

# The role of functional uniqueness and spatial aggregation in explaining rarity in trees

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## Abstract

**Aim:** Determining the drivers of species rarity is fundamental for understanding and conserving biodiversity. Rarity of a given species within its community may arise due to exclusion by other ecologically similar species. Conversely, rare species may occupy habitats that are rare in the landscape or they may be ill-suited to all available habitats. The first mechanism would lead to common and rare species occupying similar ecological space defined by functional traits. The second mechanism would result in common and rare species occupying dissimilar ecological space and spatial aggregation of rare species, either because they are specialists in rare habitats or because rare species tend to be dispersal limited. Here, we quantified the contribution of locally rare species to community functional richness and the spatial aggregation of species across tree communities world-wide to address these hypotheses.

**Location:** Asia and the Americas.

**Time period:** 2002 to 2012 (period that considers the censuses for the plots used).

**Major taxa studied:** Angiosperm and Gymnosperm trees.

**Methods:** We compiled a dataset of functional traits from all the species present in eight tree plots around the world to evaluate the contribution of locally rare species to tree community func-

tional richness using multi- and univariate approaches. We also quantified the spatial aggregation of individuals within species at several spatial scales as it relates to abundance.

**Results:** Locally rare tree species in temperate and tropical forests tended to be functionally unique and are consistently spatially clustered. Furthermore, there is no evidence that this pattern is driven by pioneer species being locally rare.

**Main conclusions:** This evidence shows that locally rare tree species disproportionately contribute to community functional richness, and we can therefore reject the hypothesis that locally rare species are suppressed by ecologically similar, but numerically dominant, species. Rather, locally rare species are likely to be specialists on spatially rare habitats or they may be ill-suited to the locally available environments.

#### KEYWORDS

functional diversity, functional traits, species relative abundance, temperate forests, tree diversity, tropical forests

## 1 | INTRODUCTION

Virtually every natural community comprises a few common species and many rare species (Brown, 1995; Hubbell & Foster, 1986; Lawton, 1999; Preston, 1948; Wallace, 1878). The large number of rare species in ecological communities becomes even more pronounced in tropical regions where community ecology effectively becomes a study of rare species (Hubbell & Foster, 1986; Pitman, Terborgh, Silman, & Nunez, 1999; Ricklefs, 2000). Thus, our understanding of how ecological communities are themselves structured depends on our ability to uncover the processes driving rarity. Further, identifying the drivers of rarity is of fundamental importance for society's efforts to conserve biodiversity through space and time.

In tree communities, the rarity of species can be explained by a few, potentially overlapping, processes. First, a species may be locally rare because its niche is being occupied by ecologically similar species that are more numerically dominant in the community. For example, priority effects could promote the rarity of late-arriving species even though these late arrivals are ecologically similar to the early arriving individuals (Chase, 2007). Second, a species may be a habitat specialist and the habitat it specializes on is itself rare in the landscape (Kunin & Gaston, 1997; MacArthur, 1957; MacArthur & MacArthur, 1961; Sugihara, 1980). A prediction arising from the first possibility is that rare species should be functionally similar to common species. The second hypothesis, however, predicts that rare species should be functionally dissimilar to common species because they specialize on different and rarer habitats than common species. Further, rare species may be spatially clustered on a preferred habitat that is itself aggregated (Kunin & Gaston, 1997). Given that in undisturbed forests pioneer species, specializing on light-gap environments, may be rare in the community (Denslow, 1987; Hubbell & Foster, 1986), a possibility that emerges is that rare species will be functionally dissimilar from common species. For example, pioneer species are characterized by having low wood density, high specific leaf area and high leaf nutrients (Bazzaz, 1980) and are often clumped distributed in gaps (Seidler & Plotkin, 2006).

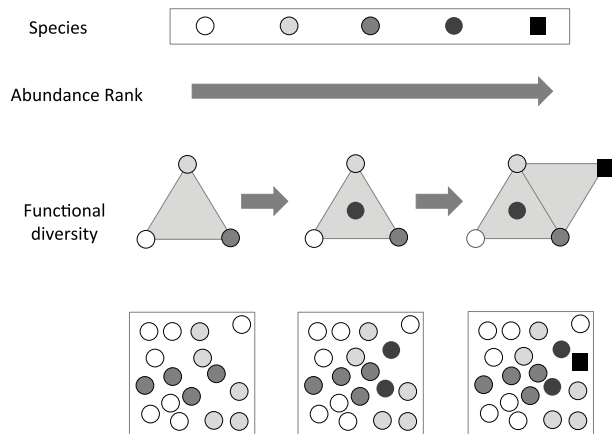
Despite the great interest in rarity in ecology (Gaston, 1994; McGill, 2006; Rabinowitz, 1981; Rabinowitz, Cairns, & Dillon, 1986), quantitative tests of the hypotheses described above are lacking. Specifically, comparative quantitative tests of the contribution of rare versus common species to community functional diversity and whether rare species tend to be spatially aggregated on spatially rare habitats are needed.

In this study we analysed long-term forest plot data from the temperate zone to the tropics. Four of the plots are located in Asia and four in the Americas. In each forest plot, we quantified several plant functional traits that are associated with species performance, functional trade-offs and ecological strategies. Our approach is a trait-based extension of a method recently proposed by Mi et al. (2012) that integrates relative abundance distributions with measures of phylogenetic diversity (Figure 1). The specific questions we addressed in this study are: (a) do locally rare tree species contribute more than expected to community functional diversity by virtue of their being on the periphery of community trait space; (b) do species with pioneer traits consistently occupy peripheral positions within the trait space of tree communities; and (c) are locally rare tree species more spatially clustered than common species? The answers to these key questions are largely consistent across forest plots from the temperate zone to the tropics on two continents. Specifically, rare species tend to contribute more than expected to community functional diversity, species with pioneer traits are not consistently occupying the peripheral positions and rare species tend to be more spatially aggregated than common species.

## 2 | METHODS

### 2.1 | Data collection

This study analysed eight forest dynamics plots from Asia and the Americas. For each forest plot, all individuals with diameter at breast height greater than or equal to 1 cm were identified, measured and spatially mapped. The Guanacaste forest plot in Costa Rica was the



**FIGURE 1** A conceptual figure depicting how the species rank abundance distribution was integrated with functional diversity. In this highly simplified example there are five individual species represented by different shades and shapes, sorted from most to least abundant based on the number of individuals in the forest plot. Note that in this example the rarest species in the community is functionally unique and that is why its shape is different from the other species. The multivariate trait volume (in this simplified example, represented by the triangular grey area) for the first three most abundant species is computed to represent the functional diversity. This measure is also referred to as functional richness. The volume is measured again including the fourth most abundant species. Here, the fourth species does not expand the volume. This process is repeated until we add the rarest species, which in this case adds substantially to the functional richness

only exception, where only individuals with diameter at breast height greater than or equal to 3 cm were recorded. The plots have experienced relatively little disturbance recently apart from the Luquillo forest plot in Puerto Rico, which experienced severe hurricane damage from Hurricane Hugo in 1989 and Hurricane Georges in 1998 (Comita et al., 2009; Zimmerman et al., 1994), and the Wabikon Lake forest plot in Wisconsin, USA which experienced selective logging in the early 1900s. The forest plots are located in temperate, subtropical and tropical regions and the plot species richness ranges from 34 with 27,861 individuals in Indiana, USA to 469 with 95,609 individuals in Xishuangbanna, China (Table 1).

At each forest plot, we compiled trait data for each of the species and calculated a species-level mean value for six functional traits: leaf area (LA), maximum height, specific leaf area (SLA), leaf nitrogen content (%N), leaf phosphorus content (%P) and wood specific gravity. The trait database for the Xishuangbanna forest plot did not contain %N, %P or wood specific gravity values. Rather, these axes of function were represented by leaf chlorophyll content and wood specific resistance (measured with a resistograph; Rennitech Co., Germany). Leaf chlorophyll content and wood resistance values have been shown to be highly correlated with %N, and %P and wood density, respectively (Isik & Li, 2003; Loh, Grabosky, & Bassuk, 2002; Netto, Campostrini, De Oliveira, & Bressan-Smith, 2005; Vos & Bom, 1993; Yang et al., 2014). Thus the leaf and wood axes of plant function were measured in each of the forest plots. Trait data were collected from the plots, or in some instances from the area immediately next to them, using standardized methodology (Cornelissen et al., 2003). For further details on trait data collection can be found in Appendix S1 in the Supporting Information.

The quantified traits approximate the position of species along a continuum of ecological strategies on several axes (Díaz et al., 2015). The SLA, %N, %P and chlorophyll content of a species are components of the 'leaf economics spectrum' (Wright et al., 2004). Leaves with low structural and high nutrient investment tend to have higher photosynthetic rates and shorter leaf life spans. The wood specific gravity and its correlate, wood specific resistance, represent the 'wood economics spectrum' (Chave et al., 2009). Species with low wood specific gravity or resistance tend to exhibit rapid volumetric growth rates and higher mortality rates than those species with higher wood specific gravity and resistance. The maximum height of species relates to the adult light niche of species and light gradient partitioning. Finally, the LA reflects the leaf area deployed for resource (i.e., light) capture and is known to vary along forest-scale abiotic gradients as well as along local light gradients (Cornelissen et al., 2003; Dolph & Dilcher, 1980).

## 2.2 | Measuring functional diversity

This work integrates functional diversity with the species rank abundance distribution in forest plots. It is important to note that this means that our approach and inferences are limited to the topic of local rarity

**TABLE 1** Location and description of the forest dynamics plots

| Forest plot                      | Latitude | Longitude | Forest type                  | Plot size (ha) | Census year | Species richness |
|----------------------------------|----------|-----------|------------------------------|----------------|-------------|------------------|
| Lilly Dickey Woods, Indiana, USA | 39.2361  | −86.2204  | Temperate forest             | 25             | 2012        | 34               |
| Wabikon Lake, Wisconsin, USA     | 45.5508  | −88.7964  | Temperate forest             | 25.6           | 2008        | 38               |
| Changbaishan, China              | 42.3833  | 128.083   | Korean pine mixed forest     | 25             | 2004        | 51               |
| Fushan, Taiwan                   | 24.7614  | 121.555   | Subtropical evergreen forest | 25             | 2002        | 110              |
| Luquillo, Puerto Rico            | 18.3262  | −65.816   | Lowland moist forest         | 16             | 2012        | 125              |
| Guanacaste, Costa Rica           | 10.8833  | −85.44    | Tropical dry forest          | 14.44          | 2006        | 136              |
| Gutianshan, China                | 29.25    | 118.117   | Subtropical evergreen forest | 24             | 2010        | 159              |
| Xishuangbanna, China             | 21.6117  | 101.574   | Tropical forest              | 20             | 2007        | 469              |

and not the regional-scale rarity of species. Our approach provides information about the relative contribution of each of the species to community functional diversity (Gaston, 2012; Mi et al., 2012). We quantified functional diversity using the functional richness (FRic) metric from Laliberté and Legendre (2010). FRic is the volume of a convex hull encompassing the multivariate trait space of the species in a sample and therefore approximates the multivariate range of traits in the samples. The FRic metric is a good indicator of environmental filtering acting on the edges of trait space and it conceptually aligns with the goals of the present work, which asks whether increasingly rare species tend to occupy the periphery of multivariate trait space (Cornwell et al., 2006). Furthermore, it does not include abundance information, which is critical for our study that requires a measure of functional diversity that is independent of the abundance distribution. We utilized the function dbFD in the R package 'FD' (Laliberté & Legendre, 2010) to calculate FRic. Trait values were log-transformed, if necessary, to approximate normality prior to the dbFD analyses. The dbFD function scales all trait data and performs a principal coordinate analysis (PCoA) to provide orthogonal axes prior to calculating FRic. The number of PCo axes selected to calculate FRic followed Laliberté and Legendre (2010) where the number of PCo axes retained is equal to the number of the species in the community minus 1.

### 2.3 | Integrating abundance distributions and functional richness

To quantify the contribution of locally rare species to community functional richness for each assemblage we integrated the standardized effect size (SES) for FRic with species rank abundance. In the following, we will describe the method to obtain the SES FRic values and how we compared it with the species abundance rank values. Our method follows that developed by Mi et al. (2012), who related phylogenetic diversity to rank abundance distributions. The first step was to calculate the observed FRic values. This method first computes the functional richness for the first and second most abundant species in the forest. Next, the third most abundant species is added to the sample and the functional richness metric is again computed and recorded. This is repeated, adding increasingly rare species to the sample until the second rarest species is added (Figure 1).

The FRic metric is correlated with species richness (Laliberté & Legendre, 2010). Thus, it is not possible to compare the value of FRic across samples including increasingly rare species that differ in their number of species. A null model is therefore necessary to produce the expected distribution of FRic values given the observed species richness of a sample. Thus, for the second step in our analyses we generated a null distribution of values to estimate standardized FRic values. The null model was accomplished by randomizing the names of species 999 times on the trait data matrix in a plot. Thus, the species pool for the randomizations consisted of only the species within each plot. The FRic values for samples with increasingly rare species were computed as before, but this time with randomized trait data. Finally we had a distribution of 999 random FRic–abundance relationships per plot that could be compared with our observed relationship. For each species

along the species abundance rank distribution we calculated a SES FRic by subtracting the mean of the null distribution of FRic values for that species from the observed FRic and dividing it by the standard deviation of the null distribution. Therefore, positive SES FRic values indicated a higher than expected observed FRic value and negative SES FRic values indicated a lower than expected observed FRic value. Since a FRic value of only one species cannot be computed, the most abundant species is never analysed by itself and the rarest species is never analysed because the standardized effect size must be 0 when all species are sampled (i.e. there is no variance in the null distribution). Finally we obtained a set of SES FRic values equal to the length of the total number of species minus 2 for each plot.

The last step was to compare the SES FRic values along the species rank abundance axis. On the left-hand side of the x axis is the sample containing only the two most abundant species and increasingly rare species are added as one moves along the x axis. A change in the y-axis value, the SES FRic, is expected if the species added to the sample (i.e., the next rarest species) increases or decreases the functional diversity more than expected based on a randomly added species. If there is a decreasing trend in SESs along the x axis this indicates that as one adds less and less abundant species to the sample, the functional diversity that accumulates is less than expected. In other words, the less abundant species are generally functionally similar to the more abundant species already in the sample. Conversely, if there is an increasing trend in the SESs along the x axis, less abundant species are more functionally diverse than expected and functionally divergent from the more abundant species already in the sample.

### 2.4 | Quantifying trends in functional diversity along the abundance distribution

Trends in the SES FRic values along the rank abundance distribution are used to indicate the relative contribution of increasingly rare species to community FRic. Thus, a critical step for interpreting FRic–rank abundance relationships is to determine the following: first, whether there are breaking points along the curve that indicate a change in the trend of the curve; and second, whether the trends in the curve are significantly increasing or decreasing, which would be indicative of rarer species adding more or less functional diversity than expected to the community. Thus, we first used piecewise regression to identify subseries (i.e., significant breakpoints) in each of the analyses and significance was assessed with a structural change test using the Chow *F*-statistic method as described in Mi et al. (2012). We used the Akaike information criterion (AIC) to compare a simple linear model with the piecewise linear model. For all the plots piecewise linear models were consistently better than a simple linear model (lower AIC values for piecewise linear models than for simple linear models; Appendix S2, Table S2.1). Second, we used a Mann–Kendall trend test to quantify whether each subseries exhibited a non-randomly increasing or decreasing trend in the values of the standardized effect size. Since the Mann–Kendall test may be sensitive to autocorrelation in the data a permutation approach using block bootstrapping is recommended (Wilks, 1997). We utilized block bootstrapping to quantify whether

trends were significant given the observed autocorrelation where block size was set at the maximum size at which continuous lag correlations were significant. Thus, blocks were randomly sampled with replacement to construct null subseries of standardized effect sizes. A Mann–Kendall trend test was then calculated for the null subseries and this was repeated 999 times to generate a null distribution with which the observed Mann–Kendall's statistic value for that subseries could be compared and a  $p$  value could be estimated. We utilized the function `MannKendal` in the R package 'Kendall' and the function `tsboots` in the R package 'boot' to perform these analyses.

## 2.5 | Evaluating individual trait ranges

In order to determine (a) whether rare species increase FRic because they are potentially pioneer species with low wood density, high leaf nutrient content (i.e., %P and %N) or high specific leaf area (Bazzaz, 1980) and (b) whether increases in FRic with rarity across all forests are generally associated with the increase in the range for a particular trait across all forests, we plotted the range of individual trait values as increasingly rare species are added. This allowed us to visualize how the range of an individual trait changes as increasingly rare species are added and it is the univariate analogue to our multivariate FRic analyses. As in our multivariate analyses, our univariate analyses also estimated breakpoints and performed the structural test using the Chow  $F$ -statistic method to evaluate whether the increases in the ranges of leaf traits and decreases in wood specific gravity were consistently associated with rare species. We used piecewise regression to identify subseries in relationships between maximum trait range and rank abundance as well as minimum trait range and rank abundance.

## 2.6 | Quantifying spatial aggregation of individuals within species

We quantified the spatial aggregation of individuals within species at several scales by computing the omega ( $\Omega$ ) metric developed by Condit et al. (2000). Omega evaluates the population density of each focal tree of each species within concentric circles with radii of 5, 10, 20, 30, 40 and 50 m. Thus, for a given species,  $\Omega$  indicates the density of conspecifics in the neighbourhood. This value is divided by the total population density of a particular species for the entire plot. Omega values equal to 1 indicate a perfectly random distribution. At short distances,  $\Omega$  values higher than 1 indicate aggregation and  $\Omega$  values lower than 1 indicate more even spacing. To ensure that our aggregation analyses were not inherently biased by differences in species abundance, we used a complete spatial randomness simulation to test whether species had  $\Omega$  values that were significantly higher or lower than expected from a randomly dispersed species. In particular, we calculated 999 random  $\Omega$  values by shuffling species names across the XY locations of all individuals in the forest plot, each time calculating an  $\Omega$  value for each species. This randomization considers the simplest null scenario assuming complete spatial randomness and independence. The mean of the null distribution of  $\Omega$  values was subtracted from the observed  $\Omega$  values and divided by the standard deviation of the null omega values to

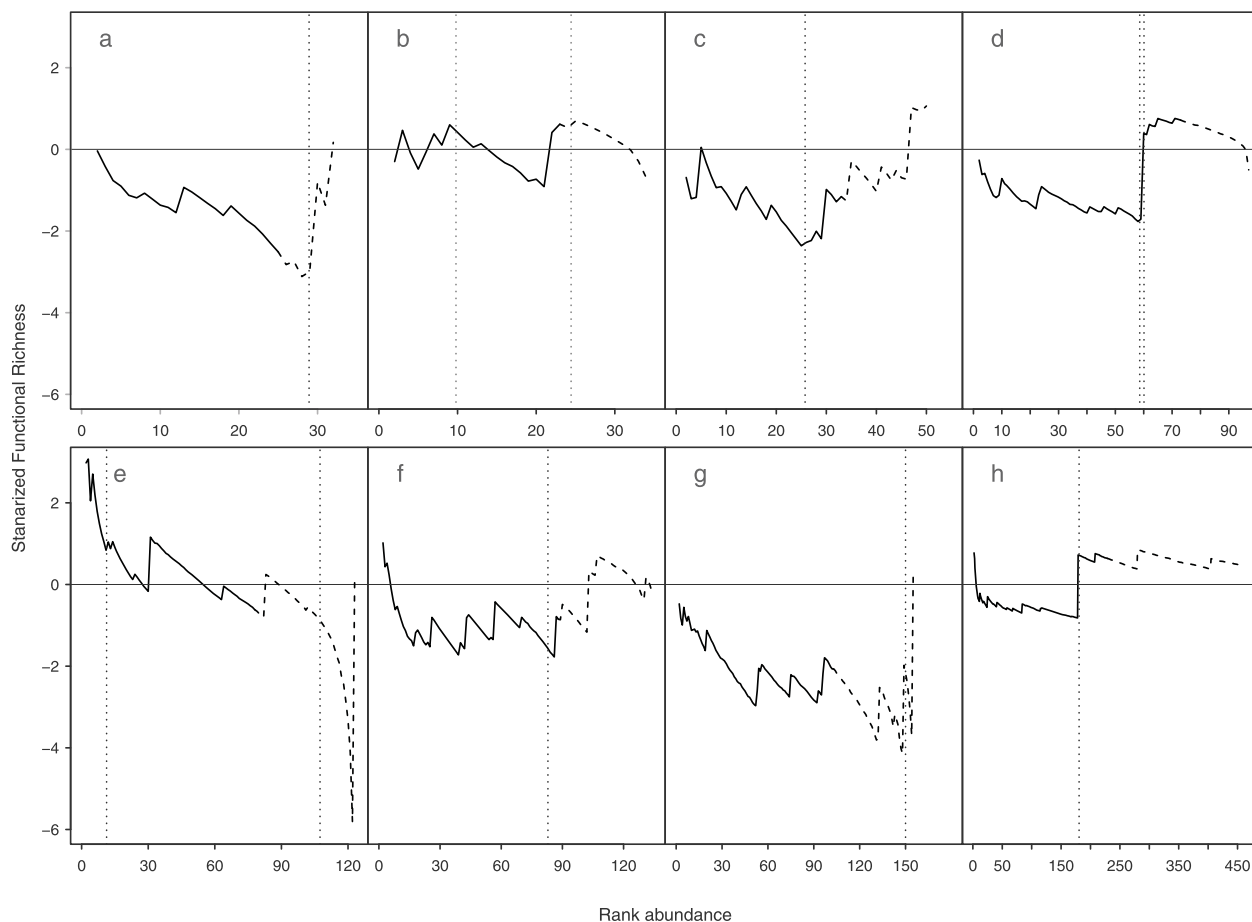
result in a standardized effect size (SES) of  $\Omega$ . A SES  $\Omega$  value greater than 0 indicates that a species is more spatially aggregated than expected, whereas a SES  $\Omega$  value of less than 0 indicates that a species is more evenly dispersed in space than expected. In order to examine whether rare species tended to be more spatially clustered than common species, we performed Spearman correlations between SES  $\Omega$  values and log-transformed species abundance. If rare species are more spatially clustered than common species, then a negative Spearman correlation is expected.

## 3 | RESULTS

The results from six of the eight forest plots (Indiana, Changbaishan, Fushan, Guanacaste, Gutianshan and Xishuangbanna) were consistent with downward trends on the left side and upward trends on the right side of the SES FRic curves (Figure 2, Tables S2.1 and S2.2 in Appendix S2). The breakpoints for these six plots were located in the right-hand part of the curve (rare species), indicating that there are significant changes of these downward trends to upward trends (Figure 2, Table S2.1 in Appendix S2). In other words, the rarest species in these forest plots added more to the overall community FRic than expected.

We further considered the results using an ad-hoc criterion for describing rare species (less than one individual of a species per hectare) (Hubbell & Foster, 1986) to evaluate if the breakpoints were associated with what may commonly be considered 'rare' species. The results show that, in general, the breakpoints were very close to values that match the criteria for 'rare' species used by Hubbell & Foster (1986) (Figure 2). Combined, the results for the trends and the breakpoints indicate that the progressively rare species add more than expected to the functional diversity of the tree community (Figure 2, Tables S2.1 and S2.2 in Appendix S2). For the other two plots (Wabikon Lake and Luquillo), the trends were more complex and rare species did not consistently contribute more than expected to the functional diversity of the community (Figure 2, Tables S2.1 and S2.2). For these two plots, the breakpoints were located on both the left- and the right-hand parts of the curve (Table S2.1), and the trends were downward (Figure 2, Table S2.2).

When the ranges of individual traits were evaluated, we found no consistent trends across the different plots, indicating that traits related to pioneer species (i.e., low wood density, high leaf nutrient content, high specific leaf area) are not consistently associated with the rarest species (Table S2.3, Figs S2.1–S2.8 in Appendix S2). Specifically, for Indiana, Changbaishan, Fushan, Guanacaste, Gutianshan and Xishuangbanna plots, the breakpoints on the right hand of the curve (rare species) were not consistently found for leaf trait maximum values and wood density minimum values (Table S2.3, Figs S2.1–S2.8). The results for the plots with historical disturbance, Wabikon Lake and Luquillo, showed significant changes in the trends in the left-hand of the curves (common species), but again the traits were not always consistent with the expectation for pioneer species (Table S2.3). Overall, we found no consistent support that our results were due to pioneer species being rare.



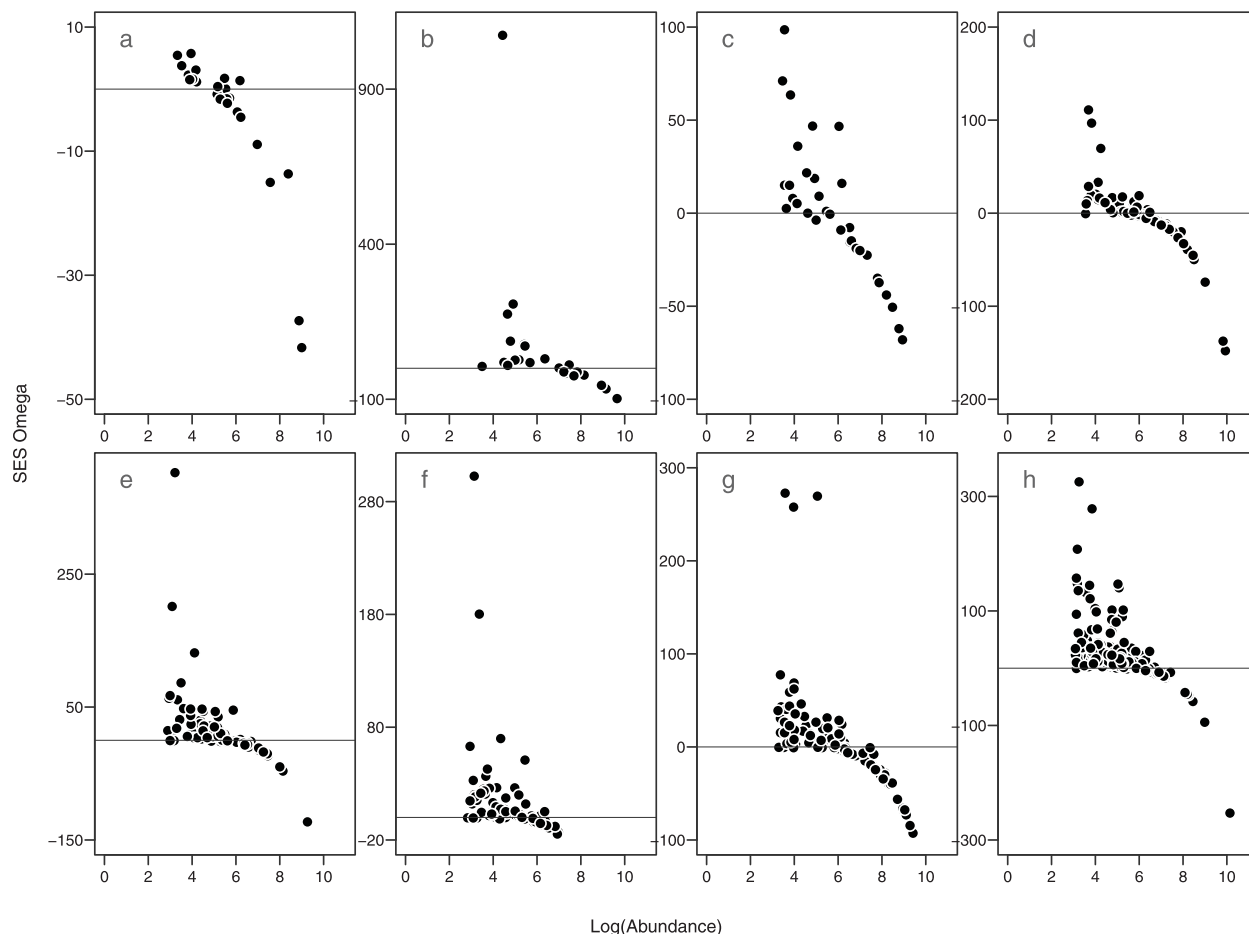
**FIGURE 2** The standardized effect sizes of functional diversity: (a) Indiana, USA; (b) Wisconsin, USA; (c) Changbaishan, China; (d) Fushan, Taiwan; (e) Luquillo, Puerto Rico; (f) Guanacaste, Costa Rica; (g) Gutianshan, China; (h) Xishuangbanna, China. Positive values on the y axis indicate that the species included in that calculation contribute more than expected to the functional diversity, and negative values indicate that they contribute less than expected to the functional diversity. Positive trends indicate that increasingly rare species are disproportionately increasing the functional diversity of the system. Vertical dotted grey lines in the panels indicate significant breakpoints in the piecewise regression (Table S2.1 in Appendix S2). Dashed portions of the trend lines indicate species that have less than one individual per hectare, which is a commonly used categorization for 'rarity' in tree communities

We further tested for evidence regarding whether rare species are spatially aggregated. This was done by evaluating the correlation between species abundance and SES  $\Omega$  values. The results show strong evidence that rare species tend to be more spatially aggregated than common species in all forests and spatial scales (Figure 3, Table S2.4 in Appendix S2). Common species tended to have negative SES  $\Omega$  values while rare species tended to have positive SES  $\Omega$  values. Some rare species were highly clustered distributed at the smallest annulus size (5 m) (Figure 3) as shown in the Wisconsin, Luquillo, Guanacaste and Gutianshan plots (Figure 3b, e–g).

#### 4 | DISCUSSION

A central goal of this study was to quantify whether rare species are functionally distinct from more common species, thereby adding more functional diversity than expected to tree communities world-wide (Gaston, 2012; Lawton, 1999). Our results show that in six of the eight plots, rare species tend to be functionally unique, indicating that rare

species are not rare because functionally similar species have pre-empted or excluded them. These results suggest that species abundance distribution is not only the result of historically contingent factors where the sequence and timing of arrival of functionally similar species is the main determinant of their abundance (Chase, 2003, 2007; Fukami, 2015). Instead, the combination of traits that characterize rare species may allow them to exploit different resources and therefore play an alternative role within the community, as suggested by similar results for other taxa (Leitaõ et al., 2016; Moullot, Villéger, Scherer-Lorenzen, & Mason, 2011; Moullot et al., 2013). However, in two of our study plots, Wabikon Lake, Wisconsin and Luquillo, Puerto Rico, the results showed different trends and the breakpoints were associated with common species. These two forests have both experienced past human disturbance via selective logging. The Luquillo plot has experienced two major hurricanes in the past 30 years (Thompson et al., 2002) and the dynamics at Luquillo plot have shown a higher functional turnover during the last 10 years compared with an undisturbed tropical forest in Panama (Swenson et al., 2012). It is possible



**FIGURE 3** The degree of spatial aggregation of individuals within a species. Standardized effect size (SES)  $\Omega$  values were plotted against their forest-wide abundance. The radius of the circle ( $\Omega$ ) surrounding each individual used for this figure was 5 m. Positive SES  $\Omega$  values indicate a higher degree of spatial aggregation. All correlations were statistically significant ( $p < .01$ ). Species with no conspecific individuals within the 5-m radius were omitted from these analyses but the correlations were still significant. Overall the trends show that rare species tend to be more clustered than common species. (a) Indiana, USA, (b) Wisconsin, USA, (c) Changbaishan, China, (d) Fushan, Taiwan, (e) Luquillo, Puerto Rico, (f) Guanacaste, Costa Rica, (g) Gutianshan, China, (h) Xishuangbanna, China

that this disturbance has affected the dynamics of these forests, having an important effect on the functional composition of the plant communities. As forested ecosystems become increasingly disturbed in the future, it may well be that functional diversity will be reduced through the loss of rare functionally divergent species, and functional homogenization through space and along the abundance distribution may become more common.

#### 4.1 | Rarity and specialization

A potential explanation for unifying the results for the eight plots is that weedy pioneer tree species with unique peripheral trait values (Bazzaz, 1980) are driving all the observed results across forests. Specifically, in the six undisturbed forests, pioneer species, usually described as rare members of pristine communities and specialized on rare gap environments, might be the species responsible for the observed pattern of functionally distinct rare species (Hubbell & Foster, 1986). Under this scenario, rarity would primarily be driven by the availability of habitats and functional specialization. However, upon

examination of increases in individual trait ranges as progressively rare species are added in each forest plot, we find no clear and consistent evidence that pioneer species with unique trait values are the determinant of our results. For example, some leaf traits showed increases associated with rare species, as is the case for *Trevesia palmata* (Araliaceae), a tree characterized by big leaves and no side branches, which is a very rare species in the Xishuangbanna tree community. However, the increases in leaf traits for other undisturbed forest plots were not always evident or were also associated with significant decreases in leaf trait values. For example, *Lonicera monantha* (Caprifoliaceae) is one of the rarest species in the Changbaishan plot, but it is not a pioneer species, instead is a shade-tolerant understorey tree. Therefore, these results provide little support for the pioneer habitat specialization hypothesis linked to rarity.

Rare species might not be necessarily pioneers, but they may be specialized in other ways. We attempted to explore this possibility by analysing the strength of the association between rare species and elevationally rare habitats compared with common species, suggesting potential specialization to particular elevations (Appendix S3).

Elevation, often linked to other topographical variables, has been found to play an important role in determining species distribution in tropical forest and is potentially a key factor determining habitat associations (Baldeck et al., 2013). We evaluated the preferred elevation of species, ordered from rarest to commonest, against the relative abundance of the elevation bins ordered from rarest to commonest. We failed to find evidence supporting the habitat specialization for rare species, apart from a very weak positive correlation in a few plots which was consistent across bin sizes (Appendix S3). However, we caution that the analytical approach used had several flaws that hinder our ability to completely reject the rare species–specialists relationship. Specifically, other habitat variables which were not measured that are not correlated (or are loosely correlated) with elevation in the plots may be axes upon which rare species specialize. Furthermore, it is also important to recall that our analyses concern local rarity both in species and elevation and we cannot say whether the rare species–specialists relationship is supported at larger spatial scales.

## 4.2 | Rarity and spatial aggregation

We further tested whether locally rare species are spatially aggregated. Our results show that locally rare species are more spatially aggregated than common species in all forests and spatial scales, suggesting that populations of locally rare species are small because (a) they are specialized on rare habitats or (b) locally rare species are sink populations and their spatial dispersion is limited due to rare dispersal events and a lack of reproduction and population spread, which combined drive the clustered individual spatial patterns. Although previous studies have found similar patterns, where locally rare species tend to be more clumped than common species (Condit, 2000; Hubbell, 1979; Li et al., 2009), one additional aspect that would help to clarify the role of rare species would be to evaluate their performance. In this respect, Hubbell (1979) showed that for a tropical forest analysed in this study (Guanacaste, Costa Rica), rare species tend to exhibit poor reproductive performance compared with common species, suggesting that specialization might not be the main factor driving rarity. Supporting these results, recent work by Mangan et al. (2010) experimentally demonstrated that rare species are more susceptible to pathogens. However, previous work by Wills et al. (2006), which included two of our study forests, showed that rare species have preferential recruitment; but, quantifying demographic rates for rare species can be challenging (Condit et al., 2006). Wills et al. (2006) argued that their results were evidence of frequency-dependent selection favouring rare species, thereby maintaining tree diversity. Thus, more studies are needed in order to fully support or reject the specialization hypothesis.

In some ways, it may be useful to consider our results in the context of the core–satellite hypothesis (Hanski, 1982). Hanski (1982) presented a classification of species according to their abundance and spatial distribution (regionally). In this context, locally small populations in a region may be considered satellite and perhaps sink populations, whereas locally large populations in a region may be considered core and perhaps source populations. One prediction arising from this would be that the locally rare populations, like those we analyse here, are satellite and perhaps sink populations ill-suited to the local environment. Due to data

limitations we were unable to address whether locally rare species were ill-suited to local conditions, and we have in many cases little information regarding whether the species in our forest plots are locally *and* regionally rare. Thus, at present we cannot fully address the predictions arising from the core–satellite literature. It is interesting to note, however, that recent work by Ricklefs and Renner (2012) has indicated that there is phylogenetic signal in local abundance in forest plots world-wide. This may indicate that there is inherent rarity in lineages that is evident locally and regionally, but it is still unclear from this evidence whether this rarity is due to specialization on rare habitats or some other process.

Together, our results fail to support the notion that rarity is driven by ecological similarity between rare species and competitively superior or earlier arriving common species. Also, we present tentative evidence that did not support the link between specialization and rarity based upon our analyses of elevational data and shade tolerance strategies. We do note, however, that soil nutrient and light data would be preferred for such an analysis, and future work on this topic is merited. Our results have additional implications beyond those for community structure and assembly. First, because locally rare species disproportionately contribute to community functional diversity it is expected that they may also disproportionately contribute to ecosystem function (Mouillot et al., 2011; Tilman et al., 1997). Recent work has indicated this may be the case in several tropical systems (Mouillot et al., 2013). The present work shows that rare species tend to be functionally unique, but they may not be disproportionately influencing present-day functioning. However, functionally unique rare species are still likely to be critical for the stability of ecosystems undergoing change. Thus, the loss of rare species in ecosystems not only reduces the species and functional dimensions of biological diversity (Hector & Bagchi, 2007) but probably also has the potential to negatively impact the ability of ecosystems to respond to change or forcing. Second, a great deal of emphasis is now being placed on building large plant trait and spatial datasets for the purpose of mapping the distribution and diversity of plant function world-wide to facilitate vegetation modelling and biodiversity science (Kattge et al., 2011; Lamanna et al., 2014; van Bodegom, Douma, & Verheijen, 2014). Such databases will inevitably be biased towards the inclusion of locally common species and the exclusion of locally rare species. This problem will be exacerbated in tropical systems, where it is likely that such efforts will be prone to underestimate tropical functional diversity compared with temperate functional diversity. Thus, future analyses should attempt to avoid such biases and, just as importantly, a great deal more information regarding the functional diversity of entire tropical assemblages will be needed.

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## AUTHOR CONTRIBUTIONS

M.N.U. and N.G.S. designed the study; all authors conducted the study; M.N.U., N.G.S., X.M., I.-F.S., D.J. and Y.I. performed all data analyses; M.N.U. and N.G.S. wrote the manuscript; M.C., B.E., Z.H., R.H., D.J., Y.I., L.L., X.L., K.M., I.-F.S., J.T., M.U., X.W., A.W., J.Y. and J.K.Z. commented on and edited the manuscript.

Census and trait data are available on (to be filled upon acceptance).

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## BIOSKETCH

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## SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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