

How does a plant species swarm maintain coexistence on an isolated mountain in northern Madagascar?

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Abstract

Background and aims – Madagascar's rich flora originated mostly from in situ diversification, and the large-scale plant species richness pattern is mainly explained by spatial heterogeneity. However, mechanisms underlying plant community assembly remain largely unexplored. We aimed to understand the coexistence of a species swarm in the Malagasy olive (*Noronhia*, Oleaceae) on the northern massif of Montagne d'Ambre and to gain insights into the factors influencing community assembly.

Material and methods – We used 13 environmental and 17 trait variables sampled across 24 plots and 13 species on the mountain, respectively. We determined likely trait-environment relationships across space using the multivariate RLQ analysis, the bivariate fourth-corner method, and their combination. We also checked for phylogenetic signal (Blomberg's *K* and Moran's *I*) among traits and assessed the phylogenetic community structure (SES.MPD and SES.MNTD) using nested spatial and phylogenetic scales.

Key results – Significant trait-environment relationships were recovered with the multivariate and the combined multi-bivariate analyses at a large spatial scale, whereas patterns at small spatial scales were unclear. Distinct assemblages at lower and higher elevations were identified and appeared to be influenced by bioclimate and soil gradients. Strong phylogenetic signals were detected in seven traits across spatial scales, regardless of phylogenetic scales. The communities exhibited an overall pattern of phylogenetic clustering with a large phylogenetic scale, while a hint of overdispersion emerged in the low-elevation assemblage with a small phylogenetic scale.

Conclusion – Multiple mechanisms may influence the coexistence of the *Noronhia* swarm on Montagne d'Ambre, with environmental filtering and niche partitioning seemingly acting on vegetative and reproductive functions, respectively. More focus on reproductive biology will provide further insights into the assembly of Malagasy plant communities. This study also highlights the conservation values of Montagne d'Ambre as a unique ecosystem supporting the flora, fauna, and human populations of the northernmost region of Madagascar.

Keywords

Montagne d'Ambre, *Noronhia*, Oleaceae, phylogenetic community structure, trait-environment relationships

INTRODUCTION

Madagascar's unique and threatened biota resulted in this island ranking among the world's biodiversity hotspots (Myers et al. 2000). This pivotal assessment was a catalyst for numerous studies and actions that aimed either at understanding the origin and maintenance of the island's

biodiversity (Wilmé et al. 2006; Pearson and Raxworthy 2009; Vences et al. 2009; Antonelli et al. 2022) or at conserving what has remained of it (Norris 2006; Kremen et al. 2008; Ralimanana et al. 2022). However, achieving these goals remains a challenge due to factors involved in ecological processes that underlie the island's biodiversity, which are still poorly documented. The island's flora is

rich of some 14,000 species, 87% of which are endemic (Lowry et al. 2018) and 63% of the endemic trees have been assessed as threatened globally (Beech et al. 2021), with deforestation at an annual rate of 1.4–4.7% (Achard et al. 2002) being one of the major threats to the Malagasy plant species. Knowledge of patterns and processes across spatial and temporal scales is still generally lacking for Malagasy plants (but see Rakotoarinivo et al. 2013; Antonelli et al. 2022; Karimi and Hanes 2024; Liu et al. 2024; Omollo et al. 2024), and more so at the local level where relevant processes affecting species diversity and coexistence can be identified (Huston 1999).

“Species swarms”, or local assemblages composed of multiple congeneric species (Gentry 1982), are commonly observed in Madagascar (Grubb 2003). However, attempts to explain how these Malagasy closely related plant species assemble and locally co-occur are scarce (e.g. Zjhra 2008). Spatial heterogeneity is thought to be one of the drivers of plant species diversity and assembly on the island (Hong-Wa et al. unpubl. data, <http://2008.botanyconference.org/engine/search/index.php?func=detail&aid=843> [accessed 01.12.2025]; Karimi and Hanes 2024), which is characterized by an abiotic complexity that results in diverse habitats. While this can be true at a relatively large to medium spatial scale, its role and importance are unclear when the scale is reduced. Indeed, local assemblages may be structured by environmental conditions, evolutionary forces, and biotic interactions (HilleRisLambers et al. 2012). In particular, competition may be particularly strong among congeneric species, which are expected to display greater morphological and ecological overlaps due to a recent shared ancestry (Sfenthourakis et al. 2006), although support for this argument has been rather weak (Gotelli and McCabe 2002; Sfenthourakis et al. 2006). Partitioning of abiotic and biotic resources at a fine spatial scale is another strategy that allows for co-occurrence (Siepielski and McPeck 2010), likely more so for congeneric species. These closely related species ought to be divergent enough to be able to use local resources differently and to assume different ecological roles within their shared ecosystem (Chase and Leibold 2003; Silvertown et al. 2006; Losos 2008). Insights into community assembly in Madagascar usually come from studies of animals, mostly primates, revealing most often the role of competition for resources as a driving factor shaping communities (e.g. Dammhahn and Kappeler 2008; Schäffler et al. 2015; Herrera 2016). Empirical studies are still largely unavailable for Malagasy plants, but they may exhibit patterns similar to those of the animals that spread their pollen and seeds. Besides, climate and soil conditions may also exert different pressures not readily seen in animals.

Studies of tropical plant species swarms show a lack of general trends, with phylogenetic clustering and phylogenetic overdispersion observed in communities of sympatric congeneric species (e.g. *Banksia* L.f., Merwin et al. 2012; *Psychotria* L., Sedio et al. 2012; *Piper* L., Salazar et al. 2016; *Inga* Mill., Dexter et al. 2017; *Cyrtandra* J.R.Forst.

& G.Forst., Johnson 2023). Community assembly can be generally explained by competitive exclusion, wherein species with shared niches cannot coexist or will shift their niches to coexist (niche partitioning). Alternatively, community assembly can be explained by environmental filtering, wherein abiotic and biotic conditions permit only coexistence to those species with similar traits (Webb et al. 2002), although neutral processes can also influence co-occurrence patterns (Hubbell 2001). Studies of community structure interpret the presence of phylogenetic or phenotypic overdispersion as evidence of competitive exclusion, whereas phylogenetic or phenotypic clustering is taken as evidence of environmental filtering. Although congeneric species may represent a special case in that common ancestry is recent, this attribute also offers a unique opportunity to assess the relative roles of alternative processes in structuring local species assemblages.

The detection of a phylogenetic signal within communities can be dependent on both the spatial and the phylogenetic scales of the studies (Webb et al. 2002; Cavender-Bares et al. 2006; Losos 2008). Environmental filtering may be the dominant process shaping communities when the spatial scale is large, as there is more habitat complexity allowing for closely related species to co-occur (phylogenetic clustering). More habitat homogeneity is expected when the spatial scale under consideration is smaller, which results in higher competition and reduced co-occurrence of closely related species (phylogenetic evenness or overdispersion). These hypotheses assume that closely related species are ecologically similar. Likewise, the degree of phylogenetic signal within a community is assumed to increase with the completeness of the phylogeny, although such a correlation requires further assessment (Losos 2008). Therefore, a nested approach that assesses patterns at different spatial and phylogenetic scales helps to capture the signatures of processes operating within communities (Webb et al. 2002; Losos 2008; Merwin et al. 2012; Asefa et al. 2017).

In this study, we focus on understanding plant species swarms in Madagascar, using the genus *Noronhia* Stadtm. ex Thouars (Oleaceae) as a model and exploring coexistence patterns of its sympatric species at various spatial and phylogenetic scales. The genus occurs in Africa and the Malagasy region, i.e. including the Comoro and Mascarene Islands (Hong-Wa and Besnard 2013). It is most diverse in Madagascar, where 83 currently described species, of which 82 are endemic, occur across the entire island under a wide range of environmental conditions (Hong-Wa 2016). Its distribution on the island is marked by a high concentration of species in some areas that are also noticeably topographically complex, in apparently a less random fashion than would be expected. These include, for instance, the grid cells that encompass the massifs of Montagne d’Ambre, Montagne des Français, and Manongarivo in the North, with 21, 19, and 14 species per grid cell of 5,166 km² (82 × 63 km), respectively, and

the Anosy-Vohimena chains in the South, with also 21 species per grid cell of the same size (grid cells 1–4 in Fig. 1A; Hong-Wa 2016). These mountainous areas are generally considered as cradles of species diversity in Madagascar, for both the animal and the plant kingdoms (Brown et al. 2016; Camacho et al. 2021; Antonelli et al. 2022; Omollo et al. 2024). The coincidence of high species richness and topographically complex areas thus supports the view that spatial heterogeneity plays a major role in generating and maintaining species diversity, at least to a certain scale. Interestingly enough, however, centres of endemism in *Noronhia* did not show similar topographic pattern (Hong-Wa 2016).

Because of its discrete boundaries, long isolation, and unique climate regime, the isolated massif of Montagne d’Ambre (MDA) is an ideal setting to examine the influences of ecological and evolutionary processes on the coexistence of sympatric congeneric species. Fifteen species of *Noronhia*, of which two are putatively new, occur on MDA (Hong-Wa and Besnard 2014; Hong-Wa 2016). Diversification of *Noronhia* in Madagascar may have started ca 15–12 Mya (Hong-Wa and Besnard 2013; Olofsson et al. 2019; Dupin et al. 2024) while the massif is estimated to be ca 14 My old (IUCN Conservation Monitoring Centre 1987), suggesting that in situ speciation on MDA may be a possibility given that some of the species are estimated to postdate the mountain formation. Apart from three widespread species (*Noronhia brevītuba* H.Perrier, *N. gracilipes* H.Perrier, and *N. pervilleana* (Knobl.) H.Perrier), the *Noronhia* species

that co-occur on MDA are only known from the northern region of Madagascar (Hong-Wa 2016). Because of its reliance on animals for pollen and seed dispersal, patterns and processes of community assembly within *Noronhia* may be expected to mirror those of its pollinators (mostly bees) and seed dispersers (birds, primates, and possibly rodents). This would promote competition as the driving force behind *Noronhia* species assembly on MDA, where the 15 congeneric species compete for the available biotic resources (e.g. eight species of lemurs for seed dispersal). However, because of plants’ abiotic requirements and the diversity of habitats on MDA, we expect to detect the influence of different processes on the assembly of *Noronhia* species across spatial scales and to capture stronger trait-environment relationships at higher spatial scale as a reflection of more pronounced habitat heterogeneity (Fig. 2). Specifically, to understand coexistence patterns of sympatric *Noronhia* species across spatial scales on MDA, we aim to assess (1) the patterns of species and habitat diversity to characterize the biological and ecological aspects of the study area, (2) the relationships between species traits and environmental variables to detect the factors that organize community, (3) the phylogenetic signal in traits to identify ecological similarity among species and the nature of the traits within a community (conserved or convergent), and (4) the phylogenetic community structure to determine the mechanisms (environmental filtering or niche partitioning) that permit coexistence of this species swarm.

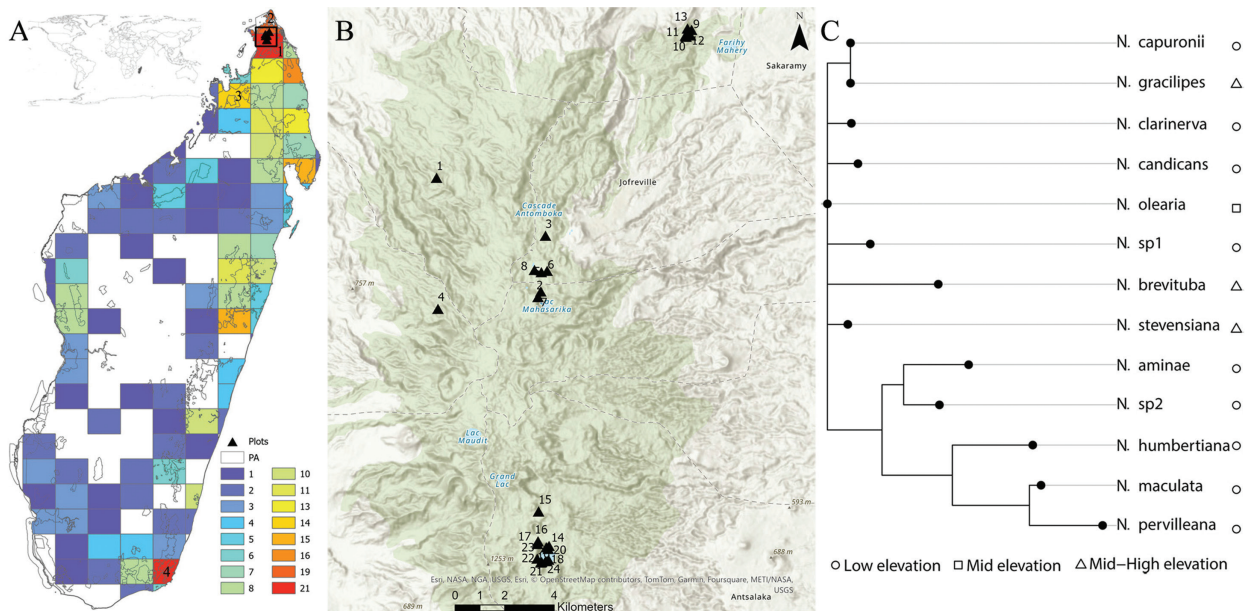


Figure 1. Summary information on the study region and the focal taxon. **A.** Spatial pattern of *Noronhia* species richness (quantified as the number of species present per grid cell) across Madagascar, highlighting species richness on Montagne d’Ambre (MDA) framed in bold black (adapted from Hong-Wa 2016); PA (overlaid areas on map) means protected areas, which include MDA; numbers inside grid cells indicate the cells that contain MDA (1), Montagne des Français (2), Manongarivo (3), and Anosy-Vohimena (4). **B.** Location of the 24 sampling plots (black triangles) on MDA (darker green on the map). **C.** Phylogenetic tree representing the 13 species of *Noronhia* encountered in the MDA plots. All maps were prepared with ESRI’s ArcGis Pro v.2.7.

MATERIAL AND METHODS

Study area and sampling

This study focuses on the massif of Montagne d'Ambre (MDA; 12°32'S, 49°10'E), a mountainous region in northern Madagascar and one of the most plant species-rich areas on the island (Hong-Wa et al. unpubl. data, <http://2008.botanyconference.org/engine/search/index.php?func=detail&aid=843> [accessed 01.12.2025]; Omollo et al. 2024), with reportedly more than 720 plant species occurring in an area of 30,538 ha (FAPBM 2020). Although this entire, isolated community of plants lends itself well to exploring patterns of species coexistence, the objective of this study is particularly on the coexistence and assembly of sympatric congeneric species that form a species swarm. The mountain is approximately 30 × 10 km in size (IUCN Conservation Monitoring Centre 1987). It starts at 200–300 m and peaks at 1,475 m elevation (Nicoll and Langrand 1989), and shows marked altitudinal gradients in rainfall and temperature, with a distinctive humid microclimate at higher elevations. The mean annual temperature and the rainfall on the mountain range from 18 to 26°C and from ca 1,000 to 4,000 mm, respectively (Hong-Wa 2018). It encompasses a humid montane forest above 800 m elevation, surrounded by a belt of lowland transitional rainforest between 300 and 800 m elevation (Raxworthy and Nussbaum 1994), and lies within a matrix of dry forest and savanna (0–300 m elevation). It is now completely isolated from other rainforests in Madagascar (Fig. 1B), and the isolation may date to millions of years given the age of the mountain.

Twenty-four 50 × 20 m study plots were randomly set up on MDA from May to July 2010 (Fig. 1B). This 0.1-ha plot size is standard for studies of tropical trees and was used to account for the diversity of growth forms and sizes of the *Noronhia* species found in the area, which vary from small understory shrubs to large canopy trees (Hong-Wa 2016). These plots were randomly established in three different sites of increasing rainfall and elevation, but within the constraints of terrain roughness and accessibility, from

north to south: five around Lac Mahery near the town of Sakaramy, eight around Station des Roussettes near the town of Joffreville, and 11 around Lac Texier near the town of Antsalaka (Fig. 1B), hereafter referred to only as Mahery, Roussettes, and Texier, respectively. There are gradients of elevation and precipitation along this north–south axis, with Mahery (elevation = 300–500 m, annual rainfall = 1,000–1,500 mm) being the lowest and driest, Roussettes (elevation = 800–1,200 m, annual rainfall ≥ 2,000 mm (≥ 3,000 mm above 1,000 m elevation)) forming a transitional zone, and Texier (elevation = 1,000–1,300 m, annual rainfall ≥ 3,000 mm) being the highest and wettest (Barat 1958; Hong-Wa 2018). These study sites are separated from each other at least by 8 km at straight distance: Mahery–Roussettes = 9.7 km; Roussettes–Texier = 8.6 km; Mahery–Texier = 19.9 km (Fig. 1B). We estimated the species beta diversity (as the sum of its turnover and nestedness components) among the sites and their environmental heterogeneity using the Bray-Curtis index and the Hellinger distance, respectively, with the R packages betapart v.1.6.1 (Baselga and Orme 2012) and vegan v.2.6-4 (Oksanen et al. 2022) in R v.4.3.1 (R Core Team 2023). The Bray-Curtis index varies from 0 to 1, which indicate identical composition and no shared species, respectively. Results can be displayed in a biplot and tested for significance with an analysis of variance (ANOVA). For the Hellinger distance, values also range from 0 to 1, with increasing habitat heterogeneity.

During fieldwork, *Noronhia* individuals with both stem diameter ≥ 1 cm and stem height ≥ 50 cm were counted, sampled for later measurements, and identified to species. These thresholds were set to exclude seedlings and to sample without excessive harm to plant growth. Thirteen species of *Noronhia* (among the 15 present on MDA) were encountered in the study plots (Suppl. material 1, Table S1), all of which had previously been included in morphological and phylogenetic assessments (Hong-Wa and Besnard 2014). Flowers and fruits are unknown for three and two species, respectively, with two (*N. sp1* and *N. sp2*) as yet undescribed. So, to be able to include reproductive features in this study, missing values

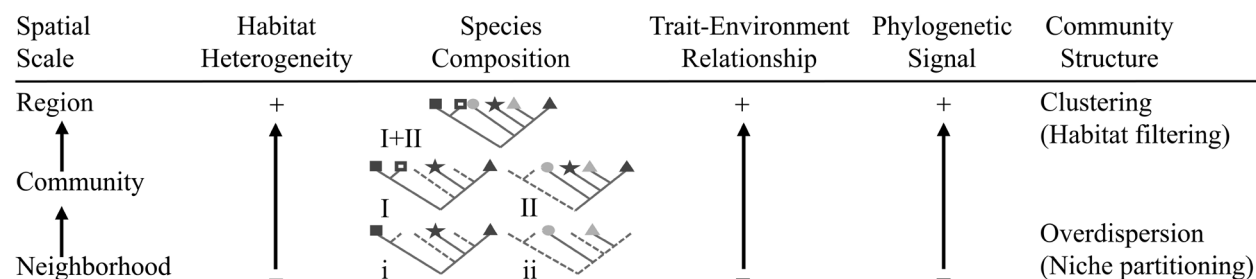


Figure 2. Working hypotheses integrating environment and traits across spatial and phylogenetic scales to understand patterns of species coexistence in *Noronhia* on Montagne d'Ambre (MDA). For species composition, symbol shape and colour represent species and trait, respectively. Numerals indicate different assemblages of species, with increasing richness and relatedness from the scale of neighbourhood (lowercase) to the scales of community (uppercase) and region (sum of all communities). Less habitat heterogeneity at a small spatial scale leads to a coexistence pattern mediated by niche partitioning among species exhibiting traits that improve their survival in the environment. At a large spatial scale, environmental filters organize communities along ecological gradients.

in reproductive traits for the three species were replaced with the respective column average of each reproductive character.

Spatial scales

We used three spatial scales at which to assess patterns of assembly. These are the mountain (i.e. MDA), the site (i.e. Mahery, Roussettes, Texier), and the plot levels, which fit well with the regional (10–1,000 km), community (0.1–10 km), and neighbourhood (< 100 m) scales described in Webb et al. (2002). The mountain, with a size of 30 × 10 km, is well-encompassed within the standard grid cell sizes at which spatial patterns of plant species richness have been studied in Madagascar, which mostly range between 50 × 50 km and 100 × 100 km (Hong-Wa et al. unpubl. data, <http://2008.botanyconference.org/engine/search/index.php?func=detail&aid=843> [accessed 01.12.2025]; Hong-Wa 2016; Karimi and Hanes 2024; Omollo et al. 2024). The sites lay within a radius of 1 km (Mahery and Texier) to 3.5 km (Roussettes). We acknowledge that there could still be some spatial heterogeneity within that extent; however, these sites fall within the same rainfall and temperature regimes and are considered homogeneous in that sense. Lastly, the plots of 50 × 20 m in size permit the identification of the influence of variables other than climate and topography.

Environmental variables

To better understand the roles of ecological factors on the coexistence of sympatric congeneric species, we explored a range of environmental characteristics (Suppl. material 1, Table S2). We used only abiotic variables given the complexity of studying biotic interactions. Biotic agents are largely unknown for *Noronhia* and would require thorough investigations that are beyond the scope of this study. However, some of the functional traits used are suggestive of pollination, seed dispersal, and herbivory syndromes and can serve as proxies for biotic interactions. Within each study plot, variables characterizing the forest structure, soil properties, and topography were recorded. In particular, the forest structure was quantified as: the percentage of canopy cover, the canopy height, tree density (abundance of all trees with a diameter at breast height (DBH) equal to or greater than 10 cm divided by the plot size), and litter depth. Soil properties were represented by: pH, electrical conductivity (EC), nitrogen (N), organic carbon (C), carbon-to-nitrogen ratio (C/N), organic matter (OM), phosphorus (P), calcium (Ca), potassium (K), and magnesium (Mg). Soil samples were taken from each plot and sent for analysis at the Laboratoire de Pédologie at the Centre National de la Recherche Appliquée au Développement Rural (Antananarivo, Madagascar), which used the methods of the Ministère de la Coopération et du Développement (1991). Elevation recorded within each plot represented topography. Moreover, the microclimate was represented by 19 bioclimatic variables at a resolution of 30 s (ca 1

km) obtained from the WorldClim database (<https://www.worldclim.org>). Correlated variables (Pearson's $R \geq 0.7$) were dropped, and spatial autocorrelation (Suppl. material 1, Table S3) among the remaining variables was checked using the Geary-Moran test through the R packages *ade4* v.1.7-22 (Dray and Dufour 2007) and *spdep* v.1.2-8 (Bivand et al. 2022). The final dataset included 13 environmental variables, of which three forest variables (canopy cover (Cover), tree density (TreeDs), litter depth (LitDp)), seven soil variables (EC, C/N, OM, P, Ca, K, Mg), and three bioclimatic variables (mean diurnal range (BIO2), isothermality (BIO3), precipitation of coldest quarter (BIO19)). Bioclimatic variables obtained at a resolution of ca 1 km² could not be used in some site- and plot-level analyses as they were uniform at that scale.

Functional traits

We included a variety of traits that represent six categories of functions (e.g. biomechanics, hydraulics, photosynthesis, productivity, regeneration, and survival; Table 1), although they focused only on above-ground characteristics. The traits used (Table 1), gathered from field observations and from literature (Hong-Wa 2016), are expected to reflect the strategies for acquiring above-ground (light, pollen and seed dispersers) and below-ground (water and nutrient) resources among these sympatric congeners, which range from understory shrubs to canopy trees, vary greatly in vegetative and reproductive features, and grow along a marked environmental gradient (e.g. bioclimate, elevation, soil); all of which may facilitate their swarming on MDA. The species maximum height (Hmax), along with two stem attributes (twig diameter (TwigD) and bark thickness (BarkT)), seven leaf features (petiole length (PetioL); leaf thickness (LeafT); leaf size (LeafS) as the product of the lamina length and width with a shape correction factor of 0.7; acumen length (AcumL); number of major veins (Vein); number of domatia per five successive veins (Domat); leaf toughness (Tough)), and five reproductive characteristics (corolla length (CoroL); fruit length (FruitL); pericarp thickness (PeriT); seed length (SeedL) and diameter (SeedD)) were included as continuous variables. Although leaf thickness was measured only on dry materials, studies have shown a strong correlation between the thickness of dry and fresh leaf tissues (Perez et al. 2020). Additionally, two other vegetative traits were noted as categorical variables. These were leaf pubescence (Pubes: absent = 0, present = 1) and petiole woodiness (PetioWd: not woody = 0, not-to-partially = 1, partially = 2, partially-to-entirely = 3, entirely = 4).

In many cases, the functions of these traits are straightforward, but the traits may also hold other significance (Table 1). For instance, plant height and leaf size are measures of competitive ability for sunlight acquisition and are thus directly involved in photosynthetic efficiency, which may particularly be important for these *Noronhia* species that occupy different layers of the forest

Table 1. Plant traits and functional significance grouped into six major categories: biomechanics (B, e.g. protection, rigidity/flexibility, support); hydraulics (H, e.g. transport); photosynthetic efficiency (PE, e.g. light capture, thermoregulation); productivity (P, e.g. growth, biomass, storage); regeneration (R, e.g. lifetime reproductive output, pollination, seed dispersal); and survival (S, e.g. metabolism, resistance, tolerance, defence).

Trait	Significance	References
Maximum height (Hmax – m)	PE; R	Cornelissen et al. (2003); Falster and Westoby (2003); Moles et al. (2004)
Twig diameter (TwigD – mm)	B; P; S	Sun et al. (2019); Westoby and Wright (2003)
Twig Bark thickness (BarkT – mm)	B; H; P; S	Baraloto et al. (2010); Paine et al. (2010); Rosell et al. (2014); Rosell (2016)
Petiole length (PetiL – mm)	PE	Takenaka (1994); Chenu et al. (2005)
Leaf size (LeafS – cm ²)	PE; S	Wright et al. (2017); Kozlov et al. (2022); Wang et al. (2022)
Leaf thickness (LeafT – mm)	P; PE	Niinemets (2001); Vile et al. (2005)
Major Veins number (Vein – #)	B; H; P; PE	Sack et al. (2013); Peng et al. (2022)
Acumen length (AcumL – mm)	S	Ivey and DeSilva (2001); Malhado et al. (2012); Wang et al. (2020)
Corolla length (CoroL – mm)	R	Pauw (2013); McCarren et al. (2023)
Fruit length (FruitL – mm)	R	Bollen et al. (2005); Yu et al. (2024)
Pericarp thickness (PeriT – mm)	R	Gautier-Hion et al. (1985); Lei et al. (2012)
Seed length (SeedL – mm)	R	Saatkamp et al. (2019); Valenta and Nevo (2020)
Seed diameter (SeedD – mm)	R	Saatkamp et al. (2019); Valenta and Nevo (2020)
Domatia (Domat – #)	P; S	Agrawal et al. (2000); Oren et al. (2001); Romero and Benson (2005); Ma et al. (2007); O’Connell et al. (2010)
Leaf toughness (Tough – N)	P; PE; S	Kitajima and Poorter (2010); Liu et al. (2010); Nardini (2022)
Leaf pubescence (Pubes)	PE; S	Johnson (1975); Press (1999)
Petiole woodiness (PetiWd)	B; S	Inferred in this study; Yamada et al. (1999; petiole thickness rather than woodiness)

(Razanajatovo 2009; Hong-Wa 2016). Additionally, plant height informs about lifetime reproductive output (i.e. regeneration), while leaf size relates to stress tolerance and adaptation to moisture and temperature gradients (i.e. survival) (Cornelissen et al. 2003; Falster and Westoby 2003; Moles et al. 2004; Wright et al. 2017; Kozlov et al. 2022; Wang et al. 2022). Similarly, leaf toughness has a defensive role against drought and herbivory, is involved in photosynthetic efficiency through thermoregulation, and is a good predictor of leaf lifespan, sapling survival, and plant growth rate (Kitajima and Poorter 2010; Liu et al. 2010; Onoda et al. 2011; Nardini 2022). The presence of domatia correlates positively with foliar carbon concentration (O’Connell et al. 2010), which facilitates plant growth despite soil nutrient stress (Oren et al. 2001; Ma et al. 2007). Domatia are also involved in defence mechanisms against herbivores and pathogens through mutualistic associations with mites (Agrawal et al. 2000; Romero and Benson 2005). Leaf acumen length is an adaptation to extreme humidity and rainfall to increase water shedding and reduce fungal growth (Ivey and DeSilva 2001; Malhado et al. 2012). Petiole length optimizes light capture by preventing mutual shading (Takenaka 1994; Chenu et al. 2005). Petiole woodiness is a particular attribute of *Noronhia* within the Oleaceae family – the petiole can develop secondary tissues along part or all of its length and becomes stem-like or it can be “naked”, making this woodiness a good diagnostic feature.

While the particular function of this woodiness is unclear, we can assume a role in protecting the petiolar vascular system and in providing stronger support to the leaves. With these different functional traits, our expectation is to capture as much of the trait-environment relationships that underlie the coexistence of this *Noronhia* swarm on MDA.

Associations between traits and environment

We used the RLQ framework to assess trait and community responses to environmental gradients across spatial scales, i.e. the regional/mountain (MDA) and community/site (Mahery, Roussettes, Texier) scales. The RLQ ordination is a multivariate analysis in which the matrix R (environment data) is linked with the matrix Q (trait data) through the matrix L (species composition data). This approach identifies environmental factors underlying community organization by assessing the combinations of traits and environmental characteristics that covary the most (Dolédec et al. 1996; Dray et al. 2014). The three matrices were first analysed separately through different ordination techniques. The matrix R (24 plots × 13 environmental variables), the matrix L (13 species abundances × 24 plots), and the matrix Q (13 species × 17 traits) were respectively analysed with a principal component analysis (PCA), a correspondence analysis (CA), and a Hill-Smith analysis that accounts for mixed type variables. Then, the three ordinations were

linked through the RLQ analysis to identify environment-trait relationships mediated by species abundances (Dray et al. 2014). Quantitative variables were log-transformed to achieve normality of the data, and environmental variables were also standardized by the range. Results of the RLQ analysis can be visualized in an ordination plot whose axes show the trait-environment covariance. The significance of the RLQ ($p \leq 0.05$) against null hypotheses (H_0) was assessed with a global permutation test that uses two independent models (Model 2 and Model 4). For Model 2, H_0 posits that the environment has no effect on the spatial distribution of species with fixed traits, whereas H_0 for Model 4 is that traits have no effect on species composition given fixed environmental conditions (ter Braak et al. 2012; Dray et al. 2014).

We additionally evaluated any trait-environment relationships using the fourth-corner method. Unlike the RLQ ordination, the fourth-corner method is a bivariate analysis that tests for association between trait and environmental variables from the three matrices in a pairwise manner (Dray et al. 2014). We first ran the fourth-corner analysis alone, which involves multiple tests given the bivariate nature of the analysis and the number of environmental and trait variables. Therefore, the p values were adjusted to allow for multiple comparisons and avoid Type 1 error (using 9,999 permutations with the false discovery rate (FDR) method). Furthermore, we applied the Moran's Spectral Randomization (MSR) to the fourth-corner analysis to offset the effects of the detected spatial autocorrelation in some environmental variables (Suppl. material 1, Table S3) and any likely phylogenetic autocorrelation, as well as to further reduce Type 1 error (Braga et al. 2018). We subsequently combined the RLQ and fourth-corner analyses to allow for testing the individual associations between the RLQ axes and each of the environmental and trait variables at the significance level of $p \leq 0.05$. The result of this combined analysis can be visualized in a two-dimensional plot that shows significant and non-significant associations of environment and trait variables with the first and second axes of the RLQ. All ordination and fourth-corner analyses were performed using the R packages *ade4* v.1.7-22 (Dray and Dufour 2007) and *adespatial* v.0.3-24 (Dray et al. 2024).

Phylogenetic patterns

The phylogenetic tree of Hong-Wa and Besnard (2014) was used to infer relationships among *Noronhia* species found on MDA. The original phylogeny, reconstructed using a combination of plastid (*trnL-F*, *trnT-L*, *trnS-G*, *trnK-matK*) and nuclear (ITS) markers, included 68 of the 87 *Noronhia* species currently known to occur in the Malagasy Region (i.e. Madagascar, the Comoros, and the Mascarenes), as well as eight *Noronhia* species from Africa and ten species representing six genera of Oleaceae found in Madagascar and elsewhere (see Hong-Wa and Besnard (2014) for additional details). This phylogenetic tree was characterized by large basal polytomies and 16

small clades and subclades with moderate to high support values (Maximum Likelihood bootstrap ≥ 70 and/or Bayesian posterior probabilities ≥ 0.90). The species encountered in this study belong to nine of those small clades and subclades. The large, inclusive phylogenetic tree was then pruned using the R package *ape* v.5.7-1 (Paradis and Schliep 2019) to include only the 13 species found in the study plots (Fig. 1C). Both the large, inclusive phylogeny (*ip*) and the pruned, community phylogeny (*cp*) were used to assess the effects of phylogenetic scale in subsequent analyses of phylogenetic signal and community structure.

Phylogenetic signal

We used the Blomberg's K (Blomberg et al. 2003) to assess phylogenetic signal in trait data across spatial scales (i.e. large scale (MDA level) and small scale (site level; Mahery, Roussettes, Texier)) and phylogenetic scales (i.e. large, inclusive phylogeny and small, community phylogeny). This index assumes a Brownian motion model of trait evolution and is demonstrably robust to changes in evolutionary rates, polytomies, and missing branch length information (Münkemüller et al. 2012). A value of $K = 1$ indicates a random walk, consistent with a Brownian motion, whereas values of $K > 1$ and $K < 1$ suggest that close relatives are more or less similar than expected, respectively (Blomberg et al. 2003). We complemented this model-based metric with one that is grounded in statistical approaches, which are useful when phylogenies are incomplete or when trait variation does not fit standard evolutionary models such as the Brownian motion (Diniz-Filho et al. 2012). For that, we used the Moran's I , a statistical method that measures autocorrelation (Moran 1950; Gittleman and Kot 1990), and whose coefficients are less sensitive to errors in the phylogeny (Diniz-Filho et al. 2012). Significant departure from zero can indicate stronger association than expected between trait data and the phylogenetic tree (Münkemüller et al. 2012). Values of $I > 0$ and $I < 0$ are indicative of stronger trait similarity and dissimilarity than expected, respectively. The R packages *ade4* v.1.1-13 (Jombart et al. 2010), *phylobase* v.0.8.10 (Bolker et al. 2024), and *phytools* v.1.9-16 (Revell 2012) were used to compute Blomberg's K and Moran's I .

Phylogenetic community structure

We assessed phylogenetic community structure at different spatial scales, given the likely influence of scale on the detection of phylogenetic signal (Losos 2008). We sampled communities at the scale of the mountain (MDA), the sites (Mahery, Roussettes, Texier), and the plots (24 plots), pooling data hierarchically from the small to the large scale, and used the mean pairwise distance (MPD), the mean nearest taxon distance (MNTD), and null models (Webb 2000; Webb et al. 2002). These metrics would generally capture patterns at slightly different levels of the phylogeny, with MPD reflecting a tree-wide phylogenetic clustering or overdispersion, and MNTD

measuring clustering or overdispersion at the branch tips. The standardized effect sizes (SES) of MPD and MNTD were assessed across 1,000 null communities using the R package *picante* v.1.8.2 (Kembel et al. 2010). Negative and positive SES values indicate phylogenetic clustering and overdispersion, respectively, at a statistical significance of $p \leq 0.05$. To be stringent, we consider only a strict zero (SES = 0.000) as random and any deviations from it as clustered (SES ≤ -0.001) or overdispersed (SES ≥ 0.001).

Similarly, we considered two phylogenetic scales with which to assess community structure, given that taxon sampling may interfere with phylogenetic signal (Losos 2008). The first one is the inclusive phylogeny that encompasses a large set of *Noronhia* from the Malagasy region and Africa along with a set of other Oleaceae genera distributed worldwide (see Phylogenetic patterns above). The second one is the pruned phylogeny representing the regional species pool of *Noronhia* only (Fig. 1C). We used the same metrics (SES.MPD and SES.MNTD) across both phylogenetic and spatial scales.

RESULTS

Species and site overview

Noronhia was recorded in lowland transitional rainforest and montane forest along a gradient of elevation that ranged from 300 to 1,375 m on Montagne d'Ambre (MDA). A total of 477 individuals (Suppl. material 1, Table S1), with both stem diameter ≥ 1 cm and stem height ≥ 50 cm, belonging to 13 species were counted across 24 \times 0.1-ha plots in three sites (i.e. Mahery, Roussettes, and Texier). The mean number of individuals of *Noronhia* per plot was 20 (min = 4; max = 63), and the mean number of species per plot was 3 (min = 1; max = 7). No single species was ubiquitous in all plots, and the lowland transitional rainforest was the most species-rich. Across all plots, *N. gracilipes* was the most abundant, with 172 individuals recorded, whereas *N. humbertiana* H.Perrier was the least abundant, with only two individuals observed. Dissimilarity in species composition among sites was picked up by the beta diversity test (Bray-Curtis (BC) index = 0.09–0.65 between Roussettes and Texier plots, and BC = 1 between plots at Mahery and those at Roussettes and Texier). This compositional change was found to be significant (ANOVA, $p = 0.001$; Suppl. material 1, Fig. S1). As for the habitat, Texier appeared to be the least heterogeneous (Hellinger distance (HD) of 0.43) compared to Mahery and Roussettes (HD of 0.70 and 0.86, respectively). Overall, these results indicate a species turnover along the elevational gradient on MDA driven by habitat heterogeneity.

Nature and spatial patterns of trait-environment relationships

At the mountain scale (MDA), the first two axes of the RLQ analysis captured 94.27% of the total inertia in the

three matrices (Fig. 3; Suppl. material 1, Table S4), with the global permutation test finding significant covariances between R (environment) and Q (trait) tables (Model 2, $p = 0.0001$; Model 4, $p = 0.0093$). On one hand, the first axis of the RLQ was largely defined by soil properties and bioclimate (Fig. 3; Suppl. material 1, Fig. S2). Its negative side identified species such as *N. gracilipes* and *N. stevensiana* Hong-Wa (Fig. 3A), with taller size and longer acumen (Fig. 3C), growing in areas (e.g. plots 17 and 18; Fig. 3B) with higher organic matter and rainfall (Fig. 3D). Its positive side highlighted species with tougher and thicker leaves, as illustrated by *N. candicans* H.Perrier and *N. clarinerva* Hong-Wa, occupying areas (e.g. plots 11 and 12) with narrower temperature range and lower availability of soil macronutrients. When the RLQ scores were mapped onto the study area (MDA), a spatial pattern emerged, where negative values on RLQ1 occurred at the higher part of the mountain that receives higher annual rainfall, whereas the positive values were located at lower elevations with less rainfall (Fig. 4A). Values closer to zero on this first axis were found at mid-elevation, although plot 1 was more positive than the others within this altitudinal range. On the other hand, the second axis of the RLQ emphasized character states (e.g. thicker bark) associated with a temperature gradient driven by mean diurnal range (BIO2) and isothermality (BIO3) on its negative side, as well as attributes (e.g. woody petiole) related to the availability of soil nutrients on its positive side. The species and plots identified on each side were, for instance, *N. olearia* Hong-Wa and plot 4 (negative), and *N. gracilipes* and plot 8 (positive) (Fig. 3; Suppl. material 1, Fig. S2). The spatial pattern for RLQ2 showed that positive values and values close to zero spanned the elevation gradient of the mountain, while highly negative values were found at mid-elevation (Fig. 4B), where temperature fluctuations are greater compared to the higher and lower parts of the mountain. Overall, the RLQ analysis recovered gradients of bioclimate and soil organizing species assemblages on MDA. Given the mountainous nature of the study area, elevation may play an important role in structuring the communities of *Noronhia*. However, RLQ results showed that lowland plots shared the same quadrants with upland plots (Fig. 3B). Furthermore, the geographic structure was not straightforward along both RLQ1 and RLQ2, with the midland sharing attributes with both the lowland and upland on RLQ1 and all elevation ranges displaying similar characteristics on RLQ2 (Figs 3B, 4A–B). This implies that the elevation gradient, or at least the elevation gradient alone, did not influence the structure of the RLQ, although elevation may interact with other factors (e.g. bioclimate). Indeed, elevation was highly correlated with bioclimatic variables ($R \geq 0.7$) but not with those retained for analyses.

The fourth-corner analysis at the mountain scale (MDA) initially showed significant relationships between individual environment and trait variables (Fig. 3E), corroborating the significance captured by the global

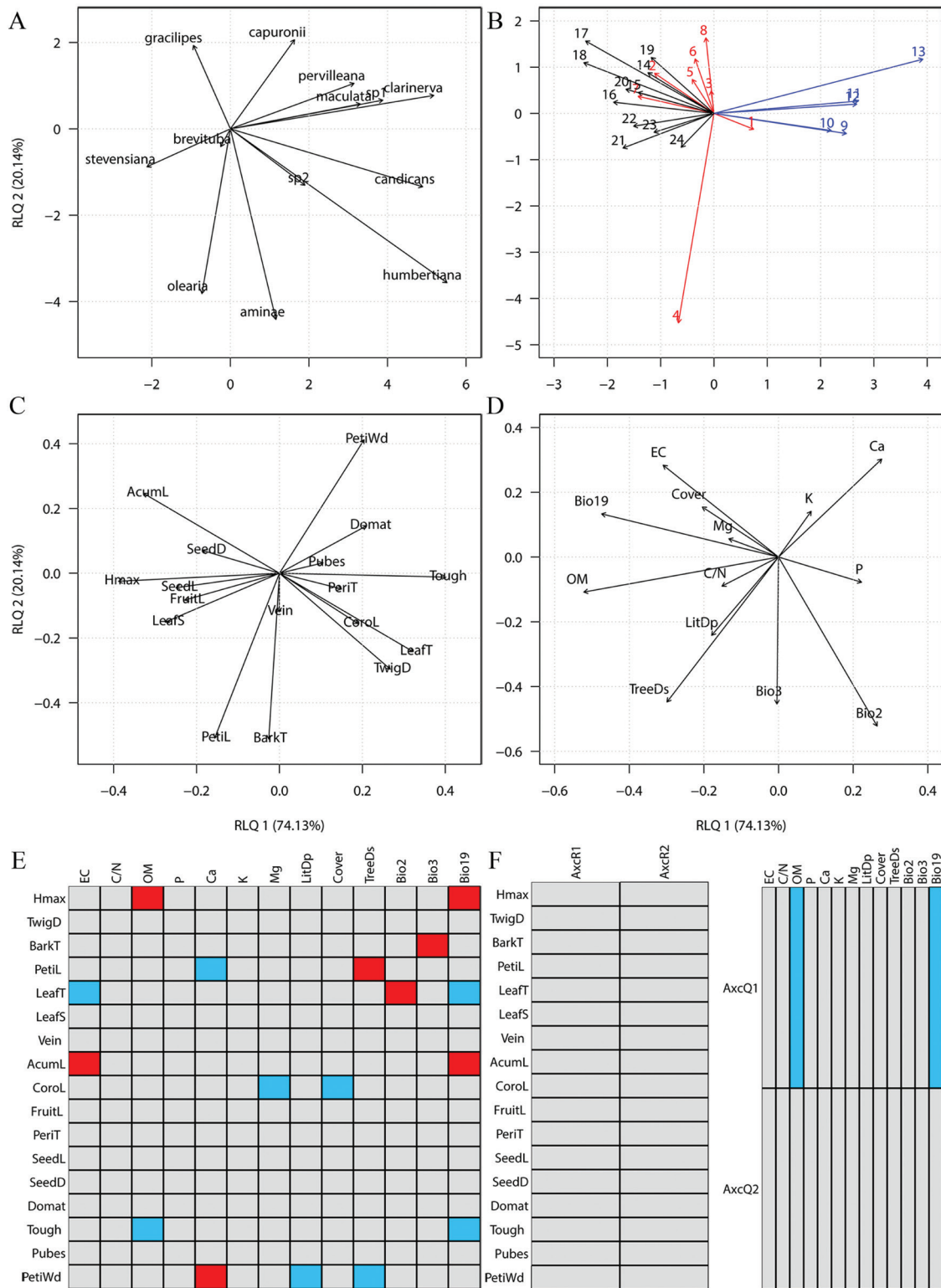


Figure 3. Associations between environmental and trait variables for Montagne d'Ambre (MDA level). **A–D.** Biplots of the RLQ analysis showing the projections of *Noronhia* species (**A**), sampling plots (in blue, Mahery; red, Roussettes; and black, Texier) (**B**), trait variables (**C**), and environmental variables (**D**) on the first two axes. **E.** Initial results of the fourth-corner analysis – Results with p values adjusted for multiple comparisons and for spatial autocorrelation using the false discovery rate (FDR) and Moran's Spectral Randomization (MSR) procedures, respectively, show no significant relationships (Suppl. material 1, Fig. S3). **F.** Results of the combined RLQ+fourth-corner analysis illustrating associations between the first two RLQ axes for traits (AxcQ1/AxcQ2) and environmental variables (right), and between the first two RLQ axes for environment (AxcR1/AxcR2) and trait variables (left). For **E** and **F**, red cells correspond to significant positive associations ($p \leq 0.05$), blue cells to significant negative associations, and grey to non-significant ones. Abbreviations for environmental and trait variables are described in Methods.

permutation test. However, the significance of these associations weakened when p values were adjusted for multiple comparisons and spatial autocorrelation to avoid Type 1 error (Suppl. material 1, Fig. S3), although spatial autocorrelation did not seem to have a major impact. The overall reduction in significance in any relationships was also observed in the combined RLQ+fourth-corner analysis when testing for individual associations between environment or trait variables and the RLQ axes (Fig. 3F), although maximum height, leaf toughness, OM, and BIO19 showed a marginally or definitely significant linkage with RLQ1 ($r_{\text{Hmax}} = -0.755$, $p_{\text{adj}} = 0.088$; $r_{\text{Tough}} = 0.781$, $p_{\text{adj}} = 0.057$; $r_{\text{OM}} = -0.748$, $p_{\text{adj}} = 0.020$; $r_{\text{BIO19}} = -0.679$, $p_{\text{adj}} = 0.020$).

Within sites, the RLQ analysis explained 85.38% (Mahery), 96.83% (Roussettes), and 100% (Texier) of the total inertia in the three matrices, but did not recover any significant covariances at all three sites (Suppl. material 1, Table S4, Figs S4–S5, S7–S8, S10–S11). Similarly, the fourth-corner analysis did not detect any individual associations when multiple comparisons and spatial autocorrelation were accounted for (Suppl. material 1, Figs S6, S9, S12). However, the combined RLQ+fourth-corner analysis revealed some linkages between RLQ1 and three traits: acumen length ($r = -0.357$, $p_{\text{adj}} = 0.014$), domatia ($r = -0.347$, $p_{\text{adj}} = 0.004$), and leaf thickness ($r = -0.3475$, $p_{\text{adj}} = 0.004$) at Texier only (Suppl. material 1, Fig. S12); whereas C/N was significantly linked to RLQ2 at Mahery ($r = -0.376$, $p_{\text{adj}} = 0.025$; Suppl. material 1, Fig. S6), and leaf size had marginally significant association with RLQ2 ($r = 0.264$, $p_{\text{adj}} = 0.076$) at Texier.

In sum, the RLQ and the adjusted fourth-corner analyses agree in their findings of non-significant relationships between traits and environment, except at the largest spatial scale, where the RLQ recovers significant associations (Fig. 3; Suppl. material 1, Figs S4–S5, S7–S8, S10–S11). In all likelihood, this discrepancy and the significant relationships recovered in the combined analyses suggest complex and/or non-linear associations. They also point to the limit of the statistical power of the fourth-corner, as it only detects significant relationships after dimensionality reduction in such complex situations (e.g. trait axis 1 negatively associated with bioclimate and soil properties). Nevertheless, these results identify bioclimate and soil as the major environmental gradients that structure the community of *Noronhia* on MDA. They also distinguish the corresponding traits that allow species to occupy these ecological spaces (Fig. 3; Suppl. material 1, Fig. S2). The opposite ends of these bioclimate and soil gradients are occupied by the Mahery and Texier assemblages, whereas the Roussettes group forms an intermediate between them (Figs 3, 4A–B; Suppl. material 1, Fig. S2D).

Functional traits and phylogenetic signal

The two indices of phylogenetic signal used in this study (i.e. Blomberg's K and Moran's I) largely corroborated each other and found significant patterns of trait similarity ($K > 1$ or $I > 0$; Table 2; Suppl. material 1, Table S5). They only disagreed in their level of support for a few traits (e.g. acumen length, bark thickness). When looking at the

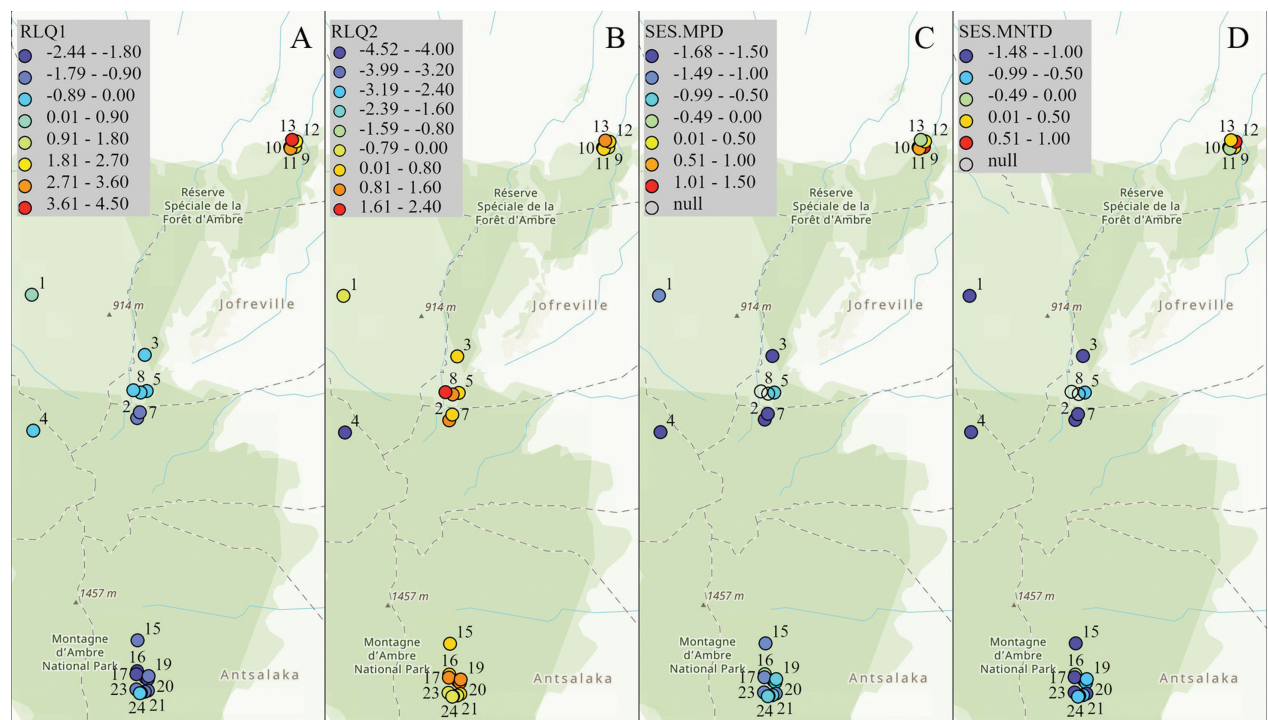


Figure 4. Spatial distribution of the scores of the RLQ axes (A and B) and the SES.MPD and SES.MNTD values of phylogenetic community structure using the small-scale phylogeny (C and D) across the 24 plots on Montagne d'Ambre (MDA). SES < 0 and SES > 0 indicate phylogenetic clustering and overdispersion, respectively.

Table 2. Phylogenetic signal in 17 functional traits at the regional (Montagne d'Ambre (MDA)) and site (Mahery, Roussettes, and Texier) levels using Blomberg's K and Moran's I . $K = 1$ or $I = 0$ indicates random trait evolution consistent with a Brownian motion model, whereas $K > 1$ or $I > 0$ and $K < 1$ or $I < 0$ suggest stronger trait similarity and dissimilarity than expected, respectively, with significance at $p < 0.1$ ('), $p \leq 0.05$ (*), $p \leq 0.01$ (**), and $p \leq 0.001$ (***). Both Blomberg's K and Moran's I were derived with 999 permutations. Subscripts refer to large, inclusive phylogeny (ip) and small, community phylogeny (cp). Moran's I could not be estimated using the inclusive phylogeny given the number of taxa absent from the regional pool. Abbreviations for trait variables are described in Methods. Exact values of K and I are provided in Suppl. material 1, Table S5.

Trait	MDA			Mahery			Roussettes			Texier		
	K_{ip}	K_{cp}	I_{cp}	K_{ip}	K_{cp}	I_{cp}	K_{ip}	K_{cp}	I_{cp}	K_{ip}	K_{cp}	I_{cp}
Hmax	<1	<1	<0	>1*	>1*	>0'	<1	<1	>0'	<1	<1	<0
TwigD	<1	<1	>0	<1	<1	<0	<1	<1	<0	<1	<1	<0
BarkT	<1**	<1**	>0'	<1*	<1*	>0'	<1	<1	<0	<1	<1	<0
PetiL	<1	<1'	>0	>1**	>1*	>0*	<1	<1	<0	<1	<1	<0
LeafT	<1	<1	>0	<1	<1	>0	<1	<1	<0'	<1	<1	<0
LeafS	<1'	<1'	<0	<1	<1	>0	<1	<1	<0	<1	<1	<0
Vein	<1	<1	<0	<1	<1'	<0	<1	<1	<0	<1	<1	<0
AcumL	<1'	<1	>0**	<1	<1	>0'	<1	<1	<0*	<1	<1	<0
CoroL	<1	<1	<0	<1	<1	<0	<1	<1	<0	<1	<1	<0
FruitL	<1	<1	<0	<1	<1	<0	>1	>1.5'	<0	>1	>1	<0
PeriT	<1	<1	>0	<1	<1	<0	<1	>1'	<0	<1	<1	<0
SeedL	<1'	<1	<0	<1	<1	<0	<1	<1	<0	<1	<1	<0
SeedD	<1	<1	>0'	<1	<1	<0	>1	>1.5'	<0	>1	>1	<0
Domat	<1	<1	>0**	>2**	>2**	>0**	<1	<1	<0	<1	<1	<0
Tough	<1	<1	<0	<1	<1	>0	>1.5*	>1.5	<0	>1.5	>1.5	<0
Pubes	<1	<1	<0	<1	<1	<0	na	na	na	na	na	na
PetiWd	<1*	<1	<0	>1.5**	>1.5**	>0*	<1	<1	<0	<1	<1	<0

effects of phylogenetic scales on phylogenetic signal, the only differences in significance recovered by the Blomberg test were at the MDA level, with petiole woodiness ($K_{ip} = 0.7516$, $p = 0.027$ vs $K_{cp} = 0.4420$, $p = 0.154$), and at the site level (Roussettes), with leaf toughness ($K_{ip} = 1.765$, $p = 0.039$ vs $K_{cp} = 1.547$, $p = 0.200$). Moran's I could not be estimated using the inclusive phylogeny given the number of taxa absent from the regional pool. With regards to the effects of spatial scales, at the MDA level, the two tests had some contrasting results. For instance, the Moran's I recovered significant trait similarity while non-significant dissimilarity was detected by the Blomberg's K for the same traits (e.g. acumen length, domatia). The opposite was also found for other traits (e.g. bark thickness). At the site level, five traits (maximum height, bark thickness, petiole length, petiole woodiness, and domatia) showed concordant and strong phylogenetic signal at Mahery (Table 2; Suppl. material 1, Table S5). The only other significance recovered was for acumen length ($I < 0$) and leaf toughness ($K > 1$) at Roussettes. A few other traits were marginally significant at the MDA and the site (Mahery and Roussettes) levels (Table 2; Suppl. material 1, Table S5). Briefly, the presence of phylogenetic signal indicates that some species within MDA in general, and within Mahery in particular, display similar ecological

requirements, and this similarity is drawn from close phylogenetic relatedness (trait conservatism). At the same time, a pattern of convergence also marks these communities.

Phylogenetic community structure

Phylogenetic structure was detected at all spatial and phylogenetic scales, with the SES.MPD and SES.MNTD trending in the same direction except in a few instances (Fig. 4C–D; Suppl. material 1, Table S6). However, these contrasting tendencies were only found at the plot level within Mahery and were not significant. Overall, the strongest structure was observed at the largest phylogenetic and spatial scales, and it was a pattern of clustering (MDA level: SES.MPD = -1.712 , $p = 0.028$; SES.MNTD = -1.843 , $p = 0.021$). At the site level, only Mahery and Roussettes received significant support for phylogenetic clustering with the inclusive and community phylogenies, respectively (Suppl. material 1, Table S6). Specifically, the two phylogenetic scales resulted in two different patterns at Mahery. On one hand, the inclusive phylogeny showed a pattern of clustering, although with varying supports for the two metrics (SES.MPD = -1.337 , $p = 0.069$; SES.MNTD = -1.516 , $p = 0.038$), which reveals more clustering at the branch tips than tree-wide. On the

other hand, the community phylogeny yielded a tendency toward overdispersion ($SES > 0$), although not significant. At the plot level, significant clustering was detected within plots located at Roussettes and Texier, but none of the patterns of clustering and overdispersion within plots at Mahery received significant support (Fig. 4C–D; Suppl. material 1, Table S6). The general lack of significance for overdispersion may stem from the incomplete resolution of the phylogenetic tree (i.e. presence of basal polytomies). In short, these results identify environmental filtering as the mechanism shaping community at a large spatial scale, whereas niche partitioning may become more important when the spatial scale decreases.

DISCUSSION

Methodological aspects

Scale effects

As expected, the multiscale spatial and phylogenetic assessments of community patterns have variable outcomes, although they generally trend in the same direction. The broader the scale, the more discernible the effects are in the analysis of trait–environment relationships through the RLQ and fourth-corner approaches (Fig. 3; Suppl. material 1, Table S4, Figs S2–S12) or the assessment of phylogenetic community structure (Fig. 4C–D; Suppl. material 1, Table S6). However, phylogenetic signals are seemingly insensitive to phylogenetic scales, with similar results obtained with both the inclusive and the community phylogenies (Table 2; Suppl. material 1, Table S5). The similarity of these results and their convergence on the same assemblage that includes a cluster of sister species (i.e. Mahery; Table 2; Fig. 1C; Suppl. material 1, Table S5) may indicate that the recovered phylogenetic signals are unlikely to be an artifact of scale, as would be expected under null models (Cavender-Bares et al. 2009).

Trait–environment relationships

The RLQ and fourth-corner analyses captured different signals of trait–environment associations (Fig. 3; Suppl. material 1, Table S4, Figs S2–S12). However, these are complementary rather than competing methods, making any comparison somewhat inadequate. The contrasting results obtained here reflect the nature, strengths, and coverage of these approaches. Indeed, the RLQ is a multivariate ordination technique that captures broad patterns of covariation between sets of environmental and trait variables. On the other hand, the fourth-corner is a bivariate method that focuses on single trait–environment pairings. While congruence is expected between their results, the lack thereof suggests complex multivariate and possibly non-linear relationships between environmental and trait variables, captured only by the ordination technique or only after dimensionality reduction in the case of the fourth-

corner (i.e. the combined analysis). Other possible explanations include insufficient sample size to derive enough statistical power to detect specific associations in the fourth-corner; insufficient representation of the full range of variation in these heterogeneous communities; omission of critical trait and/or environmental variables; or presence of confounding factors obscuring any relationships (Anderegg 2023). Bioclimate, in particular, is a complex variable intricately linked with elevation and atmospheric data including solar radiation, air pressure, and wind speed. It is possible that plant responses to these environmental conditions are more labile than expected, which could mask any particular relationships easily discernible by the fourth-corner. Soil properties are also highly complex, varying at the micro scale and affected by water availability and immediate biotic agents (e.g. plants and microbes). Moreover, studies often find mixed and/or weak plant responses to soil properties, as well as inconsistent relationships between above-ground and below-ground traits (Asefa et al. 2022; Anderegg 2023). These weak and/or inconsistent correlations can test the limit of the statistical power of a bivariate method; and in our case, only above-ground traits were used. The RLQ analysis also shows that the total inertia is generally low at small spatial scales (Mahery = 1.951, Roussettes = 8.004, and Texier = 3.796, vs 14.41 at a large spatial scale (MDA); Suppl. material 1, Table S4). As the total inertia represents the strength of the relationship between matrices R (environment) and Q (trait) through L (species) (Dolédec et al. 1996), the low inertia at the site level, especially at Mahery, indicates a rather weak trait–environment relationship for the current datasets.

Community patterns

The results support the idea of increasing environmental heterogeneity with increasing spatial scales. However, the threshold at which such a heterogeneity leaves a discernible effect on the distribution of *Noronhia* species on Montagne d’Ambre (MDA) seems also rather high. It is captured only at the scale of the mountain (30×10 km) as a significant trait–environment relationship (Suppl. material 1, Table S4). Habitat heterogeneity at a nearly similar scale ($0.1 \times 0.1^\circ$) was observed in a study of patterns of diversity of *Grewia* L. (Malvaceae) in Madagascar (Karimi and Hanes 2024). At a small spatial scale (50×50 m), spatial variations in relation to a narrow elevation gradient were detected in a study of the structure and diversity of a Malagasy woody plant community (Fujimoto et al. 2024). Elevation is highly correlated with other environmental variables in our study, and although the sites are located along a broad elevational gradient, within-site heterogeneity has only a weak signal (Suppl. material 1, Table S4). In our case, the lack of clear patterns of trait–environment relationships at scales below 10 km suggests broad ecological niches among species. Moreover, the sensitivity to detect the signal of habitat heterogeneity may differ between taxon-

specific studies (e.g. *Noronhia*, *Grewia*) and community-focused ones (e.g. an entire woody plant community).

Communities of *Noronhia* establish along bioclimate and soil gradients on MDA (Fig. 3; Suppl. material 1, Fig. S2) and exhibit signals of conservatism across spatial and phylogenetic scales (Table 2; Suppl. material 1, Table S5). These communities are characterized by an overall pattern of phylogenetic clustering, although weak signals of overdispersion emerge at small spatial scales (Fig. 4C–D; Suppl. material 1, Table S6). The poor support for overdispersion may stem from the incomplete resolution of the phylogenetic tree. Indeed, this tree is characterized by large basal polytomies, which tend to cause false negative rather than false positive outcomes resulting from a loss of statistical power with decreasing phylogenetic resolution (Swenson 2009). Thus, overdispersion is detected, but there is not enough statistical power to render a significant support. Nonetheless, reconciling these ecological and phylogenetic approaches provides insights into the likely presence of environmental filters across the mountain. Indeed, seven of the 17 traits show strong phylogenetic signals (Table 2; Suppl. material 1, Table S5). Six traits appear to be phylogenetically conserved among species, particularly among species occurring at Mahery, and seem to be an adaptation to environmental stressors (e.g. drier/warmer climate and poorer soil), which likely act as filters to community memberships. At the same time, convergence, at least in one trait, occurs within this community, which is formed by a mix of sister species and other congeners that belong to different clades (Fig. 1C). This may explain the mixed signature of conservatism and convergence that reflects a phenotypic attraction within clades (clustered) and among clades (overdispersed) mediated by habitat filtering (Webb et al. 2002).

There is a clear species turnover along the elevation gradient, with the divide occurring around Roussettes between 800 and 1,200 m elevation. Specifically, Roussettes and Texier share the same species composition, except for *N. olearia* which typically occurs at Roussettes, but none harbours the same species as Mahery. This divide was also observed in other studies. For instance, Scherz et al. (2023) found genetic divergence among amphibian and reptile taxa on MDA at 800 and 1,000–1,100 m elevation, respectively, substantiating the role of bioclimate in driving species divergence along the elevational gradient of this mountain. However, contrary to their record of highest species richness at mid-elevation, *Noronhia* species richness on MDA peaks at lower elevations, more consistent with a floristic study on the mountain that found decreased floristic richness with increasing elevation along an altitudinal range of 890 to 1,430 m (Razanajatovo et al. 2013). A study of community assembly of bryophytes in another northern mountain of Madagascar (Marojejy) also found peak richness at mid-elevation (Marline et al. 2025), pointing to different responses among different types of organisms, and possibly attributed to different environmental conditions as well. Nonetheless, the results of Scherz et al. (2023) and ours coincide in finding the

presence of well-defined species assemblages clearly adapted to the lower or the higher elevations of MDA, as well as the presence of mountain endemics only at higher elevations (e.g. *N. stevensiana*).

Determinants of coexistence in a plant species swarm

Madagascar's unique flora has been formed by external elements coming mainly from Africa and Asia and largely by in situ diversification, resulting in 87% endemism (Buerki et al. 2013; Lowry et al. 2018). Broad-scale spatial patterns of plant species richness across Madagascar are largely explained by spatial heterogeneity (Hong-Wa et al. unpubl. data, <http://2008.botanyconference.org/engine/search/index.php?func=detail&aid=843> [accessed 01.12.2025]; Antonelli et al. 2022; Liu et al. 2024; Omollo et al. 2024). But, to our knowledge, attempts to explain the mechanisms of coexistence of Malagasy congeneric plant species are scarce (Zjhra 2008; Karimi and Hanes 2024). Our study thus provides the first insights into small-scale community assembly of a Malagasy plant species swarm using community phylogenetic and trait-based approaches.

The general trend of phylogenetic clustering on MDA highlights the unique circumstance of the mountain, which harbours the only rainforest in the northern tip of Madagascar that is distant from any other rainforest block by at least 120 km (e.g. Sambirano rainforest in the Northwest, and the eastern rainforest block starting around Sambava at ca 200 km away). The composition of *Noronhia* communities on MDA, with members drawn mainly from a pool of northern-restricted species, suggests a limited role of long-distance dispersal and also supports the long isolation of this mountain. Moreover, MDA is at the intersection of two centres of endemism (centres 1 and 12 per Wilmé et al. (2006)) and may have acted as a refugium during climatic fluctuations of the Late Tertiary or Quaternary. The Mahery assemblage is composed of *Noronhia* species endemic to semi-deciduous forests of the North (centre 1), except for one widespread species (*N. pervilleana*), while the Roussettes and Texier assemblages include a species endemic to the montane forest (i.e. *N. stevensiana*; centre 12). This highlights the role of these two centres of endemism in generating and maintaining species and may explain the significant phylogenetic clustering recovered for *Noronhia* communities on MDA.

This study underscores the role of environmental heterogeneity in determining patterns of coexistence at the scale of the mountain (30 × 10 km), echoing comparable role in structuring broad-scale (50–100 × 50–100 km) patterns of plant species richness across Madagascar. As expected, based on abiotic requirements, the mechanisms driving coexistence in *Noronhia* differ from those observed in studies of animal species (e.g. lemurs), in which competition is a major factor (e.g. Dammhahn and Kappeler 2008; Schäßler et al. 2015; Herrera 2016). Decoupled large-scale phylogeographic patterns also

emerged between *Noronhia* and its potential lemur dispersers (Hong-Wa and Besnard 2014), implying that perhaps lemurs do not significantly induce evolutionary patterns in *Noronhia* and that pollination more so than seed dispersal is influenced by biotic forces in this group. Indeed, population and landscape genetics analysis of two *Noronhia* species indicated that seed dispersal may be mediated by small-range foragers (Salmona et al. 2020, 2023), whereas weak and strong patterns of isolation by distance in two sympatric *Noronhia* species denoted contrasting pollen dispersal between both taxa (Gorrilliot et al. 2021).

A noteworthy caveat is that this study features only abiotic factors and may have underestimated the range of processes mediating small-scale species distribution patterns. The poor responses of traits associated with syndromes of pollination (e.g. flower size), seed dispersal (e.g. pericarp thickness, seed size), and herbivory (e.g. leaf domatia, pubescence, toughness, and petiole woodiness) to abiotic variables suggest that biotic interactions may be the driving forces influencing community structure here. For instance, phenological data (not shown, but see Hong-Wa (2016)) indicate large overlaps in flowering and fruiting periods among species of *Noronhia*, suggesting that competition avoidance mechanisms may exist through divergent floral and seed dispersal syndromes (e.g. shape, size, colour), temporal isolation (e.g. timing, duration), and/or behavioural characteristics (e.g. display, scent, reward). Indeed, these congeneric species coexisting on MDA may display reproductive character displacement, for instance, with flowers varying in colour from cream-white (e.g. *N. amina*) to greenish-yellow (e.g. *N. brevituba*) or purplish-red (e.g. *N. candicans*), and in size from 3.5 mm long (e.g. *N. stevensiana*) to 22 mm long (e.g. *N. humbertiana*) (Hong-Wa 2016). Herbivory is also an important factor influencing plant species coexistence (Toll 2023) and has been found to occur at higher rates in tropical dry forests than in tropical humid and temperate forests (Coley and Barone 1996). The lack of significant relationships between the four herbivory-related traits and the abiotic variables at any spatial scales (p_{adj} ; Suppl. material 1, Figs S3, S6, S9, S12) implies that biotic factors could be more prominent here. For instance, domatia, which may improve plant fitness in nutrient-poor and/or herbivore-prone environments (Agrawal et al. 2000; Oren et al. 2001; Romero and Benson 2005; Ma et al. 2007; O'Connell et al. 2010) such as the drier and warmer low-elevations of MDA, showed no relationship with abiotic variables but had a strong phylogenetic signal across spatial and phylogenetic scales. This could indicate that the defensive role of domatia, through mutualistic associations with mites, may have been more useful within this community of *Noronhia* relative to its growth-supporting role, through carbon sequestration in nutrient-poor habitats. Ultimately, this suggests that biotic stress such as herbivory may have meaningfully shaped the evolution and assembly of this species swarm on MDA.

In sum, different processes may be simultaneously involved in structuring communities of *Noronhia* on MDA. Habitat filtering and niche partitioning act on vegetative and reproductive functions, respectively, as observed in *Banksia* assemblages in Australia (Merwin et al. 2012), and facilitate coexistence across spatial scales (i.e. habitat filtering at a large scale (mountain level) and niche separation at a small scale (site and plot levels)). The only study of plant species swarms that examined biotic interactions in Madagascar (Masoala Peninsula) found pollinator partitioning as the mechanism maintaining stable coexistence among members of tribe Coleeae of Bignoniaceae (Zjhra 2008). Different processes were also found to influence the assembly of bryophytes communities in northern Madagascar (Marojejy massif), with habitat filtering driving trait convergence at lower elevations, whereas niche differentiation acted more significantly at higher elevations (Marline et al. 2025).

Implications for conservation

Montagne d'Ambre (MDA) is important biologically for the unique biodiversity it shelters and economically for harbouring the headwaters of over two dozen rivers that drain the northernmost part of Madagascar (Barat 1958; Hong-Wa 2018). While MDA is a protected area, it is also under a constant human pressure, currently exacerbated by a changing climate that impacts the river system irrigating crop fields. MDA experienced recurrent drought with two extreme episodes in the last 60 years (Hong-Wa and Randrianarison 2009; Hong-Wa et al. 2010), which can affect its plant communities in two ways. First, although six decades may not be enough to induce visible changes, continuous reduced rainfall may further filter community memberships. Ultimately, this may alter species composition, thereby affecting plant communities' resilience to a changing climate. Such compositional change has already occurred on MDA owing to a millennial-long decreased precipitation (Montade et al. 2024). Second, persistent rainfall deficit has caused a conversion in agricultural practices and an increased exploitation of forest products (Hong-Wa and Randrianarison 2009; Hong-Wa 2018). This is already leading to a forest degradation that will eventually change species composition. With a pattern of phylogenetic clustering, *Noronhia*, by extension, has less evolutionary diversity on MDA, which leaves its community vulnerable to environmental changes. *Noronhia* is only but one example of taxa with species endemic to the mountain (e.g. FAPBM 2020), but it is ubiquitous in this ecosystem and provides for several species of pollinators and seed dispersers (Hong-Wa 2016). Continued preservation of the unique phylogenetic diversity on this isolated mountain that likely serves as a last refuge for countless taxa, through the reinforcement of conservation efforts and implementation of mitigation strategies, is critical not only to help further understand the evolutionary history of the Malagasy flora but also to protect the sustainability

of an ecosystem, on which the human population of the northernmost region depends for its water and other vital necessities.

CONCLUSION

Using *Noronhia* as an example to understand plant species swarms in Madagascar, this study explored its community patterns on Montagne d'Ambre (MDA) across spatial and phylogenetic scales. It found the strongest covariance between trait and environment matrices at a large spatial scale, but little effect of phylogenetic scales on phylogenetic signal or community structure. A clear species turnover was observed at mid-elevation, highlighting two species assemblages adapted to either the lower or the higher elevations. The main pattern defining communities across the mountain was phylogenetic clustering, which indicates that environmental heterogeneity acts as a filter to community memberships across MDA. However, a mixed signature of clustering and overdispersion was detected at small spatial scales at lower elevations, suggesting several mechanisms may underlie species coexistence in this *Noronhia* community. By assessing small-scale plant community assembly using community phylogenetic and trait-based approaches, this study provides new insights into the coexistence of Malagasy plant species swarms. Inquiries into *Noronhia*'s reproductive biology, especially pollination, would further elucidate the processes driving sympatric coexistence within this group; an approach that would advance current understanding of the evolution of Madagascar's flora. This study also concurs with available literature in highlighting the uniqueness of the biota on MDA, which calls for a heightened preservation of the distinctive phylogenetic diversity of this mountain in the face of a changing climate and an increased human pressure.

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SUPPLEMENTARY MATERIAL

Supplementary material 1

Data and additional results on analyses of beta diversity, trait–environment relationships and community structure across Montagne d'Ambre and within the sites of Lac Mahery, Station des Roussettes, and Lac Texier.

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