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RESEARCH ARTICLE

Species–soil relationships across Amazonia: Niche specificity and consistency in understorey ferns

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Abstract

Aims: Knowledge about species niches along environmental gradients is needed to understand community assembly and spatial variation in floristic composition and species richness. In Amazonian rainforests, such knowledge is largely lacking, although ferns have been used to infer overall floristic and edaphic patterns. Here we explore fern species distributions along an important edaphic gradient, how narrow their realised niches are and how sensitive inferences are to species commonness, data quality and the region being sampled.

Location: Amazonia.

Methods: We used a large data set (1,215 transects across lowland Amazonia) to explore the realised niches of 54 species of two fern genera (*Adiantum* and *Lindsaea*) along a soil base cation concentration gradient. We used weighted averaging to estimate species optima and niche widths, and Huisman–Olff–Fresco modelling to assess species response shapes.

Results: Overall, species optima were rather evenly spread along the soil base cation concentration gradient, but *Lindsaea* optima were limited to the lower half of the gradient, whereas *Adiantum* optima were more often in the upper half. Most species had unimodal response curves. Mean niche width was ca. 25% of the observed gradient length for *Adiantum* and 17% for *Lindsaea* and was only weakly or not at all related to different aspects of species commonness. Species optima were robust to different modelling approaches and consistent across regional subsets. However, the central Amazonian data contained no transects with high soil base cation concentration, so species with high optima were either absent or obtained a lower optimum than in the NW and SW regions.

Conclusions: Our results support niche-related species sorting as an important process that defines species co-occurrence, turnover and richness patterns within Amazonian rainforests. All *Adiantum* and *Lindsaea* species, including the most abundant ones, had

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narrow enough realised niches to be considered useful indicators of edaphic and floristic variation within the rainforest.

KEYWORDS
alpha-diversity, Amazonia, edaphic specialisation, ferns, indicator species, niche modelling, species response curves, species turnover

1 | INTRODUCTION

Information about species–environment relationships and the positions of realised niches along environmental gradients are instrumental for understanding the assembly and species composition of local communities, as well as the functioning of ecosystems (Harpole & Tilman, 2006; Kraft & Ackerly, 2014). The width of realised niches and how they are distributed along relevant environmental gradients determines local community composition. For example, two species would be expected to co-occur locally only if their niches overlap. Non-overlap of niches will tend to reduce local species richness (and thereby constrain alpha-diversity) but promote species turnover (and hence increase beta-diversity).

Plant species can differ in where along the environmental gradient they find optimal conditions (niche position) and how narrow their distributions are along those gradients (niche width). Both aspects have implications for the interpretation of community ecology. When niche positions are known, it becomes possible to infer species composition at sites with known environmental conditions and to use floristic composition (or a smaller set of indicator species) to estimate environmental conditions at sites where species occurrence data are available, but direct measurements of environmental variables are not (Ellenberg et al., 1992; Diekmann, 2003; Peppler-Lisbach, 2008; Suominen et al., 2013; Ewald & Ziche, 2017; Tyler et al., 2021; Tichý et al., 2023). Species-based environmental estimates can, in turn, be used to infer occurrence probabilities for other species (Descombes et al., 2020).

In northern Europe, indicator species are used to identify and map vegetation types, such as edaphically defined forest site types (Cajander, 1926; Pohjanmies et al., 2021). In Amazonia, some forest types have also been defined on the basis of their characteristic plant species (Encarnación, 1985; Abraão et al., 2008), and soil-related species turnover has been reported in many plant groups (Phillips et al., 2003; Fine et al., 2005; Ruokolainen et al., 2007; Baldeck et al., 2016; Tuomisto et al., 2016; Cámara-Leret et al., 2017; Moulatlet et al., 2019). Understorey ferns have been considered practical indicators of general floristic patterns and edaphic conditions, because they are both relatively common in tropical forests and easy to observe and collect (Ruokolainen et al., 1997, 2007; Kessler & Bach, 1999; Tuomisto, Poulsen, Ruokolainen, et al., 2003; Cárdenas et al., 2007; Zuquim et al., 2014).

Fern species composition has been used to infer edaphic and floristic patterns in Amazonian rainforests from local and regional extents (Tuomisto, Ruokolainen, Aguilar, et al., 2003; Salovaara et al., 2004; Sirén et al., 2013; Suominen et al., 2015; Cárdenas Ramírez et al., 2021) to the entire Amazon basin (Tuomisto et al., 2019; Zuquim et al., 2019, 2023). Edaphic preferences of some Amazonian fern species have been documented using simple edaphic classifications and/or relatively small data sets (Tuomisto & Poulsen, 1996; Tuomisto et al., 1998; Tuomisto, Ruokolainen, Aguilar, et al., 2003; Tuomisto, 2006; Cárdenas et al., 2007, but see Zuquim et al., 2014). More complete species-specific information would be valuable to improve understanding of the ecological processes behind Amazonian forest composition, to address questions related to niche evolution and adaptive radiation, and to make the indicator species approach more widely applicable as a quick means of habitat characterisation for ecological studies and conservation planning.

Observed niche position and width are affected by many factors. Some of these are purely methodological (e.g. choice of numerical niche modelling method, abundance vs presence–absence data), whereas others are fundamentally ecological (e.g. species' realised edaphic niches may vary among different climatic conditions; Diekmann & Lawesson, 1999; Reinecke et al., 2016; Hedwall et al., 2019). Sampling in different regions may give a different impression of the species' niches because of spatial variation in the environmental variables of interest (Hájková et al., 2008). For example, central Amazonia is known to differ from western Amazonia both geologically and climatically (Fittkau et al., 1975; Schobbenhaus et al., 2004; Rossetti et al., 2005; Hoorn et al., 2010). Understanding such variation is important both for drawing ecological inferences about species occurrence patterns and when using the species as environmental indicators. Ideally, indicator species would have broad distributional ranges but narrow and consistent niches, as well as a high probability of being abundant in their preferred habitat.

Here, we model the edaphic niches of two fern genera, *Adiantum* and *Lindsaea*, using an extensive data set of 1,215 quantitative field inventories. Earlier studies have mentioned several species of these genera as good indicators of specific kinds of soils (Tuomisto & Poulsen, 1996; Tuomisto, 1998; Tuomisto et al., 1998, 2002; Tuomisto, Ruokolainen, Aguilar, et al., 2003; Cárdenas et al., 2007; Zuquim et al., 2014; Lehtonen et al., 2015). Both genera share a characteristic overall appearance that makes them easy to distinguish from other Amazonian ferns in floristic inventories, and they are also common in the understorey across Amazonia, so the probability to encounter them in floristic inventories is high.

Here, we have four main aims: (1) to unravel the realised niches of Amazonian *Adiantum* and *Lindsaea* species along a soil base cation concentration gradient; (2) to explore local diversity and species turnover along the edaphic gradient, (3) to test whether niche properties are related to species commonness and rarity; and (4) to assess how consistent the niche estimates are across regions. The results are discussed in relation to community ecology and practical applications.

2 | METHODS

2.1 | Field data

Our data originate from long-term field inventory efforts of the Amazon research team of the University of Turku (UTU, Finland) and the National Institute for Amazonian Research (INPA, Brazil). Inventories of understorey ferns have been carried out along line transects that range between 2 m and 5 m in width and between 250 m and 43 km in length. For the purposes of this paper, we cut any transects longer than 500 m into non-overlapping 500-m-long segments. Henceforth, all sampling units will be called transects, whether representing original inventory lines (250 m or 500 m) or 500-m segments of longer lines.

We use those transects in which at least one surface soil sample has been analysed for exchangeable base cations (Ca, Mg and K) (Figure 1). We focused on this soil variable, because earlier studies have found soil base cation concentration to largely explain the strongest floristic gradient in Amazonia (Tuomisto, Ruokolainen, & Yli-Halla, 2003; Zuquim et al., 2014; Tuomisto et al., 2016, 2019) and it was also available from a larger number of transects than other soil variables. Field and laboratory methods have been described in detail elsewhere (Tuomisto, Poulsen, Ruokolainen, et al., 2003; Zuquim et al., 2014; Tuomisto et al., 2016).

Representative voucher specimens were collected in the field to verify species identifications and standardise them across inventories. If a matching species name could not be found for what was thought to correspond to a biological species, it was given a unique species identification number. All species identifications were cross-checked and updated by the same person for the current study. Unverified observations (corresponding to voucher specimens that were not accessible either physically or as photographs) were excluded. This resulted in false species absences, so the corresponding transects were treated as having presence-only data. Sometimes one field name had been used for two species and uncollected individuals could not be reliably identified. Such occurrences were taken into account when quantifying species richness within a transect if fully identified individuals of the same species complex were not present, but were excluded when modelling species niches. We mostly followed the nomenclature of World Ferns (https://www.worldplants.de/world-ferns/ferns-and-lycophytes-list). However, we use the name *Lindsaea pusilla* instead of *L. lancea* var. *remota*, because we believe this taxon to be distinct from *L. lancea* at the species level.

The data set consisted of 1,215 transects. Standardised abundance data (number of individuals in a 5 m × 500 m transect) were available from 403 transects, presence–absence data from 406 transects (2 m or 5 m wide, 500 m long), and presence-only data from 406 transects (mostly 2 m wide and 250 m long, some 5 m × 500 m). These categories were treated as nested sets: when analyses were based on "presence–absence data", they included also the transects for which abundance data was available (for a total of 809 transects), and analyses based on "presence-only data" included all 1,215 transects.

For regional comparisons, the transects were divided into three contrasting sets: NW Amazonia (545 transects), SW Amazonia (157 transects) and central Amazonia (513 transects) (Figure 1). The NW set has a wet, aseasonal climate (precipitation seasonality Bio15 ≤ 30 kg/m^2 as reported in CHELSA; Karger et al., 2017), whereas the SW and central set share a seasonal climate (Bio15 > 30 kg/m^2). The two western sets share biogeographical affinity to the Andes. All transects in the Andean countries were assigned to one of the western sets, as were those transects in Brazil that were situated west of 66° W. Frequency distribution of the transects along the soil base cation concentration gradient in each set is shown in Figure 1.

2.2 | Modelling of species responses

We focused on the sum of exchangeable base cation concentrations as measured in cmol(+)/kg. Because unit change is more important at low than at high nutrient concentrations, all analyses were done on logarithmically transformed values, i.e. the gradient of interest was $\log_{10}(Ca + Mg + K)$. We used weighted averaging (WA) to assess the position and width of species niches along this gradient. The species niche position (optimum) was calculated as the weighted average of the environmental variable values in the sites where the species occurred, with the species abundance at each site used as the weight. Species niche width (tolerance) was measured as one standard deviation above and below the optimum (ter Braak &van Dam, 1989; Chevalier et al., 2020). WA was done in the R statistical programming environment (R Core Team, R Foundation for Statistical Computing, Vienna, AT) using the package *rioja* (Juggins, 2022).

To assess species response shapes along the soil base cation concentration gradient, we used Huisman–Olff–Fresco (HOF) models (Huisman et al., 1993; Lawesson & Oksanen, 2002; Oksanen & Minchin, 2002; Peppler-Lisbach, 2008; Jansen & Oksanen, 2013). In increasing order of complexity, the original five response models are: no response (type I), linear (type II), plateau (type III), unimodal symmetric (type IV) and unimodal skewed (type V). Later, two bimodal models were added (types VI and VII), but we did not consider them here, because we did not have data on other potentially limiting environmental variables that might have caused the dip between the two modes. Model fitting in HOF is done by maximum likelihood estimation, with a penalisation factor derived from the number of model parameters (Jansen & Oksanen, 2013). This allows selecting the simplest model that sufficiently explains the observed pattern. We used the Akaike information criterion corrected for small sample sizes (Burnham et al., 2011) to choose the best-fitting model, because many of the fern species had small frequencies. HOF models

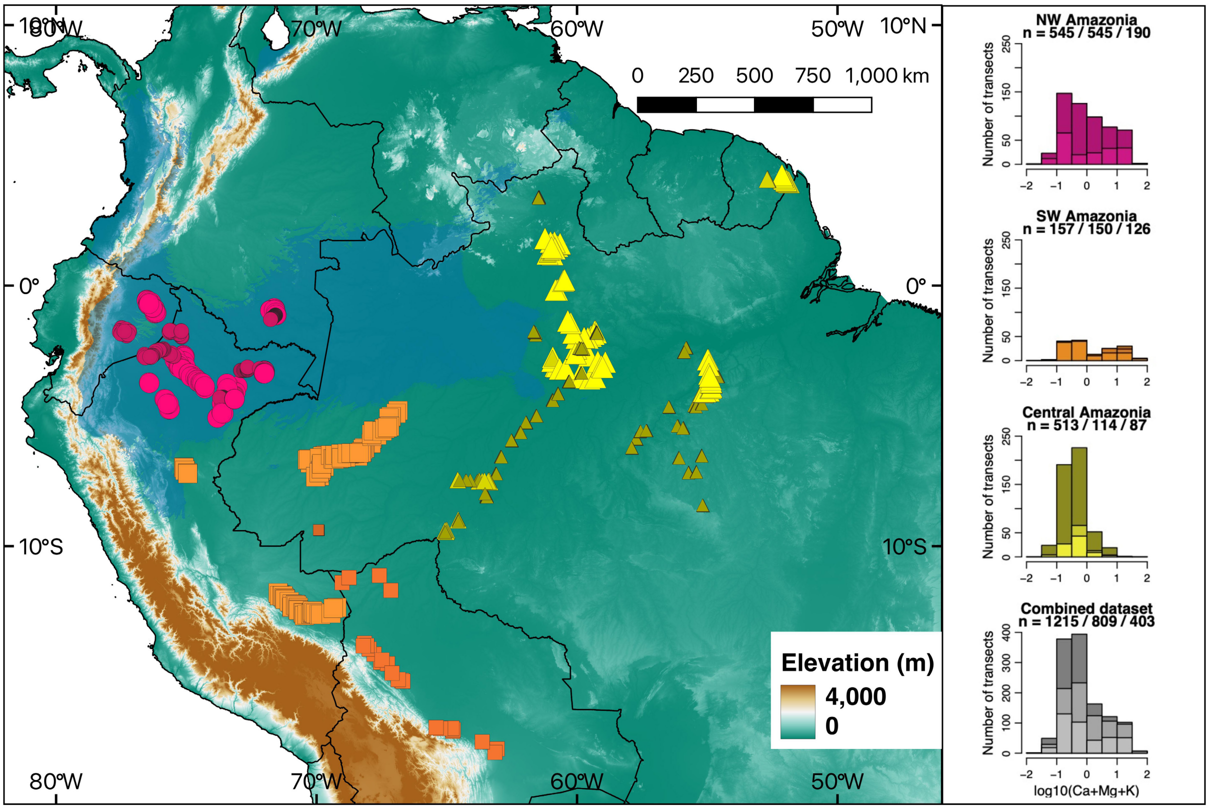

FIGURE 1 Map of northern South America with the fern inventory transects shown. NW Amazonian transects (dark pink) are aseasonal (area with precipitation seasonality Bio15 ≤ 30 kg/m^2 shown with blue shading), whereas SW (orange) and central (yellow) transects are more seasonal. Histograms show how soil base cation concentration (log$_{10}$-transformed values of Ca + Mg + K in cmol(+)/kg) varies in the three subsets and the entire data set. The number of transects is shown above each histogram for three data quality classes: at least presence data/also absence data/also abundance data. Increasing data quality is indicated by a larger symbol size in the map and a brighter colour in both the map and the histogram. Elevation is from Shuttle Radar Topography Mission (SRTM) data (https://www2.jpl.nasa.gov/srtm/cbanddataproducts.html).

were only produced if a minimum of six transects with the species present were available for modelling. To ensure that the most likely models were chosen, we used bootstrapping to run 100 HOF models for each species and chose the model that had been selected most often by the individual runs.

In HOF modelling, the species optimum is defined as the point along the environmental gradient where the response curve reaches its highest value (Jansen & Oksanen, 2013). The plateau model (type III) predicts a constant maximum value from the beginning of the plateau to one end of the gradient and reports these extremes as two optima, so we used their arithmetic mean (Michaelis & Diekmann, 2017). HOF modelling was done in R using the package *eHOF* (Jansen & Oksanen, 2013).

2.3 | Consistency of species responses

To assess the robustness of the estimated niche properties, we compared WA species optima as obtained with data sets of varying quality (abundance, presence–absence, presence-only) and from different regions (NW, SW, central Amazonia) by calculating Pearson correlations. Using the abundance–quality transects, we also compared estimates of species optima as obtained with WA vs HOF modelling. To test transferability of niche properties across regions, we ran the WA analyses first on the entire data set and then separately for the transects split into the three regional subsets, as shown in Figure 1.

Niche overlap was quantified using the Simpson and Sørensen indices as adapted to a gradient. The Simpson index quantifies the degree to which the narrower of the two niche estimates is embedded within the broader one and is insensitive to differences in niche width:

$$\text{Overlap (Simpson)} = \text{(niche overlap between two sets)} / \min\text{(niche width in set 1, niche width in set 2)}.$$

The Sørensen index takes account of differences in niche width by relating niche overlap to the mean niche width estimate:

$$\text{Overlap (Sørensen)} = \text{(niche overlap between two sets)} / \text{mean (niche width in set 1, niche width in set 2)}.$$

To address species rarity and commonness, we calculated niche width and abundance (Rabinowitz, 1981). As an approximation of Rabinowitz's niche width we used WA tolerance, and as an approximation of geographical range we used the maximum distance between two observations of a species (Choe et al., 2019). Abundance was estimated both at the local scale (as mean number of individuals per transect in those transects where the species occurred) and globally (total number of individuals) using all transects with abundance–quality data. We also calculated frequency (the percentage of transects in which a species was observed) to be able to address rarity patterns not only using the transects with abundance data, but also those with presence–absence data.

3 | RESULTS

3.1 | Species distributions along the soil gradient

We identified 92 units thought to represent biological species: 50 *Adiantum* and 42 *Lindsaea*. The focus of the current paper is on those 54 species that could be matched with a species name: 31 *Adiantum* and 23 *Lindsaea*. Many of the remaining 38 species are probably new to science, and discussing their niches will be more useful after their nomenclature has been resolved. The number of individuals registered in the 403 transects with abundance data exceeds 104,000 (>96,000 *Adiantum* and>8,000 *Lindsaea*), but the total number of individuals in the data set of 1,215 transects is unknown, because species abundances were only registered in 100.75 ha of the total inventoried area of 195.15 ha.

For *Adiantum*, alpha-diversity (mean local species density; i.e. mean species richness per transect) was lowest in transects with low soil base cation concentration and higher in transects with intermediate to high soil base cation concentration, especially in central Amazonia (Figure 2). In contrast, alpha-diversity of *Lindsaea* was highest in transects of low soil base cation concentration, and the genus was practically absent from transects with high soil base cation concentration. When both genera were considered together, alpha-diversity increased with soil base cation concentration in central Amazonia but peaked at intermediate values in the other two regions and in the combined data.

Overall, the distribution of species optima was relatively even across the observed soil base cation concentration gradient, but there was a clear difference between the two genera: most *Lindsaea* species had low optima, whereas most *Adiantum* species had high optima (Figure 3 and Appendix S1). For example, with presence–absence data (809 transects) the 9 lowest WA optima corresponded to *Lindsaea* and the 19 highest to *Adiantum*.

Niche widths varied widely among species and to some degree among genera (Figure 3). With abundance data (403 transects), mean WA niche width was ca. 20% of the total gradient length (22% with range 4%–58% for *Adiantum* and 15% with range 4–30% for *Lindsaea*). With presence–absence data (809 transects), mean WA niche widths remained almost the same (22% for all species; 25% with range 4%–41% for *Adiantum* and 17% with range 6%–29% for *Lindsaea*) (Appendix S1; only considering species with at least two occurrences).

Most of the species showed unimodal responses (HOF model types IV and V) along the soil base cation concentration gradient: 84% when using abundance data and 62% when using presence–absence data (Figures 3 and 4). With abundance data, the unimodal asymmetric model (type V) was most common, whereas using presence–absence data often led to selecting simpler models. This was the case also when the data were pooled by genus: for both *Adiantum* and *Lindsaea*, model type V was selected with abundance data and model type II with presence–absence data. None of the taxa was indifferent to the soil base cation concentration gradient (i.e. model type I was not selected for any species or genus). Full details of both genus-level and species-level HOF models are shown in Appendices S2 (abundance data) and S3 (presence–absence data).

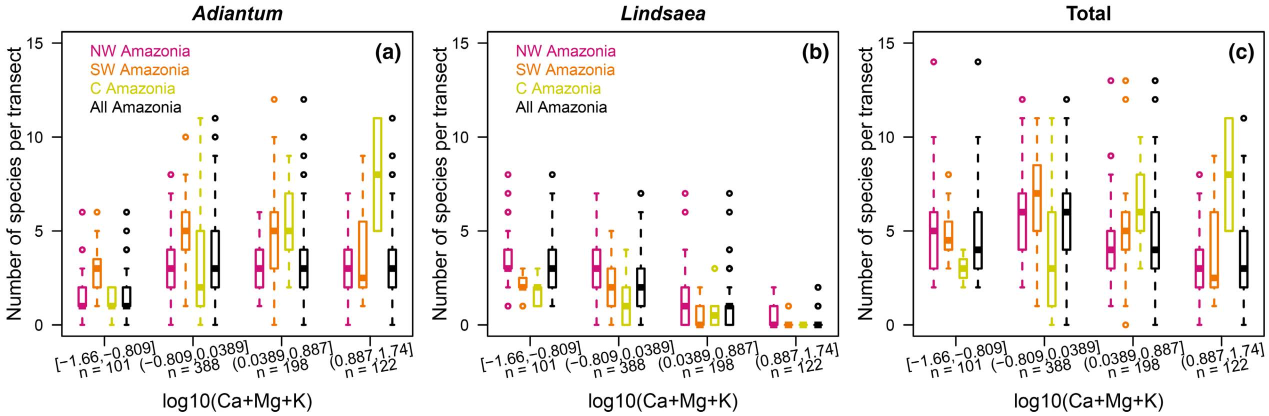

FIGURE 2 Variation in local species density of *Adiantum* (a), *Lindsaea* (b) and both together (c) as observed in 809 presence–absence transects grouped into equally long quarters of the soil gradient. For each quarter, the limits [in $\log_{10}$-transformed soil base cation concentration as expressed in cmol(+)/kg] and number of transects (*n*) are shown.

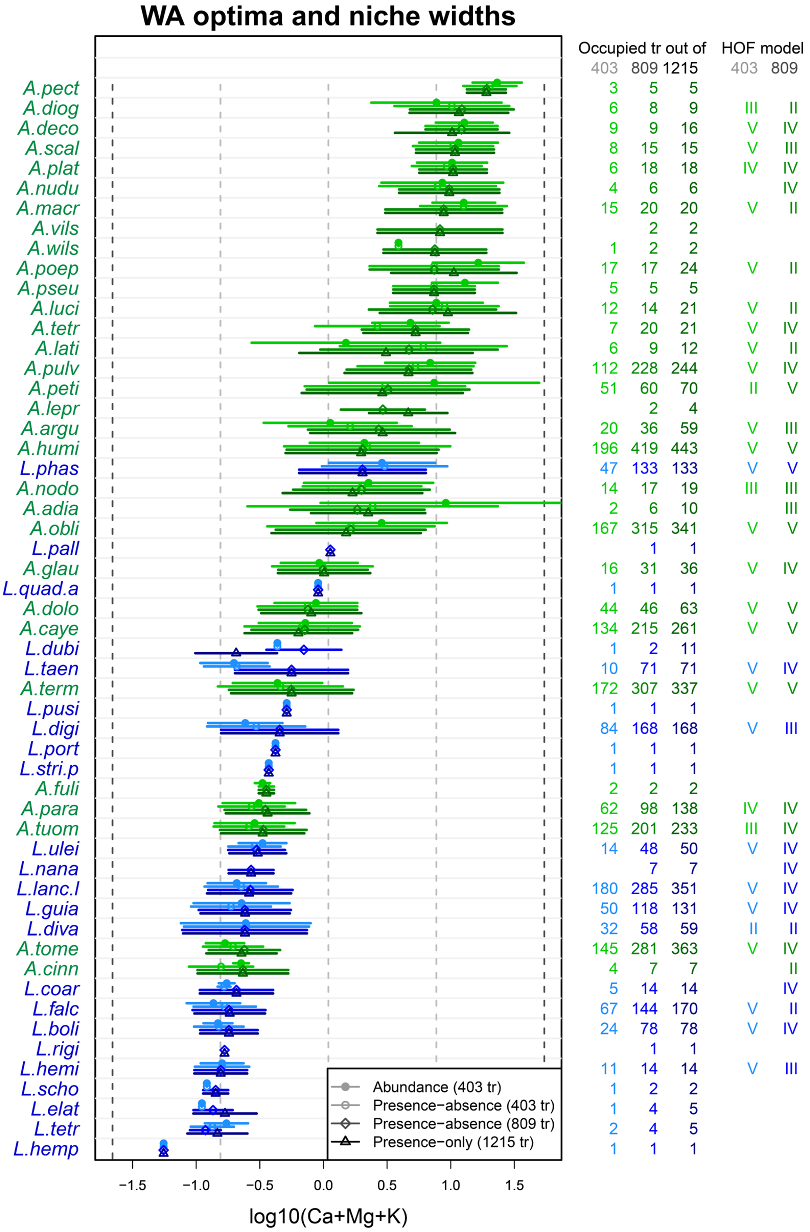

FIGURE 3 Optima and niche widths from weighted averaging (WA) of Amazonian *Adiantum* and *Lindsaea* species along a gradient of soil base cation concentration as measured in cmol(+)/kg in 1,215 Amazonian transects. Estimates were obtained separately for three nested quality classes. The number of transects in each is shown at the right, together with the Huisman–Olff–Fresco (HOF) model types obtained with abundance data from 403 transects and presence–absence data from 809 transects. For the 403 abundance-quality transects, separate optima and niche widths were calculated with abundance data and with presence–absence data. All 54 named species are listed from bottom to top in the order of increasing optimum as estimated with the 809 presence–absence transects. For geographical distribution of the transects, see Figure 1. For HOF models of the species that occurred in at least six transects, see Figure 4.

3.2 | Species commonness and rarity

There was enormous variation in the commonness of the observed species. The most abundant species overall was *Adiantum humile*, which occurred in 52% of the 809 transects with presence–absence data and had >41,000 individuals in the 403 transects with abundance data. The next most abundant species was *A. pulverulentum*, which had >13,000 individuals in 28% of the transects. Other common species were *A. obliquum*, *A. terminatum*, *A. tomentosum* and *Lindsaea lancea* var. *lancea*, each of which occurred in 35%–39% of the transects and had between 2,750 and 11,900 individuals. A total of 13 species (24%) were represented in >10% of the 809 presence–absence transects, whereas 22 species (41%) were represented in <1% of the transects.

The average density of the species at sites where they were present varied widely, from a single individual per 0.25 ha to almost 350 (median = 14, mean = 42) (Appendix S1). *Adiantum* species were generally more abundant than *Lindsaea* species, with mean total abundance

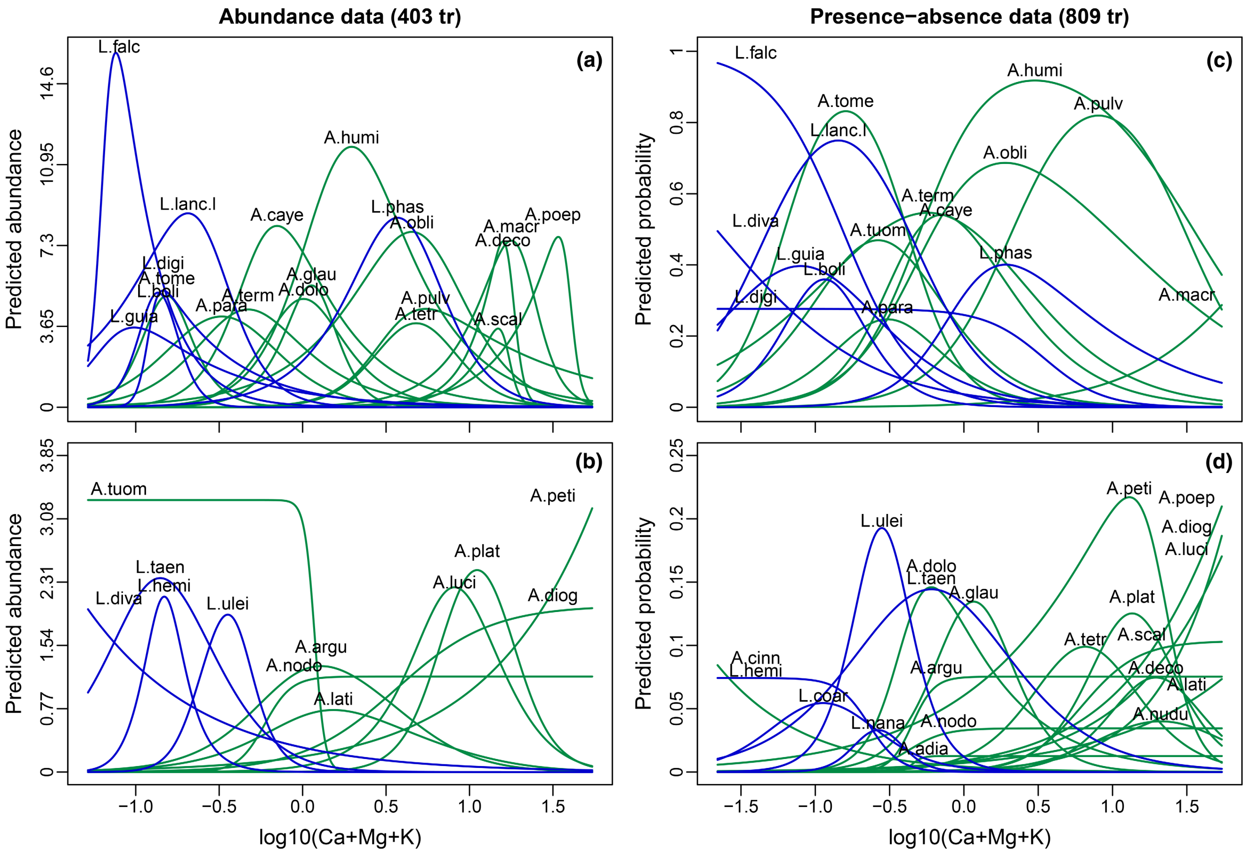

FIGURE 4 Best Huisman–Olff–Fresco (HOF) model response curves for *Adiantum* (green) and *Lindsaea* (blue) species in lowland Amazonia. Modelling used either abundance data (a, b; 403 transects) or presence–absence data (c, d; 809 transects). To avoid clutter, species with high maximum predicted response (a, c) are shown separately from species with low maximum predicted response (b, d). Only species observed in at least six of the relevant transects were modelled. For more details on each model, see Appendices S2 and S3.

of 3,324 vs 410 individuals and mean density when present of 60 vs 15 individuals/0.25 ha, respectively. *Adiantum* species also had higher mean frequency, 10% of the presence–absence transects vs 6% for *Lindsaea*. High total abundance was related to both high frequency (Pearson's $R=0.62$, $p<0.001$) and large geographical range (Pearson's $R=0.57$, $p<0.001$), but high density when present was not related to either (Pearson's $R<0.2$, $p>0.2$ in both cases). In other words, frequently encountered or widespread species were locally no more abundant than infrequent or geographically more restricted species.

Niche width significantly increased with geographical range size when calculated using presence-only data, but not when calculated using abundance data (Appendix S4a,b). No significant correlations were found between niche width and either frequency, total abundance or local abundance. However, minimum niche width calculated with presence-only data seemed to increase with frequency (Appendix S4c–f).

3.3 | Consistency of niche estimates

The species optima estimated by WA and HOF modelling were highly correlated irrespective of data quality (Figure 5a,b and Appendix S5). The correspondence was especially tight for species with unimodal HOF models (types IV and V), in agreement with the implicit assumption of unimodality in WA. At the extremes of the gradient, where the observations fit less well with this assumption, WA optima tended to be closer to the overall gradient midpoint than HOF optima; i.e. higher at the low end and lower at the high end. The correspondence between optima based on abundance data and presence–absence data was very high, especially for WA (Figure 5c,d).

Niche positions of the 26 species that occurred in at least two of the regions (NW, SW and central Amazonia) were rather similar between regions (Figure 6). Correlations between WA optima based on SW and NW Amazonian data were especially high (Pearson's $R=0.95–0.98$), independently of data quality subset. The WA optima based on central Amazonian data were slightly less correlated with optima from SW and especially NW Amazonia (Pearson's $R=0.91–0.95$ and $0.83–0.92$, respectively). Correlations involving HOF optima were lower than those only involving WA optima throughout, indicating higher sensitivity of HOF to data set properties (Appendix S5).

The optima based on central Amazonian data had a narrower spread than those from western Amazonia, mostly because the highest optima were estimated to be lower (Figure 6). Nevertheless, the niche estimates a species obtained were highly overlapping between both regions and data qualities (means between SW and NW

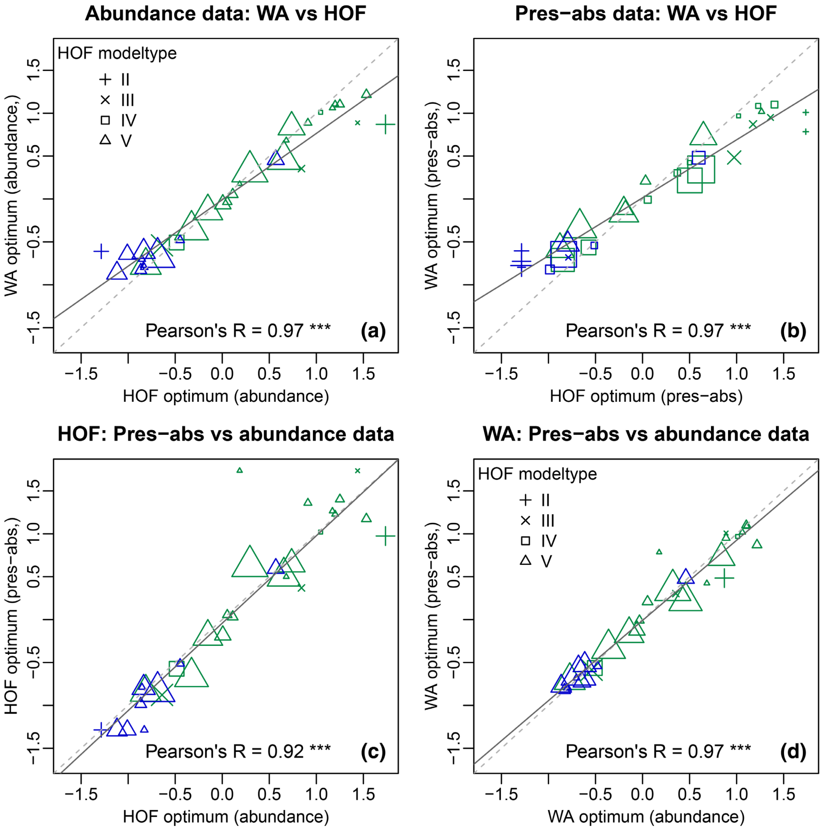

FIGURE 5 Comparisons of optima in soil base cation concentration ($\log_{10}$-transformed values of Ca + Mg + K in cmol(+)/kg) of Amazonian *Adiantum* (green) and *Lindsaea* (blue) species as estimated with different combinations of Huisman–Olff–Fresco (HOF) modelling vs weighted averaging (a, b) and abundance data vs presence–absence data (c, d). All comparisons are based on 403 abundance-quality transects. Only species that occurred in at least six of the transects are included, with symbol size reflecting the number of transects occupied. The grey dotted line shows the 1:1 relationship, the black solid line the actual linear relationship. Panel (b) shows HOF model types based on presence–absence data, the other panels those based on abundance data. ***$p < 0.001$.

Amazonia: Simpson overlap 0.78–0.91, Sørensen overlap 0.51–0.66; between either of the western areas and central Amazonia: Simpson overlap 0.66–0.88, Sørensen overlap 0.48–0.66).

4 | DISCUSSION

4.1 | Species distributions along the soil gradient

Different species of *Adiantum* and *Lindsaea* clearly reached their peak occurrence probabilities and abundances at different parts of the soil base cation concentration gradient. This clarifies why some species often co-occur in the field, whereas many have never been found together, and contributes to understanding the role of edaphic niches in driving community assembly, species composition and compositional turnover in tropical rainforests.

Our results corroborate earlier findings for those *Adiantum* and *Lindsaea* species that were included in previous studies. For example, *A. tomentosum*, *L. lancea*, *L. schomburgkii*, *L. divaricata* and *L. hemiglossa* have been reported from poor sandy to loamy soils, whereas *A. pulverulentum*, *A. obliquum*, *A. humile*, *A. argutum* and *L. phassa* have been reported from more nutrient-rich clay soils (van der Werff, 1992; Tuomisto & Poulsen, 1996; Tuomisto, 1998; Tuomisto et al., 1998; Tuomisto, Ruokolainen, Aguilar, et al., 2003; Zuquim et al., 2014). Our results provide improved understanding of niche position and niche width based on an updated taxonomy, a larger number of observations, a larger study area and a longer base cation concentration gradient. For many species, this is the first time that any aspect of their niche is quantified.

When *Adiantum* and *Lindsaea* were pooled, species optima were spread rather evenly over the entire soil base cation concentration gradient, as has been found for Amazonian *Polybotrya* ferns (Tuomisto, 2006). Nevertheless, *Lindsaea* optima were more narrowly distributed and generally lower than *Adiantum* optima. This suggests that edaphic specificity has been more conserved in the evolutionary history of *Lindsaea* than in that of *Adiantum*, which may partly explain why *Lindsaea* has fewer species within Amazonia. Globally, however, both genera have similar richness (ca. 250 species), and clarifying how niche specificity varies among species in other parts of the world could be very informative about the underlying evolutionary processes.

Plant responses to base cation concentrations may interact with their responses to other relevant gradients (Lawesson & Oksanen, 2002), such as water availability. In Amazonia, climatic

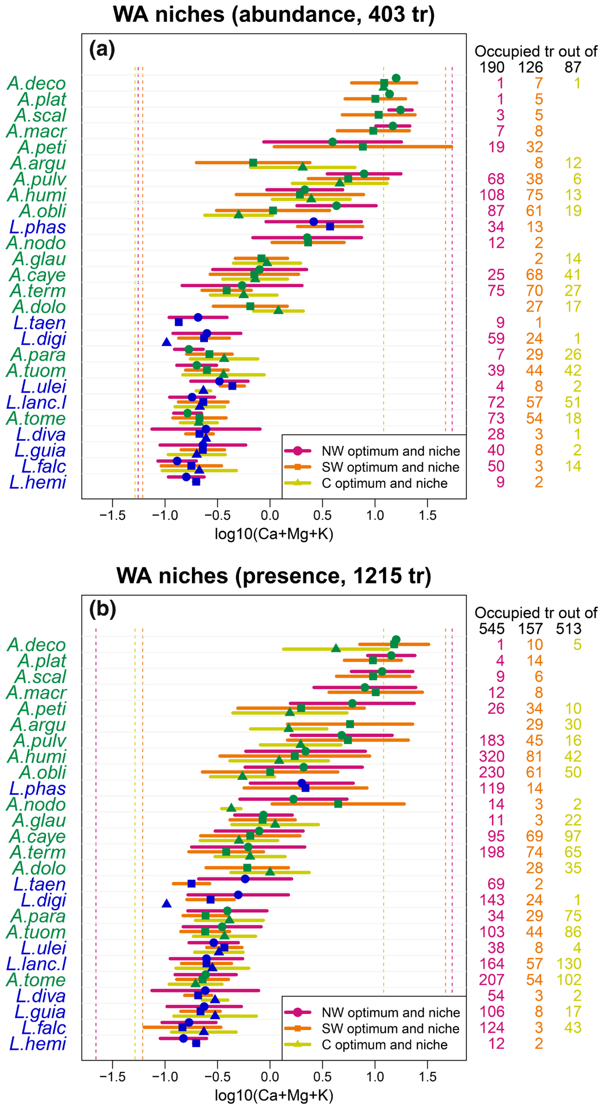

FIGURE 6 Comparison of optima and niche widths obtained from weighted averaging for *Adiantum* and *Lindsaea* species in three regions: NW, SW and central (C) Amazonia. The 26 species with abundance data for at least two of the regions are shown, listed from bottom to top in the order of increasing presence-based optimum in NW Amazonia. The vertical dashed lines give the limits of the soil base cation concentration gradient as observed in the transects from each region. At the right, total number of transects in each region is shown in black and the number of transects occupied by each species is shown in the colour corresponding to the region.

humidity tends to increase towards the equatorial Andes, just like soil base cation concentration does (Quesada et al., 2010). However, water availability to plants also depends on drainage, which is regulated by local topography and soil texture and can affect estimates of species responses to soil base cation concentration (Schietti et al., 2014; Moulatlet et al., 2019, 2022). Of the ten species with the broadest cation niches in our abundance data, eight were found predominantly in flood-prone creek banks and wet valley bottoms, and five of these were also among the six species with the broadest cation niches in the presence-only data: *Adiantum argutum*, *A. humile*, *A. latifolium*, *A. nodosum* and *A. petiolatum* (Figure 4). It remains to be clarified whether humid-site species really have broader than average base cation niches, or their niche widths have just been overestimated because most of the soil samples were taken at higher topographic positions and may not be representative of creek side conditions, especially at sites with high topographic and edaphic heterogeneity (Vormisto et al., 2004).

The two species that had broad base cation niches but were not primarily found in wet microsites span different drainage conditions: *Lindsaea divaricata* was mostly in white sand forests but also in swamps, and *Adiantum obliquum* was mostly on higher terrain but also in the floodplains of creeks. The niche of *L. divaricata* is now narrower than it would have been before *L. digitata* was segregated from it (Lehtonen & Tuomisto, 2007), because the latter is confined to well-drained terrain and does not occur on white sand. This demonstrates the importance of taxonomic resolution for species–environment relationships. *Adiantum obliquum* is morphologically very variable and probably also a species complex, and the same is true of the most abundant species in our data, *A. humile*. These still need taxonomical attention to identify the biologically most relevant units.

Theoretically, all species responses are unimodal on an infinitely long gradient (Austin, 1987, 2002; Oksanen & Minchin, 2002; Rydgren et al., 2003). The high proportion of unimodal HOF response curves (Figure 4) suggests that we have sampled most of the soil base cation gradient that is present in Amazonia, although the non-unimodal plateau model (type III) was common with presence–absence data. In the cation-poor end of the gradient, it is likely that some of the non-unimodal HOF models correspond to unimodal models that were truncated as a result if incomplete sampling, because the most nutrient-poor white sand forests were not well represented in our data set. It is also possible that soils with base cation concentrations much higher than those in our data set exist (e.g. in soils derived from serpentine rock), and that more species responses would become unimodal if such extreme sites were represented in the data. However, if such conditions exist in Amazonia, they are likely to be rare and restricted to the western regions close to the Andes. Therefore, it is possible that some species obtain non-unimodal response curves simply because high enough base cation concentrations to become harmful do not exist within their distributional range.

Some earlier studies on trees and palms have argued that many Amazonian species are generalists (Pitman et al., 2001; Toledo et al., 2012; ter Steege et al., 2013; Arellano et al., 2017), although others have found the base cation concentration to be an important environmental determinant of their abundance and distribution (Phillips et al., 2003; John et al., 2007; Baldeck et al., 2016; Cámara-Leret et al., 2017). All *Adiantum and Lindsaea* species showed significant responses to the soil base cation gradient. It is possible that ferns and trees are inherently different in this respect: ferns are not as dispersal-limited as trees are, so ferns may be able to specialise to a narrower soil niche (Zuquim et al., 2012). However, the differences may also reflect data quality: it is considerably more difficult to obtain representative samples of trees than of understorey ferns, which may lead to more noisy data for trees and failure to detect a relationship that is actually there (Jones et al., 2008).

4.2 | Species commonness and rarity

It has been proposed that Amazonian forests are dominated by a few generalist, hyperabundant tree species, whereas most species, including the specialists, are rare (Pitman et al., 2001, 2013; ter Steege et al., 2013; Cooper et al., 2024). Our results conform with the notion that some species are abundant whereas many are rare, but there was no relationship between commonness and niche width, whether commonness was measured as the number of transects occupied, total number of individuals or mean local density of individuals when present. In other words, common species were no more likely to be generalists in relation to the soil base cation concentration gradient than rare species were.

In her original typology of rarity, Rabinowitz (1981) proposed that it is unusual for species with broad niches to be geographically restricted. In our data, there indeed was a positive correlation between species niche width and range size, but it was rather weak. The geographical distribution and commonness of the preferred habitat must be an important determinant of species range size and overall abundance, but it remains to be clarified how these interact with other factors, like stress tolerance, competitiveness and dispersal ability. Mean density when present varied widely among species, but was not correlated with either niche width, frequency or range size in our data. A given species could have very different abundances at sites with similar base cation concentrations. This is no doubt related to both within-transect heterogeneity in base cation concentration and variation in unmeasured environmental factors and biotic interactions.

Although our data set is large, extensive areas have not been sampled at all, and it is likely that the full range of environmental variation in Amazonia has not yet been encountered. Based on our results, this probably has a larger effect on the estimates of range size (which can only grow, sometimes dramatically, when data from a new area becomes available) than it does on the estimates of niche position and width (whose estimates are less biased and just become more robust with more data). It is noteworthy how many of the highest optima belong to infrequent *Adiantum* species. This is related to the fact that only a small proportion of the inventoried transects had high-cation soils, so it was impossible for species specialised to these habitats to obtain high frequencies.

The stability of HOF model choice increases with the amount of data, and rare species (<50 occurrence points) have been suggested to obtain predominantly HOF model types I–III (Coudun & Gégout, 2006; Jansen & Oksanen, 2013; Michaelis & Diekmann, 2017). None of our species obtained model type I, but with presence–absence data, most of the species observed in 6–50 transects indeed obtained a non-unimodal model type (II or III), whereas few of the species observed in >50 transects did. With abundance data, almost all species obtained a unimodal model type irrespective of frequency.

These results have implications for interpreting variation in fern species composition. Because niche specificity is similar between rare and abundant species, inferences on overall community composition and the underlying soils can be based on the most common, easy-to-find species. The common species are also better represented in herbaria and therefore easier to identify than the rare ones, which is important in tropical rainforests with their relatively poorly known floras (Ruokolainen et al., 2002). An ideal indicator species would have a narrow niche but wide geographical range, and it would be consistently present and locally abundant in its preferred habitat. Some very good indicator species, in order of increasing base cation concentration optimum, are: *Lindsaea schomburgkii*, *L. falcata*, *Adiantum tomentosum*, *L. lancea* var. *lancea*, *A. terminatum*, *A. cajennense*, *L. phassa* and *A. pulverulentum*. In fact, all 54 species analysed here have a sufficiently narrow niche to be useful as indicators of soil base cation concentration, but some are so infrequent (at least in our data) that they are most useful as a part of a larger species set.

Together, *Adiantum* and *Lindsaea* cover the entire Amazonian soil base cation concentration gradient, and species of at least one of them were present in almost all transects. This means that a preliminary characterisation of an Amazonian forest site can be achieved very rapidly if one is able to identify the 54 species analysed here, or at least the 20 most common of them. The taxonomical challenge is thereby dramatically reduced when compared with identifying all ferns (maybe 600 species, as 500 have been documented in Brazilian Amazonia alone; Prado et al., 2015) or all trees (maybe 16,000 species; ter Steege et al., 2020).

4.3 | Consistency of niche estimates

The species optima produced with different estimation methods (HOF vs WA, presence–absence data vs abundance data) were in close agreement. The highest and lowest optima were somewhat less extreme when calculated with WA than HOF, because the WA optimum is an average of observed values, whereas the HOF optimum can equal the most extreme value. The largest deviations between different optima mostly concerned infrequent species, whose results are most tentative anyway. With HOF modelling, instability was often related to choosing a different model type for presence–absence and abundance data.

Overall, estimates of the response curve shape seemed more sensitive to sampling issues than estimates of niche position and niche width. In addition, the WA optima were more stable across data subsets and data qualities than the HOF optima. This suggests that the WA optima can be used as the starting point in any studies or practical applications that need information on species niche position, which is good news given how simple the WA optima are to calculate.

In principle, abundance data allow seeing details and producing more nuanced models than presence–absence data do, and the latter may be more sensitive to individuals randomly occurring in habitats that are suboptimal for the species (sink populations; Soberón, 2007). On the other hand, models based on abundance data are sensitive to observations with exceptionally high abundances. Local abundance may, more strongly than species presence, be affected by factors other than soil base cation concentration, such as soil drainage, light conditions or biotic interactions. A few of the species addressed here are able to spread via long-creeping rhizomes and can attain very high local densities (e.g. *Adiantum argutum*, *A. latifolium* and *A. pseudocajennense*), and for these species the difference between optima based on abundance vs presence–absence data was relatively large.

Species niches may contract because of harsh overall environmental conditions, expand because of competitive release, or shift towards the regionally predominant part of the gradient because of local adaptation (Diekmann & Lawesson, 1999; Hájková et al., 2008; Reinecke et al., 2016). In our case, the regional comparisons showed that many of the species with high base cation optima were either absent from central Amazonia or their optima were lower than in NW and SW Amazonia. This is consistent with the observation that the highest base cation concentrations observed in central Amazonia were considerably lower than those observed in NW and SW Amazonia, which reflects general geological differences among the regions (Fittkau et al., 1975; Quesada et al., 2010). Whether local adaptation is also involved remains to be tested.

A weaker trend was that species with the lowest base cation optima tended to have higher optima in central Amazonia than in NW or SW Amazonia. This might reflect a niche shift, because the higher rainfall seasonality in central Amazonia may render the poorest soils too inhospitable for ferns to thrive on. Overall fern species richness has indeed been found especially low at sites that combine poor soils with low annual rainfall (Tuomisto et al., 2014). Comparable niche shifts can be observed in Europe, where many species grow on acidic or neutral soils in the southern part of their range but shift towards more base-rich sites with increasing latitude and harsher climate (Reinecke et al., 2016).

5 | CONCLUSIONS

We found that Amazonian *Adiantum* and *Lindsaea* species have relatively narrow soil base cation concentration niches that are well distributed along the gradient. This supports the idea that community assembly and compositional turnover in Amazonian rainforests are to a large degree edaphically determined, even for abundant and widespread species. Estimates of species optima were robust to variation in sampling and modelling approaches, validating the use of these genera as base cation concentration indicators. *Adiantum* and *Lindsaea* differed in which part of the gradient they were most diverse, and integrating their realised niches with phylogenetic information can be expected to clarify questions related to the drivers of speciation, the evolutionary origin of edaphic specialisation, and niche conservatism.

AUTHOR CONTRIBUTIONS

HT and LS conceived the ideas, analysed the data and led the writing; HT, AA, GC, SL, GMM, EP, AS, PW and GZ collected the data and did initial species identifications; HT cross-checked the identifications; all authors participated in discussions about the manuscript, contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The data used in the analyses have been deposited in *Zenodo* with doi: 10.5281/zenodo.12193413.

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SUPPORTING INFORMATION

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

Appendix S1. Occurrence and niche characteristics of Amazonian *Adiantum* and *Lindsaea* species.

Appendix S2. Abundance-based HOF models for 32 Amazonian *Adiantum* and *Lindsaea* species.

Appendix S3. Presence-absence-based HOF models for 37 Amazonian *Adiantum* and *Lindsaea* species.

Appendix S4. Comparison of different aspects of rarity among Amazonian *Adiantum* and *Lindsaea* species.

Appendix S5. Pearson correlation coefficients between species optima as calculated with different methods.

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