

# Community context, resource dynamics, and body size differences shape multidimensional niche overlap among avian frugivores in South Asian tropics

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## Research Article

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# Abstract

Understanding how niche overlap is structured across multiple dimensions is central to explaining species coexistence. Most studies examining niche overlap focus on a single axis, and our understanding of ecological conditions that promote niche overlap is limited. Here, we examined multidimensional niche overlap among avian frugivores along dietary, vertical space-use, and temporal axes in tropical evergreen forests of Anamalai and Namdapha Tiger Reserves in the Western Ghats and eastern Himalaya, respectively. These sites differed in frugivore species richness but were otherwise environmentally similar. Using > 1100 hours of focal observations, we quantified pairwise frugivore niche overlap and tested how they varied with frugivore species richness, fruit abundance, tree identity, and body-size differences between species. Observed pairwise overlaps were lower than expected by chance across all niche dimensions, and were 1.6–2.2 times lower in Namdapha, the more species-rich site, indicating stronger niche differentiation in the more diverse assemblage. Overlap increased on trees with larger fruit crops and was particularly higher on *Ficus*. Overlap declined with increasing body-size differences between interacting frugivores. Our findings suggest that multidimensional niche overlap in tropical frugivore assemblages is structured by competition, local resource context, and species traits, thereby providing useful insights into the mechanisms promoting coexistence in diverse tropical communities.

## INTRODUCTION

A central challenge in community ecology is explaining how numerous ecologically similar species coexist within local communities. Because species' niches are inherently multidimensional (Hutchinson 1957), differentiation may occur along dietary, spatial, or temporal dimensions, or through combinations of these dimensions. The extent to which sympatric species overlap in resource use influences the strength of interspecific interactions and the potential for stable coexistence (Pastore et al. 2021; Reyes-Puig et al. 2025). Even within a single foraging guild, species may differ in the types of resources they consume (Kartzinel et al. 2015), their use of vertical space (Thiel et al. 2021), or their temporal activity patterns (Albrecht and Gotelli 2001). Understanding how niche overlap is structured across multiple dimensions is therefore critical for explaining the maintenance of high species diversity, particularly in tropical assemblages.

The degree of niche overlap among coexisting species is context-dependent. Previous studies have highlighted resource breadth and availability, and the number of co-occurring species (i.e., local species richness) in the community as key factors in influencing niche overlap (Sushma and Singh 2006; Costa-Pereira et al. 2019). The size of the local species pool may shape patterns of overlap by altering the intensity of competition and opportunities for resource sharing, thereby allowing multiple species to coexist. Abundant resources may reduce competitive constraints and permit greater niche overlap among species (Perry and Pianka 1997). The effect of resource abundance on niche overlap, particularly when resources are concentrated, has produced idiosyncratic results, with studies reporting both positive (Correa and Winemiller 2014) and no relationships (Perini and Vieira 2026). Nevertheless, while

many studies have emphasised niche differentiation as a mechanism of coexistence, comparatively less attention has been given to the ecological conditions that may promote overlap among sympatric species (but see Costa-Pereira et al. 2019).

In tropical ecosystems, plant–frugivore interactions are particularly important, as nearly 90% of woody plant species produce fleshy fruits and a substantial proportion of bird species depend heavily on fruits for nutrition (Jordano 2000). These interactions are shaped by multiple factors, including fruit and seed traits, frugivore morphology, and resource availability (Bender et al. 2018; Palacio and Ordano 2018; Rojas et al. 2021). From the plant’s perspective, seed dispersal by a diverse assemblage of frugivores can provide complementary dispersal services, allowing escape from density-dependent mortality, access to suitable recruitment sites, gene flow, and range expansion (Janzen 1970; García and Martínez 2012). For frugivores, fruits are often patchily distributed in space and time (Levey 1988; van Schaik et al. 1993), potentially intensifying competition, particularly during periods of low fruit availability. Consequently, plant–frugivore systems offer an interesting opportunity for examining how species partition resources across multiple niche dimensions. Understanding how frugivores overlap and segregate along dietary, spatial, and temporal axes is therefore key to explaining how numerous frugivores coexist in diverse assemblages in tropical forests.

Past studies of frugivore assemblages have documented dietary differentiation (Kitamura et al. 2002), dominance hierarchies during foraging (French and Smith 2005), and evidence for vertical stratification within forest canopies (Thiel et al. 2021). However, most investigations have examined these niche dimensions in isolation. Temporal partitioning among frugivores, in particular, remains comparatively understudied (but see Li et al. 2026). In addition, simultaneous evaluation of dietary, spatial, and temporal axes is rare. Yet coexistence may not require complete segregation across every dimension; rather, substantial overlap along one axis could be offset by differentiation along another (Hutchinson 1957; Ayebare et al. 2023). A multidimensional approach is therefore necessary to understand how overlap and segregation interact to structure frugivore communities.

Variation in the richness of the local species pool may further influence patterns of niche overlap. Local assemblages are shaped by both historical processes (e.g., speciation and biogeographic history) and ecological assembly processes such as environmental filtering, biotic filtering, and dispersal limitation (HilleRisLambers et al. 2012). Tropical forest sites that are climatically similar, differ in species richness, and have nested frugivore assemblages can provide a natural framework for testing how community context shapes niche overlap (Swenson et al. 2016).

Fruit resource availability is also likely to mediate overlap among frugivores. Because fruits are spatially and temporally patchy, frugivores often track trees with large fruit crops (Ortiz-Pulido and Rico-Gray 2000). High crop sizes may concentrate individuals (Abrahão et al. 2024), potentially promoting spatial and temporal overlap. In addition, fruit crop size often covaries with seed size and tree species identity (Palacio and Ordano 2018), and different fruit types may vary in their influence on frugivore assemblages. For instance, *Ficus* has been shown to have higher species strength (a measure of their

importance to frugivores) than even other small-seeded trees (Naniwadekar et al. 2021), suggesting that certain resource types may disproportionately structure patterns of niche overlap. Together, these mechanisms indicate that both the quantity and identity of fruit resources may influence niche overlap patterns across different dimensions.

In addition to resource context, species traits may further shape patterns of niche overlap. Ecological theory predicts that sympatric species, particularly those that are functionally similar and closely related, may diverge in resource use to reduce competitive overlap (MacArthur and Levins 1967; Schoener 1974). At the same time, morphological constraints can limit the range of resources a frugivore can exploit. The morphological trait-matching hypothesis posits that frugivore body size and gape width constrain the size and type of fruits that can be handled efficiently (Wheelwright 1985; McFadden et al. 2022). Thus, while competition may promote niche differentiation among similar species, shared morphological constraints may simultaneously promote convergence in resource use. The trade-off between these opposing factors could determine whether morphological similarity enhances or reduces niche overlap within frugivore assemblages.

Given this background, we examined how niche overlap among sympatric avian frugivores is structured by community context, resource dynamics, and species traits across three niche dimensions. We compared patterns of overlap in diet, vertical space use, and temporal activity at two wet tropical forest sites differing in species richness, and evaluated how fruit resource availability and identity (*Ficus* and non-*Ficus* small-, medium-, and large-seeded species) influenced overlap across vertical and temporal dimensions. Finally, we assessed whether these patterns are mediated by differences in frugivore body size, reflecting morphological constraints on resource use. We predicted that 1) the extent of overlap would differ among niche dimensions, 2) overlap would be lower in the species-rich assemblage if stronger competitive interactions promote niche differentiation, 3) higher fruit crop sizes would facilitate greater overlap by relaxing resource limitation, 4) *Ficus*, given its disproportionate importance in frugivore networks, would promote greater overlap relative to other categories of fruiting trees, and 5) greater differences in body size would be associated with reduced overlap due to trait-based constraints on fruit resource use. By integrating community context, resource availability, resource identity, and functional traits, this study provides a multidimensional understanding of the factors shaping niche overlap in tropical frugivore assemblages.

## MATERIALS AND METHODS

### Study area

We conducted this study in two evergreen forest sites in India: Hornbill Plateau in the Namdapha Tiger Reserve (27°23'–27°39'N and 96°15'–96°58'E; duration: November 2022 to April 2023; elevation range: 550–800 m asl) in the Eastern Himalaya, and Manamboli and Ulandy Ranges in the Anamalai Tiger Reserve (10°12'–10°35'N and 76°49'–77°24'E; duration: November 2023 to May 2024; elevation range: 650–1000 m asl) in the Western Ghats. Both sites lie within protected areas with minimal anthropogenic

disturbances and receive approximately 2,500 mm of annual rainfall, primarily during the southwest monsoon (June-September) and the northeast monsoon (November-December). The forests at both sites are classified as wet tropical rainforests (Proctor et al. 1998; Muthuramkumar et al. 2006) and fall within the “Tropical and Subtropical Moist Broadleaf Forests” biome (Olson et al. 2001). Despite being located in two distinct biodiversity hotspots (Himalaya and Western Ghats-Sri Lanka Biodiversity Hotspots), the sites share several key frugivore lineages, including hornbills (Bucerotidae), barbets (*Psilopogon* spp.), bulbuls (Pycnonotidae), Asian fairy bluebird (*Irena puella*), hill myna (*Gracula* spp.), green-pigeons (*Treron* spp.) and imperial-pigeons (*Ducula* spp.), as well as representatives of key bird-dispersed woody plant families, including Lauraceae, Moraceae, Meliaceae, Myristicaceae, and Oleaceae. However, the two assemblages differ in overall frugivore species richness (Anamalai: 26; Namdapha: 40 species recorded during the study period), allowing meaningful comparison of niche overlap patterns across contrasting community contexts.

## Plant–frugivore interactions

We searched for bird-dispersed tree species bearing ripe fruits along existing trails. Upon finding fruiting trees, we conducted focal tree watches on a total of 67 trees in Namdapha and 119 trees in Anamalai, representing 28 tree species at each site. We began each focal tree watch around sunrise and continued for six hours, following established methods (Naniwadekar et al. 2025), using 8 × 40 or 8 × 42 binoculars. During each focal watch, we recorded the identity and number of visiting birds, arrival and departure times, initial foraging height (measured from the base of the focal tree in five-metre bins using a Bushnell Engage/Prime 1700 laser range finder), and feeding interactions (whether consuming fruits or not). For analyses of vertical space use, each visit was assigned to the height stratum at which the bird was first observed. Subsequent movements within the tree during the same visit were not considered and were not significantly different from the initial height where the bird was observed (Fig. S4). We classified bird species as frugivores for a given tree species only if they were observed consuming at least one fruit, following previous studies (Naniwadekar et al. 2019). Observations where bird species visited a tree species but never consumed a fruit during the study period at a site were excluded from the analysis. Ripe fruit crop size (FCS) of each focal tree was estimated by counting the number of ripe fruits on multiple branches and estimating it for the entire canopy for small-seeded species, dividing the foliage into four quarters and counting fruits in one quarter and extrapolating it to others for medium- and large-seeded plant species, and doing total counts for certain large-seeded species (e.g., *Myristica*) following Davidar and Morton (1986) and Naniwadekar et al. (2025).

## Fruit and frugivore traits

Tree species were grouped into four categories: *Ficus* (all trees belonging to the genus *Ficus*), non-*Ficus* small-seeded (seed width < 5 mm), non-*Ficus* medium-seeded (5–15 mm), and non-*Ficus* large-seeded (> 15 mm), following Naniwadekar et al. (2021). *Ficus* was treated as a separate category due to its high ecological significance to tropical frugivores (Lambert and Marshall 1991). Species-level body mass

data for all avian frugivores were obtained from the 'Avonet' global bird trait database (Tobias et al. 2022).

## Statistical analyses

### Pairwise frugivore niche overlap across dietary, vertical and temporal axes

We quantified pairwise niche overlap among frugivore species using Pianka's index (Pianka 1973):

$$O_{jk} = \sum (p_{ij} \times p_{ik}) / \sqrt{[(\sum p_{ij}^2)(\sum p_{ik}^2)]}$$

where  $O_{jk}$  is Pianka's index of niche overlap between species  $j$  and  $k$ , and  $p_{ij}$  and  $p_{ik}$  are the proportional use of resource  $i$  by species  $j$  and  $k$ , respectively. Pianka's index ( $O$ ) ranges from 0 (no overlap) to 1 (complete overlap). Overlap was calculated separately for dietary, vertical, and temporal niche dimensions at each site. For dietary overlap calculation, we constructed weighted plant–frugivore interaction matrices in which each cell represented the visitation rate (number of bird visits per hour) of a given frugivore species to a fruiting tree species, thereby standardising interactions for sampling effort. We calculated vertical overlap from matrices representing frugivore counts across five-metre height classes within each focal tree (measured from the base of the focal tree). We calculated temporal overlap using matrices of frugivore counts in five-minute time bins for each focal tree during each six-hour focal watch, irrespective of their vertical position within the tree. Five-minute time bins were selected based on the minimum mean visit duration across frugivore species (Fig. S3).

To test whether observed niche overlap differed from random expectations, we generated 999 null interaction matrices for each niche dimension (dietary, vertical, and temporal) separately for each site. In each case, we preserved row and column totals while randomly redistributing visits among cells. For each null matrix, pairwise Pianka's niche overlap index was recalculated, and the mean overlap was computed. The observed mean overlap was then standardised relative to the null distribution using standardised effect sizes (SES; z-scores). Positive SES values ( $> 2$ ) indicate greater overlap than expected by chance, whereas negative values ( $< -2$ ) indicate lower-than-expected overlap. To assess whether observed overlap differed between Anamalai and Namdapha, null models were run independently for each site, and for each iteration, the difference in mean overlap between sites was calculated. The observed difference was then compared to the resulting null distribution of differences.

### Ripe fruit availability and frugivore overlap in vertical space and time

To examine whether fruit availability influenced Pianka's niche overlap index at the scale of individual trees, we calculated pairwise vertical overlap (based on five-metre height classes discussed above) and temporal overlap (based on five-minute time bins) for all possible frugivore species pairs visiting each

focal tree individual that was used by at least two frugivore species. Because the distribution of overlap values was strongly zero-inflated (~ 90% values were zeros), we modelled the occurrence of overlap (absence = 0, any overlap = 1) as a function of log-transformed fruit crop size using binomial generalised linear mixed-effects models as implemented by the R package 'glmmTMB'. A log transformation was applied because fruit crop sizes varied by several orders of magnitude across tree watches. Individual focal tree identity was included as a random intercept to account for multiple frugivore species pairs per tree. In addition, the identities of both frugivore species within each interacting pair were included as random intercepts to account for non-independence arising from shared species across multiple pairs. Separate models were fitted for vertical and temporal overlap at each site. Since the dietary overlap among frugivore species pairs was estimated at the tree species level and not at the individual tree level, we did not carry out this analysis for dietary overlap.

## Tree type and frugivore niche overlap

Seed size and tree type are known to influence the diversity and abundance of frugivores visiting fruiting trees (Naniwadekar et al. 2021, 2025). We therefore examined whether a particular tree category facilitated greater frugivore overlap in vertical space and time at each study site. Trees were categorised as mentioned earlier: *Ficus*, non-*Ficus* small-seeded, medium-seeded, and large-seeded. Despite having small seeds, we classified *Ficus* in a different category because they have been reported to have significantly higher species strengths than other small-seeded trees (Naniwadekar et al. 2021). To assess the contribution of each tree type to overlap across niche dimensions, we recalculated overlap after sequentially excluding interactions associated with a given tree category. We compared these values with those from the full dataset, including all tree types. A tree type was considered to contribute significantly to niche overlap if the 95% confidence intervals of overlap estimates from the reduced dataset did not include the mean overlap value from the full dataset, indicating a clear shift in overlap following its exclusion (Cumming et al. 2007).

## Body size of interacting frugivores and niche overlap

We analysed the relationship between pairwise niche overlap and body-mass difference (difference between log-transformed body masses of interacting species) of frugivore species pairs using separate generalised linear mixed-effects models (GLMMs) for each combination of overlap type (dietary, vertical, temporal) and study site (Anamalai and Namdapha) using the R package 'glmmTMB'. Overlap values (Pianka's index) for all three niche axes in our study were continuous and bounded between 0 and 1; therefore, we fitted each model with a beta error distribution and logit link. Overlap values of 0 or 1 were adjusted slightly to fall within the open interval (0, 1). In each model, we included frugivore body mass difference as a fixed effect. In addition, to account for non-independence arising from repeated appearances of species across multiple pairs, we included the identities of each frugivore in a species pair as random intercepts. Models were fitted separately for each site and overlap axis to allow effect

sizes to vary independently across ecological contexts. We carried out all analyses in this study using R (ver. 4.4.1).

## RESULTS

We recorded a total of 26 and 40 avian frugivore species during our sampling periods in Anamalai and Namdapha, respectively. However, many species visited focal trees infrequently, as is typical of community ecology data (Preston 1980; McGill et al. 2007). To ensure meaningful interpretation of pairwise niche overlap, we restricted analyses to frugivore species that visited > 10% of focal tree individuals at each site. Consequently, our analyses included the nine relatively frequently observed frugivore species in Anamalai (yielding 36 unique frugivore species pairs) and 18 species in Namdapha (yielding 153 unique species pairs) (Table S1). Among all frugivore species pairs in Anamalai, Malabar Barbet *Psilopogon malabaricus* and Southern Hill Myna *Gracula indica* exhibited the highest overlap along the dietary (Pianka's index: 0.93) and temporal (0.28) niche axes, whereas Asian Fairy-bluebird *Irena puella* and White-cheeked Barbet *Psilopogon viridis* showed the greatest overlap in vertical space use (0.50) (Fig. 1). In Namdapha, Asian Fairy-bluebird *Irena puella* and Blue-winged Minla *Actinodura cyanouroptera* showed the highest overlap in the dietary (0.90) and vertical axes (0.70), whereas Blue-winged Minla *Actinodura cyanouroptera* and Rufous-backed Sibia *Leioptila annectens* exhibited the greatest temporal overlap (0.41) (Fig. 1).

## Pairwise niche overlap along dietary, vertical and temporal axes

Across all niche dimensions (dietary, vertical, and temporal) in both Anamalai and Namdapha, the observed mean pairwise niche overlap was significantly lower than expected under the null model (Table 1). Standardised effect sizes were strongly negative at both sites across all three axes, indicating significantly lower niche overlap than expected by chance. Null model means were similar between Anamalai and Namdapha across all niche dimensions, suggesting comparable null expectations despite differences in species richness. Frugivorous birds showed greater dietary, intermediate vertical, and low temporal overlap, all of which were significantly lower than the niche overlap expected by chance. Observed overlap was consistently higher in Anamalai (the species-poor site) than in Namdapha (the species-rich site) across all three niche axes (Table 1; Fig. 2). Specifically, mean (95% CI) dietary overlap in Anamalai (0.45; 95% CI: 0.38–0.53) was 2.2 times higher than in Namdapha (0.21; 95% CI: 0.18–0.24) (Table 1, Fig. 2). Similarly, vertical overlap was 1.6 times higher in Anamalai (0.21; 95% CI: 0.17–0.26) compared to Namdapha (0.13; 95% CI: 0.11–0.15) (Table 1, Fig. 2). Temporal overlap was 2.2 times higher in Anamalai (0.11; 95% CI: 0.08–0.13) than in Namdapha (0.05; 95% CI: 0.04–0.06) (Table 1, Fig. 2).

Table 1

Observed and null model estimates of mean pairwise niche overlap among frugivores (using Pianka's index) along dietary, vertical, and temporal niche dimensions in Anamalai (species-poor site) and Namdapha (species-rich site). Standard deviations (SD) and standardised effect sizes (z-score) from the null models are also reported. Observed niche overlap values across all dimensions in both sites are consistently lower than null expectations, and the observed values in Anamalai are higher than in Namdapha. Interestingly, the null mean values for both Anamalai and Namdapha are very similar.

| Site/Inter-site comparison | Niche dimension | Observed value | Null mean | Null SD | z-score |
|----------------------------|-----------------|----------------|-----------|---------|---------|
| Anamalai                   | Dietary         | 0.452          | 0.713     | 0.034   | -7.68   |
| Namdapha                   | Dietary         | 0.210          | 0.697     | 0.025   | -19.42  |
| Anamalai                   | Vertical        | 0.211          | 0.737     | 0.014   | -37.63  |
| Namdapha                   | Vertical        | 0.130          | 0.747     | 0.012   | -50.30  |
| Anamalai                   | Temporal        | 0.106          | 0.381     | 0.005   | -60.98  |
| Namdapha                   | Temporal        | 0.047          | 0.477     | 0.005   | -85.73  |
| Anamalai – Namdapha        | Dietary         | 0.242          | 0.016     | 0.043   | 5.31    |
| Anamalai – Namdapha        | Vertical        | 0.081          | -0.010    | 0.019   | 4.85    |
| Anamalai – Namdapha        | Temporal        | 0.059          | -0.096    | 0.007   | 22.50   |

## Role of ripe fruit availability in influencing frugivore niche overlap

The GLMM results suggested that the probability of pairwise frugivore niche overlap in both vertical space and time increased significantly with ripe fruit availability at the level of individual fruiting trees in both our study sites, Anamalai and Namdapha (Fig. 3, Table S2). In addition, variation in the probability of overlap was explained by differences among focal trees and among frugivore species identities, with random-effect variance attributed to focal tree individuals and to frugivore species within each frugivore species pair (Table S3).

## Tree type and frugivore niche overlap

The mean overlap values did not differ from the original ones after we dropped non-*Ficus* small-seeded trees (except for dietary axis in Namdapha, where the mean (95% CI) overlap increased from 0.21 (0.18–0.24) to 0.29 (0.25–0.33)), non-*Ficus* medium-seeded trees (except for dietary axis in Anamalai, where the mean (95% CI) overlap increased from 0.45 (0.38–0.52) to 0.53 (0.46–0.60)), and non-*Ficus* large-seeded trees (except for dietary axis in Namdapha, where the mean (95% CI) overlap increased from 0.21 (0.18–0.24) to 0.26 (0.22–0.29)) (Fig. 4). However, they decreased significantly after we dropped *Ficus* from the analysis (except for dietary axis in Anamalai) (Fig. 4). Specifically, for dietary axis, the mean (95% CI) overlap decreased from 0.21 (0.18–0.24) to 0.10 (0.07–0.13) in Namdapha, for vertical

axis the mean (95% CI) overlap decreased from 0.21 (0.16–0.26) to 0.15 (0.10–0.20) in Anamalai and from 0.13 (0.11–0.15) to 0.06 (0.04–0.08) in Namdapha, and for temporal axis the mean (95% CI) overlap decreased from 0.11 (0.08–0.13) to 0.06 (0.04–0.08) in Anamalai and from 0.05 (0.04–0.06) to 0.02 (0.01–0.03) in Namdapha (Fig. 4). Taken together, these results suggest that among all tree types examined in our study, *Ficus* allowed significantly higher frugivore niche overlap on them in all niche axes, especially in species-rich site, Namdapha. This is despite *Ficus* having similar fruit crop sizes as non-*Ficus* small-seeded tree species (Fig. S2).

## Body size of interacting frugivores and pairwise niche overlap

Among frugivore species observed during tree watches, both sites encompassed a similar range of body masses. Specifically, the heaviest frugivore at both sites was the Great Hornbill *Buceros bicornis* (2,791 g). In contrast, the lightest species incorporated in the analyses were the Flame-throated Bulbul *Rubigula gularis* (29.3 g) in Anamalai and the Whiskered Yuhina *Yuhina flavicollis* (16.9 grams) in Namdapha. Across niche dimensions, pairwise overlap generally declined with increasing body mass difference between frugivore species in a pair (Fig. 5, Table S4). This negative relationship was evident for vertical and temporal overlap at both sites, and for dietary overlap in Namdapha, but was weak in Anamalai. What is also evident is that, for smaller body-size differences, niche overlap was low to moderate, whereas for large body-size differences, it was consistently low. Overall, these patterns indicate that morphologically similar species may exhibit greater niche overlap, whereas species differing substantially in body size are more strongly partitioned across niche dimensions.

## DISCUSSION

In this study, we examined patterns of niche overlap among avian frugivores across three key dimensions: diet, vertical space, and time, across multiple ecological contexts, including variation in species pool size, fruit crop size, plant functional type, and body-size differences among sympatric frugivore species. Multidimensional niche overlap among frugivore species pairs was generally low (< 50%) across both study sites, indicating substantial segregation along one or more axes. Notably, overlap was consistently lower at the species-rich site, Namdapha, than at the relatively species-poor site, Anamalai, suggesting stronger niche partitioning in the more diverse assemblage. Beyond differences in species richness, niche overlap increased with fruit crop size, indicating that greater resource availability may promote niche overlap. Tree type also influenced niche overlap patterns, with *Ficus* fostering greater overlap among frugivore pairs across niche dimensions, reflecting its role as a keystone resource. Additionally, morphologically similar species exhibited greater overlap across most niche dimensions, highlighting the role of body size in influencing resource use and partitioning. Taken together, these findings suggest fine-scale, multidimensional niche segregation facilitating coexistence in species-rich tropical frugivore assemblages, while also underscoring the influence of species pool, resource availability, resource type, and body size in shaping overlap patterns.

Our multidimensional approach to quantifying niche overlap reveals consistently low overlap among frugivore species across dietary, vertical, and temporal axes. Such limited overlap across multiple dimensions suggests that fine-scale niche segregation facilitates the coexistence of numerous sympatric frugivores in tropical forests (Todeschini et al. 2020). Importantly, overlap was consistently lower in the relatively species-rich site than in the species-poor site, indicating stronger niche differentiation in the more diverse assemblage. Interestingly, the sampling effort in terms of the duration of study and human hours invested is similar across both sites, and we found an identical number of fruiting tree species at both sites in the given time duration, suggesting that the underlying differences in fleshy-fruited tree diversity may not be influencing the observed patterns. Furthermore, the similarity in null expectations across sites for each niche dimension, together with the consistency of observed overlap after controlling for sampling effort and frugivore group representation (Fig. S1), indicates that the lower overlap observed in the species-rich site is unlikely to be an artefact of data structure. Instead, these patterns are consistent with stronger niche differentiation in the higher-diversity assemblage (Schoener 1974; Pastore et al. 2021). These findings contrast with previous work, which reported greater niche overlap with increasing frugivore species richness (Dehling et al. 2022). However, that study examined niche overlap primarily in relation to plant functional traits along the dietary axis only. By contrast, our study utilised foraging observations and did not rely on plant functional traits to infer overlap patterns.

In addition to dietary partitioning, our multidimensional framework captures segregation across spatial and temporal dimensions, too, revealing patterns that may not be evident when diet is considered alone. While we have not estimated stabilising fitness differences, these metrics provide process-informed proxies of realised niche similarity among species (Levine et al. 2025). Lower overlap across multiple dimensions suggests stronger niche differentiation, which is predicted to enhance stabilising coexistence mechanisms. The lower overlap observed at the species-rich site is consistent with the richness–specialisation hypothesis, which predicts a positive relationship between species richness and niche specialisation (Belmaker et al. 2012; Pellissier et al. 2018), as documented in a recent study (Mandal et al. 2026). Frugivores’ diets are known to be plastic and context-dependent (Naniwadekar et al. 2021), with evidence for dietary niche expansion in the absence of competitors (Bolnick et al. 2010). We speculate that similar expansion may occur not only in diet but also along vertical and temporal axes in species-poor assemblages, resulting in comparatively greater multidimensional niche overlap.

Competition theory predicts that the strength of niche partitioning depends on the intensity of resource limitation (Chesson 2000). When resources are scarce, interspecific competition is expected to promote stronger niche differentiation (MacArthur and Levins 1967). Conversely, when resource availability is high, competitive constraints may relax, allowing species to expand their realised niche and increasing overlap (Colwell and Futuyma 1971). In line with this expectation, we observed greater dietary, vertical and temporal overlap on trees with larger fruit crops. High fruit abundance may reduce direct competitive interactions by relaxing resource limitation, thereby permitting greater behavioural plasticity across niche dimensions. Similar context-dependent increases in dietary overlap under high resource availability have been reported in rodents during mast years (Stephens et al. 2019), in frugivorous fishes

during the period of high fruit abundance (Correa and Winemiller 2014), and in pollinators during periods of floral abundance (Casanelles-Abella et al. 2023). Furthermore, the relatively higher temporal overlap observed among similarly-sized species pairs may also reflect heterospecific facilitation, particularly under conditions of high resource availability. For example, the arrival of a frugivore at a fruiting tree may provide cues (e.g. vocalisations or movement) that attract other individuals, leading to increased temporal co-occurrence, as has been reported for mass-fruiting trees (Gu et al. 2017).

Small-seeded bird-dispersed species often produce larger fruit crops than large-seeded species, consistent with the quality-quantity trade-off in fleshy fruits and the greater accessibility of small fruits to a wider range of frugivores; therefore, they are expected to facilitate greater niche overlap (Wheelwright 1985; Hazell et al. 2023). However, among small-seeded trees, *Ficus* permitted significantly higher overlap than non-*Ficus* species, even though fruit crop size did not differ significantly between them (Fig. S2). This indicates that factors beyond crop size, per se, drive the elevated overlap observed on figs. *Ficus* species are widely regarded as keystone resources in tropical ecosystems due to their asynchronous fruiting phenology, which provides reliable food during periods of general fruit scarcity (Lambert and Marshall 1991; Kattan and Valenzuela 2013). By offering predictable and often temporally buffered resources, figs may act as focal aggregation points where multiple frugivore species converge, particularly during lean fruiting periods. Such convergence could increase fine-scale dietary, spatial, and temporal overlap. In addition, most *Ficus* species in our study were large canopy trees, and tree stature has been shown to influence frugivore visitation rates positively (Jayanth et al. 2024). Thus, structural prominence may further enhance aggregation at figs. Nutritional attributes of figs, including high calcium content (O'Brien et al. 1998), may also increase attractiveness to frugivores. Together, these characteristics suggest that *Ficus* function as ecological hubs that concentrate frugivore activity and thereby modulate patterns of niche overlap. Future work should explicitly test whether overlap on *Ficus* is strongest during periods of landscape-level fruit scarcity and disentangle the relative contributions of phenology, crop size, and tree stature to frugivore co-occurrence patterns.

Most temporal overlap studies aggregate observations across multiple locations, thereby estimating landscape-level similarity without accounting for fine-scale spatial segregation (Marinho et al. 2020; Murray et al. 2023). However, temporal co-occurrence does not necessarily translate into competitive interaction if species are spatially separated. By quantifying temporal overlap at the level of individual fruiting trees, we incorporate spatial context directly into the analysis. Because competition requires co-occurrence in both space and time, tree-level estimates provide a more ecologically meaningful measure of potential interaction strength. Our results show that temporal overlap at this fine spatial scale is relatively low, suggesting that apparent temporal similarity at broader scales may overestimate the likelihood of direct competitive encounters. This spatially explicit perspective aligns with the modern coexistence theory, which emphasises that interaction strength depends on realised encounters rather than broad-scale similarity alone (Chesson 2000; Hart et al. 2017). Incorporating spatial context, therefore, refines inferences about stabilising niche differences.

We found that morphologically divergent species pairs consistently exhibited low niche overlap across multiple dimensions. This pattern aligns with the concept of limiting similarity (MacArthur and Levins 1967) and modern coexistence theory (Chesson 2000), whereby greater trait differences reduce interspecific competition by enhancing stabilising niche differences. Body size is a key functional trait influencing resource acquisition, movement, and foraging behaviour (Brown et al. 2004), and thus can mediate dietary, vertical, and temporal segregation among frugivores. Morphological constraints on resource use, such as gape limitation, have been shown to drive dietary differentiation (Dehling et al. 2016; Naniwadekar et al. 2019), while vertical stratification further promotes partitioning among foraging guilds, with larger-bodied species such as hornbills predominantly using the upper canopy and smaller frugivores such as bulbuls foraging in lower strata (Shanahan and Compton 2001). It is interesting to note that morphologically divergent species pairs in our study exhibited minimal temporal overlap. This could be a likely outcome of differing activity patterns of large- and small-bodied species (van Schaik and Griffiths 1996), an aspect that needs further investigation.

While species pairs with similar body sizes tended to exhibit greater niche overlap, they also exhibited a wider range of overlap values across niche dimensions, especially in Namdapha (Fig. 5). For smaller values of body-mass differences, niche overlap values could be high or low. This suggests that morphologically similar species may either occupy similar niches due to shared constraints or reduce competition by segregating along different niche axes. Such variability points to a balance between optimal foraging and competitive interactions in shaping realised niches. While species may preferentially exploit similar resources based on morphological suitability, interspecific competition, through both exploitative and interference mechanisms, can drive niche divergence (Schoener 1974). Empirical studies of Asian frugivore assemblages support this view, showing that closely-related and similarly-sized hornbill species can differ in both diet composition and canopy use (Hadiprakarsa and Kinnaird 2004). Specifically, sympatric hornbills vary in their reliance on figs versus non-fig fruits and in how they partition vertical space, with some species foraging predominantly in the upper canopy and others in mid- or lower strata. Together, these patterns highlight that the trait similarity does not necessarily translate into niche equivalence, but instead allows for flexible partitioning across multiple niche dimensions.

## CONCLUSIONS

Empirical studies that examine species niches at fine spatial and temporal scales while explicitly considering multiple niche dimensions remain relatively rare (but see Ayebare et al. 2023). To our knowledge, our study is among the first to quantify overlap patterns among co-occurring tropical avian frugivores across multiple niche dimensions and to evaluate how pairwise niche overlap in vertical space and foraging time are influenced by fruit resource availability at the level of individual fruiting trees. Using standardised sampling across two ecologically comparable tropical forest sites differing in species richness, we show that multidimensional niche differentiation is a key feature of frugivore assemblages. Lower niche overlap in the relatively species-rich assemblage suggests stronger partitioning across dietary, vertical, and temporal axes. In addition, we demonstrate that niche overlap is context-dependent,

increasing with local resource availability and varying across tree types, with *Ficus* likely functioning as important aggregation points that may facilitate co-occurrence. Finally, trait differences, particularly body size, further structure niche relationships, with morphologically divergent species exhibiting consistently low overlap. These findings highlight how the interplay between species richness, resource dynamics, and functional traits shapes multidimensional niche structure, providing insights into the mechanisms that may facilitate coexistence in diverse tropical communities.

## DECLARATIONS

### Declaration of authorship

All authors contributed substantially to this work, approved the final version of the manuscript, and agreed to its submission to Oecologia. The manuscript has not been published previously and is not under consideration for publication elsewhere.

### Conflicts of interest:

The authors have no conflicts of interest to declare.

#### **Ethics approval:**

This was an observational study and did not require ethical approval from a human subject or animal approval committee. However, we secured the necessary permissions from the respective forest departments to conduct the study in the protected areas: Anamalai (Permission no. WL5(A)/18255/2023) and Namdapha (Permission no. NNP(TR)/D/13–14/Vol-V/2968-73).

#### **Consent to participate:**

All patients included in this study gave written informed consent to participate in this research.

#### **Consent for publication:**

All patients provided written informed consent to publish the data contained within this article.

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## Authors' contributions:

RN, RM and AO originally formulated the idea and developed the methodology. RM, HL, ND and RK conducted fieldwork. RM and RN performed statistical analyses with inputs from AO. RM and RN led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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## Availability of data and material:

The data associated with this manuscript will be uploaded to a digital repository and made publicly available upon acceptance of the manuscript.

## Code availability:

The code will also be uploaded to a digital repository, along with the data.

## REFERENCES

1. Abrahão M, Buckeridge MS, Missagia CCC et al (2024) Influence of crop size and sugar content on bird fruit feeding patterns on two sympatric *Miconia* (Melastomataceae) species on a continental island in the Brazilian Atlantic Forest domain. *Ornithol Res* 32:310–321. <https://doi.org/10.1007/s43388-024-00202-3>
2. Albrecht M, Gotelli NJ (2001) Spatial and temporal niche partitioning in grassland ants. *Oecologia* 126:134–141. <https://doi.org/10.1007/s004420000494>
3. Ayebare S, Doser JW, Plumptre AJ et al (2023) An environmental habitat gradient and within-habitat segregation enable co-existence of ecologically similar bird species. *Proc R Soc B Biol Sci* 290:20230467. <https://doi.org/10.1098/rspb.2023.0467>

4. Belmaker J, Sekercioglu CH, Jetz W (2012) Global patterns of specialization and coexistence in bird assemblages. *J Biogeogr* 39:193–203. <https://doi.org/10.1111/j.1365-2699.2011.02591.x>
5. Bender IMA, Kissling WD, Blendinger PG et al (2018) Morphological trait matching shapes plant–frugivore networks across the Andes. *Ecography* 41:1910–1919. <https://doi.org/10.1111/ecog.03396>
6. Bolnick DI, Ingram T, Stutz WE et al (2010) Ecological release from interspecific competition leads to decoupled changes in population and individual niche width. *Proc R Soc B Biol Sci* 277:1789–1797. <https://doi.org/10.1098/rspb.2010.0018>
7. Brown JH, Gillooly JF, Allen AP et al (2004) Toward a Metabolic Theory of Ecology. *Ecology* 85:1771–1789. <https://doi.org/10.1890/03-9000>
8. Casanelles-Abella J, Fontana S, Fournier B et al (2023) Low resource availability drives feeding niche partitioning between wild bees and honeybees in a European city. *Ecol Appl* 33:e2727. <https://doi.org/10.1002/eap.2727>
9. Chesson P (2000) Mechanisms of Maintenance of Species Diversity. *Annu Rev Ecol Syst* 31:343–366. <https://doi.org/10.1146/annurev.ecolsys.31.1.343>
10. Colwell RK, Futuyma DJ (1971) On the Measurement of Niche Breadth and Overlap. *Ecology* 52:567–576. <https://doi.org/10.2307/1934144>
11. Correa SB, Winemiller KO (2014) Niche partitioning among frugivorous fishes in response to fluctuating resources in the Amazonian floodplain forest. *Ecology* 95:210–224. <https://doi.org/10.1890/13-0393.1>
12. Costa-Pereira R, Araújo MS, Souza FL, Ingram T (2019) Competition and resource breadth shape niche variation and overlap in multiple trophic dimensions. *Proc R Soc B Biol Sci* 286:20190369. <https://doi.org/10.1098/rspb.2019.0369>
13. Cumming G, Fidler F, Vaux DL (2007) Error bars in experimental biology. *J Cell Biol* 177:7–11. <https://doi.org/10.1083/jcb.200611141>
14. Davidar P, Morton ES (1986) The Relationship Between Fruit Crop Sizes and Fruit Removal Rates by Birds. *Ecology* 67:262–265. <https://doi.org/10.2307/1938529>
15. Dehling DM, Dalla Riva GV, Hutchinson MC, Stouffer DB (2022) Niche Packing and Local Coexistence in a Megadiverse Guild of Frugivorous Birds Are Mediated by Fruit Dependence and Shifts in Interaction Frequencies. *Am Nat* 199:855–868. <https://doi.org/10.1086/718684>
16. Dehling DM, Jordano P, Schaefer HM et al (2016) Morphology predicts species’ functional roles and their degree of specialization in plant–frugivore interactions. *Proc R Soc B Biol Sci* 283:20152444. <https://doi.org/10.1098/rspb.2015.2444>
17. French AR, Smith TB (2005) Importance of Body Size in Determining Dominance Hierarchies among Diverse Tropical Frugivores. *Biotropica* 37:96–101. <https://doi.org/10.1111/j.1744-7429.2005.04051.x>
18. García D, Martínez D (2012) Species richness matters for the quality of ecosystem services: a test using seed dispersal by frugivorous birds. *Proc R Soc B Biol Sci* 279:3106–3113.

<https://doi.org/10.1098/rspb.2012.0175>

19. Gu H, Chen J, Ewing H et al (2017) Heterospecific attraction to the vocalizations of birds in mass-fruited trees. *Behav Ecol Sociobiol* 71:82. <https://doi.org/10.1007/s00265-017-2312-6>
20. Hadiprakarsa Y-Y, Kinnaird MF (2004) Foraging characteristics of an assemblage of four Sumatran hornbill species. *Bird Conserv Int* 14:S53–S62. <https://doi.org/10.1017/S0959270905000225>
21. Hart SP, Usinowicz J, Levine JM (2017) The spatial scales of species coexistence. *Nat Ecol Evol* 1:1066–1073. <https://doi.org/10.1038/s41559-017-0230-7>
22. Hazell RJ, Sam K, Sreekar R et al (2023) Bird preferences for fruit size, but not color, vary in accordance with fruit traits along a tropical elevational gradient. *Ecol Evol* 13:e9835. <https://doi.org/10.1002/ece3.9835>
23. HilleRisLambers J, Adler PB, Harpole WS et al (2012) Rethinking Community Assembly through the Lens of Coexistence Theory. *Annu Rev Ecol Evol Syst* 43:227–248. <https://doi.org/10.1146/annurev-ecolsys-110411-160411>
24. Hutchinson GE (1957) Concluding Remarks. *Cold Spring Harb Symp Quant Biol* 22:415–427. <https://doi.org/10.1101/SQB.1957.022.01.039>
25. Janzen DH (1970) Herbivores and the Number of Tree Species in Tropical Forests. *Am Nat* 104:501–528. <https://doi.org/10.1086/282687>
26. Jayanth A, Isvaran K, Naniwadekar R (2024) Drivers of intraspecific variation in seed dispersal can differ across two species of fleshy-fruited savanna plants. *Biotropica* 56:e13322. <https://doi.org/10.1111/btp.13322>
27. Jordano P (2000) Fruits and frugivory. In: *Seeds: the ecology of regeneration in plant communities*. pp 125–165
28. Kartzinel TR, Chen PA, Coverdale TC et al (2015) DNA metabarcoding illuminates dietary niche partitioning by African large herbivores. *Proc Natl Acad Sci* 112:8019–8024. <https://doi.org/10.1073/pnas.1503283112>
29. Kattan GH, Valenzuela LA (2013) Phenology, abundance and consumers of figs (*Ficus* spp.) in a tropical cloud forest: evaluation of a potential keystone resource. *J Trop Ecol* 29:401–407
30. Kitamura S, Yumoto T, Poonswad P et al (2002) Interactions between fleshy fruits and frugivores in a tropical seasonal forest in Thailand. *Oecologia* 133:559–572. <https://doi.org/10.1007/s00442-002-1073-7>
31. Lambert FR, Marshall AG (1991) Keystone Characteristics of Bird-Dispersed *Ficus* in a Malaysian Lowland Rain Forest. *J Ecol* 79:793–809. <https://doi.org/10.2307/2260668>
32. Levey DJ (1988) Spatial and Temporal Variation in Costa Rican Fruit and Fruit-Eating Bird Abundance. *Ecol Monogr* 58:251–269. <https://doi.org/https://doi.org/10.2307/1942539>
33. Levine JI, An R, Kraft NJB et al (2025) Why ecologists struggle to predict coexistence from functional traits. *Trends Ecol Evol* 40:147–158. <https://doi.org/10.1016/j.tree.2024.10.002>

34. Li W, Grass I, Zhu C et al (2026) Temporal niche partitioning by nocturnal arboreal mammals increases the modularity of plant–frugivore networks in a fragmented subtropical landscape. *Funct Ecol* 40:463–475. <https://doi.org/10.1111/1365-2435.70235>
35. Macarthur R, Levins R (1967) The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *Am Nat* 101:377–385. <https://doi.org/10.1086/282505>
36. Mandal R, Gopal A, Jayanth A et al (2026) Frugivore species richness influences dietary specialisation and network properties in Asian wet tropical forests. 2026.01.31.703054
37. Marinho PH, Fonseca CR, Sarmiento P et al (2020) Temporal niche overlap among mesocarnivores in a Caatinga dry forest. *Eur J Wildl Res* 66:34. <https://doi.org/10.1007/s10344-020-1371-6>
38. McFadden IR, Fritz SA, Zimmermann NE et al (2022) Global plant-frugivore trait matching is shaped by climate and biogeographic history. *Ecol Lett* 25:686–696. <https://doi.org/10.1111/ele.13890>
39. McGill BJ, Etienne RS, Gray JS et al (2007) Species abundance distributions: moving beyond single prediction theories to integration within an ecological framework. *Ecol Lett* 10:995–1015. <https://doi.org/10.1111/j.1461-0248.2007.01094.x>
40. Murray DL, Gobin J, Scully A, Thornton DH (2023) Conventional niche overlap measurements are not effective for assessing interspecific competition. *Front Ecol Evol* 11. <https://doi.org/10.3389/fevo.2023.1281108>
41. Muthuramkumar S, Ayyappan N, Parthasarathy N et al (2006) Plant Community Structure in Tropical Rain Forest Fragments of the Western Ghats, India. *Biotropica* 38:143–160. <https://doi.org/10.1111/j.1744-7429.2006.00118.x>
42. Naniwadekar R, Chaplod S, Datta A et al (2019) Large frugivores matter: Insights from network and seed dispersal effectiveness approaches. *J Anim Ecol* 88:1250–1262. <https://doi.org/https://doi.org/10.1111/1365-2656.13005>
43. Naniwadekar R, Gopal A, Mandal R et al (2025) Effects of frugivore species pool and seed size on the diversity and functional composition of frugivores visiting fruiting trees. *Proc R Soc B Biol Sci* 292:20251775. <https://doi.org/10.1098/rspb.2025.1775>
44. Naniwadekar R, Gopal A, Page N et al (2021) Large frugivores matter more on an island: Insights from island-mainland comparison of plant–frugivore communities. *Ecol Evol* 11:1399–1412. <https://doi.org/10.1002/ece3.7151>
45. O'Brien TG, Kinnaird MF, Dierenfeld ES et al (1998) What's so special about figs? *Nature* 392:668–668. <https://doi.org/10.1038/33580>
46. Olson DM, Dinerstein E, Wikramanayake ED et al (2001) Terrestrial Ecoregions of the World: A New Map of Life on Earth: A new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *BioScience* 51:933–938. [https://doi.org/10.1641/0006-3568\(2001\)051%5B0933:TEOTWA%5D2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051%5B0933:TEOTWA%5D2.0.CO;2)
47. Ortiz-Pulido R, Rico-Gray V (2000) The effect of spatio-temporal variation in understanding the fruit crop size hypothesis. *Oikos* 91:523–527. <https://doi.org/10.1034/j.1600-0706.2000.910314.x>

48. Palacio FX, Ordano M (2018) The Strength and Drivers of Bird-Mediated Selection on Fruit Crop Size: A Meta-Analysis. *Front Ecol Evol* 6:18. <https://doi.org/10.3389/fevo.2018.00018>
49. Pastore AI, Barabás G, Bimler MD et al (2021) The evolution of niche overlap and competitive differences. *Nat Ecol Evol* 5:330–337. <https://doi.org/10.1038/s41559-020-01383-y>
50. Pellissier V, Barnagaud J-Y, Kissling WD et al (2018) Niche packing and expansion account for species richness–productivity relationships in global bird assemblages. *Glob Ecol Biogeogr* 27:604–615. <https://doi.org/10.1111/geb.12723>
51. Perini AA, Vieira EM (2026) Availability of a Keystone Plant Resource Reduces Niche Overlap and Drives Distinct Species-Specific Changes in Niche Breadth Among Small Rodents. <https://doi.org/10.1111/1749-4877.70105>. *Integr Zool* n/a
52. Perry G, Pianka ER (1997) Animal foraging: past, present and future. *Trends Ecol Evol* 12:360–364. [https://doi.org/10.1016/S0169-5347\(97\)01097-5](https://doi.org/10.1016/S0169-5347(97)01097-5)
53. Pianka ER (1973) The Structure of Lizard Communities. *Annu Rev Ecol Syst* 4:53–74
54. Preston FW (1980) Noncanonical Distributions of Commonness and Rarity. *Ecology* 61:88–97. <https://doi.org/10.2307/1937159>
55. Proctor J, Haridasan K, Smith (1998) How far north does Lowland Evergreen Tropical Rain Forest go? *Glob Ecol Biogeogr Lett* 7:141–146. <https://doi.org/10.1111/j.1466-8238.1998.00270.x>
56. Reyes-Puig C, Enriquez-Urzelai U, Sillero N, Kaliontzopoulou A (2025) Niche Differences in Coexisting Species: Ecological Insights Into the Role of Activity Patterns, Space Use, and Environmental Preferences. *Ecol Evol* 15:e71802. <https://doi.org/10.1002/ece3.71802>
57. Rojas TN, Bruzzone OA, Zampini IC et al (2021) A combination of rules govern fruit trait preference by frugivorous bat and bird species: nutrients, defence and size. *Anim Behav* 176:111–123. <https://doi.org/10.1016/j.anbehav.2021.04.001>
58. Schoener TW (1974) Resource Partitioning in Ecological Communities. *Science* 185:27–39. <https://doi.org/10.1126/science.185.4145.27>
59. Shanahan M, Compton SG (2001) Vertical stratification of figs and fig-eaters in a Bornean lowland rain forest: how is the canopy different? *Plant Ecol* 153:121–132. <https://doi.org/10.1023/A:1017537707010>
60. Stephens RB, Hobbie EA, Lee TD, Rowe RJ (2019) Pulsed resource availability changes dietary niche breadth and partitioning between generalist rodent consumers. *Ecol Evol* 9:10681–10693. <https://doi.org/10.1002/ece3.5587>
61. Sushma HS, Singh M (2006) Resource partitioning and interspecific interactions among sympatric rain forest arboreal mammals of the Western Ghats, India. *Behav Ecol* 17:479–490. <https://doi.org/10.1093/beheco/arj058>
62. Swenson NG, Weiser MD, Mao L et al (2016) Constancy in Functional Space across a Species Richness Anomaly. *Am Nat* 187:E83–E92. <https://doi.org/10.1086/685083>

63. Thiel S, Tschapka M, Heymann EW, Heer K (2021) Vertical stratification of seed-dispersing vertebrate communities and their interactions with plants in tropical forests. *Biol Rev* 96:454–469. <https://doi.org/10.1111/brv.12664>
64. Tobias JA, Sheard C, Pigot AL et al (2022) AVONET: morphological, ecological and geographical data for all birds. *Ecol Lett* 25:581–597. <https://doi.org/10.1111/ele.13898>
65. Todeschini F, de Toledo JJ, Rosalino LM, Hilário RR (2020) Niche differentiation mechanisms among canopy frugivores and zoochoric trees in the northeastern extreme of the Amazon. *Acta Amaz* 50:263–272. <https://doi.org/https://doi.org/10.1590/1809-4392202000732>
66. van Schaik CP, Griffiths M (1996) Activity Periods of Indonesian Rain Forest Mammals. *Biotropica* 28:105–112. <https://doi.org/10.2307/2388775>
67. van Schaik CP, Terborgh JW, Wright SJ (1993) The Phenology of Tropical Forests: Adaptive Significance and Consequences for Primary Consumers. *Annu Rev Ecol Syst* 24:353–377
68. Wheelwright NT (1985) Fruit-Size, Gape Width, and the Diets of Fruit-Eating Birds. *Ecology* 66:808–818. <https://doi.org/10.2307/1940542>

## Figures

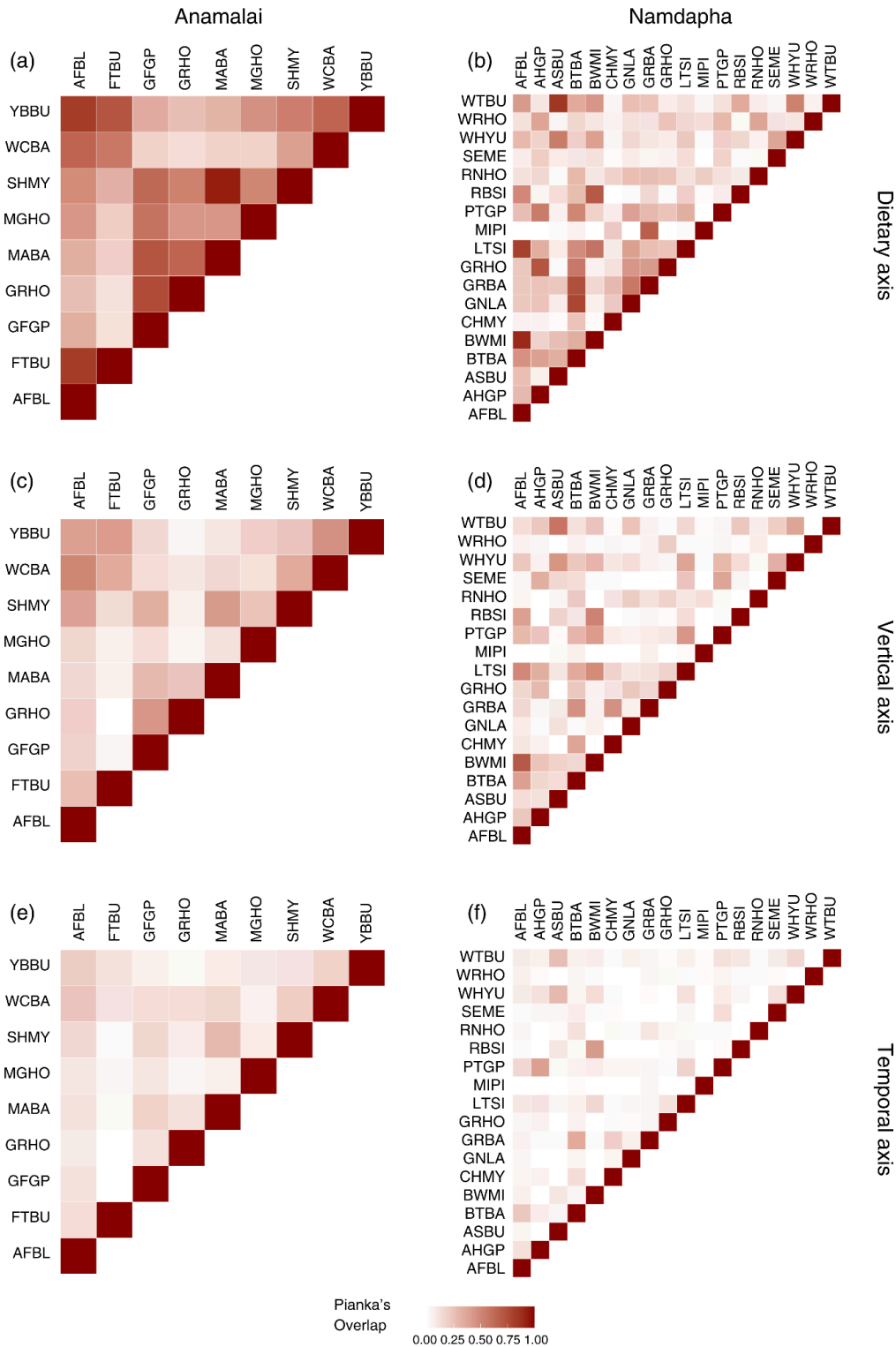


**Figure 1**

Heatmaps showing pairwise overlap values between frugivore species in Anamalai (left column) and Namdapha (right column) for three niche dimensions: dietary overlap (a, b), vertical overlap (c, d), and temporal overlap (e, f). Each cell represents the pairwise overlap between two species, quantified using Pianka's niche overlap index, where values range from 0 (no overlap) to 1 (complete overlap). Diagonal

cells represent self-overlap (value = 1). Warmer colours indicate greater overlap. Scientific names associated with the bird species codes shown on both axes are listed in Table S1.

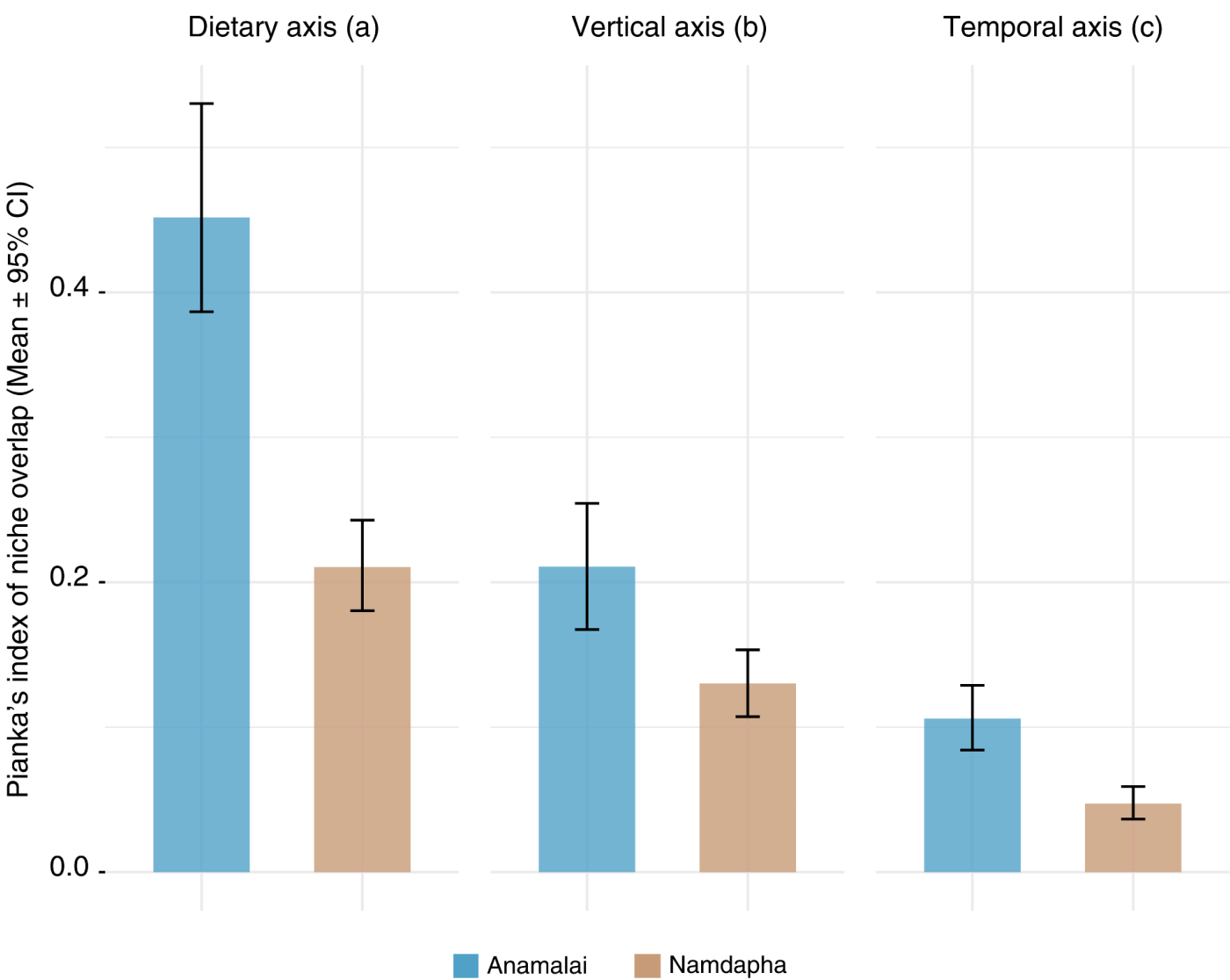


**Figure 2**

Mean ( $\pm$  95% CIs) pairwise frugivore overlap across three niche axes – dietary (a), vertical (b), and temporal (c) – calculated using Pianka's index of niche overlap at the two study sites, Anamalai and Namdapha.

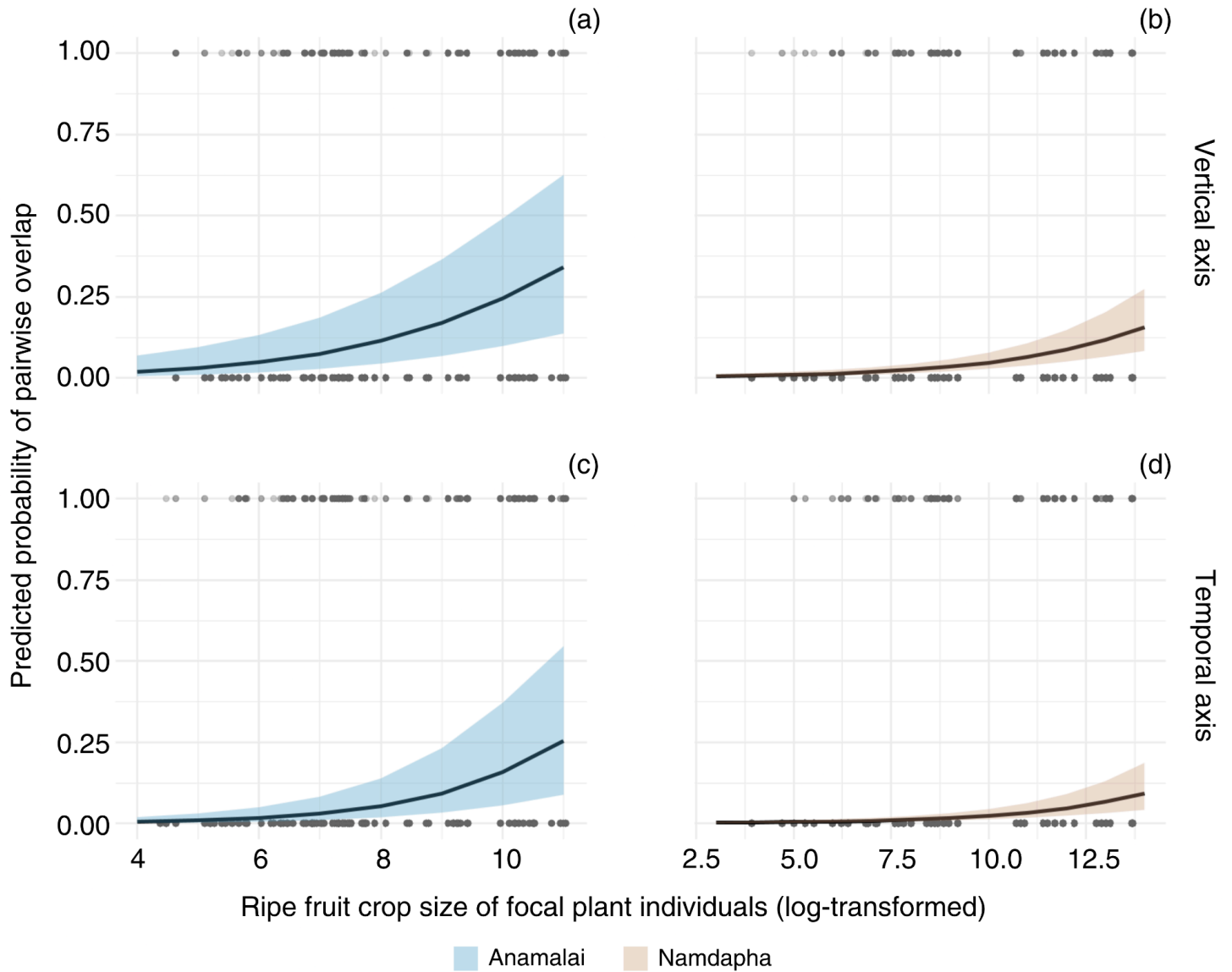


**Figure 3**

Predicted probability of pairwise frugivore overlap as a function of log-transformed ripe fruit crop size of focal tree individuals across two niche axes: vertical space (a, b) and time (c, d), at the two study sites, Anamalai and Namdapha. Black lines represent predictions from a binomial generalised linear mixed-effects model (GLMM), shaded bands indicate 95% confidence intervals, and grey points denote observed presence (1) or absence (0) of pairwise overlap on fruiting trees.

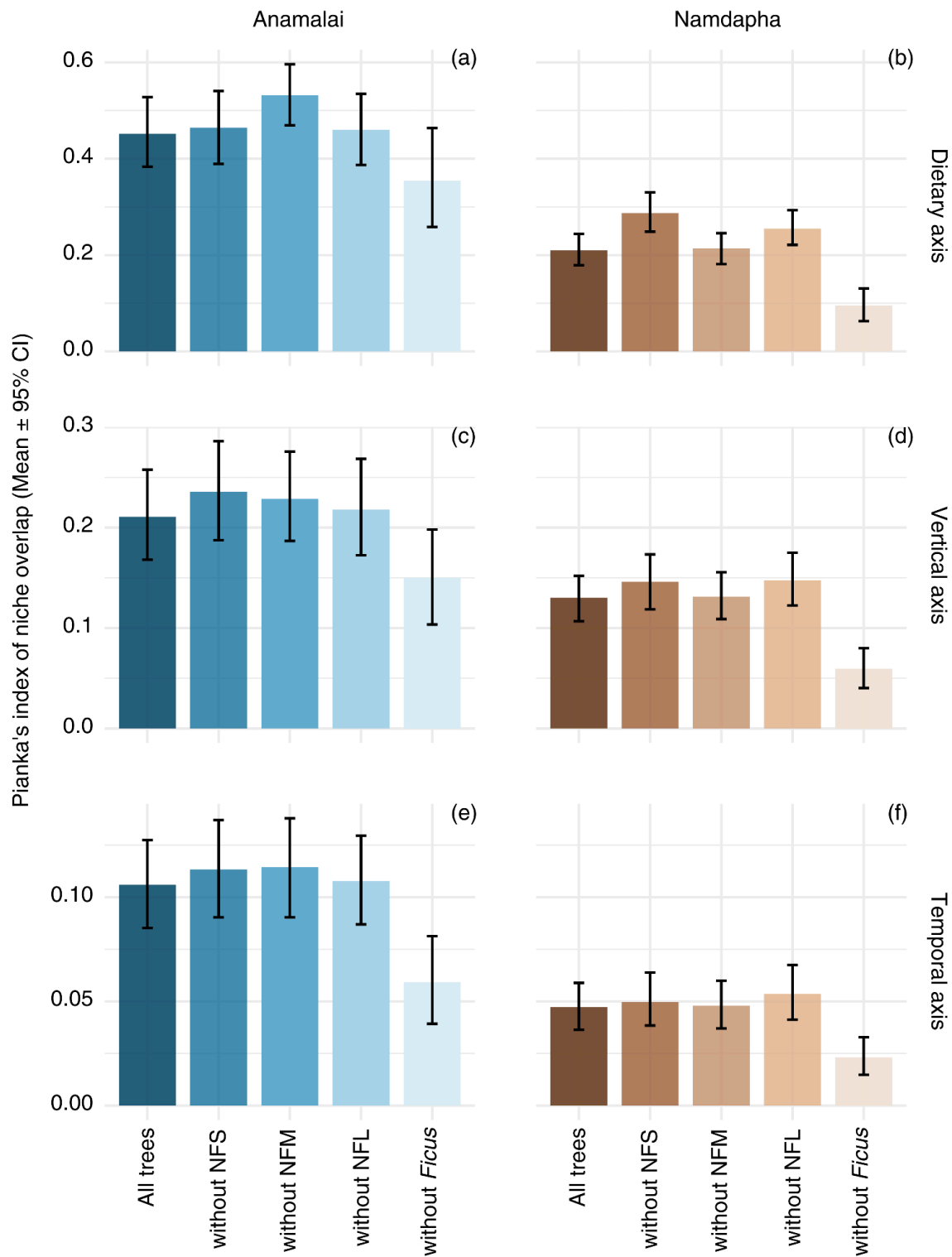


**Figure 4**

Pianka's overlap comparisons (mean  $\pm$  95% CIs) between original values (including all tree species) and values recalculated after excluding specific tree categories across dietary (a–b), vertical (c–d), and temporal (e–f) niche axes in Anamalai (left) and Namdapha (right). For each panel, overlap values are shown for the full dataset ("All trees") and after sequentially excluding specific tree categories: non-

*Ficus* small-seeded (without NFS), non-*Ficus* medium-seeded (without NFM), non-*Ficus* large-seeded (without NFL), and all *Ficus* species (without *Ficus*).

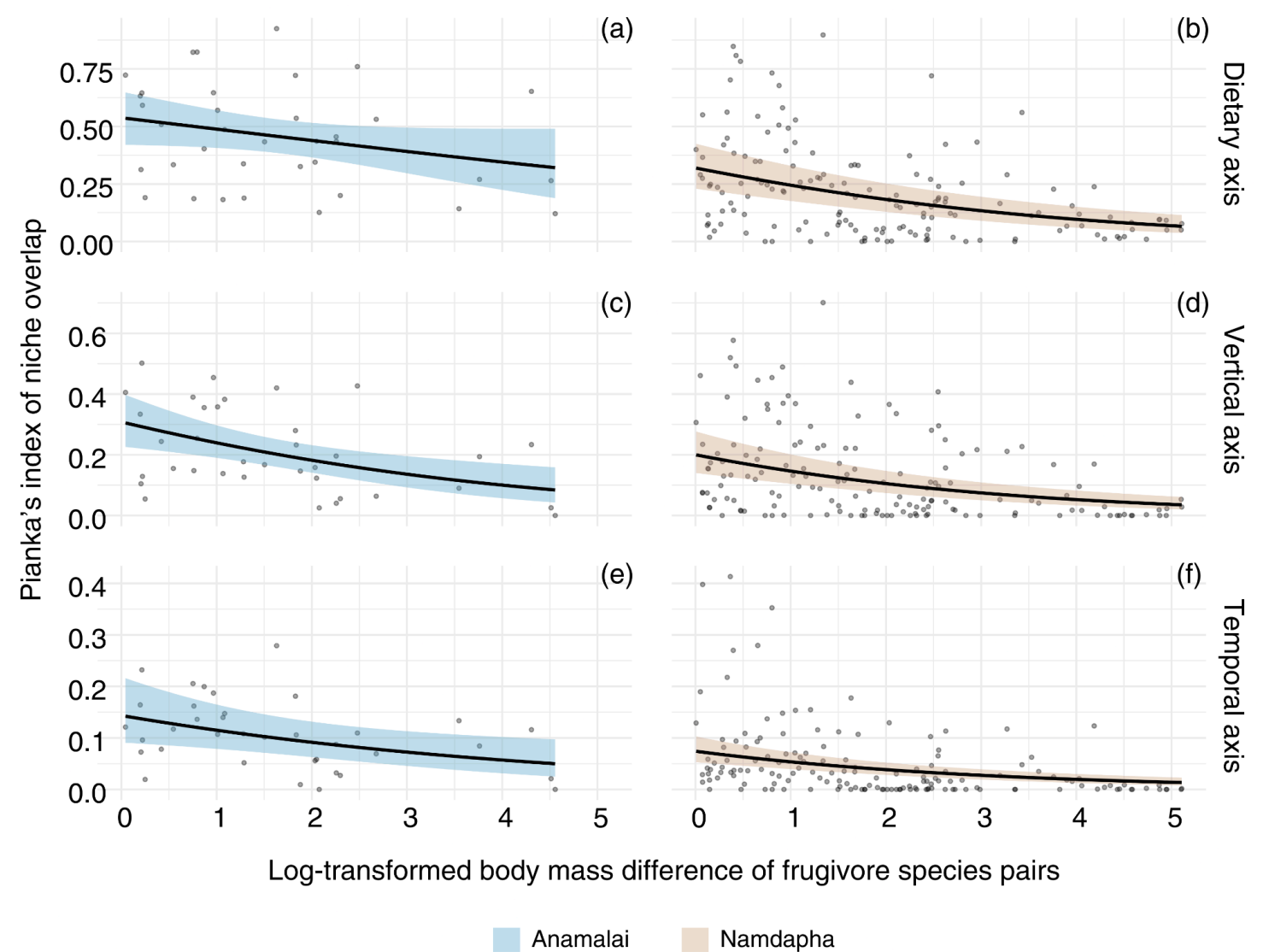


Figure 5

Results of the generalised linear mixed-effects models (GLMMs) with beta error structure and logit link examining the relationship between body mass difference (difference in log-transformed body mass) of interacting frugivore species pairs and pairwise overlap in each niche dimension: dietary, vertical, and temporal in two study sites: Anamalai (a, c, e) and Namdapha (b, d, f). Solid black lines represent the fitted GLMM predictions, and shaded bands indicate 95% confidence intervals.

## Supplementary Files

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