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Turnover importance: Operationalizing beta diversity to quantify the generalism continuum

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Abstract

1. Generalization is difficult to quantify, and many classifications exist. A beta diversity framework can be used to establish a numeric measure of generalist tendencies that jointly describes many important features of species interactions, namely spatiotemporal heterogeneity. This framework is promising for studying generalized symbiotic relationships of any form.
2. We formulated a novel index, turnover importance (*T*). *T* describes spatiotemporal heterogeneity in interactor assemblages, an inherent feature of generalist relationships that is not captured by available metrics. We simulated the behaviour of *T* relative to other available metrics, calculated *T* for native North American orchid-insect relationships, and tested correlations between *T* and eco-geographic variables. We performed case studies to demonstrate applications of *T* for conservation and eco-evolutionary studies.
3. *T* behaves predictably across simulations, and dynamically interacts with site number, gamma diversity, and species range sizes. *T* is moderately sensitive to sampling depth. Orchids with higher *T* scores occupy larger ranges and broader climatic niches.
4. Alternative interactor-specific measures of generalism are best employed for local-level community networks over short timespans. While these interactor metrics can assess use versus availability in local communities, *T* can be used to measure spatiotemporal patterns of variation in interactor assemblages across a focal species' range. This study provides a roadmap for future work focused on better understanding the patterns and consequences of generalized relationships.

KEYWORDS
generalization, orchids, pollination, spatiotemporal heterogeneity, specialization, species interactions, symbiotic relationships

1 | INTRODUCTION

The evolutionary and ecological consequences of specialization versus generalization have long been of interest (Brown & Pavlovic, 1992; Futuyma & Moreno, 1988; Jinks & Connolly, 1973; Kassen, 2002; Van Tienderen, 1991), but the boundaries between the two terms are often vague and complex. As typically defined, a specialist depends on a single kind of resource, while a generalist uses many. In terms of ecological niche breadth, a generalist has a broad niche, whereas a specialist has a narrow one. Importantly, a species can be specialized in one niche dimension while being generalized in another. This complex nature of multidimensional niche space makes it difficult to classify species as strictly generalists or specialists (WallisDeVries, 2014). Indeed, putting species' ecological interactions and niche requirements into discrete categories is often based on qualitative or arbitrary criteria (Habel & Schmitt, 2012). Researchers often disagree over the number and kind of niche dimensions that should qualify species as generalists, and it may very well be the case that no species is a generalist in all niche dimensions. Because of this, using the specialist/generalist dichotomy ignores the fact that all species occupy unique ecological niches and are, in at least one dimension, specialized (Loxdale et al., 2019). Still, it remains an important task to understand how broadening or narrowing of particular niche dimensions might contribute to the persistence or extinction of lineages (Dapporto & Dennis, 2013). Accordingly, many authors have argued for abandoning discrete categories and using measures that place species along a continuum from specialism to generalism (WallisDeVries, 2014). Instead of asking: 'Is this species a generalist or a specialist?', we now ask: 'To what degree is this species a generalist versus a specialist?'.

We consider modern quantifications of generalism to fall into two basic categories: niche-specific and interactor-specific. Niche-specific measures address the extent to which species' entire niches are generalized or specialized. They typically rely on weighted means or principal coordinates of many niche dimensions and can be used to quantify generalist tendencies across geographic and ecological space (Dapporto & Dennis, 2013; Habel & Schmitt, 2012; Wallis et al., 2016). Interactor-specific measures describe the extent to which particular relationships are specialized. Most interactor-specific methods are descriptions of species diversity at the community level, where generalism of a focal species is measured with respect to the diversity of its interactors, or use versus availability of interactors (Blüthgen et al., 2006; Poisot et al., 2015; Sahli & Conner, 2006; Shefferson et al., 2019). Regardless of category, all measures depend on species richness (e.g. the number of pollinators a plant has) to quantify generalism. That is, all these methods rely on the traditional ideation that a species is more of a generalist when they have more interactors, and less of a generalist when they have fewer.

We argue that modern methods ignore a critical feature of generalized relationships: that they are variably manifested in space and time. For example, we can infer that an orchid species specialized to one pollinator will only interact with that pollinator throughout its range. However, an orchid species with two pollinators may interact with both species throughout its range (Figure 1a), or it could interact with one in one part, and the other elsewhere (Figure 1b). In the latter scenario, the orchid species is specialized in every part of its range, whereas in the former it is not. Further, a species may be equally specialized or generalized across its range, but the interactors that compose each community could be taxonomically distinct (Figure 1b). In this way, species interactions can form spatial or temporal mosaics akin to the coevolutionary mosaics proposed by Thompson (1994, 1997). Measures that only account for species richness at single sites, or total species richness regardless of spatial structure, ignore these critical distinctions. Such spatiotemporal variation impacts evolutionary

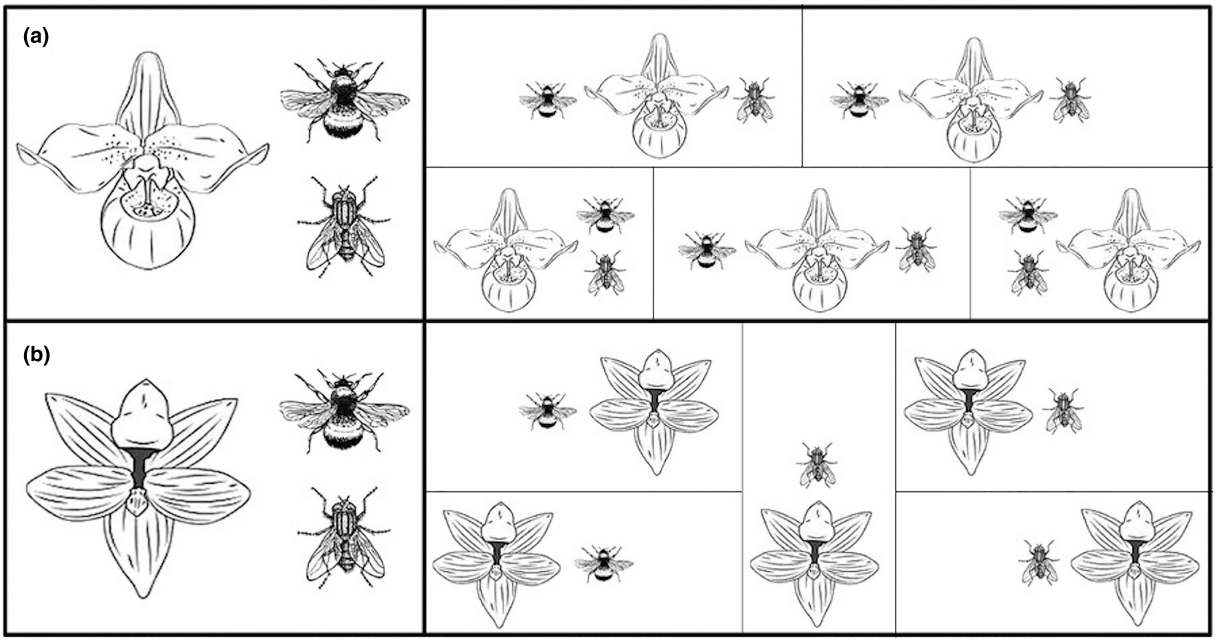

FIGURE 1 Visualization of different scenarios of spatial manifestation of interactor species. In both (a) and (b), each species has a total interactor species richness of 2. In (a), both interactor species occur in each area of the focal species' range. In (b), only one species occurs in each area of the focal species' range. Additionally, while the focal species in (b) is locally functionally specialized across its entire range, the interactor species with which it associates are variable across its range, leading to homogeneity in local specialization, but heterogeneity in taxonomic composition.

and ecological trajectories of focal species in ways that cannot be predicted by accounting for species richness alone. Neither interactor-specific nor niche-specific methods are designed to capture spatiotemporal variation in the identity of the interactors that comprise quantifications of generalism. This limits the applicability of current methods to local-scale analyses of interactions within single populations. But interspecies interactions exist beyond a single population, and they persist over evolutionary time. A method that can account for changes in relationship dynamics between a focal species and its interactors across its entire range would allow us to better understand how species may withstand changes to available niche space over time, whether certain interactors pose limiting factors on the ranges of focal species, and how variation in interactor community structure might contribute to population, and eventually species, divergence.

Shefferson et al. (2019) discuss the difference between apparent generalism and true generalism. In their schema, an apparent generalist is one who associates with a core set of species, but may also add others, while the core assemblage remains unchanged. A true generalist is one whose interactors are relatively interchangeable and is prone to frequent host switching. While they consider this difference in the context of evolutionary time, we can also use this distinction to better understand how different generalist relationships might manifest over space. In this context, a true generalist is a species with high turnover in its interactors over its range, while an apparent generalist is a species whose core interactors remain unchanged throughout its range, but with some additional interactors in subsets of its range.

Beta diversity, a measure of compositional differentiation among sites within a region, is an integral aspect of species diversity. We argue that analysing interspecies associations broadly characterized as generalist is best accomplished under a beta diversity framework because it enables us to account for spatiotemporal variation in those associations. However, there are myriad ways to calculate beta diversity, and different methods often yield contrasting results using identical data. Koleff et al. (2003) identified 24 beta diversity metrics applicable for presence-absence data, which they categorize as either being sensitive to, or independent of, community-level differences in species richness. That is, some measures can disentangle the contributions of changes in species richness (nestedness) versus compositional turnover to overall beta diversity, while others cannot. One of the most common ways to calculate beta diversity is to use the *Betapart* package (Baselga & Orme, 2012) for either multi-site or pairwise scenarios, which automatically partitions a total beta diversity score into its nestedness and turnover components (Bevilacqua & Terlizzi, 2020; Gao et al., 2020; Legendre & De Cáceres, 2013; Mariani et al., 2019).

Compositional turnover and nestedness are critical components of beta diversity that individually contribute to our understanding of generalist versus specialist relationships. In the context of species interactions, compositional turnover indicates that species interact with distinct communities of symbionts across their range. When compositional turnover contributes to beta diversity, it means that differentiation between sites is attributable to unique species assemblages that are not shared among sites (Figure 2a). Species with high turnover in their interactions are likely to depend on unique sets of interactors in different parts of their range, and to engage in frequent host switching. Unlike compositional turnover, nestedness measures the progressive loss of species richness between sites (Figure 2b). Species with high nestedness in their interactions are likely to depend on a core set of interactors across their range, with additions to that core assemblage in some parts.

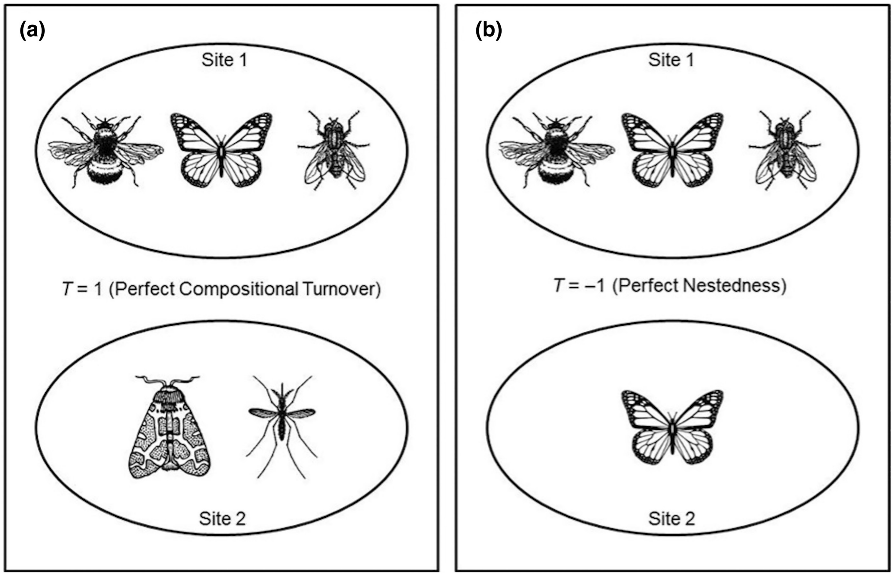

FIGURE 2 Conceptual differences between nestedness and compositional turnover. (a) A situation in which differences between sites are entirely attributable to compositional turnover. Assemblages are unique with respect to each other. In this case, $T = 1$. (b) A situation in which one area is a perfect subset of another, that is perfect nestedness. Differences between sites are entirely attributable to progressive loss of species richness. In this case, $T = -1$.

Whether total beta diversity is primarily attributable to compositional turnover among sites or progressive loss of species richness between sites is an important distinction. For example, orchids with strong compositional differences in pollinators are more likely to experience restrictions to gene flow between populations. They may also exhibit marked morphological variation in response to different selective pressures imposed by unique sets of pollinators throughout their range (Moeller, 2006). Orchids with significant pollinator richness losses between sites are likely to be more pollinator limited in some parts of their range than others, and they may have an increased contribution of rare species to their interactors (Baselga, 2012).

Here, we introduce turnover importance (*T*), a novel interactor-specific quantification of generalism that uses the beta diversity framework developed by Baselga (2010) to characterize the specialist-generalist continuum by explicitly accounting for the spatial or temporal heterogeneity in ecological relationships and its underlying components (compositional turnover vs. nestedness). We then perform simulations to assess its performance, interpretability, and sensitivity compared to other available interactor-specific methods (Table 1). Using a dataset on orchid pollinators, we (a) examine the relationships between range size, abiotic niche breadth, and *T*, (b) assess phylogenetic signal in *T*, and (c) detail taxonomic and geographic gaps in orchid floral visitor sampling effort and provide a roadmap for future studies. While pollinator relationships are merely one biotic factor out of many contributing to orchid range dynamics, we choose to focus on it here to illuminate the utility of *T* for evaluating relationships on the generalist continuum. We finish by presenting case studies that characterize different degrees of *T*, and explicate its utility for eco-evolutionary studies and conservation endeavours.

TABLE 1 Summary of available metrics for quantifying interactor-specific diversity and attributes of each measure (Y = yes; N = no).

Measure	Range-wide	Data-intensive	Abundance-based
d'	N	Y	Y
S	N	Y	N
Simpson diversity index	N	Y	Y
Species richness	Y	N	N
Turnover importance	Y	N	Y/N

2 | MATERIALS AND METHODS

2.1 | Quantifying *T* and assessing its behaviour

We used the R package *Betapart* v.1.5.5 (Baselga & Orme, 2012) to calculate multi-site dissimilarity measures for focal species based on the composition of their interactor species across their total range for both simulated datasets and our orchid dataset. Three metrics were calculated and are symbolized in the style of Baselga (2010) (Table 2; Figure S1):

1. B_{SOR}: the Sorenson multi-site dissimilarity measure (which is equal to $B_{NES} + B_{SIM}$). B_{SOR} was used to represent total beta diversity. B_{SOR} can take any value from 0 to 1, where 0 = no site dissimilarity, and 1 = total site dissimilarity (Baselga, 2010).
2. B_{SIM}: The turnover-resultant component of B_{SOR}, calculated as the Simpson multi-site dissimilarity measure.
3. B_{NES}: The nestedness-resultant component of total beta diversity.

To analyse the relative importance of compositional turnover, B_{SIM} was modified to account for: (1) site-number dependence of B_{SOR}, and (2) identical signals of zero generated by different underlying phenomena. Turnover and nestedness are both necessarily zero when total beta diversity is zero, but they can also take zero values when one or the other comprises 100% of the contribution to total beta diversity. For example, turnover is 0 when nestedness is 1. This means that the raw value of $B_{SIM} = 0$ can either be caused

TABLE 2 Summary of all beta diversity metrics calculated, where: 'S_i is the total number of species in site *i*, S_T is the total number of species in all sites considered together and b_{ij}, b_{ji} are the number of species exclusive to sites *i* and *j*, respectively, when compared by pairs' (Baselga, 2010).

Functional name	Term	Formula	References
Total beta diversity	B_{SOR}	$\dfrac{\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]+\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}{2\left[\sum_{i}S_iS_T\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]+\left[\sum_{i<j}\max(b_{ij},b_{ji})\right]}$	Baselga (2010)
Turnover-resultant component of total beta diversity	B_{SIM}	$\dfrac{\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}{\left[\sum_{i}S_iS_T\right]+\left[\sum_{i<j}\min(b_{ij},b_{ji})\right]}$	Baselga (2010)
Nestedness-resultant component of total beta diversity	B_{NES}	$B_{NES} = B_{SOR} - B_{SIM}$	Baselga (2010)
Turnover importance	T	$T = \frac{B_{SIM} - B_{NES}}{B_{SOR}}$	This paper
Interactor richness	G	Total number of interactors (count)	This paper

by complete spatial homogeneity or perfect nestedness. Thus, to accurately represent the difference between these cases, Turnover Importance, T, was calculated as:

4. $T = \frac{B_{SIM} - B_{NES}}{B_{SOR}}$.

T can range from −1 to 1. When $T=1$, this means that there is perfect compositional turnover in interactor species assemblages (Figure 2a). When $T=-1$, this means that there is perfect nestedness (Figure 2b). Effectively, $T>0$ indicates increasingly higher relative importance of compositional turnover with respect to total beta diversity, while $T<0$ indicates that nestedness is increasingly important. When $T=0$, total beta diversity is also 0, indicating complete spatial homogeneity. Finally, T represents the proportional contribution of compositional turnover to total beta diversity, but it is independent of the total beta diversity value. This allows the measure to represent the underlying drivers of beta diversity scores while mitigating site-number dependence (Baselga, 2010), thus allowing T to be used broadly for comparative purposes.

In terms of the specialism/generalism continuum, species with $T>0$ are likely to depend on unique, separate sets of interactors in different parts of their ranges. They are likely to engage in frequent interactor switching. Species with $T<0$, on the other hand, are more likely to depend on a single (or small set) of associates throughout their range, with some additions to that core assemblage in some parts of their range (Figure 2).

To better understand how T behaves relative to B_{SOR} under different site-number conditions, we simulated random community matrices consisting of 100, 30, 10 and 3 sites. Site number represents the total range size of a focal species, and each site represents an occurrence location. For each site-number category, we simulated 1000 community matrices without spatial structure or limits to migration (i.e. each site had an equal chance of being occupied by any interactor species) with the R package *prabclus* (Hennig et al., 2015). We also stochastically varied the total number of interactor species (species richness), and the ranges of those species, resulting in a total of 4000 simulated community matrices with varying levels of species richness and range sizes.

We then tested whether (a) the range of possible T and B_{SOR} values were identical across site-number scenarios; (b) identical T values indicated the same interactor assemblage patterns across site-number scenarios; and (c) the relationship between species richness, T, and B_{SOR} was preserved across site-number scenarios.

2.2 | Comparing *T* to other measures of generalism

To understand (a) whether other metrics can capture the features of generalism described by T; (b) the extent to which metrics are sensitive to sampling depth; and (c) how metrics correspond to interactor species richness and focal species range size, we again simulated community matrices. Because the methods differ in their required input data, we simulated a single community matrix that represented the ranges of all interactor species (e.g. orchid pollinators) over a total area of 100 cells and used this as the basis for generating subsequent datasets. Within these cells, interactor species ranges were randomly varied between 1 and 100 without spatial structure. Then, we randomly selected the ranges of 25 focal species (e.g. orchid species), again with range sizes randomly varied between 1 to 100 cells without structure. Finally, we randomly selected interactor species for each focal species. This process was repeated 258 times for a total of 6450 focal-interactor networks. From each focal-interactor network, we created the three community matrices variously required by the generalism metrics. Matrix 1: a presence-absence community matrix, where rows are focal species and columns are interactor species. In this case, 1 represents presence of an interaction, 0 represents absence of an interaction. This matrix is needed to calculate the S metric (Table S1). Matrix 2: an abundance-based community matrix, where rows are focal species and columns are interactor species. In this case, 0 still represents absence of an interaction, but values >0 represent the number of times an interactor species and focal species co-occur across their respective ranges. This matrix is needed to calculate D prime and the Simpson diversity index (Table S1). Matrices 1 and 2 represent all interactions across focal species' ranges, that is there is no spatial partitioning. Matrix 3: a presence-absence community matrix, where rows are sites and columns are interactor species. This matrix is identical in kind to the ones used in our first set of simulations, and is needed to calculate T, D diff, and D mean.

Using these matrices, we calculated six different metrics using the R packages bipartite (Dormann et al., 2008), vegan (Dixon, 2003), and betapart (Baselga & Orme, 2012):

1. *T*.
2. D prime, which measures interactor specificity relative to interactor availability (Blüthgen et al., 2006). D prime is only calculated for a single community matrix at a single site or over all sites at once (e.g. a single community matrix representing the entire range of a focal species).
3. D diff, which is the mean difference in D prime scores among sites across a focal species range.
4. D mean, which is the mean d prime score among sites across a focal species range.
5. S, which measures the use of interactors relative to all available interactors (Poisot et al., 2015).
6. Simpson diversity index, which measures the frequency or strength of interactions relative to interactor species richness (Sahli & Conner, 2006). All metrics, required calculations, references, and required matrices are summarized in Table S1.

To assess sensitivity to sampling depth, each of the 1650 focal-interactor networks were randomly subsampled six times, and all metrics were re-calculated to represent 90%, 75%, and 50% interactor sampling, and 90%, 75%, and 50% focal species range sampling. For example, we randomly sampled 90% of the interactor species from the original focal-interactor network, and re-calculated all metrics.

To understand how metrics vary with respect to interactor species richness and focal species range size in general, we calculated Pearson's correlation coefficients between calculated metrics and interactor species richness, and between calculated metrics and focal species range size.

2.3 | Native North American orchids and their floral visitors

Our orchid insect dataset was created over the span of several years with the help of interns, students, and volunteers in the Spalink Lab, and researchers from the Smithsonian's North American Orchid Conservation Center and National Museum of Natural History. Published records from the last ~80 years were scored for any verified incidences of floral visitation or pollination by an animal for orchid species native to the continental United States and Canada. Pollinator identifications ranged from species to family-level. For the purposes of this investigation, only species-level interactor observations were retained. Taxonomic inconsistencies among publications and datasets were resolved for both orchids and their pollinators using the R package *Taxize* v.0.9.99 (Chamberlain & Szöcs, 2013).

The cleaned dataset was a presence-absence matrix with orchid species as rows, and pollinator species as columns (Morley et al., 2024). The matrix consisted of 110 out of 208 North American orchid species with known floral visitor observations, representing 40 out of 66 total genera. Interactor observations totaled 442, spanning 272 (mostly insect) species.

Given the difficulty of distinguishing between floral visitors and pollinators, we included both verified pollinators and floral visitors. Thus, our matrix represents the maximal possible set of pollinators for an orchid based on available information. In this way, *T* describes the spatial patterns that underlie orchid-insect interactions, not necessarily actual pollination. We note that this distinction between visitation and pollination is largely inconsequential for the main purpose of this paper—namely, to improve our understanding of the spatial and ecological structure of the generalist-specialist continuum in biotic interactions—and we emphasize the importance of ongoing efforts to improve the density of confirmed pollinator relationships in this study system.

2.3.1 | Distribution data and calculating *T*

Occurrence records for pollinators and orchids were collected from the Global Biodiversity Information Facility (GBIF) using the R package *rgbif* v.3.7.0 (Chamberlain et al., 2017), and cleaned with *CoordinateCleaner* v.2.0.20 (Zizka et al., 2019). Both datasets were also manually cleaned on a per-species basis to remove any occurrence points outside of species' accepted ranges. To minimize bias due to missing data, only orchids that co-occurred with a known interactor species over at least 90% of their total range were retained; other species were discarded in downstream analyses.

A shapefile comprising 758 equal-area grid cells (area = 5733 km^2) over North America was created following (Zizka, 2018) with *rgdal* v.1.5.29 (Bivand et al., 2015), *magrittr* v.2.0.2 (Bache et al., 2022), *raster* v.3.5.15 (Hijmans et al., 2015), and *speciesgeocodeR* v.2.0.10 (Zizka, 2017). We used this coarse resolution to account for the bias and missingness in both orchid and pollinator distribution datasets. After binning, orchids and pollinator occurrence points were reduced to presence-absence within each grid cell and transformed to community matrices. Again, we treat co-occurrence records as the maximal possible set of pollinators based on available data. These data are considered estimates of the spatial heterogeneity underlying orchid-insect interactions, and actual use of insects and pollinators should be verified on a per-species and per-site basis.

2.3.2 | Correlates of *T*

All WorldClim2 (Fick & Hijmans, 2017) variables plus elevation were retrieved with the R package *Dismo* v.1.3.5 (Hijmans et al., 2017). Point values were calculated for each occurrence record for each orchid species. To reduce covariance among variables while retaining those of putative importance for orchid distributions, we performed Pearson's correlation tests in R, and retained only a subset for analysis (SI 1.1; Table S4). To represent niche breadth, we performed a PCA on retained environmental variables and used PC1 as the independent variable (SI 1.2; Table S4; Figure S4). Area of Occupancy (AOO) and Extent of Occurrence (EOO) were calculated as the number of cells an orchid occupies and the maximum haversine distance between two occurrence points, respectively. These were used to represent range size (SI 1.3).

2.3.3 | Phylogenetic signal

Sequence data were gathered from GenBank (Sayers & Karsch-Mizrachi, 2016) for all available native North American orchid species. Representative non-North American taxa were chosen for genera that extended outside of our study region. Loci with <15% coverage were removed to minimize missing data while maximizing taxa present in the final tree. After filtering, 18S, ITS1, 5.8S, ITS2, 26S, rbcL, Matk, trnK, PsaB and ycf1 were retained for alignment and concatenation (SI 2; Table S5). We constructed a maximum likelihood tree with 1000 ultrafast bootstrap replicates using the IQ Tree online portal (Nguyen et al., 2015). The full tree consists of 182 orchid species, representing 59 out of 66 North American genera (Morley et al., 2024). To assess phylogenetic signal in *T*, we calculated Pagel's Lambda and Blomberg's *K* for the subset of orchids that also had adequate insect distribution data.

2.3.4 | Phylogenetic and spatial sampling gaps

To assess the extent to which lineages are under-sampled with respect to insect associations, we plotted data completeness along our phylogeny. To identify geographic areas that are under sampled, we calculated the percentage of all orchids in an area for which their known insect associate(s) also occurred in that area. These data can serve as a roadmap for future orchid-insect work and provide critical information for the protection and restoration of endangered orchid species.

2.3.5 | Case studies

To explicate the behaviour of *T*, we selected three orchid species from our above dataset that had similar values of beta diversity but contrasting *T* scores: *Spiranthes casei* (low *T*; −1), *Spiranthes lacera* (high *T*; 0.952) and *Isotria verticillata* (intermediate *T*; 0.01). Then, we created interactor richness gradients and assessed areas of taxonomic compositional similarity. Richness gradients reflect changes in the number of co-occurring interactors across occupied cells for a focal orchid species. We assessed areas of taxonomic similarity by first calculating a Jaccard distance matrix for each community matrix using the R package *Vegan* (Dixon, 2003). Then, we implemented a UPGMA clustering algorithm using the R package *clustsig* (Whitaker et al., 2014), which groups areas by taxonomic similarity in interactor assemblage.

2.4 | Limitations

Although our orchid-insect data was compiled from an extensive literature review, our dataset is likely incomplete. Thus, we emphasize that this paper is intended to introduce *T* as a quantification of generalism, and we use orchid-insect associations to demonstrate that *T* can illuminate how variation among generalist relationships impact ecological, geographic, and evolutionary dynamics. We argue that our exploration of orchid-insect relationships in terms of *T* further supports the importance of increased efforts to observe and characterize orchid-insect interactions across focal species' ranges.

3 | RESULTS

3.1 | Quantifying *T* and assessing its behaviour

The range of *T* scores was −1 to 1 for all simulated site-number scenarios. However, the distribution of non-zero B_{SOR} values varied depending on the number of sites (Figure S2). As site number increased, B_{SOR} also increased. At 100 sites, the minimum non-zero B_{SOR} value was 0.5, and for 30 sites, it was 0.25. Despite disparity in value ranges, mean *T* (like B_{SOR}) was significantly different across site-numbers (Table S2).

When plotted in space, we found that, despite variation in B_{SOR} and site number, all four scenarios exhibited a spatial pattern of assembly such that 100% of the dissimilarity among sites was attributable to nestedness when $T=-1$. That is, cells with decreased diversity were proper subsets of more speciose cells (Figure S3).

The relationship between *T* and interactor species richness was preserved across site-number scenarios (Table S3). As interactor species number increases, the total number of possible unique combinations also increases, and on average, a greater number of unique combinations of interactor species as interactor species number increases. The relationship between B_{SOR} and interactor species richness was inconstant between site-number scenarios, which should be expected (Table S3).

3.2 | Comparing *T* to other measures of generalism

Changes in *T* are poorly tracked by other available metrics. While all other methods were significantly correlated with *T*, correlations were low, and scatterplots show substantial variation in other metric values as *T* increases and decreases (Figure 3).

T is moderately sensitive to interactor sampling depth, with only a 0.77 correlation between true *T* scores and observed *T* scores at 50% interactor species sampling. Error was highest for extremely low or extremely high values of *T*, with nestedness tending to be overestimated as sampling depth decreased (Figure S5). Other available measures tended to be less sensitive to interactor sampling depth, with the Simpson diversity index performing the best (Table 3).

T is less sensitive to focal species range sampling depth than interactor sampling depth, with a correlation value of 0.89 at 50% depth. S, Simpson diversity, and D prime are also less sensitive to focal species range sampling depth, with very high fidelity at 50% depth. D mean and D diff, on the other hand, are substantially more sensitive to gaps in focal species range sampling, with correlation values of 0.72 and 0.52 at 50% sampling depth respectively (Table 3).

Changes in interactor species richness track changes in all generalism metrics. D prime and Simpson diversity index showed the strongest relationships, with interactor species richness explaining 90% and 100% of variation in scores respectively. Interactor species richness explained 44% of variation in *T* (Table 4).

While all relationships were significant, focal species range size explained less variation in metric values than interactor species richness. D diff showed the strongest relationship with focal species range size, at a correlation value of −0.4 (Table 4).

3.3 | Correlates of *T*

Niche breadth, AOO and EOO were significantly positively correlated with *T* ($R=0.508, 0.59, 0.396$ respectively; Figure S6) indicating that compositional turnover in floral visitor assemblages increases with the size of occupied geographic and ecological space. EOO and AOO were strongly positively correlated with niche breadth, indicating that orchids with larger ranges occupy broader niches. However, orchids with zero total beta diversity confounded the relationships between eco-geographic space occupancy and *T* (Figure S6).

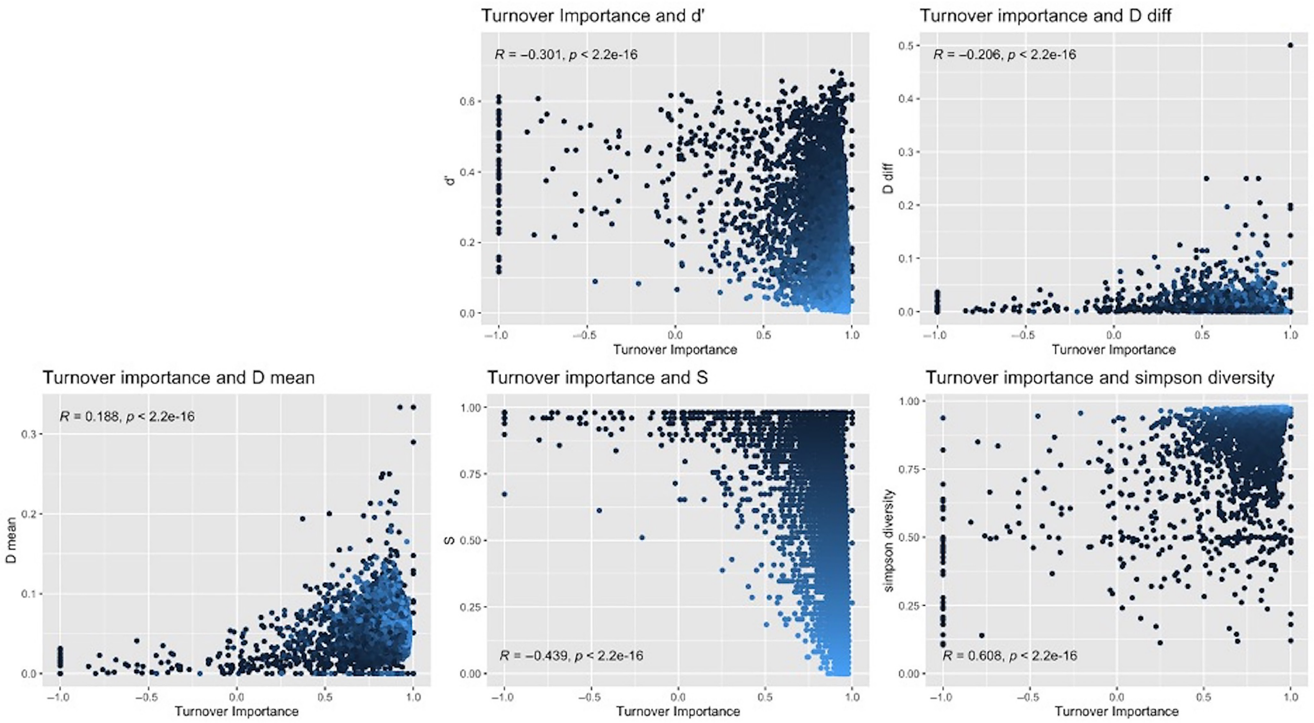

FIGURE 3 Relationships between *T* and other metrics across all simulations. While some variation is shared, all metrics poorly track changes in *T*.

TABLE 3 Summary of correlations between observed values at specified sampling depths and true values for all metrics across all simulations.

Measure	90% interactor sampling	75% interactor sampling	50% interactor sampling	90% focal range sampling	75% focal range sampling	50% focal range sampling
T	0.973	0.889	0.795	0.984	0.941	0.893
d' (D prime)	0.995	0.978	0.895	0.9998	0.999	0.997
D diff	0.971	0.867	0.707	0.974	0.606	0.524
D mean	0.963	0.898	0.782	0.977	0.839	0.724
S	0.9997	0.9996	0.999	0.9997	0.999	0.996
Simpson diversity	0.998	0.980	0.944	0.9997	0.998	0.997

Note: All correlations were significant at $p < 0.0002$.

3.4 | Phylogenetic signal

Pagel's Lambda and Blomberg's *K* were nearly zero and insignificant (Lambda <0.000006, $p=1$; $K<0.004$, $p=0.91$). This indicates that differences in *T* cannot be attributed solely to phylogenetic structure. In other words, a Brownian model of evolution alone is insufficient to explain observed variation in *T*. Notably, values of *T* are diffuse across the phylogeny, indicating that position along the generalism continuum is phylogenetically labile (Figure S7).

3.5 | Floral visitor sampling gaps

While most species across the phylogeny have some pollinator data (89%), far fewer have sufficient species-level observations across their ranges (26%; Figure S8). Epidendroideae is the most sparsely sampled: only 10% of all represented species have sufficient pollinator observations across their range. Members of the Orchidoideae outside of *Spiranthes* and *Platanthera* are also under sampled with respect to pollinator observations. Eastern North

TABLE 4 Correlations between measures and interactor species richness, and measures and focal species range size across all simulations.

Measure	Interactor species richness	Focal species range size
T	0.44	0.37
d'	−0.9	0.15
D diff	−0.18	−0.4
D mean	0.2	0.37
S	−1	−0.13
Simpson diversity	0.62	0.14

Note: All correlations are significant at $p < 0.002$.

America and much of the south appear to be well sampled areas, while the west, intermountain west, and Florida are under sampled (Figure S9).

3.6 | Case studies

Spiranthes casei ($T=-1$) displayed an insect richness gradient identical to its areas of taxonomic similarity (Figure 4a,b), exemplifying that compositional changes in insect assemblages are entirely attributable to progressive loss of species richness when $T=-1$. *Spiranthes lacera* ($T=0.952$) exhibited somewhat of a latitudinal richness gradient in its interactor insect species (Figure 4c). Insect compositional patterns were not identical to richness gradients, and three significant interactor taxonomic clusters were recovered, with distinct central, northern, and southern parts of its range (Figure 4d). *Isotria verticillata* ($T=0.01$) exhibited a latitudinal insect richness gradient (Figure 4e). Four significant interactor clusters were recovered. Taxonomic similarity mirrored richness changes for some clusters, but not others (Figure 4f).

4 | DISCUSSION

4.1 | Quantifying *T* and assessing its behaviour

Across site-number scenarios, T generates predictable and transferrable patterns, allowing for biologically meaningful comparative analyses. In general, site number, along with interactor species richness and focal species range sizes, should impact the distribution of T values due simply to the effects of random matrix filling. Through our analyses of T, we can generate expectations for how it will behave under different conditions: (1) increases in site number and interactor species richness should correspond to increases in mean T values; and (2) the probability that rare species will contribute to nestedness versus turnover depends on site number and interactor species richness.

The relative contribution of turnover in a landscape should be higher more often in larger areas because of increased opportunity for non-overlapping ranges when interactor species are randomly distributed. Thus, mean T values should increase with increasing site-number, but we should not expect the range of T values to change across site-number scenarios. In other words, independent of site number, 100% contribution of nestedness to interactor species beta diversity should be possible, as well as 100% contribution of compositional turnover, and every value in between.

At the same time, as interactor species richness increases, the total number of possible unique combinations also increases. For example, for four interactor species, there are 15 possible combinations that could be observed at any single site. If all sites are proper subsets of one most speciose site containing all four species, and all species have equal probability of occurring in any cell, then any site has a 1/196 chance of yielding an identical species combination to another site. For only three species, that chance increases to 1/36. Thus, higher interactor species richness increases the probability that two sites will have distinct species combinations under random matrix filling, decreasing the contribution of nestedness to overall dissimilarity, even when all sites are a proper subset of one site.

Baselga (2012) demonstrated that the nestedness component of B_{SOR} is highest when the most speciose region is composed of species with small ranges, and few species have larger ranges. We should expect that species' range sizes alone should differentially contribute to T depending on site-number under random matrix-filling. Given that increases in site number should decrease the chances of range overlap, it follows that rare species should also be less likely to overlap. In this way, the likelihood that rarer species will increase the impact of nestedness depends on site number.

Importantly, we should not assume that our expectations for the behaviour of T under random matrix-filling will always hold true in real world scenarios. Species distributions are determined, in part, by the distributions of other species—either via mutualisms, competition, or common evolutionary descent (Štípková et al., 2020). Thus, the distribution of T values for any given study system will also depend on the ecological, evolutionary, and historical context in which the system exists.

4.2 | Comparing *T* to other metrics

We have shown that, while T is more sensitive to sampling depth than other available metrics, it captures a unique feature of generalism ignored by other metrics. Specifically, variation in available metrics is not interpretable in terms of interactor beta diversity. Even D diff, which is intended to measure variation in D prime scores, was a poor indicator of T. This is because D diff only indicates how different D prime is among sites across a focal species' range, and D prime only measures the extent to which a focal species is specialized within a community, not the uniqueness of that local community with respect to the rest of the focal species' range. In this way, T describes an inherent feature of generalist relationships that is not captured by available metrics: spatiotemporal heterogeneity in interactor assemblages.

The strong relationship between the Simpson diversity index, D prime, S, and interactor species richness indicates that these methods primarily describe generalism as a feature of the number of interactors a focal species has, while T describes generalism as a feature of spatiotemporal variation in interactor species communities across a focal species' range. In addition, methods that depend on local community matrices and make use of both interactors and non-interactors (such as D prime and S) are uniquely vulnerable to the exclusion of non-interactors. That is, for any given focal species, metrics like D prime require knowledge of not only a focal species' interactors but also of the other species in the local (or global) community that the focal species does not interact with. Combined with dependence on abundance data for interactor species, these methods become increasingly data intensive—scaling up to the entire range of a focal species would ideally require intimate ecological knowledge of every community of which the focal species is a part. At the same time, Blüthgen et al. (2006) discourage using D prime

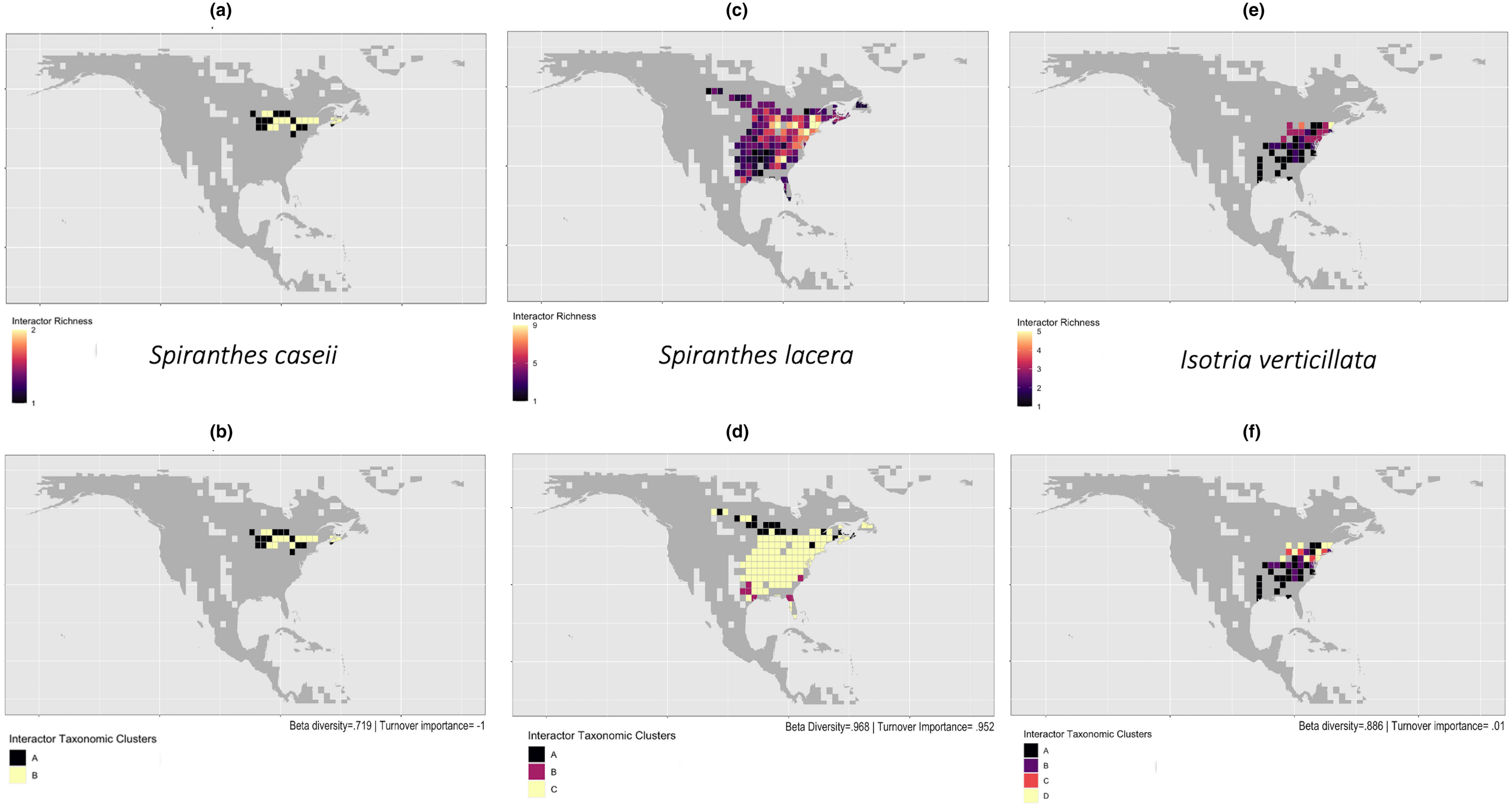

FIGURE 4 (a) Interactor richness gradient over the range of *Spiranthes casei* (total beta diversity = 0.719; $T = -1$). (b) Compositional clusters across the range of *Spiranthes casei*. Lettered groups define significantly similar pollinator clusters. As expected, compositional differentiation exactly mirrors changes in richness. (c) Interactor richness gradient over the range of *Spiranthes lacera* (total beta diversity = 0.968; $T = 0.953$). There appears to be a slight latitudinal richness gradient, as well as a longitudinal richness gradient, with interactors being the most speciose near the Appalachian Mountains. (d) Interactor compositional clusters across the range of *Spiranthes lacera*. Lettered groups define significantly similar interactor clusters. Group C occurs over much of *S. lacera*'s range, but unique clusters can be seen in the northern and southern borders of *S. lacera*'s range. (e) Interactor richness gradient over the range of *Isotria verticillate* (total beta diversity = 0.886; $T = 0.01$). Richness appears to follow a latitudinal gradient. (f) Interactor compositional clusters across the range of *Isotria verticillata*. Lettered groups define significantly similar pollinator clusters. The largest compositional cluster mirrors areas of lowest species richness, but some others occur in areas with similar richness, exemplifying the fact that both nestedness and compositional turnover contribute to *I. verticillata*'s high beta diversity value.

over large areas or over prolonged periods of time due to measures of specialization potentially being misled by phenomena other than resource preference. Considering these factors, available interactor-specific measures of generalism are best employed for local-level community networks over short timespans. In this way, *T* is complementary to these metrics: while available metrics can be used to assess use versus availability in local communities, *T* can be used to assess spatiotemporal patterns of variation in interactor assemblages across a focal species' range. Identifying a focal species with exceptionally low *T* could prove extremely useful in identifying areas of its range where they are already interactor limited, and therefore at greater risk of population loss upon habitat disturbance (climatic or physical) (Crain & Tremblay, 2014). On the other hand, discovering high *T* values can direct conservation strategies to identify potentially different sets of interactors, and their needs, in different parts of an orchid's range. For restoration efforts, understanding whether a focal species is disposed more towards turnover or nestedness is essential: the choice of appropriate habitat depends largely on predicting where, and to what extent, certain interactors are active in the maintenance of healthy focal species populations.

However, *T* might only capture one axis of variation along the generalism continuum, and in many contexts other features of variation might be important to include. For example, differences in *T* values do not necessarily correspond to differences in local functional specialization. Both exceptionally high and low values of *T* can reflect local functional specialization. On one hand, high *T* values indicate a strong effect of compositional turnover in resource use/availability across a species' range. In this case, local functional specialization is possible, but not necessarily expected. This is because *T* is independent of changes in species richness among sites. High *T* values mean that sites are compositionally different—those sites can have uniformly high or low richness, or richness can vary considerably among sites. Exceptionally low values of *T* imply higher rates of local functional specialization in some areas of a species' range compared to others. This is because low *T* values indicate a strong effect of nestedness, which necessitates progressive loss of richness among sites across a species' range. So, when local community assemblages are of interest, metrics like D prime can be used in concert with *T* to yield more holistic analyses of focal species' generalist tendencies.

4.3 | Correlates of *T*

It appears that orchids occupying colder, more seasonal climates in higher altitudes tend to exhibit higher *T* than orchids that occupy only warmer, more stable climates (Figure S6). These results might point to the impact of historic glaciation events in shaping North American orchid pollinator strategies (Kennedy & Walker, 2007). It might have been advantageous to retain low specificity and a capacity for frequent host switching (high *T*) in areas that were historically volatile (Saladin et al., 2020). Since many studies have demonstrated decreasing species diversity in increasingly colder climates (Hillebrand, 2004; Sanbonmatsu & Spalink, 2022), one might assume that orchids in colder climates have access to fewer total insects and depend on small, nested subsets of insects throughout their range (Štípková et al., 2020; Sun et al., 2014). These results, however, suggest the opposite: orchids with smaller areas of occupancy in less seasonal, warmer areas exhibit increasingly lower *T* compared to orchids that occupy larger ranges in colder, more seasonally volatile areas.

Many researchers have shown that increased specialization corresponds with decreased niche and range sizes (Kolanowska et al., 2017; Phillips et al., 2020). It would therefore be reasonable to expect that specialized native North American orchids would exhibit similar range sizes or abiotic niche breadths. But despite adhering to the relationships observed between range size and niche breadth, species exhibiting zero total pollinator beta diversity confounded the relationships involving *T* (Figure S6), displaying no pattern whatsoever. This could mean that the selective forces driving North American orchids to specialize on a single pollinator differ from those in other regions, where interspecific competition among sympatric orchid species plays a large role in determining not only insect associations, but also geographic and ecological space occupancy (Baguette et al., 2020).

4.4 | Phylogenetic signal

Generalist strategies are often considered a response to volatile or variable ecological conditions, and the climatic and geographic history of North America certainly fits this description (Fildani et al., 2018; Wallis et al., 2016). It is possible that such lability in generalist tendencies could characterize temperate orchid evolution in general, but future work should determine whether temperate orchids outside of North America follow these same patterns. Interestingly, some groups displayed uniformly high *T* values (e.g. *Cypripedium*), while others displayed highly variable *T* values. It appears that many high *T* species are in close phylogenetic proximity to low *T* species (e.g. *Platanthera*). It may be that for some clades, high *T* species eventually lead to divergence events in which one taxon occupies a smaller subset of the ancestral pollinator niche than the other, leading to the observed pattern of high *T* paired with low *T*. With more phylogenetic and pollinator data, future work should explore the causes and correlates of uniform vs variable *T* values within and between clades.

4.5 | Floral visitor sampling gaps

Our results indicated that central eastern North America is the best represented with respect to insect observations. Approximately 25% of native North American orchid species ($n = 53$) have a known floral visitor co-occurrence in at least half of their total range, while ~50% of species lack any information about their floral visitors at the species level. Those 53 species with known pollinator observations are mostly in the Orchidoideae, while the North American Epidendroideae are under-sampled. Because the Orchidoideae were over-represented in our study, future work should focus on increasing sampling effort among the epidendroids to verify whether the patterns we observed are common across native North American orchids or unique to terrestrial orchids. At the same time, and perhaps most importantly, it is clear that within-species sampling is sparse across the board: orchid-insect studies that do exist often rely on observations that take place in a single location.

Further, many orchids that are globally secure are imperilled or vulnerable in some parts of their range (Crain & Tremblay, 2014), so future work should focus on understanding how pollinator assemblages vary among areas for which a focal orchid is secure versus threatened. We emphasize the lack of available insect data for globally threatened and Imperilled orchid species (SI 3). Without these crucial data, we can say very little about the relationships between *T* and global orchid rarity when it comes to insect associations.

Considering the prevalence of spatial heterogeneity in orchid-insect associations, even orchids with known pollinators/insect associates do not have enough data for anyone to confidently assess insect/pollinator utility—merely insect/pollinator availability. To better understand true rates of *T*, and its causes and consequences, future work should be designed to explore insect associations and pollinator relationships across the ranges of individual orchids, rather than at single locations.

4.6 | *T* in the real world

We can use our case studies to better understand the utility of *T* relative to common definitions of generalism, especially for focal species like *I. verticillata* ($T=0.01$). Considering only *T*, we understand that the nature of its insect relationships is defined by a combination of compositional turnover and nestedness. Some areas are compositionally distinct from one another, but others contain nested subsets of more speciose locations. In this way, categorizing *I. verticillata* as a 'true generalist' or an 'apparent generalist' would ignore potentially important variation across its range. When intermediate values of *T* are common, simplifying a species' interactor relationships into discrete categories eliminates observable variation that could play an important role in shaping ecological and evolutionary trajectories of focal species. At the same time, it is also clear that an index of generalization/specialization that focuses on only a single part of a focal species' range cannot always be extrapolated to other parts of that same species' range. Our introduction of *T* operationalizes the beta diversity framework to capture key complexities of generalized relationships that will facilitate improved ecological, evolutionary and conservation assessments.

AUTHOR CONTRIBUTIONS

Lydia Morley and Daniel Spalink conceived the project. Lydia Morley conceptualized *T*, performed the analyses, and led the manuscript writing. Gary Krupnick and Benjamin J. Crain provided the original floral visitor data matrix. All authors contributed to manuscript preparation and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

PEER REVIEW

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DATA AVAILABILITY STATEMENT

All datasets and scripts (including the function for calculating *T* and the master orchid-insect table with citations) can be found Zenodo and Github: https://zenodo.org/doi/10.5281/zenodo.10840140.

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SUPPORTING INFORMATION

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

Table S1: All metrics used in this paper.

Table S2: *p* values for pairwise Wilcoxon tests of mean T values between site number scenarios.

Table S3: Correlations between total number of species (Gamma diversity) and T, and Gamma diversity and B_{SOR}.

Table S4: Loadings for all retained ecological variables along PC1.

Table S5: Best fit models of nucleotide evolution, number parsimony informative characters, and total characters for each gene used to construct the orchid phylogeny.

Figure S1: Typical workflow for compiling interspecies co-occurrence data and calculating *T*.

Figure S2: Differences in value range between *T* and B_{SOR} among site-number scenarios.

Figure S3: patterns of assembly across site-number scenarios for identical *T* values.

Figure S4: PCA of climatic niche variables for all orchids with available occurrence data.

Figure S5: Distribution of error in *T* (measured as observed value-true value) in different sampling depth scenarios.

Figure S6: Correlations between *T*, climatic niche breadth, area of occupancy, and extent of occurrence.

Figure S7: Phylogenetic signal and patterns of *T* across the native North American orchid phylogeny.

Figure S8: Sampling effort across the native North American orchid phylogeny.

Figure S9: Proportion of orchids for which there is a known insect associate occurrence in that same cell.

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