrepose Contracting, the New-Caledonia Government, the Reef Foundation, FNRS (Belgium) and the Belgian National Lottery. Daniel Johnson, Miguel Acevedo and Phil Hahn provided valuable input on data visualisation and statistical analyses. We thank curators of institutional insect collections: Maxwell Barclay (NHM, London), Lourdes Chamorro (USNM, Washington DC), Harald Schilhammer (NHMW, Vienna), and Gyozo Szel and Ferenc Lakatos (HNHM, Budapest). Y.D., S.S., A.J.J. and J.H. were supported by the National Science Foundation and by the USDA Forest Service. V.N. was supported by the Praemium Academiae award from the Czech Academy of Sciences.

FUNDING INFORMATION

This work was supported by the Prince Albert II of Monaco Foundation, the Stavros Niarchos Foundation, the Total Foundation, the

Fondation d'entreprise EDF, the Fonds Pacifique, Spiecapag, Entrepose Contracting, the New-Caledonia Government, the Reef Foundation, FNRS (Belgium) and the Belgian National Lottery.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.26502538.

ORCID

Yiyi Dong https://orcid.org/0000-0003-1119-2063
Sierra Shepherd https://orcid.org/0009-0001-6334-6629
Nigel E. Stork https://orcid.org/0000-0001-7812-2452
Andrew J. Johnson https://orcid.org/0000-0003-3139-2257
Sarah M. Smith https://orcid.org/0000-0002-5173-3736
Vojtech Novotny https://orcid.org/0000-0001-7918-8023
Jiri Hulcr https://orcid.org/0000-0002-8706-4618

REFERENCES

Ash, J. (1987) Nothofagus (Fagaceae) forest on Mt Giluwe, New Guinea. *New Zealand Journal of Botany*, 26(2), 245–258. Available from: https://doi.org/10.1080/0028825X.1988.10410116

Atkinson, T.H. & Equihua, A. (1986) Biology of the Scolytidae and Platypodidae (Coleoptera) in a tropical deciduous forest at Chamela, Jalisco, Mexico. *Florida Entomologist*, 69(2), 303–310. Available from: https://doi.org/10.2307/3494933

Atkinson, T.H. & Martínez, A.E. (1985) Notes on biology and distribution of Mexican and Central American Scolytidae (Coleoptera). I. Hylesininae, Scolytinae except Cryphalini and Corthylini. *The Coleopterists Bulletin*, 39, 227–238.

Bale, J., Masters, G., Hodkinson, I., Awmack, C., Bezemer, T., Brown, V. et al. (2002) Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. *Global Change Biology*, 8(1), 1–16. Available from: https://doi.org/10.1046/j.1365-2486.2002.00451.x

Barrows, L., Matainaho, T., Ireland, C., Miller, S., Carter, G., Bugni, T. et al. (2009) Making the most of Papua New Guinea's biodiversity: establishment of an integrated set of programs that link botanical survey with pharmacological assessment in "the land of the unexpected". *Pharmaceutical Biology*, 47(8), 795–808. Available from: https://doi.org/10.1080/13880200902991599

Baselga, A. (2010) Partitioning the turnover and nestedness components of beta diversity. *Global Ecology and Biogeography*, 19(1), 134–143. Available from: https://doi.org/10.1111/j.1466-8238.2009.00490.x

Baselga, A. & Orme, C.D.L. (2012) Betapart: an R package for the study of beta diversity. *Methods in Ecology and Evolution*, 3, 808–812. Available from: https://doi.org/10.1111/j.2041-210X.2012.00224.x

Basset, Y., Dahl, C., Ctvrtecka, R., Gripenberg, S., Lewis, O.T., Segar, S.T. et al. (2018) A cross-continental comparison of assemblages of seed- and fruit-feeding insects in tropical rainforests: faunal composition and rates of attack. *Journal of Biogeography*, 45(6), 1–18. Available from: https://doi.org/10.1111/jbi.13211

Bazzaz, F.A. (1998) Tropical forests in a future climate: changes in biological diversity and impact on the global carbon cycle. In: Markham, A. (Ed.) *Potential impacts of climate change on tropical forest ecosystems*. Dordrecht: Springer, pp. 177–196.

Beaver, R.A. & Browne, F.G. (1978). The scolytidae and platypodidae (Coleoptera) of Penang, Malaysia. *Oriental Insects*, 12(4), 575–624. Available from: https://doi.org/10.1080/00305316.1978.10432538

Beaver, R. (1979) Host specificity of temperate and tropical animals. *Nature*, 281(5727), 139–141. Available from: https://doi.org/10.1038/281139a0

Beck, J., Altermatt, F., Hagmann, R. & Lang, S. (2010) Seasonality in the altitude–diversity pattern of Alpine moths. *Basic and Applied Ecology*, 11(8), 714–722. Available from: https://doi.org/10.1016/j.baae.2010.08.009

Biedermann, P.H. & Taborsky, M. (2011) Larval helpers and age polyethism in ambrosia beetles. *Proceedings of the National Academy of Sciences*, 108(41), 17064–17069. Available from: https://doi.org/10.1073/pnas.1107758108

Bishop, T.R., Robertson, M.P., van Rensburg, B.J. & Parr, C.L. (2014) Elevation–diversity patterns through space and time: ant communities of the Maloti-Drakensberg Mountains of southern Africa. *Journal of Biogeography*, 41(12), 2256–2268.

Brehm, G. & Fiedler, K. (2003) Faunal composition of geometrid moths changes with altitude in an Andean montane rain forest. *Journal of Biogeography*, 30(3), 431–440. Available from: https://doi.org/10.1046/j.1365-2699.2003.00832.x

Browne, F.G. (1961) The biology of Malayan Scolytidae and Platypodidae. *Malyan Forest Records*, 22, 1–255.

Bussler, H., Bouget, C., Brustel, H., Brändle, M., Riedinger, V., Brandl, R. et al. (2011) Abundance and pest classification of scolytid species (Coleoptera: Curculionidae, Scolytinae) follow different patterns. *Forest Ecology and Management*, 262(9), 1887–1894. Available from: https://doi.org/10.1016/j.foreco.2011.08.011

Camara-Leret, R., Frodin, D., Adema, F., Anderson, C., Appelhans, M., Argent, G. et al. (2020) New Guinea has the world's richest island flora. *Nature*, 584(7822), 579. Available from: https://doi.org/10.1038/s41586-020-2549-5

Chao, A. (1984) Nonparametric-estimation of the number of classes in a population. *Scandinavian Journal of Statistics*, 11(4), 265–270.

Chao, A., Chiu, C.H. & Jost, L. (2014) Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers. *Annual Review of Ecology, Evolution, and Systematics*, 45(1), 297–324.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. et al. (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84(1), 45–67. Available from: https://doi.org/10.1890/13-0133.1

Chao, A. & Jost, L. (2012) Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, 93(12), 2533–2547.

Chao, A., Thorn, S., Chiu, C.H., Moyes, F., Hu, K.H., Chazdon, R.L. et al. (2023) Rarefaction and extrapolation with beta diversity under a framework of Hill numbers: the iNEXT. beta3D standardization. *Ecological Monographs*, 93(4), e1588. Available from: https://doi.org/10.1002/ecm.1588

Chinellato, F., Faccoli, M., Marini, L. & Battisti, A. (2014) Distribution of Norway spruce bark and wood-boring beetles along alpine elevational gradients. *Agricultural and Forest Entomology*, 16(2), 111–118. Available from: https://doi.org/10.1111/afe.12040

Cirimwami, L., Doumenge, C., Kahindo, J. & Amani, C. (2019) The effect of elevation on species richness in tropical forests depends on the considered lifeform: results from an East African mountain forest. *Tropical Ecology*, 60(4), 473–484. Available from: https://doi.org/10.1007/s42965-019-00050-z

Colinet, C., Exbrayat, M., Robillard, T. & Legendre, F. (2016) Species richness and composition in cockroaches (Dictyoptera: Blattodea) along an elevational gradient in Papua New Guinea. In: Robillard, T., Legendre, F., Villemant, C. & Leponce, M. (Eds.) *Insects of Mount Wilhelm, Papua New Guinea*. *Mémoires du Muséum National d'Histoire Naturelle*, Vol. 209, pp. 129–140.

Colwell, R.K. & Coddington, J.A. (1994) Estimating terrestrial biodiversity through extrapolation. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, 345(1311), 101–118.

Colwell, R.K., Rahbek, C. & Gotelli, N.J. (2004) The mid-domain effect and species richness patterns: what have we learned so far? *The American Naturalist*, 163(3), E1–E23.

Colwell, R.K., Gotelli, N.J., Ashton, L.A., Beck, J., Brehm, G., Fayle, T.M. et al. (2016). Midpoint attractors and species richness: modelling the interaction between environmental drivers and geometric constraints. *Ecology letters*, 19(9), 1009–1022. Available from: https://doi.org/10.1111/ele.12640

Corcos, D., Cerretti, P., Mei, M., Taglianti, A., Paniccia, D., Santoiemma, G. et al. (2018) Predator and parasitoid insects along elevational gradients: role of temperature and habitat diversity. *Oecologia*, 188(1), 193–202. Available from: https://doi.org/10.1007/s00442-018-4169-4

Dahl, C., Richards, S.J., Basien, I., Mungkaje, A.J. & Novotny, V. (2024). Local and regional diversity of frog communities along an extensive rainforest elevation gradient in Papua New Guinea. *Biotropica*, 56(1), 90–97. Available from: https://doi.org/10.1111/btp.13283

Dole, S.A., Hulcr, J. & Cognato, A.I. (2021) Species-rich bark and ambrosia beetle fauna (Coleoptera, Curculionidae, Scolytinae) of the Ecuadorian Amazonian Forest Canopy. *ZooKeys*, 1044, 797–813.

Dolson, S.J. & Kharouba, H.M. (2024) 30 years of terrestrial insect richness patterns across elevation: what have we learned? A global meta-analysis. *Journal of Animal Ecology*, 93, 1819–1829. Available from: https://doi.org/10.1111/1365-2656.14193

Dong, Y., Marais, C., Wang, B., Lin, W., Chen, Y., Li, Y. et al. (2024) Pre-invasion assessment of potential invasive wood borers on North American tree species in Chinese sentinel gardens. *Entomologia Generalis*, 44(4), 905–913. Available from: https://doi.org/10.1127/entomologia/2024/2489

Dorey, J., Groom, S., Freedman, E., Matthews, C., Davies, O., Deans, E. et al. (2020) Radiation of tropical island bees and the role of phylogenetic niche conservatism as an important driver of biodiversity. *Proceedings of the Royal Society B: Biological Sciences*, 287(1925), 20200045. Available from: https://doi.org/10.1098/rspb.2020.0045

Fleishman, R. (2022) *Papua New Guinea, climate, and security*. The Center for Climate and Security. Briefer.

Garrick, R.C., Arantes, Í.C., Stubbs, M.B. & Havill, N.P. (2021) Weak spatial-genetic structure in a native invasive, the southern pine beetle (*Dendroctonus frontalis*), across the eastern United States. *PeerJ*, 9, e11947. Available from: https://doi.org/10.7717/peerj.11947

Gaston, K.J. (2007) Latitudinal gradient in species richness. *Current Biology*, 17(15), R574.

Gaylord, M.L., Kolb, T.E., Wallin, K.F. & Wagner, M.R. (2006) Seasonality and lure preference of bark beetles (Curculionidae: Scolytinae) and associates in a Northern Arizona ponderosa pine forest. *Environmental Entomology*, 35, 37–47.

Ge, X., Jiang, C., Chen, L., Qiu, S., Zhao, Y., Wang, T. et al. (2018) Predicting the potential distribution in China of *Euwallacea fornicatus* (Eichhoff) under current and future climate conditions (vol 7, 2017). *Scientific Reports*, 8, 5772.

Grégoire, J.C., Jactel, H., Hulcr, J., Battisti, A., Inward, D., Petter, F. et al. (2023) Cosmopolitan Scolytinae: strong common drivers, but too many singularities for accurate prediction. *NeoBiota*, 84, 81–105.

Griffiths, A., Silman, M., Farfan-Rios, W., Feeley, K., Cabrera, K., Meir, P. et al. (2021) Evolutionary diversity peaks at mid-elevations along an Amazon-to-Andes elevation gradient. *Frontiers in Ecology and Evolution*, 9, 680041. Available from: https://doi.org/10.3389/fevo.2021.680041

Gripenberg, S., Basset, Y., Lewis, O.T., Terry, J.C.D., Wright, S.J., Simón, I. et al. (2019) A highly resolved food web for insect seed predators in a species-rich tropical forest. *Ecology Letters*, 22, 1638–1649. Available from: https://doi.org/10.1111/ele.13359

Gusmão, R.S., Filho, O.P., Dorval, A., de Souza, M.D. & do Nascimento, D.A. (2020) Use of etanol in the collector recipiente of ethanolic traps as attractive bait for Scolytinae (Coleoptera: Curculionidae) in eucalyptus stands in region of Cerrado. *IDESIA (Chile)*, 38(1), 99–104.

Harrington, R.A., Poff, N.L. & Kondratieff, B.C. (2016) Aquatic insect β-diversity is not dependent on elevation in Southern Rocky Mountain streams. *Freshwater Biology*, 61(2), 195–205. Available from: https://doi.org/10.1111/fwb.12693

Hill, G.M., Kawahara, A.Y., Daniels, J.C., Bateman, C.C. & Scheffers, B.R. (2021) Climate change effects on animal ecology: butterflies and moths as a case study. *Biological Reviews*, 96(5), 2113–2126.

Hnatiuk, R.J., McVean, D.M. & Smith, J.M.B. (1976). *Mt Wilhelm studies II. The climate. Dept. Biogeography and Geomorphology*, *Publ. BG/4*, Australian National University, Canberra.

Hodkinson, I. (2005) Terrestrial insects along elevation gradients: species and community responses to altitude. *Biological Reviews*, 80(3), 489–513. Available from: https://doi.org/10.1017/S1464793105006767

Hulcr, J., Beaver, R.A., Puranasakul, W., Dole, S.A. & Sonthichai, S. (2008) A comparison of bark and ambrosia beetle communities in two forest types in northern Thailand (Coleoptera: Curculionidae: Scolytinae and Platypodinae). *Environmental Entomology*, 37(6), 1461–1470.

Hulcr, J. & Cognato, A.I. (2013) *Xyleborini of New Guinea, a taxonomic monograph (Coleoptera: Curculionidae: Scolytinae)*, Vol. 33. Annapolis, MD: Entomological Society of America.

Hulcr, J., Mogia, M., Isua, B. & Novotny, V. (2007) Host specificity of ambrosia and bark beetles (Col., Curculionidae: Scolytinae and Platypodinae) in a New Guinea rainforest. *Ecological Entomology*, 32(6), 762–772. Available from: https://doi.org/10.1111/j.1365-2311.2007.00939.x

Hulcr, J., Novotny, V., Maurer, B. & Cognato, A. (2008) Low beta diversity of ambrosia beetles (Coleoptera: Curculionidae: Scolytinae and Platypodinae) in lowland rainforests of Papua New Guinea. *Oikos*, 117(2), 214–222. Available from: https://doi.org/10.1111/j.2007.0030-1299.16343.x

Hulcr, J., Black, A., Prior, K., Chen, C.Y., & Li, H.F. (2017). Studies of ambrosia beetles (Coleoptera: Curculionidae) in their native ranges help predict invasion impact. *Florida Entomologist*, 100(2), 257–261.

Hulcr, J. & Skelton, J. (2023) Ambrosia beetles. In: Allison D., Paine J., Slippers T.D., & Wingfield, M.J. (Eds.). *Forest entomology and pathology: volume 1: entomology*. Cham: Springer International Publishing, pp. 339–360.

Johns, R.J. (1982) Plant zonation. In: Gressitt, J.L. (Ed.) *Biogeography and ecology of New Guinea*. *Monographiae Biologicae*, Vol. 42. Dordrecht: Springer. Available from: https://doi.org/10.1007/978-94-009-8632-9_13

Johnson, A.J., Hulcr, J., Knížek, M., Atkinson, T.H., Mandelshtam, M.Y., Smith, S.M. et al. (2020) Revision of the bark beetle genera within the former Cryphalini (Curculionidae: Scolytinae). *Insect Systematics and Diversity*, 4(3), 1. Available from: https://doi.org/10.1093/isd/ixaa002

Johnson, A.J., Kendra, P.E., Skelton, J. & Hulcr, J. (2016) Species diversity, phenology, and temporal flight patterns of *Hypothenemus* pygmy borers (Coleoptera: Curculionidae: Scolytinae) in South Florida. *Environmental Entomology*, 45(3), 627–632.

Johnson, A.J., McKenna, D.D., Jordal, B.H., Cognato, A.I., Smith, S.M., Lemmon, A.R. et al. (2018) Phylogenomics clarifies repeated evolutionary origins of inbreeding and fungus farming in bark beetles (Curculionidae, Scolytinae). *Molecular Phylogenetics and Evolution*, 127, 229–238. Available from: https://doi.org/10.1016/j.ympev.2018.05.028

Jones, K., Shegelski, V., Marculis, N., Wijerathna, A. & Evenden, M. (2019) Factors influencing dispersal by flight in bark beetles (Coleoptera: Curculionidae: Scolytinae): from genes to landscapes. *Canadian Journal of Forest Research*, 49(9), 1024–1041. Available from: https://doi.org/10.1139/cjfr-2018-0304

Jordal, B.H., Normark, B.B., Farrell, B.D. & Kirkendall, L.R. (2002) Extraordinary haplotype diversity in haplodiploid inbreeders: phylogenetics and evolution of the bark beetle genus *Coccotrypes*. *Molecular Phylogenetics and Evolution*, 23(2), 171–188.

Kim, B., Shin, J., Guevarra, R., Lee, J., Kim, D., Seol, K. et al. (2017) Deciphering diversity indices for a better understanding of microbial communities. *Journal of Microbiology and Biotechnology*, 27(12), 2089–2093. Available from: https://doi.org/10.4014/jmb.1709.09027

Kirkendall, L., Biedermann, P. & Jordal, B. (2015) Evolution and diversity of bark and ambrosia beetles. In: Jordal, B. (Ed.) *Bark beetles: biology and ecology of native and invasive species*, Elsevier. pp. 85–165. Available from: https://doi.org/10.1016/B978-0-12-417156-5.00003-4

Knížek, M. & Beaver, R. (2004) Taxonomy and systematics of bark and ambrosia beetles. In: Lieutier, F., Day, K.R., Battisti, A., Grégoire, J.-C. & Evans, H.F. (Eds.) *Bark and wood boring insects in living trees in Europe, a synthesis*. Dordrecht: Springer, pp. 41–54.

Koleff, P., Gaston, K.J. & Lennon, J.J. (2003) Measuring beta diversity for presence–absence data. *Journal of Animal Ecology*, 72(3), 367–382. Available from: https://doi.org/10.1046/j.1365-2656.2003.00710.x

Le Cesne, M., Wilson, S. & Soulier-Perkins, A. (2015) Elevational gradient of Hemiptera (Heteroptera, Auchenorrhyncha) on a tropical mountain in Papua New Guinea. *PeerJ*, 3, e978. Available from: https://doi.org/10.7717/peerj.978

Legendre, P., Borcard, D. & Peres-Neto, P.R. (2005) Analyzing beta diversity: partitioning the spatial variation of community composition data. *Ecological Monographs*, 75(4), 435–450. Available from: https://doi.org/10.1890/05-0549

LeMay, G.A., Johnson, A.J. & Hulcr, J. (2024) Integrative taxonomy sheds light on species boundaries and relationships in the inbred haplodiploid ambrosia beetle genus *Xyleborus*. *Insect Systematics & Evolution*, 56(1), 47–63.

Leponce, M., Novotny, V., Pascal, O., Robillard, T., Legendre, F., Villemant, C. et al. (2016) Land module of our planet reviewed – Papua New Guinea: aims, methods and first taxonomical results. In: Robillard, T., Legendre, F., Villemant, C. & Leponce, M. (Eds.) *Insects of Mount Wilhelm, Papua New Guinea*. Mémoires du Muséum national d'Histoire naturelle, pp. 13–48.

Leponce, M., Pascal, O., Basset, Y. & Novotny, V. (2020) Organizing large-scale inventories of biodiversity in the tropics: the genesis and lessons of the project our planet reviewed Papua New Guinea – land component. In: Robillard, T., Legendre, F., Villemant, C. & Leponce, M. (Eds.) *Insects of Mount Wilhelm, Papua New Guinea*, Vol. 2. Paris: Muséum national d'Histoire naturelle, pp. 11–40.

Lira-Noriega, A., Soberon, J. & Equihua, J. (2018) Potential invasion of exotic ambrosia beetles *Xyleborus glabratus* and *Euwallacea* sp. in Mexico: a major threat for native and cultivated forest ecosystems. *Scientific Reports*, 8, 10179. Available from: https://doi.org/10.1038/s41598-018-28517-4

Logan, J., Macfarlane, W. & Willcox, L. (2010) White bark pine vulnerability to climate-driven mountain pine beetle disturbance in the Greater Yellowstone Ecosystem. *Ecological Applications*, 20(4), 895–902. Available from: https://doi.org/10.1890/09-0655.1

Lomolino, M.V. (2001) Elevation gradients of species-density: historical and prospective views. *Global Ecology and Biogeography*, 10(1), 3–13.

Luo, F., Meng, L., Wang, J. & Liu, Y. (2022) The patterns of co-occurrence variation are explained by the low dependence of bark beetles (Coleoptera: Scolytinae and Platypodinae) on hosts along altitude gradients. *Frontiers in Zoology*, 19(1), 10. Available from: https://doi.org/10.1186/s12983-022-00455-y

Maeto, K. & Fukuyama, K. (2003) Vertical stratification of ambrosia beetle assemblages in a lowland forest at Pasoh, peninsular Malaysia. In: Okuda, T., Manokaran, N., Matsumoto, Y., Niiyama, K., Thomas, S.C. & Ashton, P.S. (Eds.) *Pasoh: ecology of a lowland rain forest in Southeast Asia*. Tokyo: Springer, pp. 325–336.

Marathe, A., Shanker, K., Krishnaswamy, J. & Priyadarsanan, D.R. (2021) Species and functional group composition of ant communities across an elevational gradient in the Eastern Himalaya. *Journal of Asia-Pacific Entomology*, 24(4), 1244–1250. Available from: https://doi.org/10.1016/j.aspen.2021.08.009

Mayor, J., Sanders, N., Classen, A., Bardgett, R., Clement, J., Fajardo, A. et al. (2017) Elevation alters ecosystem properties across temperate treelines globally. *Nature*, 542(7639), 91–95. Available from: https://doi.org/10.1038/nature21027

McCain, C. (2007) Could temperature and water availability drive elevational species richness patterns? A global case study for bats. *Global Ecology and Biogeography*, 16(1), 1–13. Available from: https://doi.org/10.1111/j.1466-8238.2006.00263.x

McCain, C. & Grytnes, J. (2010) *Elevational gradients in species richness*. Chichester: John Wiley & Sons, Ltd.

Mech, A.M., Thomas, K.A., Marsico, T.D., Herms, D.A., Allen, C.R., Ayres, M.P. et al. (2019) Evolutionary history predicts high-impact invasions by herbivorous insects. *Ecology and Evolution*, 9(21), 12216–12230. Available from: https://doi.org/10.1002/ece3.5709

Meng, L., Wang, J. & Liu, Y. (2022) Impact of vegetation and climate types on vertical stratification of wood-boring longhorn and bark beetles (Coleoptera: Cerambycidae and Scolytinae) along altitude gradients in Yunnan, Southwest China. *Agricultural and Forest Entomology*, 24(3), 320–331. Available from: https://doi.org/10.1111/afe.12496

Miller, J., Jolley-Rogers, G., Mishler, B. & Thornhill, A. (2018) Phylogenetic diversity is a better measure of biodiversity than taxon counting. *Journal of Systematics and Evolution*, 56(6), 663–667. Available from: https://doi.org/10.1111/jse.12436

Morris, E., Caruso, T., Buscot, F., Fischer, M., Hancock, C., Maier, T. et al. (2014) Choosing and using diversity indices: insights for ecological applications from the German Biodiversity Exploratories. *Ecology and Evolution*, 4(18), 3514–3524. Available from: https://doi.org/10.1002/ece3.1155

Neves, D., Dexter, K., Baker, T., de Souza, F., Oliveira-Filho, A., Queiroz, L. et al. (2020) Evolutionary diversity in tropical tree communities peaks at intermediate precipitation. *Scientific Reports*, 10(1), 1188. Available from: https://doi.org/10.1038/s41598-019-55621-w

Novotny, V. & Basset, Y. (2005) Host specificity of insect herbivores in tropical forests. *Proceedings of the Royal Society B: Biological Sciences*, 272(1568), 1083–1090. Available from: https://doi.org/10.1098/rspb.2004.3023

Novotny, V., Miller, S.E., Baje, L., Balagawi, S., Basset, Y., Cizek, L. et al. (2010) Guild-specific patterns of species richness and host specialization in plant-herbivore food webs from a tropical forest. *Journal of Animal Ecology*, 79(6), 193–203. Available from: https://doi.org/10.1111/j.1365-2656.2010.01728.x

Novotny, V., Miller, S.E., Hulcr, J., Drew, R.A.I., Basset, Y., Janda, M. et al. (2007) Low beta diversity of herbivorous insects in tropical forests. *Nature*, 448, 692–695.

Peltonen, M., Heliövaara, K., Väisänen, R. & Keronen, J. (1998) Bark beetle diversity at different spatial scales. *Ecography*, 21(5), 510–517. Available from: https://doi.org/10.1111/j.1600-0587.1998.tb00442.x

R Core Team. (2013) *R: a language and environment for statistical computing*. Vienna: Foundation for Statistical Computing.

Rahbek, C. (2005) The role of spatial scale and the perception of large-scale species-richness patterns. *Ecology Letters*, 8(2), 224–239. Available from: https://doi.org/10.1111/j.1461-0248.2004.00701.x

Ranger, C. (2016) Bark beetles: biology and ecology of native and invasive species. *American Entomologist*, 62(3), 196–198.

Roepke, W. (1919) *Thamnurgides myristicae*, eine neue javanische Ipide (Col.: Scolytoidea) aus Muskat Nüssen. *Treubia*, 1, 23–29.

Rubin-Aguirre, A., Saenz-Romero, C., Lindig-Cisneros, R., del-Rio-Mora, A.A., Tena-Morelos, C.A., Campos-Bolaños, R. et al. (2015) Bark beetle pests in an altitudinal gradient of a Mexican managed forest. *Forest Ecology and Management*, 343, 73–79.

Sam, K. & Koane, B. (2014) New avian records along the elevational gradient of Mt. Wilhelm, Papua New Guinea. *Bulletin of the British Ornithologists Club*, 134(2), 116–133.

Sam, K., Koane, B., Bardos, D.C., Jeppy, S. & Novotny, V. (2019). Species richness of birds along a complete rain forest elevational gradient in the tropics: Habitat complexity and food resources matter. *Journal of Biogeography*, 46(2), 279–290.

Sivault, E., Amick, P., Armstrong, K., Novotny, V. & Sam, K. (2023) Species richness and assemblages of bats along a forest elevational transect in Papua New Guinea. *Biotropica*, 55(1), 81–94. Available from: https://doi.org/10.1111/btp.13161

Smith, S.M., Beaver, R.A. & Cognato, A.I. (2020) A monograph of the Xyleborini (Coleoptera, Curculionidae, Scolytinae) of the Indochinese peninsula (except Malaysia) and China. *ZooKeys*, 983, 1–442. Available from: https://doi.org/10.3897/zookeys.983.52630

Smith, S.M., Gomez, D.F., Beaver, R.A., Hulcr, J. & Cognato, A.I. (2019) Reassessment of the species in the *Euwallacea fornicatus* (Coleoptera: Curculionidae: Scolytinae) complex after the rediscovery of the "lost" type specimen. *Insects*, 10(9), 261. Available from: https://doi.org/10.3390/insects10090261

Stork, N.E. & Grimbacher, P.S. (2006) Beetle assemblages from an Australian tropical rainforest show that the canopy and the ground strata contribute equally to biodiversity. *Proceedings of the Royal Society B: Biological Sciences*, 273(1596), 1969–1975. Available from: https://doi.org/10.1098/rspb.2006.3521

Stouthamer, R., Rugman-Jones, P., Thu, P., Eskalen, A., Thibault, T., Hulcr, J. et al. (2017) Tracing the origin of a cryptic invader: phylogeography of the *Euwallacea fornicatus* (Coleoptera: Curculionidae: Scolytinae) species complex. *Agricultural and Forest Entomology*, 19(4), 366–375. Available from: https://doi.org/10.1111/afe.12215

Tavakilian, G., Berkov, A., Meurer-Grimes, B. & Mori, S. (1997) Neotropical tree species and their faunas of xylophagous longicorns (Coleoptera: Cerambycidae) in French Guiana. *The Botanical Review*, 63(4), 303–355. Available from: https://doi.org/10.1007/bf02856596

Ugland, K., Gray, J. & Ellingsen, K. (2003) The species-accumulation curve and estimation of species richness. *Journal of Animal Ecology*, 72(5), 888–897. Available from: https://doi.org/10.1046/j.1365-2656.2003.00748.x

Wang, Z., Li, Y., Ernstsons, A.S., Sun, R., Hulcr, J. & Gao, L. (2021) The infestation and habitat of the ambrosia beetle *Euwallacea interjectus* (Coleoptera: Curculionidae: Scolytinae) in the riparian zone of Shanghai, China. *Agricultural and Forest Entomology*, 23(1), 104–109. Available from: https://doi.org/10.1111/afe.12405

White, T., Bickley, P., Brown, C., Busch, D., Dutson, G., Freifeld, H. et al. (2021) Quantifying threats to biodiversity and prioritizing responses: an example from Papua New Guinea. *Diversity*, 13(6), 248. Available from: https://doi.org/10.3390/d13060248

Williams, K.K., McMillin, J.D., DeGomez, T.E., Clancy, K.M. & Miller, A. (2008) Influence of elevation on bark beetle (Coleoptera: Curculionidae, Scolytinae) community structure and flight periodicity in ponderosa pine forests of Arizona. *Environmental Entomology*, 37(1), 94–109. Available from: https://doi.org/10.1603/0046-225X(2008)37[94:IOEOBB]2.0.CO;2

Yombai, J., Klimes, P., Dargusch, P., Posman, A., Mottl, O., Mani, A. et al. (2021) Ant species diversity, distribution, and community composition in different forest types in Papua New Guinea. *Case Studies in the Environment*, 5(1), 1342727. Available from: https://doi.org/10.1525/cse.2021.1342727

Zhang, W., Huang, D., Wang, R., Liu, J. & Du, N. (2016) Altitudinal patterns of species diversity and phylogenetic diversity across temperate mountain forests of northern China. *PLoS One*, 11(7), e0159995. Available from: https://doi.org/10.1371/journal.pone.0159995

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1. Abundance of bark beetles across elevations. The number of individuals per trap was calculated for each elevation. Statistical significance levels were determined using the Kruskal–Wallis test. * represents p value <0.05; ** represents 0.01 < p value ≤ 0.05; *** represents 0.001 < p value ≤0.01; **** represents p value <0.001; ns represents no significant.

Figure S2. Predicted proportion of undescribed species along the elevation gradient. The grey dots represent the observed proportion of undescribed species at each elevation. The solid line represents the fitted regression curve based on the predictions from the binomial logistic regression model.

Table S1. Comprehensive list of species collected in this study. Link to Dataset: https://doi.org/10.6084/m9.figshare.26502538.

How to cite this article: Dong, Y., Shepherd, S., Stork, N.E., Johnson, A.J., Smith, S.M., Wardhaugh, C. et al. (2025) Scolytine beetle diversity along an altitudinal gradient in Papua New Guinea. *Insect Conservation and Diversity*, 18(4), 552–566. Available from: https://doi.org/10.1111/icad.12824