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RESEARCH ARTICLE

A multi-site method to capture turnover in rare to common interactions in bipartite species networks

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Abstract

1. Ecological network structure is maintained by a generalist core of common species. However, rare species contribute substantially to both the species and functional diversity of networks. Capturing changes in species composition and interactions, measured as turnover, is central to understanding the contribution of rare and common species and their interactions. Due to a large contribution of rare interactions, the pairwise metrics used to quantify interaction turnover are, however, sensitive to compositional change in the interactions of, often rare, peripheral specialists rather than common generalists in the network.
2. Here we expand on pairwise interaction turnover using a multi-site metric that enables quantifying turnover in rare to common interactions (in terms of occurrence of interactions). The metric further separates this turnover into interaction turnover due to species turnover and interaction rewiring.
3. We demonstrate the application and value of this method using a host–parasitoid system sampled along gradients of environmental modification.
4. In the study system, both the type and amount of habitat needed to maintain interaction composition depended on the properties of the interactions considered, that is, from rare to common. The analyses further revealed the potential of host switching to prevent or delay species loss, and thereby buffer the system from perturbation.
5. Multi-site interaction turnover provides a comprehensive measure of network change that can, for example, detect ecological thresholds to habitat loss for rare to common interactions. Accurate description of turnover in common, in addition to rare, species and their interactions is particularly relevant for understanding how network structure and function can be maintained.

KEYWORDS
ecological networks, environmental modification, habitat loss thresholds, host–parasitoid interactions, interaction turnover, multi-site turnover, rewiring

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1 | INTRODUCTION

Communities are composed of rare and common species that contribute in different but important ways to ecosystem diversity and function (Gaston, 2010; Mouillot et al., 2013). In ecological networks, this relative contribution is expressed in the 'core-periphery' structure (Miele et al., 2020). A core of generalist, often common, species are central to maintaining network structure because they tend to be associated with many interactions (Kaiser-Bunbury et al., 2010; Miele et al., 2020). These core generalists interact with both specialists and other generalists, and their loss can lead to cascading species loss and change in network function (Bascompte et al., 2003; Memmott et al., 2007). In contrast, rare species, or those with some combination of high habitat specificity, narrow geographical ranges and small local population sizes (Rabinowitz, 1981), are vulnerable to extinction, particularly when locally suitable resources are limited or patchily distributed (Cagnolo et al., 2009) and are considered peripheral to network structure (Bascompte et al., 2003; Miele et al., 2020). Nonetheless, they jointly contribute substantially to both species and functional diversity (Mouillot et al., 2013). Analytical approaches that are sensitive to changes in the interactions of both core and peripheral species are needed for a comprehensive understanding of network diversity and function.

Interaction turnover is a metric that is used to quantify changes in network composition, specifically the difference between pairs of networks (i.e. interaction beta diversity), and species identity is implicit in the quantification of this change (Novotny, 2009; Poisot et al., 2012). Using interaction turnover, changes in locally realised interactions between two networks can be partitioned into (a) species turnover (i.e. interactions that change across sites because one or both interaction partners are absent) and (b) interaction rewiring (i.e. interactions that change even though both species remain; Novotny, 2009; Poisot et al., 2012). This metric has been used, for example, in pollination networks to estimate the rate of compositional change in interactions along spatial and temporal gradients (CaraDonna et al., 2017; Carstensen et al., 2014; Olesen et al., 2011; Trøjelsgaard et al., 2015) and to examine the potential for interaction rewiring to act as a buffer against environmental change (Nielsen & Totland, 2014; Simanonok & Burkle, 2014).

One constraint of turnover metrics that rely on pairwise comparisons of networks is that they are likely to be more sensitive to the compositional change in the interactions of rare, peripheral specialists than to the interactions of common species in the generalist core of the network. This is due to the large contribution of turnover in interactions shared by few networks, because interactions that are rare across networks are more likely to differ between any two networks than interactions that are common across networks. The relative insensitivity of pairwise metrics to the turnover of common species is recognised as a limitation to assessing community structural change more generally (Diserud & Ødegaard, 2007; Hui & McGeoch, 2014; Jost, 2007; McGeoch et al., 2019).

Since interaction turnover was first introduced (Novotny, 2009), different variations of the metric have been suggested, all of which rely on pairwise network comparisons. This includes, for example, methods that focus on different components of interaction turnover (e.g. Nielsen & Totland, 2014; Poisot et al., 2012), compare local network realisations to the metaweb representing all species and their interactions across networks (Noreika et al., 2019; Poisot et al., 2012) and incorporate interaction probabilities into turnover metrics (Ohlmann et al., 2019). These measures all add unique perspectives on the nature of network change. Nonetheless, a method that can quantify turnover in not just rare but also common interactions has not yet been explored. Such a metric would provide a more comprehensive and information-rich understanding of network change and enable modelling of environmental drivers of change across rare to common interactions.

To fully understand compositional change in ecological networks, the relative contributions of rare to common species and their interactions need to be disentangled. Here we present a multi-site interaction turnover metric that quantifies the compositional change of species and interactions that vary in their degree of commonness (i.e. ranging from rare to common) and their environmental drivers. Degree of commonness is defined here in terms of the occurrence (i.e. presence or absence) of species and interactions across networks, that is, species and interactions that occur in few to many networks. While abundance is another important component of commonness (McGeoch & Latombe, 2016; Rabinowitz, 1981), and weighted metrics are widely used in network analysis (e.g. Noreika et al., 2019; Ohlmann et al., 2019), it is not the focus here.

We illustrate the ecological insights and information gained with this method using a host–parasitoid network of gall wasps and their natural enemies sampled along multiple modification gradients. We show (a) that compositional change in rare to common interactions is differently driven by interaction rewiring and species turnover, and (b) that interactions of rare to common species have different threshold tolerances to habitat loss. Disentangling the roles of environment, species commonness, rewiring and species turnover for changes in species interactions therefore provides information-rich insights on the nature of network change, with crucial implications for the understanding and management of ecosystems.

2 | MATERIALS AND METHODS

2.1 | Extending pairwise interaction turnover to multi-site interaction turnover

In communities, compositional change of rare to common species is quantified using the zeta diversity metric (ζ_n), defined as the mean number of species shared by n sites (Hui & McGeoch, 2014). Zeta diversity is incidence based, and rarity and commonness are therefore defined in terms of relative occurrence, that is, species having narrow to wide geographical ranges, respectively (McGeoch et al., 2019). The number of sites, n, is referred to as the zeta order, with order 2 equivalent to pairwise, incidence-based calculations of beta diversity, whereas order 3 and beyond extend the concept to

comparisons across three to multiple sites (Hui & McGeoch, 2014). As the order of zeta increases, with more sites considered in the calculation of turnover, only the species that are widespread across sites remain shared. Low orders of zeta are, therefore, dominated by the turnover in rare species, while high orders of zeta represent turnover in common species only (Hui & McGeoch, 2014). Zeta diversity has been used to provide novel insights on compositional change and its drivers in multiple taxa and contexts (Krasnov et al., 2020; Leihy et al., 2018; Simons et al., 2019), but not yet applied to quantify turnover in species interactions.

Here, we expand on the pairwise interaction turnover formulated by Novotny (2009; β_{int}, i.e. interaction beta diversity) to quantify interaction turnover across multiple sites, using zeta diversity (Box 1). Other multisite turnover metrics exist but we use zeta diversity due to its unique ability to quantify turnover along a gradient of increasing commonness. Commonness is here defined as interaction occurrence across networks, not local abundance. In networks, the causal relationship between occurrence and abundance, as well as degree of specialisation and sampling, remains to be determined (e.g. Fort et al., 2016; Vázquez & Aizen, 2004) but the relationship is as a rule positive (i.e. the occupancy–abundance relationship (Gaston et al., 2000); see also the positive relationship for the study system; Supporting Information S1, Figure S1.17).

Novotny (2009) quantified interaction turnover (β_{int}) as the number of interactions that are dissimilar between two bipartite interaction networks, M_1 and M_2, divided by the total number of interactions across both networks (Box 1). To quantify the full range of compositional change in interactions, including both relatively rare and common interactions, we define a measure of zeta dissimilarity and use it to expand pairwise interaction turnover to multi-site comparisons. Given *n* networks, we define multi-site interaction dissimilarity (${}^{c}\zeta_n = 1 - \zeta_n$) as the number of interactions that occur in at least one, but not all, of *n* networks divided by the total number of interactions across the *n* networks (i.e. corresponding to normalised zeta diversity similarity; McGeoch et al., 2019). In this form, normalised, second-order zeta dissimilarity (${}^{c}\zeta_2$) is therefore equivalent to the Jaccard dissimilarity measure for pairwise interaction turnover, β_{int} (Novotny, 2009).

Total pairwise interaction turnover (β_{int}) can be partitioned into interactions that change because (a) one or both of the species included in the interaction are missing (i.e. interaction turnover due to species turnover; β_{st}), or because (b) the two species do not interact even though both are present (i.e. interaction rewiring, β_{rw}; Novotny, 2009). The total pairwise interaction turnover β_{int} is, therefore:

$$\beta_{int} = \beta_{st} + \beta_{rw}. \quad (1)$$

When more than two networks are considered, total interaction turnover (${}^{c}\zeta_{n,int}$) must be partitioned into three additive components (Figure 1): interaction turnover due to species turnover ${}^{c}\zeta_{n,st}$ (where interactions are dissimilar across *n* networks because one or both interaction partners are missing in one or more networks, but interactions are always observed if both species are present, equivalent to β_{st} for two networks), interaction rewiring ${}^{c}\zeta_{n,rw}$ (where both interaction partners are present across all *n* networks but their interaction is absent in one or more networks, equivalent to β_{rw} for two networks) and a mixture of both ${}^{c}\zeta_{n,strw}$ (where interactions are dissimilar due to species turnover between some of the *n* networks compared and due to interaction rewiring in others).

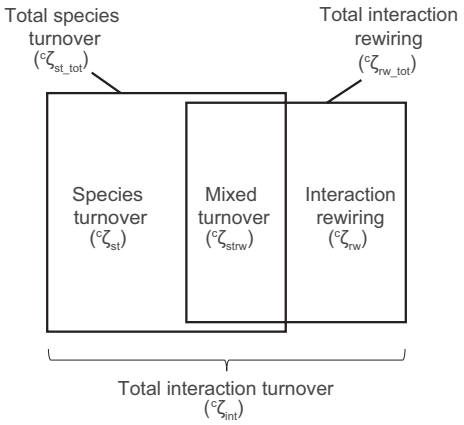


FIGURE 1 Schematic showing how total interaction turnover for multiple sites is partitioned into three components. Total interaction turnover (${}^{c}\zeta_{int}$) can be partitioned into interaction turnover due to species turnover only (${}^{c}\zeta_{st}$), interaction turnover due to rewiring only (${}^{c}\zeta_{rw}$) and turnover due to a mixture of both (${}^{c}\zeta_{strw}$). Thus, ${}^{c}\zeta_{st_tot}$ is turnover involving some component of species turnover and ${}^{c}\zeta_{rw_tot}$ is turnover involving some component of interaction rewiring. For pairwise turnover, there is no overlap between species turnover and interaction rewiring (i.e. no mixed turnover component)

Total interaction turnover is therefore partitioned as:

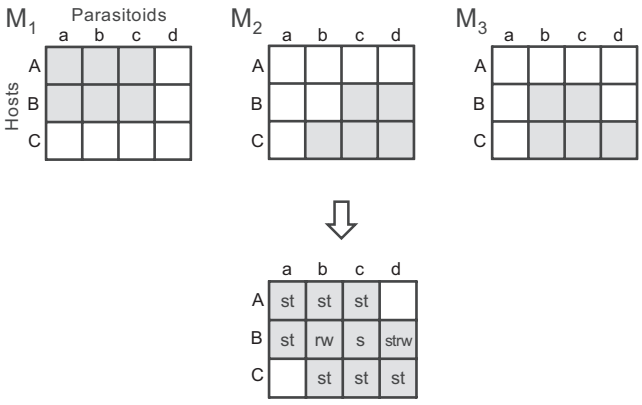
$${}^{c}\zeta_{n,int} = {}^{c}\zeta_{n,st} + {}^{c}\zeta_{n,rw} + {}^{c}\zeta_{n,strw}. \quad (2)$$

We show the calculation of interaction turnover in Box 1 for three networks and similar calculations can be made for any number of networks (i.e. two, four or more networks). Following this approach, the turnover of rare to common interactions (i.e. across few to many sites compared) of any type and size of network can be quantified. Computation of multi-site interaction turnover is fully formulated in Supporting Information S1 and the R code is provided in Supporting Information S2.

The contribution of common interactions to total interaction turnover will increase with the number of networks compared. Meanwhile, the pure species turnover component (${}^{c}\zeta_{n,st}$) is increasingly influenced by common interactions that change only due to species turnover (Figure 2). Thus, these are the interactions of species with high partner fidelity (Trøjelsgaard et al., 2015) that only change their interactions if their interaction partners are absent. The pure rewiring component (${}^{c}\zeta_{n,rw}$) will be dominated by species that co-occur in all *n* networks compared but vary in the local realisation of their interactions. When many networks are compared, the pure

BOX 1 Calculation of multi-site interaction turnover

Using an example of three theoretical host–parasitoid networks (M_1, M_2 and M_3), below we show how the components of multi-site interaction turnover are quantified as the dissimilarity in interactions between three interaction matrices (i.e. zeta order 3), normalised by the total number of interactions across networks (${}^{c}\zeta_{3,int}$). To quantify change in interaction composition, species across all networks (i.e. three host and four parasitoid species) are included in binary interaction matrices with presence (grey) and absence (white) of interactions. When no interaction occurs for a species in a network, the species is considered absent (e.g. see species C and d in M_1 or A and a in M_2 below).



Based on the interaction matrices above, all interactions across networks can be categorised as shared (s; i.e. species B and c interact in all networks), dissimilar due to species turnover (st; e.g. A and b interact in M_1 but the interaction is absent in M_2 and M_3 because species A is absent in both), dissimilar due to interaction rewiring (rw; i.e. species B and b interact in M_1 and M_3 but not in M_2 even though both species are present in the network) or dissimilar due to a mix of both species turnover and interaction rewiring (species B and d interact in M_2 but the interaction is absent from M_1 due to species turnover, i.e. species d missing from M_1, and is absent from M_3 due to interaction rewiring, i.e. both species are present in M_3 without interacting).

Across the three matrices, (a) one interaction is shared (s), (b) seven interactions are dissimilar because one or both interaction partners are missing from one or two networks (st, i.e. the number of interactions that are dissimilar due to species turnover), (c) one interaction is dissimilar even though both interaction partners are always present (rw, i.e. the number of interactions that are dissimilar due to rewiring), and (d) one interaction is dissimilar between two matrices (M_1 and M_2) because an interaction partner is missing while the interaction is dissimilar between two other matrices (M_2 and M_3). This is despite both interaction partners being present in both matrices (strw, i.e. the number of interactions that are dissimilar due to both species turnover and rewiring).

Pairwise interaction dissimilarity as defined by Novotny (2009) is calculated as Jaccard dissimilarity = 1 − Jaccard similarity = $1 - x/(x + y + z) = (y + z)/(x + y + z)$ where x is the number of entities shared between two assemblages (M_1 and M_2), and y and z are the number of entities unique to assemblage M_1 and M_2, respectively. Each component of interaction turnover is then quantified as:

$$\beta_{st} = \mathrm{st}/(x + y + z), \tag{3}$$

$$\beta_{rw} = \mathrm{rw}/(x + y + z), \tag{4}$$

where st is the total number of interactions in assemblage M_1 and M_2 that are dissimilar due to species turnover and rw is the number of interactions in assemblage M_1 and M_2 that are dissimilar due to interaction rewiring.

Similarly, the components of multi-site interaction turnover for the three networks illustrated above can be calculated as:

$${}^{c}\zeta_{3,rw} = \mathrm{rw}/(\mathrm{rw} + \mathrm{st} + \mathrm{strw} + \mathrm{s}) = 1/(1 + 7 + 1 + 1) = 0.1, \tag{5}$$

$${}^{c}\zeta_{3,st} = \mathrm{st}/(\mathrm{rw} + \mathrm{st} + \mathrm{strw} + \mathrm{s}) = 7/(1 + 7 + 1 + 1) = 0.7, \tag{6}$$

$${}^{c}\zeta_{3,strw} = \mathrm{strw}/(\mathrm{rw} + \mathrm{st} + \mathrm{strw} + \mathrm{s}) = 1/(1 + 7 + 1 + 1) = 0.1. \tag{7}$$

Total interaction turnover is then:

$${}^{c}\zeta_{3,int} = {}^{c}\zeta_{3,st} + {}^{c}\zeta_{3,rw} + {}^{c}\zeta_{3,strw} = 0.7 + 0.1 + 0.1 = 0.9. \tag{8}$$

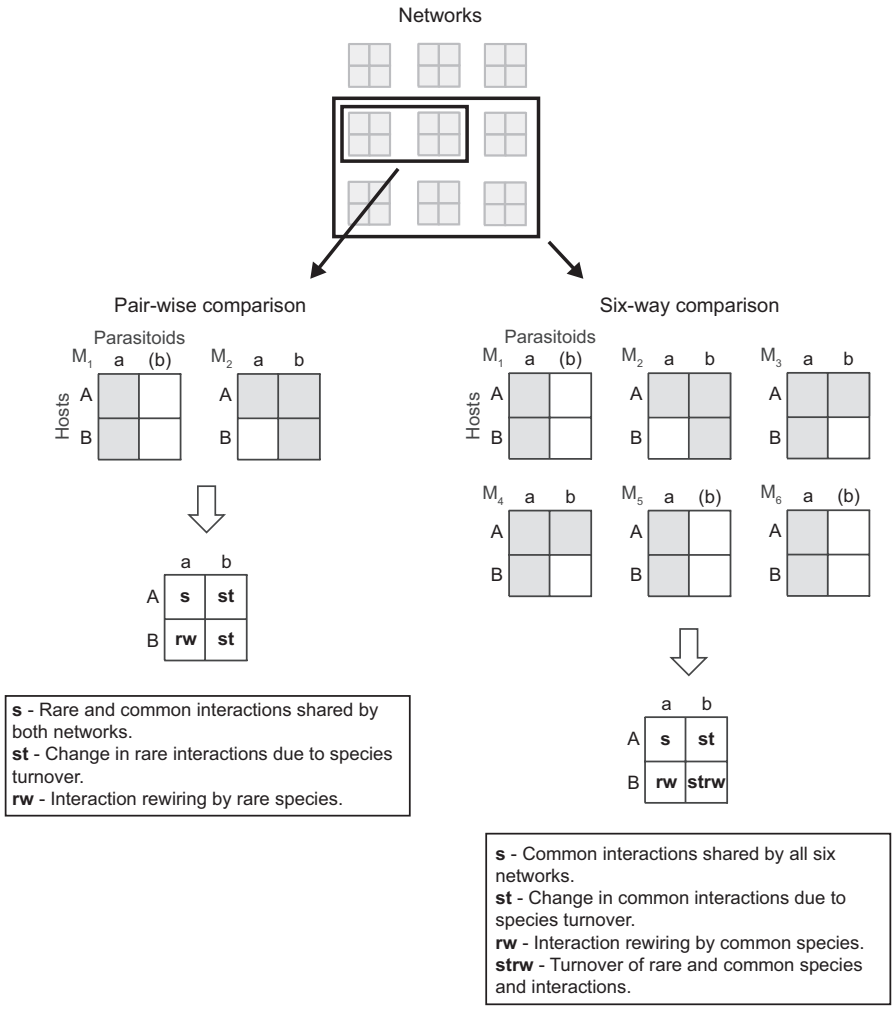


FIGURE 2 How to interpret the interaction turnover components when comparing few (pairwise comparison) and many (six-way comparison) networks in which turnover is dominated by rare and relatively common interactions, respectively. This is shown for a strongly simplified system consisting of nine spatially distinct networks (top) with no more than two host and two parasitoid species each. Interactions are indicated as present (in grey) or absent (in white). Absent species are shown in parentheses. When two randomly chosen networks are compared (left), turnover between networks is due to changes in rare species and interactions which are the ones most likely to change between any two networks. Turnover in a six-way comparison (right) is dominated by changes in relatively common species and interactions which are likely to change among any subset of six randomly chosen networks. Only the most common interactions are likely to be shared between any six networks

rewiring component therefore represents interaction rewiring by the most common species across networks (Figure 2).

The likelihood of rewiring and species turnover happening simultaneously across multiple networks increases with the number of networks compared since there are more networks involved in which species can make different partner choices (interaction rewiring) or be absent from one or more networks (species turnover). Because of this, the mixed component of interaction turnover (${}^{c}\zeta_{n,\mathrm{strw}}$) is expected to increase with the number of networks compared.

2.2 | Relationship between multi-site interaction turnover and environmental change

To demonstrate the information gained by this multi-site method, we quantified the relationship between environmental variables and multi-site interaction turnover by adapting an existing multi-site generalised dissimilarity modelling approach (MS-GDM; Latombe et al., 2017). This will reveal if rare to common interactions in the network are explained by different environmental predictors. MS-GDM predicts nonlinear changes in species composition across multiple sites from changes in environmental and spatial drivers and is a multi-site extension of pairwise generalised dissimilarity modelling (GDM; Ferrier et al., 2007). In MS-GDM, the average environmental difference between pairs of sites in a given combination is used for the predictors (Latombe et al., 2017). MS-GDM accommodates two types of nonlinearity in the relationship between compositional interaction dissimilarity and environmental distance (Krasnov et al., 2020; Latombe et al., 2017). First, because the measure of interaction turnover is constrained between zero and one, its relationship with the environmental distance must be curvilinear. Second, the impact of environmental distance can vary along the range of the value of each environmental variable. I-splines are thus used to transform the original environmental variables and a generalised linear model with a binomial distribution is fitted to the transformed environmental variables (see Ferrier et al., 2007; Latombe et al., 2017 for details).

The shape of the I-splines fitted for each environmental variable in the MS-GDM describes the relationship between compositional and environmental dissimilarity in two ways: (a) the maximum height of each curve indicates the relative importance of the environmental variable in explaining compositional change compared to other variables for the same order of zeta, and (b) the slope of the curve indicates the rate of turnover along the environmental gradient (Ferrier et al., 2007; Latombe et al., 2017). This analytical approach allowed

us to quantify both the relative difference in importance between environmental variables (difference in maximum curve height) and the points along each environmental gradient at which interaction composition changes most rapidly (steep slopes along the curve). Points of rapid network change will indicate potential thresholds at which small changes in habitat availability and fragmentation could result in large shifts in composition (Yin et al., 2017). MS-GDM was run in R 3.2.2 (R Core Team, 2015) by adapting the Zeta.msgdm function from the ZETADIV package (Latombe et al., 2016) to use the novel metric of multi-site interaction turnover (the R code is provided in Supporting Information S2).

2.3 | Study system used to apply the multi-site interaction turnover method

We used a system of gall wasps and their natural enemies to illustrate our method because host–parasitoid networks are useful systems for studying complex interactions across trophic levels (van Veen et al., 2006), especially in a spatial context where networks must be sampled from multiple localities. The often small, host–parasitoid networks are well defined (i.e. a guild of herbivores and their natural enemies) and relatively easy to sample (van Veen et al., 2006). Host–parasitoid networks have been used to examine complex direct and indirect interactions, such as anthropogenic impacts on networks (Tylianakis et al., 2007), indirect interactions between herbivores (Morris et al., 2004) and consequences of multi-trophic interactions for biocontrol (Gagic et al., 2011).

The study system is a ubiquitous insect herbivore–natural enemy network native to Australia. It includes three *Trichilogaster* (Hymenoptera: Pteromalidae) gall wasp herbivores (*T. acaciaelongifoliae* [Froggatt], *T. signiventris* [Girault] and *T. maideni* [Froggatt]) and 18 Hymenopteran natural enemies (Henriksen et al., 2017, 2019). Each of these gall wasps is highly specific to between one to two *Acacia* host plants (Fabaceae; i.e. *T. acaciaelongifoliae* occur on *A. longifolia* (Andrews) Willd. and *A. floribunda* (Vent.) Willd., *T. signiventris* occur on *A. pycnantha* Benth. and *T. maideni* occur on *A. implexa* Benth.; Prinsloo & Neser, 2007).

To relate compositional change in species and interactions to the degree of environmental modification, galls of the three gall wasp species were collected across 13 sites within an extent of 525 km^2 in the eastern suburbs of Melbourne, Victoria, Australia (37°50′45 S, 145°04′25 E) and reared in the laboratory. Galls were sampled in urban parks and reserves where the gall wasps were prevalent (Henriksen et al., 2017, 2019). This was a landscape with strong human impact where the effects of multiple modification gradients could be tested, including different responses of rare and common species along these gradients. The natural enemy assemblage consisted of parasitoid and gall inquiline species (Figure S1.17). While parasitoids feed directly on the gall wasp larvae, gall inquilines feed on gall tissue and thereby directly or indirectly kill their host (Ronquist, 1994). Both species and interactions were sampled to a high completeness (measured as the proportion of estimated richness observed; Chacoff et al., 2012), with a mean sampling completeness of 0.83 for species and 0.80 for interactions (Henriksen et al., 2019). See Supporting Information S1 and Henriksen et al. (2017, 2019) for more detail on sampling and insect identification. Permits for collection of plant material were given by the Department of Environment and Primary Industries, Victoria, Australia (permit numbers 10006916 and 10008025). No ethical approval was required.

An interaction matrix (A_{hp}) containing the presence and absence of interactions between each gall wasp host species and their natural enemies was constructed for each site (hereafter referred to as host–parasitoid networks). Multi-site interaction turnover and its components were then quantified for the 13 networks.

To assess the extent to which environmental predictors may be related to compositional change of common and rare interactions (using MS-GDM modified for multi-site interactions), we selected habitat modification variables known to influence insect community diversity and structure across trophic levels, that is, measures of habitat availability and fragmentation (Tscharntke & Brandl, 2004; Öckinger et al., 2009). We used measures of availability and fragmentation of two different habitat types in the urban matrix—forest cover and green space. The two habitat types were quantified from independent spatial datasets of land-use zones (green space) and tree vegetation obtained through remote sensing (forest cover; described fully in Supporting Information S1). The full MS-GDM contained six environmental predictors: two measures of forest cover (forest patch perimeter:area ratio and *Acacia* host plant abundance), two measures of green space (proportional cover and mean patch fractal dimension, *D*; Krummel et al., 1987) and two covariates (interaction richness and geographical distance) that were included to control for local variation in richness and spatial autocorrelation. Quantification and selection of model variables is described in full in Supporting Information S1 (including habitat availability and fragmentation across spatial scales, choice of covariates and elimination of collinear predictor variables). For pairwise comparisons (i.e. zeta order 2, ${}^{c}\zeta_2$), model significance and inclusion of environmental variables were tested with permutation tests in the GDM package (Manion et al., 2017) as detailed in Supporting Information S1. Permutation tests are not supported in the Zeta.msgdm function, as it is too computationally intensive to run permutation tests for high orders of zeta (Latombe et al., 2016). Model significance and the significance of landscape variables could, therefore, not be predicted for high orders of zeta. Instead, MS-GDM was run 30 times for random samples of 400 site combinations, therefore resulting in a different spline for each variable for each MS-GDM run (except for zeta 2 and 3, because the total number of possible site combinations is <400, i.e. 78 and 286, respectively). The variability in the splines for a given variable over these 30 replicates provides a level of confidence in the relationship between turnover and the change in the variable.

3 | RESULTS

3.1 | Characteristics of the study system

Across the 13 networks, the natural enemy assemblage consisted of six parasitoid species and 12 gall inquilines and included 34 gall wasp–natural enemy interactions (Figure S1.17). Most of the gall inquilines were relatively rare, occurring in three or fewer networks. The most common species, occurring in 11 or more networks, were all parasitoids (Figure S1.17). Few species had an intermediate level of occurrence (Figure S1.17). In the following results, turnover in rare interactions will therefore be dominated by interactions of inquilines with their hosts while turnover in common interactions is increasingly influenced by interactions involving parasitoids.

3.2 | Components of multi-site interaction turnover

On average, more than half of the interactions were shared between pairs of networks while <10% of interactions were common enough to be shared across all 13 networks (Figure 3). Thus, total interaction turnover (i.e. interaction dissimilarity) was 0.49 for rare interactions (i.e. pairwise network comparison; ${}^{c}\zeta_{2,int}$) and increased to 0.91 with an increasing influence of common interactions (when all 13 networks were compared; ${}^{c}\zeta_{13,int}$; Figure 3; Figure S3.1).

The contribution of species turnover to interaction turnover increased with the number of networks compared (Figure 3). For example, the proportion of interactions that changed due to species turnover was 39% for the rarest interactions (${}^{c}\zeta_{2,st} = 0.39$) and 53% for the relatively common interactions in six-way comparisons (${}^{c}\zeta_{6,st} = 0.53$). The species turnover component declined again towards the most common interactions (e.g. ${}^{c}\zeta_{13,st} = 0.44$) as a result of increasing contribution of mixed turnover (${}^{c}\zeta_{strw}$; Figure 3).

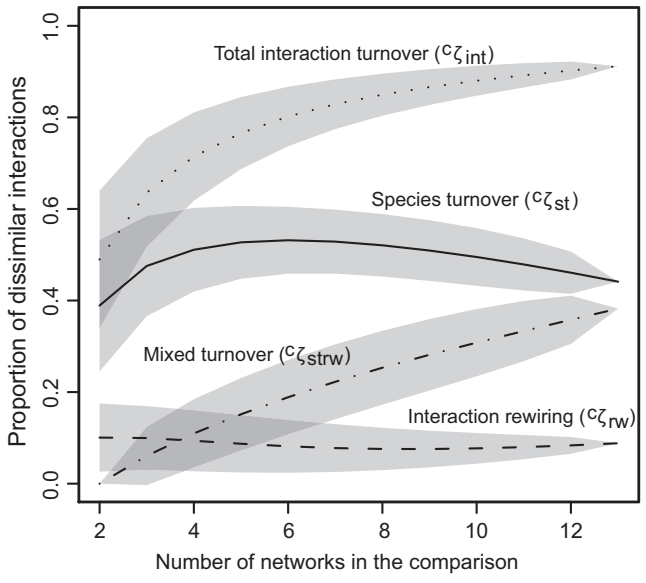


FIGURE 3 Multi-site interaction turnover (±*SD*) found across the host–parasitoid networks in an urban landscape, showing the contributions of components of interaction turnover (measured as zeta dissimilarity, i.e. the mean proportion of interactions dissimilar for a particular number of networks). Total interaction turnover is the result of its three additive components: species turnover, interaction rewiring and mixed turnover. The contribution of mixed turnover increases with the number of networks compared as expected due to varying environmental conditions across sites

Interaction rewiring (${}^{c}\zeta_{rw}$) remained a small (e.g. ${}^{c}\zeta_{2,rw} = 0.10$), but consistent, contributor to interaction turnover (Figure 3). About 10% of total interaction turnover was consistent due to interaction rewiring regardless of whether the species involved were rare or common.

3.3 | Relative importance of environmental variables related to interaction turnover

Pairwise network turnover: When measured as pairwise turnover, total interaction turnover and the species turnover component were significantly related to green space cover (${}^{c}\zeta_{2,int}$ and ${}^{c}\zeta_{2,st}$, respectively; Table 1). They were also both significantly related to interaction richness (Table 1). Interaction rewiring was significantly related to host plant abundance (i.e. ${}^{c}\zeta_{2,rw}$; Table 1). All three measures of interaction turnover were, furthermore, significantly related to geographical distance between sites, although geographical distance was always much less important than other variables included in the final model (i.e. the variable explaining the smallest proportion of deviance; Table 1).

Turnover across multiple networks: We excluded zeta diversity orders higher than six in the MS-GDM since change in mixed turnover was by far the most dominant contributor to the increase in total interaction turnover at high orders (Figure 3). Additional orders therefore provide little information about the contribution of the pure species turnover and rewiring components to total interaction turnover. The relative importance of habitat variables across multiple networks mirrored those of the tested pairwise relationships (Table 1) as shown by the maximum height of each I-spline curve in the MS-GDM (Figure 4). Overall, green space cover, fragmentation and host plant abundance were all important for turnover. Green space cover was most important for total interaction turnover and its species turnover component, whereas host plant abundance was most important for interaction rewiring (Figure 4). Fragmentation was an important explanatory variable for both interaction turnover components (Figure 4b,c). These relationships were consistent when quantified multiple times from a reduced number of samples both in terms of relative importance and shape of the individual I-splines, as shown by the low variability across replicates (Supporting Information S3, Figure S3.3–5).

However, when considering the multi-site aspect of the analysis (from the top towards the bottom of Figure 4), shifts in relative importance of habitat variables for turnover dominated by rare towards more common interactions were evident. For the species turnover component, fragmentation became increasingly important compared to green space cover with increasing commonness (Figure 4b). For interaction rewiring, the relative importance of host

TABLE 1 Contribution of landscape modification to explaining interaction turnover. Values are given as the percentage deviance explained (with bootstrapped *p*-values indicating significance) by each landscape variable (i.e. relative contribution) in the body of the table and the total deviance explained for GDM models (pairwise turnover). Bootstrapped *p*-values for the inclusion of each landscape variable are given in parentheses. Dashes indicate variables excluded from the final models through step-wise backwards elimination of the least significant variables until only significant terms remained

	Model		
Environmental variable	**Total interaction turnover ($^{c}\zeta_{2,int}$)**	**Species turnover ($^{c}\zeta_{2,st}$)**	**Interaction rewiring ($^{c}\zeta_{2,rw}$)**
Geographical distance	0.07 (<0.001)	0.01 (<0.001)	1.84 (0.034)
Interaction richness	20.89 (<0.001)	30.58 (<0.001)	—
Host plant abundance	—	—	89.46 (<0.001)
Forest cover–perimeter:area ratio	—	—	—
Green space–proportional cover	55.40 (<0.001)	38.47 (<0.001)	—
Green space–fragmentation (*D*)	—	—	—
Total deviance explained (%)	74.80	62.96	30.52

plant abundance and green space cover switched with species commonness. Thus, rewiring by rare species was strongly related to host plant abundance while rewiring by comparatively common species was strongly related to green space cover (Figure 4c).

3.4 | Habitat modification rates and thresholds for compositional change

Rate of turnover along an environmental gradient provides information on the environmental conditions where interactions change most rapidly. This is illustrated by the shape of each fitted I-spline in Figure 4, with steep slopes indicating a high degree of compositional change for a given value of habitat modification.

There was a steady change in total interaction turnover with declining green space cover, until a value of around 10% cover after which composition changed rapidly (0.1 rescaled range, Figure 4a). The threshold for the species turnover component was also at ~10% green space cover at which point rare interactions changed sharply (see top panel in Figure 4b), while the rate of turnover in common interactions remained comparatively steady at low green space cover (Figure 4b). A host plant abundance threshold became increasingly apparent for rewiring by common species (at around 15%–20% host plant abundance values; see bottom panel in Figure 4c).

The contribution of each of the turnover components (i.e. species turnover and interaction rewiring) to the rate of total interaction turnover was particularly evident in the shape of the I-spline fitted for green space cover. At low green space cover, rate of total interaction turnover increased rapidly, similar to the rate of the species turnover component (Figure 4a,b). At medium to high green space cover, total interaction turnover increased similar to the rate of interaction rewiring (Figure 4a,c). On the other hand, the contribution of green space fragmentation (fractal dimension) was not apparent for total interaction turnover. Green space fragmentation was, however, related to the rewiring and species turnover components, particularly when many networks were compared (bottom panels of Figure 4b,c). Thus, green space fragmentation was important for both changes to common interactions and interaction rewiring by common species.

4 | DISCUSSION

Here we show how a multi-site metric of interaction turnover provides a comprehensive measure of network compositional change that captures the contribution of both rare and common species and their interactions. This metric has the potential to enhance both the accuracy of the description of network change and our understanding of the consequences of environmental modification for network function. In the host–parasitoid network of gall wasps and their natural enemies, this was shown for changes in interactions that varied in degree of commonness, and for the environmental variables related to these changes. This included the identification of potential habitat loss thresholds for rare to common interactions. The method we present here is applicable to any network sampled repeatedly across space or time. The approach is particularly relevant for management aimed at preserving interactions to avoid cascading species loss. While turnover of rare species and interactions may indicate an overall loss of diversity, large shifts in network structure and function are more likely related to changes in the most common species and their interactions (Kaiser-Bunbury et al., 2010; Miele et al., 2020).

4.1 | A comprehensive measure of network compositional change

Given the key services and disservices contributed by common species and their interactions to ecosystem function (Baker et al., 2018; McGeoch & Latombe, 2016), a better understanding of their contribution to interaction turnover is particularly important to ensure the conservation of network structure and function. The metric presented here expands on previous pairwise interaction turnover metrics that are dominated by rare interactions (such as Novotny, 2009; Poisot et al., 2012) to include change in common

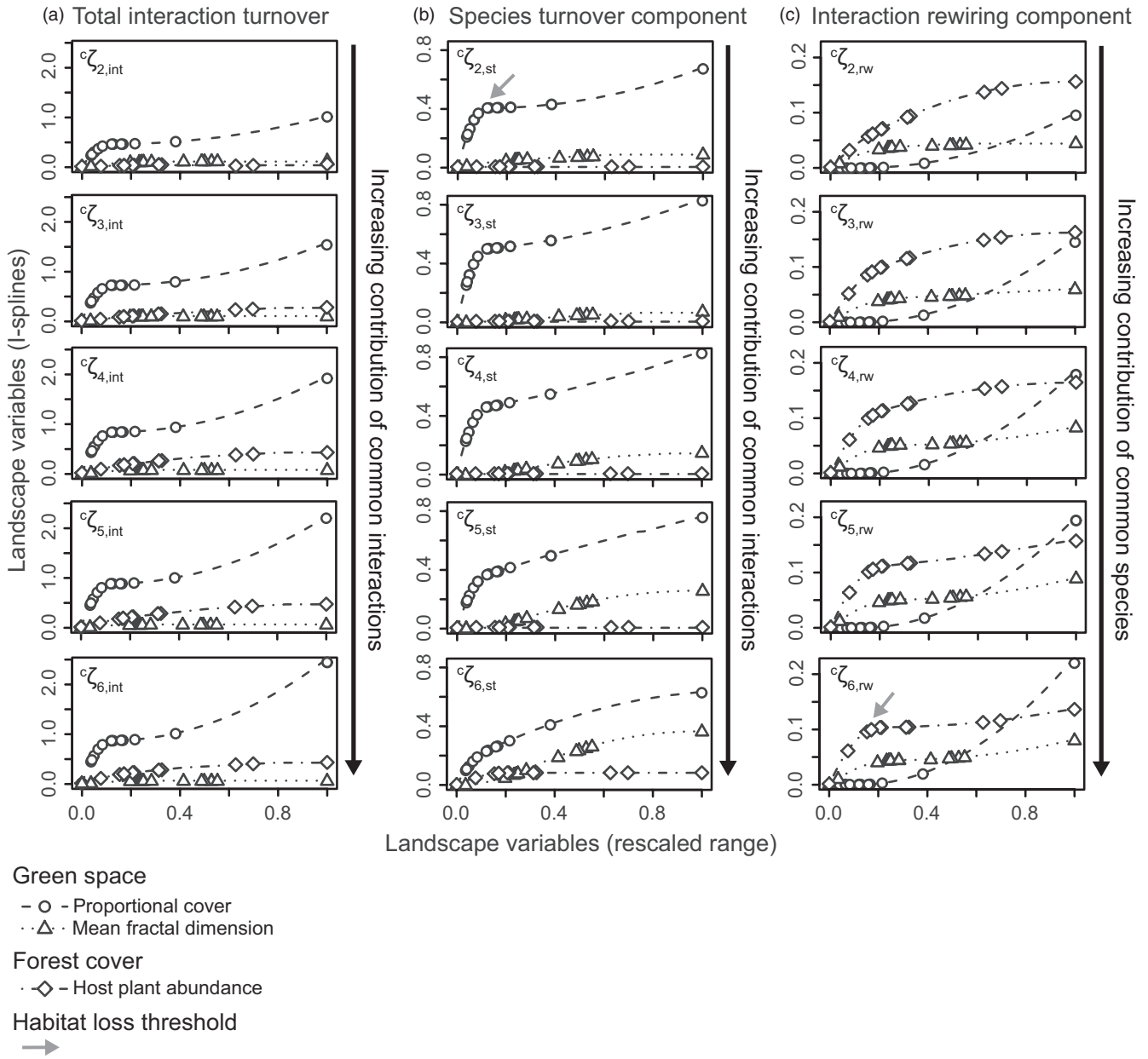


FIGURE 4 Multi-site generalised dissimilarity modelling of interaction turnover: The most important landscape variables explaining (a) total interaction turnover (${}^{c}\zeta_{int}$) and its components, (b) species turnover (${}^{c}\zeta_{sp}$) and (c) interaction rewiring (${}^{c}\zeta_{rw}$). These are shown across increasing orders of zeta diversity (i.e. from the top panel results of pairwise ${}^{c}\zeta_{2}$ to the bottom panel results of multisite, six in this case ${}^{c}\zeta_{6}$), interpreted along the arrows to the right. Interpretation of each panel: Each landscape variable is transformed using I-splines scaled from low (right) to high (left) levels of modification for each variable (e.g. low (left) to high (right) green space cover). Points show the location of the sampled sites along the landscape variable gradients. A steep slope indicates a high rate of turnover. Potential critical thresholds for habitat loss are indicated (see further explanation in the main text). Note that the y-axes scales differ between A, B and C. Results are shown for those environmental variables that had high explanatory power, that is, green space proportional cover and fragmentation (mean fractal dimension, *D*) and host plant abundance. Variables with low explanatory power and covariates are shown separately in Supporting Information S3, Figure S3.2

interactions. Using pairwise metrics, previous studies have added their own useful perspectives on interaction turnover, for example in terms of assessing turnover in quantitative networks (Poisot et al., 2012) and incorporating uncertainty in network analysis (Ohlmann et al., 2019). The metaweb approach to turnover has a different focus in that it compares locally realised interactions to all potential interactions in the metaweb (Noreika et al., 2019; Poisot et al., 2012). It is therefore interpreted as a measure of local resource selectivity (Noreika et al., 2019) rather than a direct measure of network compositional change as quantified in traditional pairwise metrics and the multi-site metric presented here. The dominance of rare interactions in any pairwise approach tells us little about interaction turnover related to species that are common across networks. Thus, the adaptation of zeta diversity

as a multi-site interaction turnover metric, and its incorporation in the MS-GDM method, allows for a comprehensive understanding of the drivers of network change including environmental change and interaction commonness.

In the gall wasp study system, the multi-site approach to turnover revealed different thresholds along habitat modification gradients where large shifts occurred in the composition of rare to common gall wasp–natural enemy interactions. For rare interactions, a strong threshold at particularly low levels of green space cover indicated the critical point along this gradient at which rare species, and their interactions, are likely to be lost from the system. The loss of these species will have consequences for overall system diversity. While common species remained in the system, a strong threshold for rewiring at low host plant abundance indicated that they were likely to change their typical interaction partners at this point (Figure 4c). Changes in the interactions of common species could have severe consequences for the overall network structure and function. Ecological thresholds (i.e. abrupt ecological responses to perturbation; Yin et al., 2017) provide valuable guidelines for management aimed at maintaining biodiversity in modified landscapes (Swift & Hannon, 2010), although specific thresholds of habitat loss and fragmentation should be interpreted with care and are species specific and area context specific (van der Hoek et al., 2015).

Rare and common *species* have previously been shown to respond differently to environmental gradients (Cagnolo et al., 2009; Latombe et al., 2019). Here we have shown that turnover of *interactions* that are rare to common are also related to different sets of environmental predictors. For example, habitat fragmentation (quantified as the mean fractal dimension of green space) was predominantly related to turnover in common, not rare, interactions and should, therefore, be considered among the variables particularly relevant for conserving the stability and function of the system. Interactions of common generalists are critical for maintaining network structure with fragmentation (Hagen et al., 2012). Fragmentation has previously been shown to impact rare, specialist parasitoids more than common ones (Cagnolo et al., 2009). In the studied system, parasitoids were relatively common while most gall inquilines were rare. Gall inquilines are generally considered less host specific than parasitoids (López-Núñez et al., 2019) and may be able to use alternative resources in the urban landscape which could explain why the rare species appear robust to habitat fragmentation. Meanwhile, if habitat fragmentation impedes the ability of parasitoids to locate their gall wasp hosts, it could explain their vulnerability to fragmentation. Species-specific differences in mobility can also influence responses to fragmentation (Concepción et al., 2015). Both niche breath and mobility should be studied in detail to determine their combined contribution to interaction turnover in this system.

Multi-site interaction turnover also illustrates the potential for host switching to buffer the system against environmental change. As illustrated by the nonlinear MS-GDM, interaction rewiring occurred throughout the green space gradient (i.e. even at sites where green space cover was relatively high), whereas the majority of species turnover happened at low green space cover when most of this habitat had been lost. This supports theoretical predictions that interactions will change prior to species along disturbance gradients (Valiente-Banuet et al., 2015). Thus, interaction rewiring may enable species to (a) avoid local extinction if they can switch between host resources (Nielsen & Totland, 2014; Simanonok & Burkle, 2014) or (b) compensate for species loss if species can perform new functional roles (Nielsen & Totland, 2014). Rewiring also indicates that networks can recover if habitats are restored (Noreika et al., 2019). The potential for interaction rewiring to occur can theoretically depend on multiple context specific conditions, such as phenotypic mismatches, narrow fundamental niches and low resource encounter rates (due to low abundances of resource species; Henri & van Veen, 2011; Vázquez et al., 2009), and may, therefore, prove to be highly system specific. Studies have found both minor and major contributions of rewiring to interaction turnover across space (Kaiser-Bunbury et al., 2010; Trøjelsgaard et al., 2015) and time (CaraDonna et al., 2017; Olesen et al., 2011). A high proportion of rewiring has been shown to occur in the generalist core (Olesen et al., 2011) but such contributions of common species are not expressed in pairwise metrics. Here rewiring was relatively low across species commonness, but the environmental drivers of rewiring differed. Thus, insights into the rewiring by rare compared to common species contribute to our understanding of the ability of core and peripheral species to buffer systems against different types of disturbance.

General challenges in ecological network studies could find some solutions in a multi-site measure of turnover that separates the change in different types of interactions (i.e. rare to common). For example, expanding interaction turnover from a pairwise to a multi-site metric provides a measure of network change that is likely to be relatively robust to under-sampling. Under-sampling of interactions in known to bias the metrics commonly used to quantify network structure (e.g. connectance, nestedness, etc.; Martinez et al., 1999; Henriksen et al., 2019), but the influence of under-sampling on interaction turnover metrics remains to be explored. At least a proportion of observed species turnover is likely due to incomplete sampling of local communities (Jost et al., 2010). The challenge of observing interactions compared to species, furthermore, makes most network studies particularly vulnerable to some degree of sampling bias (Chacoff et al., 2012). Since common species, and their interactions, are more easily observed than rare species in the network, turnover of common interactions, as quantified in the multi-site turnover metric, is likely to provide a reliable estimate of turnover. The multi-site turnover metric can, therefore, contribute to increased accuracy in the evaluation of network change.

Furthermore, multi-site interaction turnover (i.e. quantifying interactions as rare to increasingly common) can supplement traditional descriptions of species roles in ecological networks that are used to describe, for example, the role of particular species in maintaining network coherence (Trøjelsgaard & Olesen, 2016). In such studies, species are often assigned network roles in a binary fashion, as either specialists or generalists (e.g. Olesen et al., 2011), whereas

these roles are more accurately described along a gradient of multiple categories ranging from species with specialised to increasingly generalised resource use.

5 | CONCLUSIONS

Here we developed and applied a multi-site approach to interaction turnover and showed the contributions of both rare and common interactions to network change along modification gradients. Both the type and amount of habitat needed to maintain the composition of interactions were shown to depend on the properties of the interactions considered, that is, as rare to common. In so doing, this measure of interaction turnover provides an information-rich approach to measuring system-wide change. Accurate description of turnover in common interactions is particularly relevant for the conservation of ecological networks.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

AUTHORS' CONTRIBUTIONS

M.V.H. and M.A.M. developed the concept of the paper; M.V.H. and G.L. developed the method and analysed the data. All authors contributed to the writing of the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Figshare at https://doi.org/10.6084/m9.figshare.7122572 (Henriksen et al., 2018).

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