

# Parallel responses of species diversity and functional diversity to changes in patch size are driven by distinct processes

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## Abstract

1. Do species and functional trait diversity respond similarly to deterministic and random processes? Theory predicts that the contributions of random and deterministic processes to species diversity depend on patch size. Smaller patches are more strongly influenced by random sampling effects, by having fewer individuals, as well as ecological drift, which propagates the effects of small samples through stochastic birth and death processes. These random processes decrease species richness and increase compositional differences among small patches. Larger patches are predicted to be more deterministically assembled, with greater species richness and greater predictability of composition for a particular environment. The consequences of patch size for the diversity of functional traits, however, are poorly understood. Species diversity may be a poor proxy for functional diversity due to trait redundancies among species, making it unclear how random and deterministic processes alter functional diversity within patches of differing size, and how these differences scale up to determine among-patch functional diversity.
2. We report a novel experimental study of species and functional diversity across spatial scales. We manipulated patch area in an experimental plant metacommunity and used a nested sampling design to distinguish the effects of deterministic processes, ecological drift and sampling effects on species and functional trait diversity.
3. Our study revealed a pervasive influence of ecological drift and sampling effects on diversity, with distinct influences on functional traits and species composition within and among patches. Overall, drift and sampling effects caused a two- to threefold decrease in the importance of deterministic processes in small fragments. Species and functional diversity showed similar patterns with patch size; larger patches had greater within-patch (alpha) diversity and lower among-patch (beta) diversity, consistent with theory. However, our nested sampling design revealed that sampling effects (i.e. the size of the sample area) largely determined alpha species diversity and beta functional diversity, while ecological drift had a stronger influence on alpha functional diversity and beta species diversity.
4. *Synthesis.* The compositions of species and functional diversity in a community are influenced by distinct processes, resulting in divergent spatial scaling of species and their traits within patches and across landscapes.

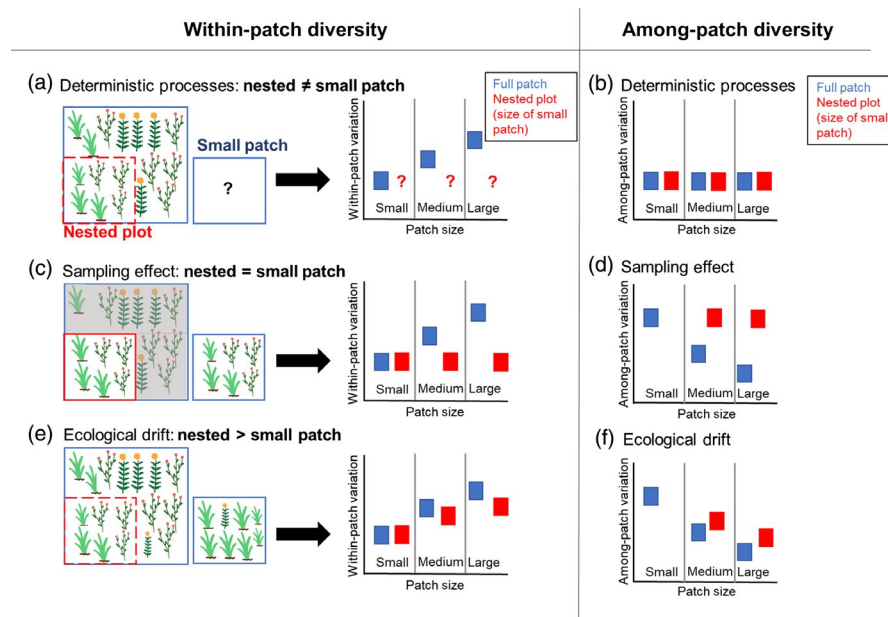
## KEYWORDS

community assembly, deterministic processes, ecological drift, functional diversity, neutral theory, sampling effect, species diversity

## 1 | INTRODUCTION

Trait-based ecology has gained popularity with the promise that easy-to-measure traits, representing well-known functions (or 'functional' traits), can replace species identity as meaningful measures of diversity (Adler et al., 2013; Díaz et al., 2016; Funk et al., 2017; Shipley et al., 2016). The distribution of functional traits within a community (functional diversity) is expected to faithfully reflect the processes that influence the survival and reproduction of individuals and, ultimately, the diversity of species (Laughlin & Messier, 2015). This logic implies an assumption that has remained largely untested; species and functional diversity should be influenced in similar ways by community assembly processes (e.g. Tredennick et al., 2017), which are well-known to structure diversity locally and at larger multi-patch scales (Starzowski et al., 2008; Vellend, 2016). Determining whether assembly processes have a similar impact on species diversity and functional diversity across spatial scales is necessary to better understand the utility of popular trait-based methods in spatial ecology.

Community responses to patch size may reveal how functional and species diversity are influenced by deterministic and random processes. Comparing the composition of habitat patches or islands that vary in size has been a longstanding method for disentangling the processes structuring species diversity and species-area relationships (for clarity, when we mention 'diversity' alone we are referring to both species and functional trait diversity unless otherwise stated; He & Legendre, 1996; Hubbell, 2001; Leibold & Chase, 2017; Vellend, 2010; MacArthur & Wilson, 1967). Island (or habitat) size is especially important when considering species turnover, as size impacts not only the number of individuals that can persist on the island, but also which types of species will be most successful (Simberloff, 1976; Simberloff & Wilson, 1969). When the size of a patch or the number of individuals in a community varies, so does the expected strength of deterministic assembly mechanisms relative to random processes such as drift and sampling effects (i.e. the effects of sample area on diversity; Gilbert & Levine, 2017; Henle et al., 2004; refer to Figure 1 for visual representations throughout).



**FIGURE 1** Graphical presentation of how sampling effects, ecological drift and deterministic processes produce distinct patterns of alpha (a) and beta (b) diversity and relative abundance within full patches of differing size, as well as a nested sample within larger patches. Deterministic processes (a) could result in multiple patterns of alpha diversity, depending on underlying abiotic conditions, but would cause the beta variation (b) in the full (blue boxes) and nested patches (red boxes) to be identical, and decreasing with patch size. Sampling effects capture a spatial subset of a larger patch, such that local spatial patterning and absolute abundances in larger patches determine the community in a smaller subset patch. If species or traits are not randomly distributed within a community, sampling effects will result in fundamentally different trends in alpha and beta diversity between the full and subset patches (c and d). Ecological drift begins with any sampling effects that arise from sampling a larger community, but species' abundances drift from this initial sample as demographic stochasticity causes birth and death rates to differ from their expected values. The net result of drift is to cause greater beta diversity (f) among smaller patches, and a greater reduction of alpha diversity (e) within patches relative to a simple sampling effect

In the absence of random processes, patches with similar environmental conditions are expected to favour similar distributions of functional traits that reflect optimal matching with abiotic conditions and biotic interactions (HilleRisLambers et al., 2012). In the absence of patch size-specific abiotic conditions, larger patches should better capture this matching due to a weaker influence of random processes (Figure 1b). Patch size is also often correlated with distinct biotic and abiotic conditions that underly deterministic assembly mechanisms, such as differences in herbivore abundances and edge to interior ratios that alter light availability (Genua et al., 2017; Laurence & Yensen, 1991). Deterministic differences between patches of different size may result in the selection of distinct functional trait values in small versus large patches (Girão et al., 2007; Henle et al., 2004; May et al., 2013). For instance, if differently sized patches differ in light availability, then distinct species may dominate in different-sized patches depending on their traits and the optimum phenotype for the light environment of each patch (Kraft et al., 2015). These kinds of deterministic mechanisms are often referred to as 'selection' in the literature (Vellend, 2016), but here we refrain to avoid confusion with other forms of selection that are also likely to impact communities that vary in size (described below). In general, larger patches are expected to better reflect deterministic processes, and differences in environmental conditions with patch size should cause patches of the same size to have similar distributions of species and traits (i.e. the similar trend in the blue and red boxes with patch size in Figure 1b).

Small patch area is expected to increase the variability of species and trait distributions through sampling effects and ecological drift. Here we use the term 'sampling effect' to describe the random influence of area on diversity, as smaller patches have fewer individuals so that we would expect species diversity to increase with patch size due to the available area alone (Srivastava et al., 2008). The impact of this random sampling effect on trait distributions is unknown, but likely depends on the traits of rare species that are frequently lost in smaller patches. If rare species have trait values that are distinct from more abundant species, sampling effects would cause a decrease in the diversity of species and functional traits in smaller patches (i.e. red box in Figure 1c). The random loss of rare species through sampling effects would result in greater variation of species and functional diversity among small patches, regardless of the size of the community these patches were sampled from (i.e. high beta diversity in all red boxes in Figure 1d; Violle et al., 2017).

In addition to sampling effects, ecological drift has predictable effects on species diversity that are particularly important in small communities. Specifically, smaller patches support small population sizes that are shown to be more highly sensitive to the impacts of demographic stochasticity, causing species to 'drift' from their expected abundances merely by random differences in births and deaths (Gilbert & Levine, 2017; Vellend, 2010). Although akin to sampling effects, drift is distinct in that it causes the effects of small sample sizes to propagate over time (Figure 1d vs. f). The impact of ecological drift on the distribution of functional traits is also unknown, but is likely to depend on trait-abundance correlations in

the same manner as sampling effects (Violle et al., 2017)—if each species has a unique set of trait values linked to the underlying environment within a small community, then drift should cause species and functional diversity to decrease (i.e. red box in Figure 1e), while increasing compositional differences among patches (i.e. beta diversity; first blue box in Figure 1f). However, species often show some degree of functional redundancy within communities (MacDougall et al., 2013), so the impact of ecological drift on functional diversity may be relatively small in larger patches in which there are likely to be more species with overlapping trait values (i.e. red boxes in Figure 1f; Violle et al., 2017; but see Wohl et al., 2004). The choice of individual traits is especially important when considering the impacts of drift, as some traits may reflect patterns of drift in a system while others may not, and so a more broad suite of traits may more accurately reflect the patterns of the 'overall functional diversity' in a system (e.g. Kraft et al., 2015).

The relationships between species and functional diversity across spatial scales may be difficult to isolate. Although two communities with identical species composition will likely have similar functional composition (even when incorporating some intraspecific variation), two communities with similar functional composition need not be comprised of the same species due to functional redundancy in species pools. By measuring the impacts of deterministic mechanisms, sampling effects and ecological drift on species and functional diversity, we can begin to disentangle how each process influences species and functional diversity across spatial scales. We can also determine if patterns of functional traits accurately reflect those of species diversity, as predicted in much of trait-based ecology (HilleRisLambers et al., 2012).

In this study, we test the influence of deterministic processes, sampling effects and ecological drift on species and functional trait distributions by manipulating patch size and using nested subsample plots to disentangle the spatial processes structuring diversity. Here and throughout, we refer to deterministic mechanisms as those which result in the perfect matching of species and/or traits to the environment, while purely random (or 'neutral') processes result in no pattern with the environment. In reality, communities lie within a continuum between completely deterministic and completely random (Gravel et al., 2006), and in this study we test how the relative importance of each process changes with patch size for species and functional diversity. We created 168 old field plant habitat patches of three sizes (0.25, 1 and 4 m<sup>2</sup>) and sampled communities and soil conditions in full patches and in nested plots (all 0.25 m<sup>2</sup> nested within the 1 and 4 m<sup>2</sup> patches) to test three hypotheses for the composition and diversity of species and functional traits. **(H1)** Diversity and composition are largely structured by deterministic processes; communities with similar soil conditions will have similar distributions of species and traits for any patch size (i.e. revealing the relative importance of deterministic mechanisms on diversity). **(H2)** Diversity is most strongly influenced by sampling effects; larger patches will be more similar in among-patch composition than smaller patches (i.e. blue boxes in Figure 1c,d), but nested plots will be more variable in composition than the full patches they reside

in (red vs. blue boxes in Figure 1d). Similarly, loss in functional or species diversity with patch size will be fully captured by nested plots. (H3) Ecological drift structures diversity; larger patches will be more similar in among-patch composition than smaller patches (blue boxes in Figure 1e,f) and nested plots will show similar but weaker patterns among patches than the extant communities (red boxes in Figure 1f). We test these hypotheses by examining changes in alpha and beta diversity, and the composition–environment relationships, in patches of differing size. We partition the effects of random processes by examining the difference in nested and full patches. Our results show mixed support for each hypothesis. Species and functional alpha diversity increase with patch size in the full patches as expected under all three hypotheses above. Nested plots, however, show an increase in functional diversity with patch size consistent with ecological drift (H1), while also showing a decline in species diversity consistent with sampling effects (H2). At the among-patch (beta diversity) scale, we see the exact opposite pattern, illustrating fundamental differences in the processes structuring the spatial diversity of species and their traits.

## 2 | MATERIALS AND METHODS

### 2.1 | Field study

We aimed to alter the relative importance of deterministic processes, sampling effects and ecological drift on species and functional diversity by manipulating patch size (Orrock & Watling, 2010). Specifically, we established replicated communities in an 8,700 m<sup>2</sup> area at the Koffler Scientific Reserve in New Market, Ontario in 2012. Surrounding fields largely contain old-field species that dispersed freely into our patches (see Borges et al., 2019; Supporting Information, for further detail on set-up and trait measurements). The area was maintained as a mowed field for horse riding for over 25 years before the experiment. In the absence of disturbance, the area would eventually succeed to deciduous forest. In 2012, we created 14 blocks, each consisting of four 0.25, 1 and 4 m<sup>2</sup> patches separated by 1 m of weed blanket (additional patches were created for another experiment but are not considered here). Each block was separated by 10 m of mowed grass. The patch sizes were chosen so that abiotic conditions would be largely homogenous within patches, and that differences in patch sizes were of an order of magnitude. In 2016, 71 species were found throughout the 168 patches.

To explore the processes governing species and functional diversity, we first quantified the relative abundance of species 4 years after establishment. We counted all individuals in the smallest patches (0.25 m<sup>2</sup>), and then repeated the process for a nested sample of the same area (0.25 m<sup>2</sup>) in the south-west corner of the larger patches (the 1 and 4 m<sup>2</sup>). These nested plots allowed us to compare species and trait distributions among plots of equal size, controlling for sampling effects (discussed below), to see if distributions of species and function in the subsamples are reflective of the larger communities in which they reside (with subsets referred to as 'nested

plots' throughout). The location of these nested plots was standardized to maximize edge effects in order to make them as similar as possible to the true 0.25 m<sup>2</sup> plots, and to avoid artificially increasing differences between these plots that may arise from sampling randomly placed nested plots. To characterize the effect of patch size on diversity at the whole-patch level, we counted and identified all remaining individuals in the larger patches (the 1 and 4 m<sup>2</sup>).

We next quantified species traits. We collected seven individuals of each species (or as many as possible for species with fewer than seven individuals) at peak flowering and measured nine functional traits (Appendix S1: Table S1). Traits included physical phenotypes (specific leaf area, leaf dry matter content, maximum height, per cent leaf nitrogen and carbon to nitrogen ratio) which correlate to various strategies of growth and reproduction (Appendix S1: Table S1), phenological characteristics (flowering phenology, vegetative to reproductive biomass and seed mass) and a measure of plant defence that correlates with other functional traits (per cent leaf herbivory; Loranger et al., 2017). For further details, Appendix S1: Table S1 discusses the functional significance of each trait measured in this study. We expect that our measured traits may vary with patch size if colonization/extinction processes are more important in smaller patches (i.e. shorter species with smaller seeds may be more common in smaller patches), and if the greater edge-interior ratios of small patches select for different traits (i.e. more 'stress' tolerant traits such as low specific leaf area, high leaf dry matter content and lower height may be more common in small patches). We used standardized methods of collection and measurement for our traits (Pérez-Harguindeguy et al., 2013). Because not all traits could be measured for all species, we supplemented our dataset from additional data resources (Appendix S1). For example, *Potentilla arguta* did not set seed in our patches, and we therefore used the TRY database (<http://www.try-db.org>; Kattge et al., 2020) to provide an estimate of seed mass. Our measurements were highly correlated with those on the TRY database for SLA ( $r = 0.98$ ), LDMC ( $r = 0.99$ ), leaf nitrogen ( $r = 0.92$ ) and height ( $r = 0.79$ ), while the remainder of our traits were not readily available on TRY for comparisons between all species.

To quantify abiotic conditions that may underly patterns driven by deterministic processes, we measured soil moisture, soil macronutrients and light in all patches in 2017. For soil moisture and light, multiple measurements were taken across the patches, and we used the average value per patch in the analyses. Soil moisture was measured with a TDR soil moisture probe, and light measurements were taken with LAI-2200C Plant Canopy Cover Analyzer. For the soil nutrient analysis, all patches had samples taken from the top 20 cm of soil after removing the top 1 cm (there was no other distinct organic humus layer due to earthworm activity). Soil samples were taken in the southwest corner of each patch (where the nested plots were located), 14 cm in from the corner towards the patch centre (see Supporting Information: Methods for full protocol). Soil samples were sent to Brookside Laboratories, Inc. for analysis. We used the soil properties (cation exchange capacity, pH and per cent organic matter) and macronutrients in our analyses below to reflect the full

breadth of the underlying abiotic conditions (i.e. nutrient availability) across our patches. Our analysis (described below) captures independent axes of enrichment or impoverishment for different sets of soil variables.

## 2.2 | Statistical analyses

### 2.2.1 | Calculating trait means and variances within patches

To quantify functional diversity within our patches, we calculated the mean trait value, reflecting a competitive optimum, and the trait variance, reflecting the range of functional strategies within the community (Kraft et al., 2015). For all full and nested communities, we calculated a community weighted mean (CWM) and the overall functional dispersion of all traits (FDis), using the `FD` package in `R` (version 3.5.5; Laliberté & Legendre, 2010). We further calculated the FDis value for each trait and we use these individual trait results in the beta diversity tests (below). The CWM measures the average trait value weighted by the relative abundance of each species within that patch. We chose FDis (the mean abundance-weighted distance of each species' trait from the CWM within a patch) because it is expected to be more independent of species richness than trait volume measures using convex hulls (Laliberté & Legendre, 2010), so we can compare differences between species and functional diversity directly. Other metrics, such as functional richness (FRic) and functional divergence (FDiv), cannot be calculated when some patches contain fewer functionally distinct species than measured functional traits (Laliberté & Legendre, 2010), as in some of our patches and nested plots.

### 2.2.2 | Measuring deterministic mechanisms

There is no direct way to test if differences in species or functional alpha diversity are deterministic, as both deterministic and random processes (drift and sampling effects) can generate an increase in diversity with patch size. However, we were able to test whether patch size explained differences in species composition or community mean trait values (i.e. the relative importance of deterministic mechanisms on species and functional composition). Similarly, partitioning the relative impacts of deterministic and random processes on community variance can be difficult, as it largely depends on the environmental variables measured, the scale at which they are measured and the amount of unexplained variation (Leibold & Chase, 2017). As a result, our measurements of deterministic effects are likely underestimated, but our tests for the changes among plot sizes (described below) are indicative measures of how the relative importance of deterministic processes change with fragment size. We also assume that each abiotic variable has the same effect on traits and species abundances across each plot sizes, and therefore has no distinct functional effect in our communities.

To measure the relative influence of deterministic effects, we used the 'adonis' function (`VEGAN` package version 2.5-2; Oksanen et al., 2018) for these tests, with species richness, Shannon diversity (to account for differences in species abundances), or CWMs as the response matrix and patch size as the predictor. Permutations were constrained within blocks to account for our experimental design. We then tested for an environmental gradient in mean soil and light conditions with increasing patch size, as well as for differences in variance of these environmental variables (using 'adonis' and 'beta-disper' functions in `vegan`, and the Euclidean environment matrix).

We next tested for signatures of deterministic processes on beta diversity, as we would expect similar species and functional composition among communities in similar environments. We examined how well abiotic conditions predicted among-patch differences in traits (CWM and FDis) and species composition. We used either CWM, FDis or species relative abundances for each patch as the response matrix in a redundancy analysis (RDA). For these analyses, each trait was used to create a single column in the CWM and FDis matrices, and the composite of all FDis traits was also included in the FDis RDA. The environmental matrix consisted of 12 principal component (PC) axes of soil macronutrients (Appendix S1: Table S2), as well as standardized soil moisture and light. We performed the PCA to ensure that our soil predictors were independent of each other, and we used all 12 PC axes in our exploratory analyses to ensure we accounted for all measured variation. Once we determined which soil axes were correlated to species diversity, trait means and trait variances, we reduced the number of axes for our later analyses as described below.

We first conducted an exploratory RDA for each response variable in each patch size and sample (i.e. either the full or nested plot). We used the 'fwd.selection' function (`ADEPATIAL` package version 0.3-8; Dray et al., 2018) to select significant variables from our environmental matrix, and created a reduced environmental matrix with only significant predictors (from all patch sizes and subsamples) for a given response variable. This first step was to ensure that all patch sizes and their nested samples had the same predictor matrix for a given response variable; this allowed for comparison of  $R^2$  values between the full and nested patches. Using the reduced environmental matrices, we tested the variation of the response variable explained for each patch size and subsample (i.e. whether it was the full or nested plot). We report the adjusted  $R^2$  values as our measure of variation explained, and for each patch size we used a jackknife procedure (i.e. resampling our analyses with one observation removed per permutation to estimate the variability in the RDA outputs) to estimate the variation in our adjusted  $R^2$  values. Our final analyses tested the deterministic effects of patch size on species and functional composition. This approach of standardizing environmental predictors and the spatial scales of our experiment was done to ensure that our measures of the relative importance of deterministic processes are equally biased in fragments of different size. It does not guarantee that we know the full deterministic signal, but it does ensure that a statistically different signal is due to our manipulation (plot size) rather than other variables known to influence the quantification of

deterministic processes, such as differences in environmental predictors. In other words, our results are robust within our system, but can only be compared qualitatively to other systems that use different fragment sizes, different plant communities or measure other environmental variables.

### 2.2.3 | Measuring sampling effects

To test for the influence of sampling effects on alpha diversity, we compared differences in FDis, species richness and Shannon diversity between our full and nested patches across patch sizes. Species diversity is known to increase with number of individuals, and FDis can be sensitive to the number of species present (Laliberté & Legendre, 2010), as can CWM when trait distributions are skewed (e.g. Díaz et al., 1998). Our nested plots capture the outcome of reduced habitat area in that they maintain the fine-scale spatial patterns that may result from species interactions or abiotic conditions. More specifically, these nested plots are rarefaction by area that does not make any assumption about the spatial distribution of individuals within patches, unlike a numerical rarefaction that necessarily assumes a random distribution (i.e. other common 'null' models). We used linear mixed effect models (LMEs; lmer function in lme4 package version 1.1-18.1; Bates et al., 2015) to test for the effects of patch size by subsample, where subsample was coded either zero (full patch) or one (0.25 m<sup>2</sup> nested within larger patch). Because patches contained two measures (full patch and nested plot), our random effect was patch nested within experimental block. We constrained all models to have a single intercept set at 0.25 m<sup>2</sup>, since the 0.25 m<sup>2</sup> patches represent the full and nested plots for our smallest patches and therefore had the same value. We tested for a main effect of patch size, nestedness and their interaction. All models were tested using likelihood ratios (Chi-squared test).

We then tested for correlations between the functional diversity within a patch and the species richness or Shannon diversity. This allowed us to determine if differences in sampling effects were masked by functional redundancies that vary with patch size. Patch size was treated as a categorical variable because we had no a priori prediction on how the correlation between species diversity and functional dispersion might differ among patches of varying size. Specifically, we used LMEs, with FDis as the response, and species diversity (either species richness or Shannon diversity, with each tested separately from the other), patch size and their interaction as fixed effects and block as a random effect. We tested nested plots and full patches separately, because of the challenge of applying our smallest patches to both sampling types.

### 2.2.4 | Measuring ecological drift

Finally, we isolated the effects of ecological drift from sampling effects and deterministic processes by comparing the among-community variation in species and functional diversity. We would expect alpha

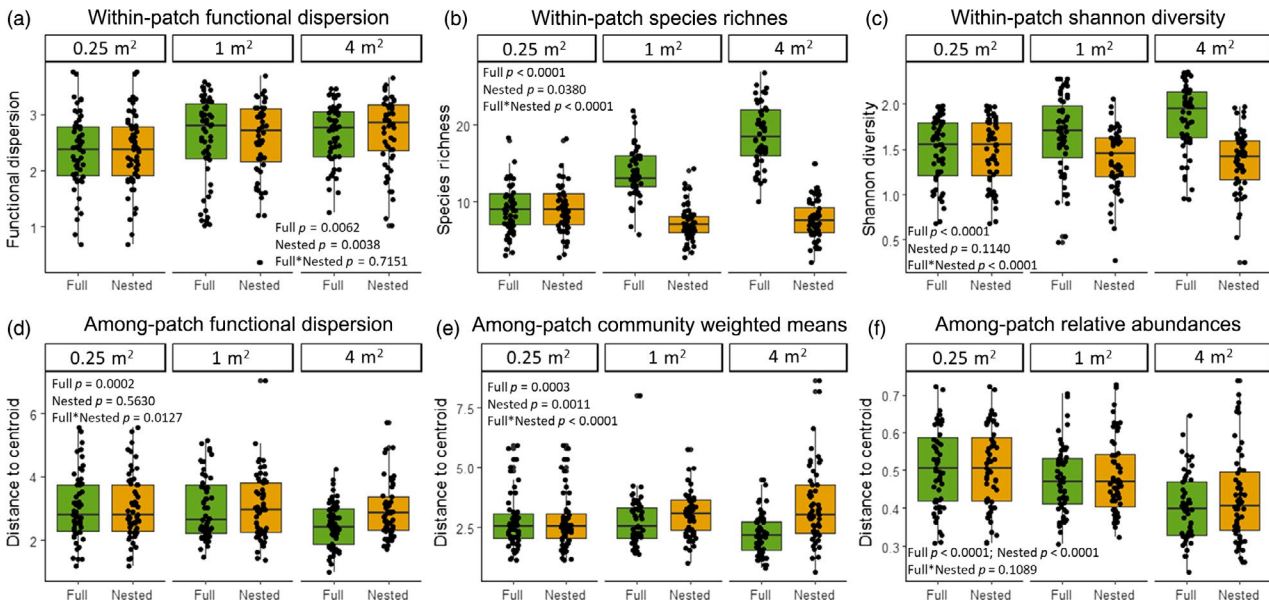
diversity to increase with patch size under drift and deterministic mechanisms, and so patterns of beta diversity should distinguish the underlying mechanisms (see Figure 1b–d). A decline in beta diversity with patch size may be the result of ecological drift given that the nested plots show a similar, but weaker decline than their respective full patches (Figure 1f). For among-community variation (beta diversity), we compared FDis and CWM of each trait, and species relative abundances (using Bray–Curtis distances) across patch sizes for full and nested plots. We calculated distances from the centroid (betadis-per function in vegan library, Oksanen et al., 2018), so that each community had a single observation. We used these distances with LMEs as detailed above. Although theory and our predictions assume monotonic effects of patch size, our tests allow for non-monotonic relationships between patch sizes at the beta-diversity scale. Our blocked design was used to ensure that each size of patch was equally represented in each block, such that variation in traits or species for patches of a given size was not due to differences in environmental variation among patches (this was confirmed in an analysis of our environmental matrix, see Section 3). All analyses were done using R3.5.1 (R Core Team, 2018).

## 3 | RESULTS

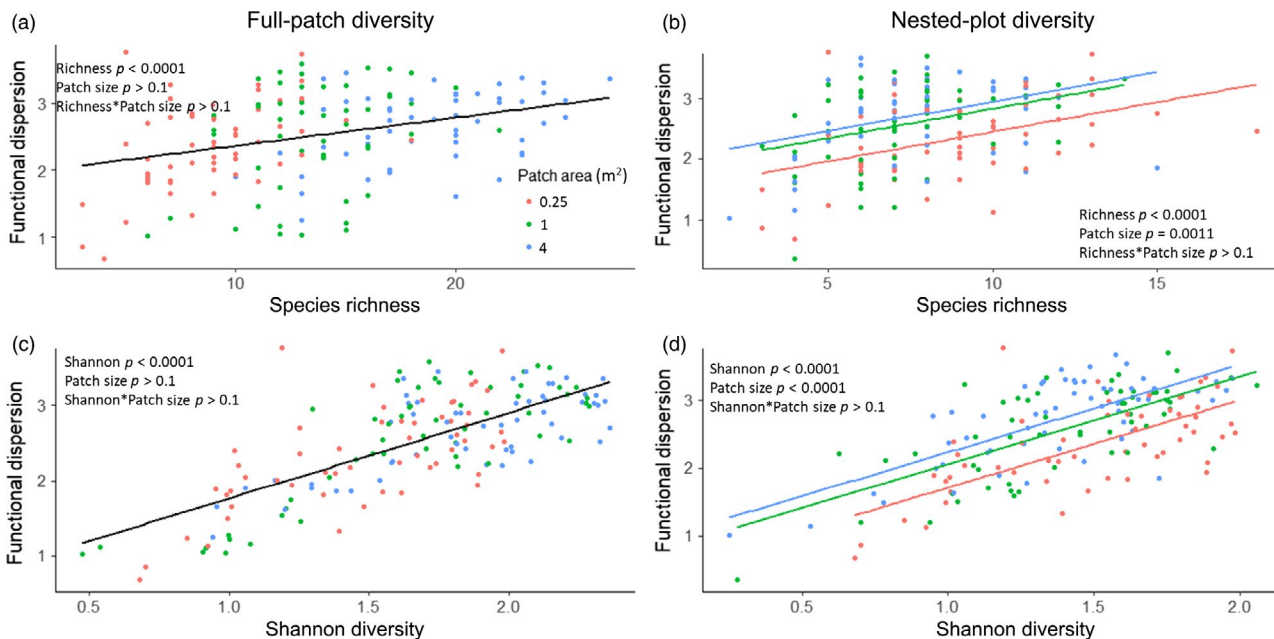
Functional trait diversity within and among patches changed with patch size in a pattern that largely reflected changes in species diversity (results for full patches in Figures 2 and 3 [green boxplots] and Figure 4a,c). The contribution of sampling effects to these changes with patch size depended on the type of diversity (functional vs. species diversity) and the scale (within- or between-patch scale) considered (Figures 2 and 3), as did the contribution of ecological drift (Figure 4). We detail how we partition and attribute these effects to deterministic processes, sampling effects and ecological drift below.

### 3.1 | The impacts of deterministic processes

We tested the importance of deterministic processes (H1) by first testing the direct effects of patch size on species composition and, second, by comparing the match of species and traits to the abiotic environment. To test for the deterministic effects of patch size on species and functional trait composition, we used a multivariate distance-based analysis with functional traits (CWMs) or species composition (Bray–Curtis distance) as the response variables. Our analysis showed no significant difference in functional composition with plot size (Figure 4a,  $R^2 = 0.001$ ,  $p = 0.8$ ). Species composition showed a statistically significant difference among patches of different sizes, but patch size nonetheless explained a nominal amount of the variation in species composition (Figure 4c,  $R^2 = 0.02$ ,  $p < 0.001$ ). These nominal differences in species composition and trait composition reflected the small environmental difference that occurred with patch size; patch size did not explain differences in soil conditions and light levels ( $R^2 = 0.01$ ,  $p = 0.61$ ), whereas the differences in



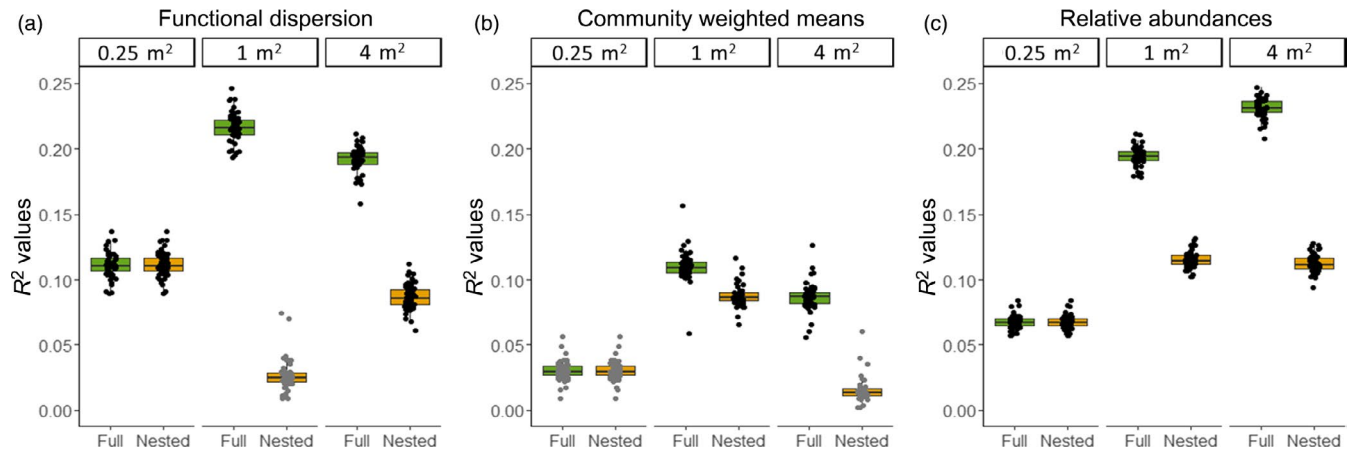
**FIGURE 2** Variation in species and functional diversity within- (top) and among- (bottom) plant communities in patches of varying size. Within-patch (alpha) diversity increased for functional (a) and species (b and c) diversity with patch size for full patches (green). This pattern is reversed for species diversity but not function (orange) when only nested plots within patches were measured, suggesting sampling effects influence species, but not trait, alpha diversity. Among-patch (beta) diversity showed the opposite trend, with a decrease in species (f) and function (d and e) for full patches, and a reverse trend only for function in the nested plots, suggesting sampling effects influence functional, but not species, beta diversity. For each patch, we analysed the full community (green) and a nested 0.25 m<sup>2</sup> subset within each patch (orange). Relationships were tested using linear mixed effect models. Distances in (f) were calculated using the Bray–Curtis metric on relative abundances



**FIGURE 3** Functional diversity increases predictably with species diversity in patches of all sizes (a, c), but nested plots within patches show distinct diversity–function relationships (b, d). Both species richness (a) and Shannon diversity (c) predicted functional dispersion for full communities (patch size was not significant although diversity was higher in larger patches on average). The nested plots in larger patches (0.25 m<sup>2</sup>, shown in b and d) had significantly greater functional dispersion, indicating that the within-patch scaling of functional and species diversity depends on patch size

environmental differences among blocks was pronounced (i.e. spatial environmental heterogeneity;  $R^2 = 0.51$ ,  $p < 0.001$ ). The deterministic effect of patch size on species composition was especially small

when compared to the deterministic effects of environmental differences on species composition for patches of a given size ( $R^2$  values ranging from 3.5 to ~10 times higher; Figure 4) or the difference



**FIGURE 4** The explanatory power ( $R^2$ ) of environmental conditions on species and functional diversity increases in large patches. From left to right, panels show adjusted  $R^2$  values of RDAs performed on (a) functional diversity, (b) community weighted means of functional traits and (c) species composition, with full communities shown in green and nested 0.25 m<sup>2</sup> plots shown in orange. Significant RDAs are shown with black points, non-significant RDAs are shown with grey points and points reflect values obtained through jackknife resampling (Methods). Numbers across the top of each panel give  $\sqrt{\text{Area}}$  (m) of patches

in variation explained due to purely random processes (change in  $R^2 \sim 0.10$ ). These results show that deterministic differences in species and trait distributions with patch size were trivial compared to differences that arose from environmental variation and purely stochastic processes.

To estimate the relative importance of deterministic drivers of beta diversity, we tested how well environmental conditions explained functional dispersion, CWMs and species relative abundances among fragments of each size (Figure 4). The variation explained by our multivariate analyses likely underestimate how well our response variables are predicted by the environment (e.g. Gilbert & Bennett, 2010). However, we used identical predictors and statistical models for all fragment sizes, so that the change in variation explained among fragments of different size reflected how the importance of deterministic processes changed with patch size.

Functional dispersion of full communities was better explained in larger patches, with adjusted  $R^2$  values almost doubling from the smallest ( $R^2 = 0.12$ ) to the two largest sizes (Figure 4a;  $R^2 = 0.23$  and  $0.19$ ; Figure 4; Figure S1; Table S3). Nested patches did not show a similar pattern—subsets of larger communities were either not statistically different from small fragments ( $R^2 = 0.10$ ) or not statistically significant (i.e.  $p > 0.05$ ; Figure 4a, grey points for 1 m<sup>2</sup>;  $R^2 = 0.03$ ). CWM values were poorly explained by patch environmental conditions, with full communities showing significant but weak relationships only in larger patches (1 and 4 m<sup>2</sup>; Figure 4b; Figure S2). Nested plots were not significant except in the intermediate (1 m<sup>2</sup>) patches, which had a weak relationship ( $R^2 = 0.07$ ,  $p = 0.035$ ). Species composition showed higher  $R^2$  values to the abiotic conditions in larger patches for full communities, with  $R^2$  values increasing more than threefold from the smallest to largest patch size (Figure 4c). Nested plots from larger patches also had greater  $R^2$  values, although they were smaller than the full patches (Figure 4c). Overall, the relative importance of deterministic processes increased 2–3 fold from small to larger patches for beta diversity of functional traits and species, with the two largest

patches showing similar influence of deterministic processes in all cases (Figure 4, green boxplots).

### 3.2 | Random processes: The impacts of sampling effects and ecological drift

To isolate sampling effects from deterministic processes and ecological drift (H2), we compared alpha diversity of species and traits within patches of each size by comparing the full and nested patches. Our inference for ecological drift (H3) was therefore based on losses in alpha diversity and increases in beta diversity in smaller patches that could not be explained by sampling effects alone. Although there are challenges to inferring random processes through pattern-based tests, we note that our analyses found no significant differences in environmental conditions (including light) among patches of different size and, similarly, differences in environmental variation among patches of different size were also not significant (both  $p > 0.25$ ; see Table S6 for the selected abiotic variables for each plot size in the original RDAs).

Functional dispersion increased with patch size for full patches (Figure 2a) and increased at the same rate in nested communities (Figure 2a; full patch size  $\times$  nested subsample  $p = 0.7151$ ), indicating that sampling effects had no influence on alpha functional dispersion. Species richness also increased significantly with patch size for full communities ( $p < 0.0001$ ) but showed a small decrease with patch size in the nested samples (Figure 2b; size  $\times$  subsample  $p < 0.0001$ ). Mean richness was nine and 19 species in the smallest and largest communities respectively, while the mean in nested plots of the largest patches was eight species. Shannon diversity also differed between full and nested plots (size  $\times$  subsample  $p < 0.0001$ ), increasing with patch size for full communities ( $p < 0.0001$ ) and showing no trend in nested plots. Overall, these results indicate that alpha species diversity and functional dispersion show similar responses to patch size, but that these patterns



are nonetheless driven by distinct processes; the different trends in nested plots indicate that sampling effects have an overwhelming impact on species alpha diversity but no detectable effect on alpha functional dispersion, suggesting that drift may be more important for functional dispersion.

To further understand how differences in alpha diversity are related to differences in functional dispersion, we tested how functional dispersion correlated with species diversity (Figure 3). Functional dispersion increased with both species richness and Shannon diversity in full patches (Figure 3a,c;  $p < 0.0001$ ). There was no additional effect of patch size on functional dispersion ( $p > 0.1$ ), although average diversity was higher in larger patches (Figures 2b,c and 3). Functional dispersion likewise increased with species richness and Shannon diversity in nested plots ( $p < 0.0001$ ), but there was also a significant effect of patch size—smaller patches had lower functional dispersion for a given species diversity (i.e.  $4 \text{ m}^2 > 1 \text{ m}^2 > 0.25 \text{ m}^2$ , Figure 3b,d;  $p < 0.001$ ). Subsequent contrasts showed that this decrease was statistically significant only for the smallest patch size (small vs. each larger, both  $p < 0.005$ ). Overall, these results highlight that random sampling effects explain the dependence of species alpha diversity on patch size, whether we measured species richness (Figure 2b) or Shannon diversity (Figure 2c). In contrast, sampling effects had no effect on alpha functional dispersion, which instead responded directly to patch size (Figures 2a and 3).

Among-patch (beta) variation in functional dispersion could not be attributed to ecological drift. Functional dispersion decreased with patch size in full patches ( $p = 0.0002$ ), but not in nested plots (Figure 2d;  $p = 0.563$ ; full vs. nested  $p = 0.0127$ ), indicating that the effect of patch size was largely driven by sampling effects. CWMs also showed different responses to patch size between full and nested samples ( $p < 0.0001$ ); variation among full communities decreased with patch size ( $p = 0.0003$ ), whereas nested samples increased (Figure 2e;  $p = 0.0011$ ). In contrast, variation in species relative abundances decreased with patch size in both nested plots and full patches (Figure 2f;  $p < 0.0001$ ; full vs. nested  $p = 0.1089$ ), suggesting that beta species diversity was largely driven by ecological drift.

Analysis of species–environment and trait–environment relationships confirmed our interpretations of beta diversity for traits and species (Figure 3). The increased importance in random processes, measured as a decrease in  $R^2$  values, was pronounced in small patches. These differences appeared to be explained by sampling effects for traits (Figure 3a,b) and by ecological drift for species (Figure 3c), and typically resulted in a 2–3 fold decrease in the importance of deterministic processes.

## 4 | DISCUSSION

Our study reveals a surprising difference in the processes that structure the diversity of species and function. In our system, sampling effects played an important role in structuring the local (alpha) diversity of species but not functional traits, and had a larger impact on the among-patch (beta) diversity of functional traits than species. Alternatively, ecological drift was more important for alpha

functional diversity and beta species diversity, in effect causing these random processes to play different roles for functional traits and species at within- and among-patch scales. Previous research has shown that species and function may respond differently to environmental change (Bergholz et al., 2017; De Bello et al., 2013; Mayfield et al., 2010), whereas similar patterns of species and function have been found in response to other underlying drivers of diversity, such as soil moisture (e.g. Spasojevic et al., 2014; but see Gallagher et al., 2013). Our study reveals that apparent similarities in the structuring of species and functional traits may be driven by fundamentally different underlying mechanisms, and offers an explanation for these apparently contradictory findings in the literature.

### 4.1 | Sampling effects alter alpha diversity of species but not functional traits

Previous research suggests that functional composition and species diversity may show distinct patterns across spatial scales (Bergholz et al., 2017), yet our results for whole-patch communities showed very similar patterns. Both species and functional diversity increased with patch size, and larger patches showed less among-patch variation, consistent with ecological drift. Our nested sampling approach, however, revealed that sampling effects exerted a strong hidden influence on alpha species diversity and beta functional diversity. Our study is the first to show decoupling of species and functional diversity across spatial scales, and suggests that decoupling in response to disturbance (Mayfield et al., 2010) or some environmental conditions (Cadotte et al., 2011), may in fact be far more widespread than generally appreciated.

The different processes underlying species and functional diversity raises the question of why traits in larger patches are distributed differently than in smaller patches. One possibility is that species interactions cause limiting similarity that acts on a neighbourhood scale, meaning that local interactions cause high trait variance even at small scales (HilleRisLambers et al., 2012; MacArthur & Levins, 1967). Research by Stubbs and Wilson (2004) on New Zealand beach communities has found evidence of similar fine-scale trait dispersion (i.e. increased functional diversity), with plants showing higher functional differentiation than expected by chance at scales smaller than  $0.01 \text{ m}^2$ . Similarly, research at our study site has shown how functional dispersion may be maintained over smaller subsets by non-random survival of species with distinct traits (Borges et al., 2019). In contrast, similar research in a saltmarsh found little empirical support for fine-scale trait dispersion (Wilson & Stubbs, 2012). Such small-scale species interactions may then scale across larger habitat patches, potentially causing the differences in species and functional diversity we observed across spatial scales. It is also possible that unmeasured variables vary among fragments of different size. While our extensive abiotic soil data did not show differences with fragment size, differences in soil biota or insect communities (e.g. Genua et al., 2017) may also alter trait distributions; such biotic differences would ultimately raise the question of the processes that structure these other biotic components of ecological communities. Regardless of the cause of this scale-dependency,

contrasting results from our study and the literature suggest that the spatial scale at which trait dispersion occurs likely varies among different communities, and the consequences of reducing patch sizes for functional dispersion are therefore also likely to differ.

## 4.2 | Sampling effects alter beta diversity of traits while drift impacts species composition

The mathematical and biological relationships between alpha and beta diversity suggest that a strong influence of a process at one level of diversity should be reflected at other levels (Chase & Knight, 2013; Starzomski et al., 2008). We found that patterns of beta diversity also differed for functional and species diversity, but in this case the trend was opposite to what we observed for alpha diversity—species beta diversity was largely insensitive to sampling effects. Previous research has shown that species beta diversity can be used to detect the effects of ecological drift (Segre et al., 2014), and larger population sizes should be less variable in community composition (Gilbert & Levine, 2017) by reducing stochastic extinction of low-density populations (Melbourne & Hastings, 2008). Our results were consistent with the effects of drift on beta species diversity, and nested plots showed lower beta diversity when residing in larger patches. This pattern, observed in other natural systems (e.g. Jones et al., 2015), highlights how patch size stabilizes species composition.

Previous research has shown that functional beta diversity frequently mirrors species beta diversity when both are driven by environmental gradients (e.g. Bergholz et al., 2017; Swenson et al., 2011). Our analysis of trait and species beta diversity seems to follow this trend from the literature, but only when entire patches are considered. The large importance of sampling effects on trait beta diversity (Figure 2d,e), but not species beta diversity (Figure 2f), indicates that different processes structure functional and species diversity at the between-patch scale. For example, the increase in CWM variation in nested plots (compared to full patches) suggests that the mean trait of a community is not consistently distributed within patches. Previous research has suggested that sampling from non-normal trait distributions could produce this type of inconsistency (e.g. Díaz et al., 1998; see Funk et al., 2017 for detailed discussion of trait distributions). Alternately, high trait variation in nested plots when species diversity is low (Figure 3) may produce shifts in mean traits, due to changes in the relationship between species and trait diversity. Regardless of the underlying cause, the high sensitivity of trait beta diversity to sampling effects suggests that any reduction of patch size is likely to cause high among-patch variation in functional traits, especially when compared to variation in species composition.

## 4.3 | Deterministic effects on diversity

The strength of the relationship between local environmental conditions and species composition or functional traits is often used as a measure of the relative importance of deterministic processes

structuring beta diversity (Germain et al., 2017; Vellend et al., 2014). We observed a clear structuring of functional traits and species by environmental conditions that is consistent with several previous studies (e.g. Borges et al., 2019; Cornwell & Ackerly, 2009; Dwyer & Laughlin, 2017), but that eroded in small patches. The environmental underpinning of functional trait distributions emphasized the large impact of sampling effects on functional composition. Overall, our results highlight an interesting and counter-intuitive characteristic of functional diversity—our nested plots had the same functional diversity as the larger patches they were in, despite a weaker correlation to the local environmental conditions. This result challenges previous findings that traits diverge at small scales and converge at larger scales (Bergholz et al., 2017; De Bello et al., 2013), and shows that species distributed within nested areas of patches are a random subset of the larger patch (Figure 2) and match the environmental conditions of the larger patch (Figure 4). In contrast, the non-random subset of functional dispersion within nested areas of patches fails to match environmental conditions in the larger patch (Figure 2a vs. Figure 4a), suggesting that patch-level interactions independent of environmental conditions are more important for functional trait distributions (Borges et al., 2019; Funk et al., 2017).

An important caveat for our study, as with most studies in trait-based ecology, is how well our measurements capture the functional traits of the community. Our study includes 71 species and nine important traits (Appendix S1: Table S1); previous research suggests this broad approach should reflect functional differences among species (e.g. HilleRisLambers et al., 2012; Kraft et al., 2015). One challenge with this number of traits and species, however, is that quantifying intraspecific differences is logistically infeasible. Intraspecific variation may alter trait distributions and how well those distributions correlate to underlying abiotic conditions (Funk et al., 2017; Loughnan & Gilbert, 2017). While it is unlikely that intraspecific variation would fundamentally alter our conclusions about the processes structuring species and functional trait distributions, as we would expect individuals of a species to respond similarly to similar environmental conditions, it nonetheless deserves further attention. A second consideration comes from testing trait–environment relationships, as these may merely reflect species–environment relationships (Peres-Neto et al., 2017). However, our study showed divergent trends for species and traits, and changing relationships between species diversity and functional dispersion; these trends would not emerge through spurious, or random correlation. Additionally, we have compared nested plots to full patches to infer short-term consequences of habitat reduction. Future work that implements this type of reduction should examine if and how species and traits change over the long term to provide insights into the temporal dimensions of community assembly processes. A final consideration is the potential impact of priority effects on the patterns of species and functional diversity. Priority effects cause early arrivers to determine the long-term composition of a community through strong, deterministic feedbacks (Fukami, 2015). Priority effects are expected to increase among-community variation by coupling strong deterministic effects (species interactions) with stochastic differences in early composition that arise from dispersal

rather than subsequent drift. Priority effects have been shown to produce scale-dependent differences in diversity at larger spatial scales than considered in our study (Seabloom et al., 2003). However, although priority effects may influence among-patch diversity, we are not aware of any theory that would explain how priority effects could produce the patterns of functional diversity we observed within our patches, nor how these patterns differ among nested plots.

In summary, our study reveals how similar distributions of species and functional diversity with patch size can be driven by different underlying processes. Sampling effects structured alpha species diversity and beta functional diversity, while ecological drift had the opposite pattern. These random processes caused a decline in the influence of abiotic conditions on the diversity of species and their traits as patches decreased in size. Given the importance of patch size to the distribution of diversity, resolving the scaling of species and functional traits is central to relating these theories to the functional importance of species diversity.

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## AUTHORS' CONTRIBUTIONS

L.Z.F. and B.G. conceived the ideas, designed methodology, analyzed the data, contributed to the writing, and gave final approval for publication. L.Z.F. collected the data.

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## DATA AVAILABILITY STATEMENT

Data are available from the Dryad Digital Repository <https://doi.org/10.5061/dryad.4tmpg4f7k> (Forsyth & Gilbert, 2020).

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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