

**Title: The prevalence and impact of transient species in ecological communities**

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Appendix

\* Table A1

\* Figures A1-A6

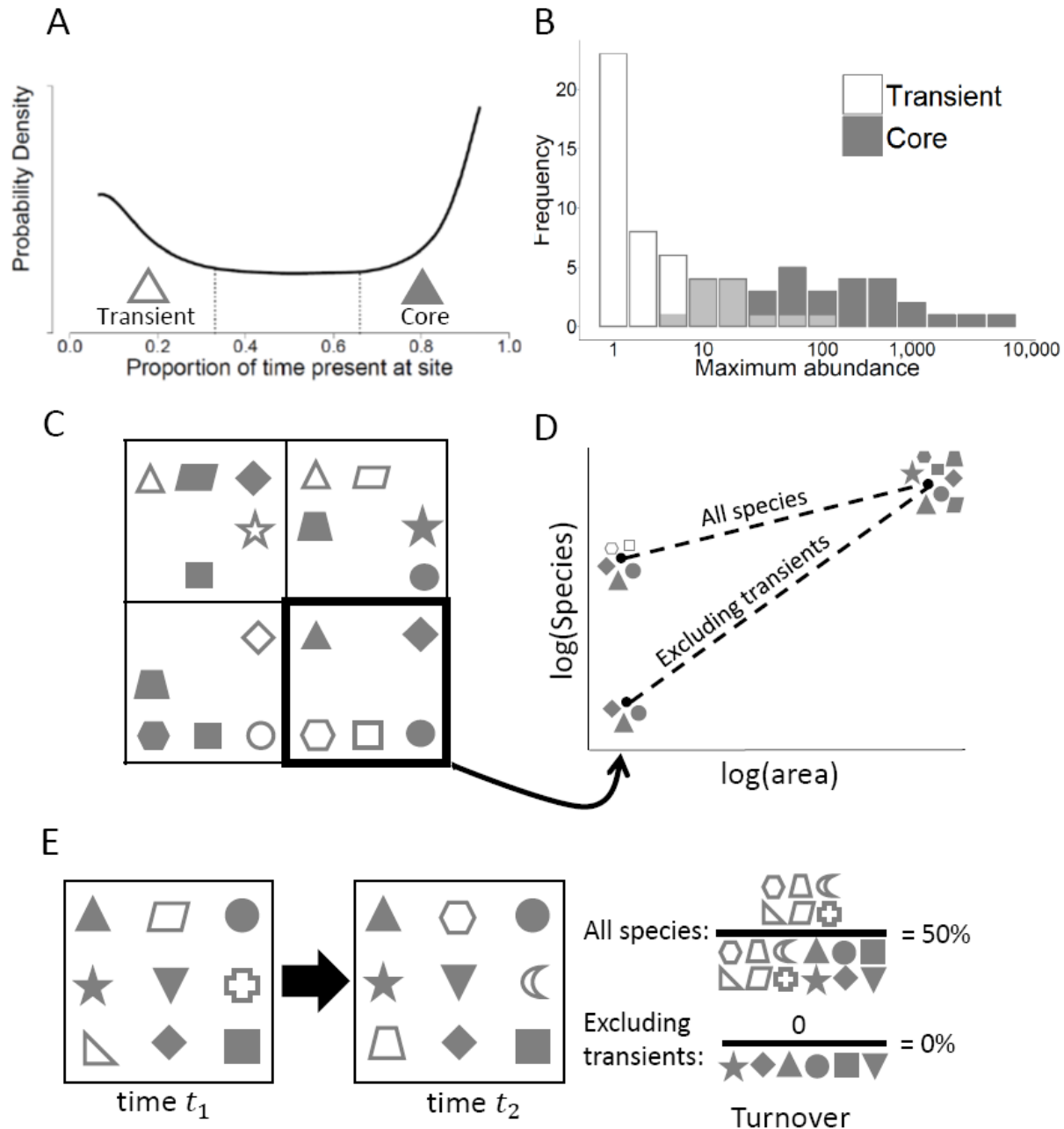
## Abstract

Transient species occur infrequently in a community over time and do not maintain viable local populations. Because transient species interact differently than non-transients with their biotic and abiotic environment, it is important to characterize the prevalence of these species and how they impact our understanding of ecological systems. We quantified the prevalence and impact of transient species in communities using data on over 17,000 community time series spanning an array of ecosystems, taxonomic groups, and spatial scales. We found that transient species are a general feature of communities regardless of taxa or ecosystem. The proportion of these species decreases with spatial scale leading to a need to control for scale in comparative work. Removing transient species from analyses influences the form of a suite of commonly studied ecological patterns including species-abundance distributions, species-energy relationships, species-area relationships, and temporal turnover. Careful consideration should be given to whether transient species are included in analyses depending on the theoretical and practical relevance of these species for the question being studied.

# **Introduction**

Ecologists frequently conduct taxonomic surveys to characterize the diversity and composition of ecological assemblages. While many of the species observed in these surveys represent local populations, some may be irregular visitors that do not maintain viable local populations, are poorly suited to the local conditions, and rarely interact with other members of the community. Grinnell (1922) first coined the term "accidental" to refer to this kind of species, which is observed inconsistently at a site over time in contrast to the more regular and predictable members of an assemblage. This group of species has also been referred to as "occasional", "vagrant", "transient", and "tourist" (Southwood et al. 1982; Costello and Myers 1996; Novotný and Basset 2000; Magurran and Henderson 2003; Ulrich and Olrik 2004; Dolan et al. 2009; Coyle et al. 2013; Petersen et al. 2015; Supp et al. 2015). Regardless of the name applied, these species (hereafter "transients") have generally been identified based on the low frequency of observations recorded in samples or surveys over time at a given location (i.e., low temporal occupancy). Several studies ranging from birds to fish to amphipods have found that temporal occupancy is frequently bimodally distributed within communities, with one distinct mode at very low occupancy reflecting transient species, and another mode at high occupancy reflecting temporally persistent "core" species (Figure 1A; Costello and Myers 1996; Magurran and Henderson 2003; Coyle et al. 2013; Umaña et al. 2017). The existence of a mode at low occupancy indicates that transient species may make up a larger proportion of ecological assemblages than has typically been acknowledged.

Transient species are expected to interact with their biotic and abiotic environments differently than core species since by definition they do not maintain viable local populations and are not necessarily well adapted to the local environments in which they are found (Magurran and Henderson 2003; Coyle et al. 2013; Umaña et al. 2017). Previous studies found that core



**Figure 1.** (A) Bimodal distribution of temporal occupancy for North American birds from Coyle et al. (2013) illustrating one mode of "core" species observed consistently at sites and a mode of low occupancy "transient" species observed irregularly. (B) Core and transient species exhibit different species abundance distributions for the Hinkley Point fish assemblage (Magurran and Henderson 2003). (C) Four contiguous quadrats in which species (different shapes) may be core (shaded) or transient (open). (D) The species-area relationships for (C) depending on whether transient species are excluded or not, using the lower right panel to represent the smallest area. Because every species is core in at least one quadrat, species richness at the largest scale is the same for the two relationships. (E) Temporal turnover (the Jaccard index of dissimilarity) is much lower when transient species are excluded from the calculation, since they are the species most driving turnover.

species presence is more strongly tied to the environment and other deterministic factors, while transient presence is more strongly determined by stochastic factors (e.g., Magurran and Henderson 2003; Coyle et al. 2013; Umaña et al. 2017). Because much of the ecological theory related to species coexistence, niche partitioning, and biodiversity assumes that species directly interact and occur only in suitable environments, the presence of these transient species has the potential to skew our understanding of ecological systems. Indeed, transient species have been shown to differ from core species with respect to the shape of species abundance distributions (Figure 1B; Magurran and Henderson 2003), the relative importance of density-dependence versus environmental stochasticity (Magurran and Henderson 2003; Ulrich and Ollik 2004), the primary drivers of species richness (Coyle et al. 2013), and life history traits (Supp et al. 2015). We expect transient species may influence the slope of species-area relationships, since species that are transient may make up a disproportionate fraction of the community at smaller spatial scales, while at large scales most species are expected to maintain persistent populations over at least some subset of the domain (Figures 1C, D). Transient species are also likely to contribute disproportionately to estimates of temporal turnover since by definition they are present in only a small proportion of samples over time (Figure 1E). Thus, a wide variety of classic ecological patterns may differ depending on whether transient species are considered, including biodiversity patterns that have the potential to influence conservation and management decisions.

Given the potential impact of transient species on understanding and managing ecological systems, it is important to understand more about how common transient species are and how their prevalence varies with taxonomic group, ecosystem types, environmental context, and scale. There are reasons to expect that several of these factors may influence the prevalence of transients. First, species from taxonomic groups with strong dispersal abilities like birds commonly show up in

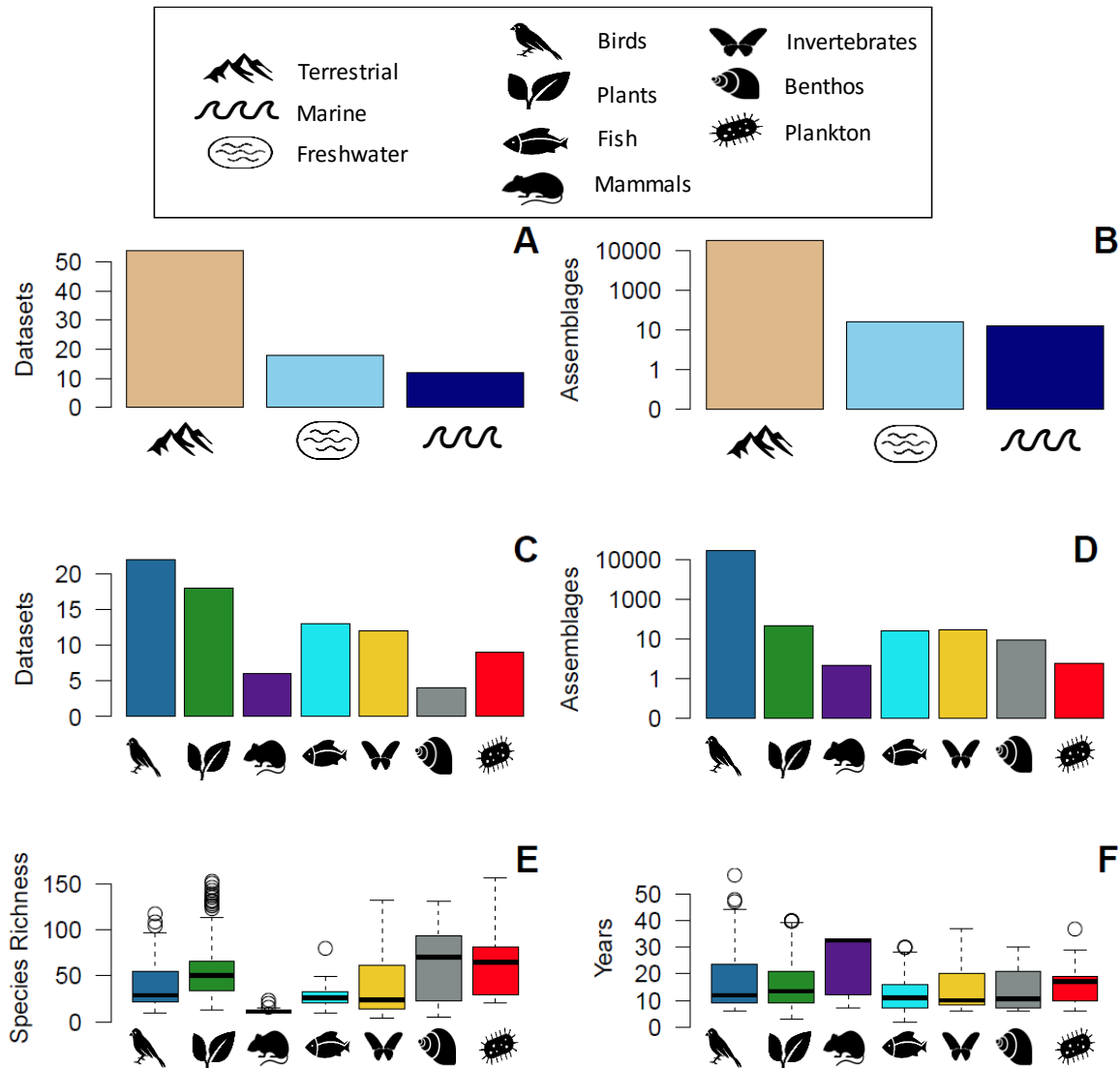
habitats and regions in which they are not expected (Grinnell 1922; Coyle et al. 2013), whereas organisms with limited dispersal should do so much less frequently. Second, assemblages located in regions of high habitat heterogeneity are expected to receive more transient individuals from adjacent habitats via mass effects (Shmida and Wilson 1985). Coyle et al. (2013) found that mountainous regions had a greater proportion of transient bird species, consistent with these predictions. Third, at small scales (e.g., below the average home range size), most organisms will only be observed occasionally and the majority will therefore be classified as transients. At large scales (e.g., an entire continent), nearly all species will maintain viable populations and be consistently observed, and almost none will be classified as transient. Understanding variation in the prevalence of transient species will improve our understanding of the factors structuring communities and help identify study systems where our understanding of ecological systems is most prone to being influenced by their presence. Making comparisons across ecosystems and taxonomic groups will require understanding the scale-dependence of transient species' prevalence because the scale at which assemblages are sampled can vary by several orders of magnitude.

Here, we undertake the first systematic evaluation of the prevalence and predictors of transient species in ecological communities. We use data from over 17,000 community time series from terrestrial, aquatic, and marine ecosystems across seven major taxonomic groups to: 1) evaluate the prevalence of transient species and how it varies with taxonomic group, ecosystem type, and habitat heterogeneity; 2) assess the scale-dependence of transient species prevalence and correct for scale to make consistent comparisons across groups; and 3) examine how the inclusion of transient species in community-level analyses impacts four commonly analyzed ecological patterns including the shape of species-abundance distributions, drivers of species richness, species-area relationships, and temporal turnover.

# Methods

## Data

We conducted an extensive search for datasets of community composition over time both online and published in the literature. We identified datasets using a combination of existing compilations (Dornelas et al. 2014; Yenni et al. 2016), searching online data catalogs such as the Ecological Data Wiki ([ecologicaldata.org](http://ecologicaldata.org), White 2016), exploring datasets available from Long-Ecological Research sites, exploring datasets in the data journal Ecological Archives, and conducting literature searches. We initially identified 330 datasets spanning seven broad taxonomic groups. We filtered these datasets to those meeting the following criteria: 1) each assemblage was sampled on at least six occasions (typically years, but occasionally for smaller organisms like plankton samples were monthly or bimonthly), 2) at least ten species were observed over the course of the study, and 3) the study had a spatially well-defined location with a fixed environmental context (e.g. communities based solely on the geographic coordinates of individual organisms, as in many marine pelagic transect studies, were not included). Of the 330 datasets examined, 86 satisfied our criteria and yielded 17,921 unique assemblages spanning terrestrial, marine and freshwater ecosystems. A complete list of datasets and sources is provided in T. The majority of datasets and community time series come from terrestrial bird and plant assemblages, with fewer datasets from marine and freshwater systems (Figure 2A-D). The duration of the studies ranged from six to 57 years and assemblage richness ranged from 10 to 276 species, with most assemblages having between 20 and 61 species (Figure 2E, F). All species names were checked for typos, and any taxa not identified to species (e.g. "Unidentified grass") were removed unless the taxon clearly did not overlap with any other taxa in the dataset (e.g. "*Sigmodon* sp." was retained only if no other *Sigmodon* species were present in the region). For datasets with uneven



**Figure 2.** Description of the compiled time-series datasets. The number of (A) datasets and (B) number of assemblages (log scaled) by ecosystem type (terrestrial, freshwater, marine) and by taxonomic group (C, D). (E) Boxplots of the number of species per assemblage by taxonomic group. Several high richness outliers for plant and plankton assemblages were excluded to improve visualizing the bulk of the data (\*). (F) Boxplots of time series length by taxonomic group.

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 150 sampling in either space or time (e.g. variable numbers of surveys per year, or variable numbers  
 151 of spatial units per survey), we standardized the level of spatial or temporal subsampling for that  
 152 site in each year of the time series (see details in Appendix, Figure A1).



## Analysis

Following Coyle et al. (2013), we operationally defined a species as transient at a site if it was observed in 33% or fewer of the temporal sampling intervals, and assessed the prevalence of transients as the proportion of species in the assemblage below this threshold (Figure 1A). We also evaluated more restrictive definitions using maximum temporal occupancy thresholds of 10% and 25% to evaluate the impact of this decision. Results were qualitatively similar for the three different thresholds (Figure A2-A6).

Although many authors have used the bimodality of temporal occupancy distributions (e.g., Figure 1A) to identify transient species in this way (Magurran and Henderson 2003; Dolan et al. 2009; Coyle et al. 2013), some species will be incorrectly classified due to imperfect detectability. Species with low detectability due to low density or traits or behaviors that make them difficult to detect may be persistent at a site but only detected in a small proportion of samples (MacKenzie et al. 2006). As such, estimates of the proportion of transient species based on observed temporal occupancy are likely higher than the true numbers. A full exploration of the detailed influence of imperfect detection is beyond the scope of this paper, but we are developing simulation-based approaches to understand precisely how it influences estimates of the proportion of transients as well as the identification of individual species (Hurlbert unpublished data).

While imperfect detection is clearly a concern for analyses of this type there is also evidence that using observed occupancy provides a reasonable first approximation of transient status. Magurran and Henderson (2003) showed that using occupancy to identify species as transient is consistent with using habitat preferences. In an examination of nearly 500 bird communities, Coyle et al. (2013) showed that transient species richness was correlated with

regional habitat heterogeneity as would be expected of true transients while it was not positively correlated with vegetation which would be expected to impede species detections. In addition, similar studies using habitat preference-based transient designations (Belmaker 2009) have yielded similar conclusions to those using occupancy based approaches (Coyle et al. 2013). Finally, the results in this paper are similar for species that are comprehensively surveyed and those that are less thoroughly sampled (see *Results* and *Considerations*). So, while there is no doubt that misclassifications will occur, for large data compilations like this one that lack both detailed habitat preference data for species and the necessary sampling methods to estimate detection probabilities, occupancy based approaches appear to provide a reasonable approximate classification. We address these issues further in the *Considerations* section of the Discussion.

We evaluated the effect of spatial scale on the perceived prevalence of transient species using the subset of datasets that included sampling at hierarchically nested spatial scales. We used a linear mixed model to quantify how the proportion of transient species in an assemblage varied with the spatial scale over which the assemblage was characterized. The model included taxonomic group as a fixed effect and dataset as a random effect, with both variables having the potential to influence both the slope and intercept of the relationship. Area was log-transformed for analysis. Because scale will be perceived differently for organisms of different size—e.g. a 1 ha quadrat is effectively much larger for ants than for birds—it may not allow for direct comparisons of "scale" among taxonomic groups. As such, we also built a similar mixed model using the median community size for all assemblages (i.e., the total number of individuals sampled in an assemblage, median = 102) as an alternative, potentially more generalizable, measure of scale.

To explore the influence of habitat heterogeneity on the prevalence of transients we used a linear mixed model to predict the proportion of transients as a function of elevational heterogeneity

(the variance in elevation within a 5 km radius of the site), with spatial scale (using community size as a proxy) as a covariate and taxonomic group as a random effect. P-values were estimated from the *t*-statistics using a normal approximation. All terrestrial datasets with geographic coordinates were used to fit the model. We used a 30 arc-second digital elevation model DEM of North America (GTOPO30), acquired from the USGS Earth Resources Observation and Science Center (EROS), to calculate the variance of elevation. We calculated a pseudo  $R^2$  for each mixed model based on the fit between predicted and observed values.

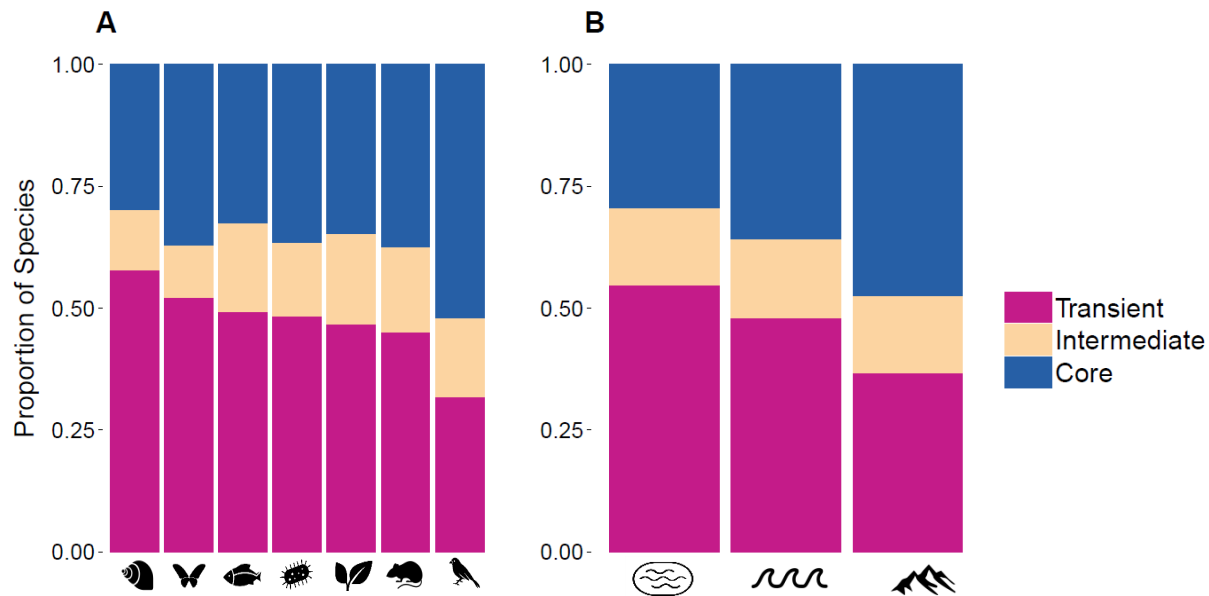
Finally, we quantified the influence of transient species on a suite of commonly studied ecological patterns including species-abundance distributions, species-area relationships, temporal turnover, and correlates of species richness. We did this by comparing the form of these patterns when using data on the entire community to the same pattern generated after excluding species that were identified as transients (i.e. those species with temporal occupancy  $\leq 33\%$ ). We fit two distributions for species-abundance, the logseries and the Poisson lognormal to the combined abundance data across years for each time-series. Magurran and Henderson (2003) proposed that transient species should be better fit by the logseries and core species by the lognormal, meaning that excluding transient species should result in improved fits by the lognormal. We compared the fits of the two distributions based on  $AIC_c$  model weights. Analysis of species-area relationships was restricted to datasets with hierarchical spatial sampling. Power function relationships were fit to each assemblage using linear regression on log-transformed data (Xiao et al. 2011) to predict the number of species observed from the area sampled. The fitted exponents of the relationships were compared. Mean temporal turnover was calculated as the mean of the Jaccard dissimilarity index (Krebs 1999; Figure 1E) between all adjacent time samples in each community time series. Analyses of the drivers of species richness were restricted to data from the Breeding Bird Survey

of North America since it was the only dataset that employed consistent sampling across large spatial scales with a large number of replicates. For this last set of analyses we used two environmental correlates that are known to be important for determining richness in this dataset, the Normalized Difference Vegetation Index (NDVI), a remotely sensed estimate of productivity, and elevation (White and Hurlbert 2010). We calculated correlation coefficients between each environmental variable and species richness (including or excluding transient species), as well as correlation coefficients for transient species richness alone to further illuminate differences.

The complete set of R scripts for data cleaning and processing are available on Github (<http://www.github.com/hurlbertlab/core-transient>) and analysis scripts for this study are archived at Data Dryad (URL to be filled in).

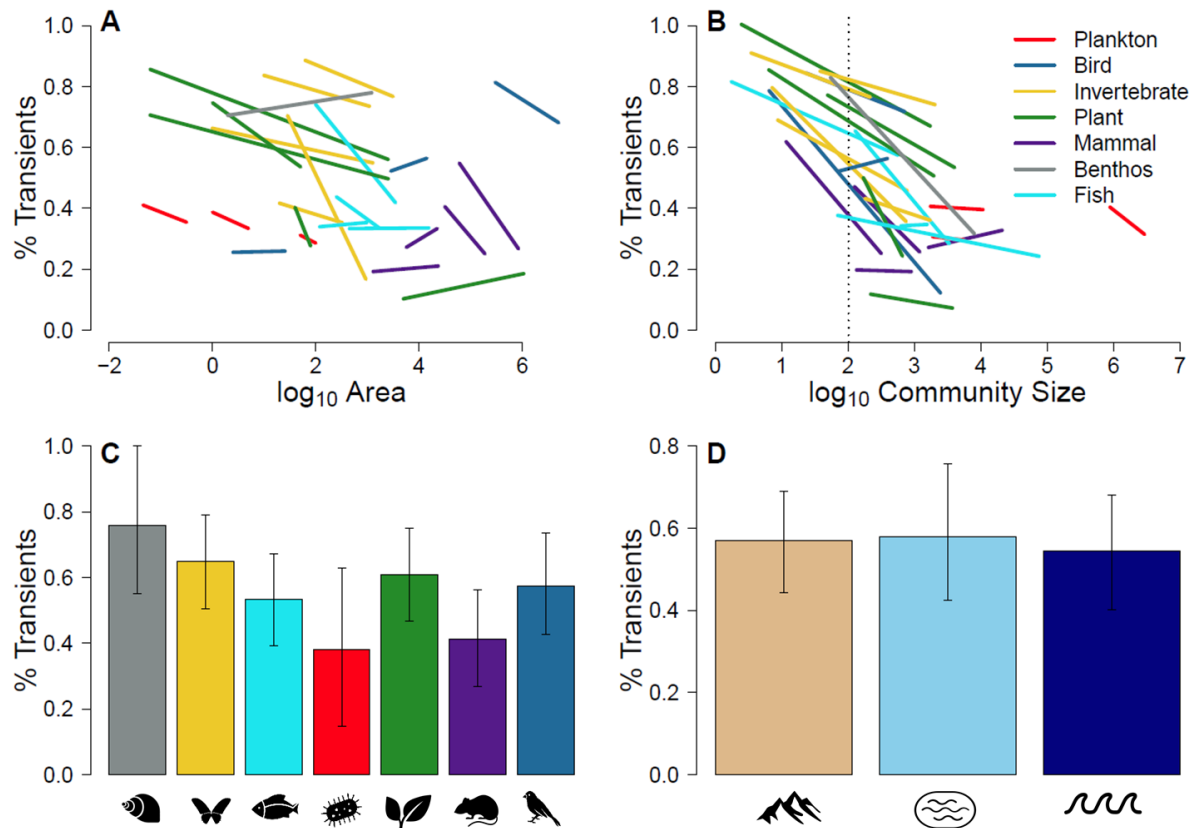
## Results

Assemblages from all ecosystem types and taxonomic groups included a substantial proportion of transient species, and relatively few species with intermediate temporal occupancies (Figure 3). The proportion of an assemblage made up of transient species varied with taxonomic group, with means ranging from 32-58%. Benthos and invertebrates had more than 50% of species characterized as transient on average. Fish, plankton, and plant communities had 46-49% transient species on average. In mammal communities, 45% of species were classified as transient, while birds had the lowest proportion of species classified as transients at 30%. Terrestrial ecosystems had the lowest proportion of transient species (37%) followed by marine (48%) and freshwater (55%) systems (Figure 3B).



**Figure 3.** The mean proportion of species in an assemblage that are transient ( $\leq 33\%$  temporal occupancy), core ( $> 66.7\%$ ), or neither, grouped by (A) taxonomic group and (B) ecosystem. See Figure 2 for icon key.

There was a negative effect of sampling area on the proportion of transients in a community ( $p < 10^{-16}$ ), but scaling relationships varied substantially in both slope and intercept across datasets and taxonomic groups (Figure 4A; pseudo  $R^2 = 0.01$ ). When we characterized the scaling relationships using total community size based on the total number of individuals in an average sample instead of sample area the relationship was considerably stronger (Figure 4B; pseudo  $R^2 = 0.32$ ). Communities at scales in which large numbers of individuals are sampled have few transient species, while communities at scales in which small numbers of individuals are sampled have proportionally more transient species, regardless of taxonomic group. After controlling for scale (community size), birds—one of the taxonomic groups with the lowest representation of transient species based on the raw survey data—became comparable to benthic and terrestrial invertebrates, which had the highest representations of transient species based on raw data (cf. Figure 3A and



**Figure 4.** Linear models of the proportion of transient species as a function of (A) sample area and (B) sample community size (number of individuals) for each dataset with a spatially hierarchical sampling scheme. Datasets are color coded by taxonomic group. The proportion of transient species expected for a hypothetical community of 102 individuals (the median community size across datasets) for a given (C) taxonomic group or (D) ecosystem based on linear mixed effects models (see text). No spatially hierarchical datasets were available to evaluate benthic invertebrates. See Figure 2 for icon key.

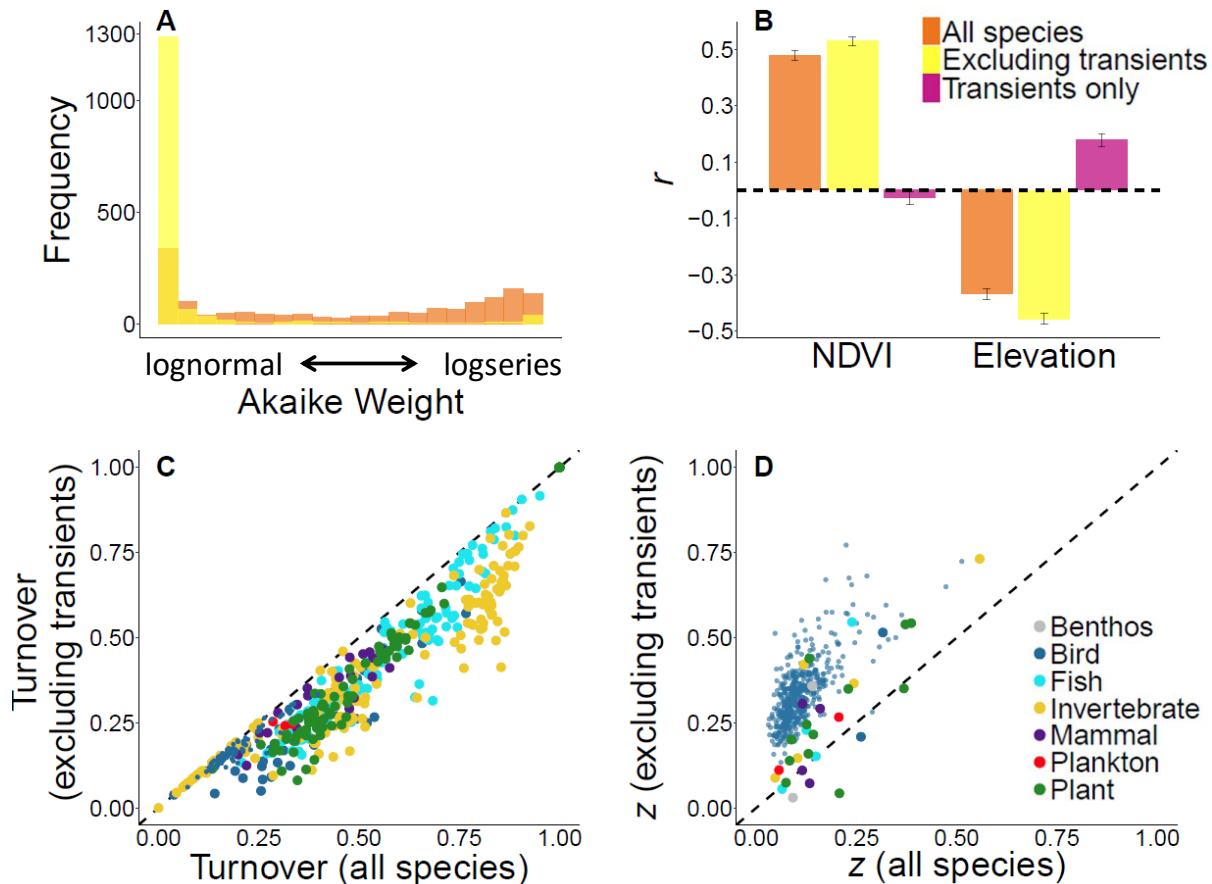
4C). Mammal and plankton communities had the lowest average proportion of transient species in scale-corrected datasets at approximately 40%. Controlling for sampling scale, the proportion of transients in an assemblage no longer varied across type of ecosystem (Figure 4D).

Elevational heterogeneity was found to have a positive effect ( $p < 0.0001$ ) on the proportion of transient species when accounting for community size as a covariate and taxonomic group as a random effect (Table 1). There was no evidence for an interaction between elevational heterogeneity and community size ( $p = 0.98$ ).

**Table 1.** Linear mixed model results for the effect of elevational heterogeneity and community size on the proportion of transients. Taxonomic group was included as a random effect.

Fixed Effect	Estimate	Standard Error	<i>t</i>	<i>p</i>
Intercept	1.08	0.054	20.0	<10 <sup>-16</sup>
log10(community size)	-0.23	0.006	-36.35	<10 <sup>-16</sup>
log10(elev. variance)	0.013	0.003	3.91	9.27e-5
log10(community size):log10(elev. variance)	-4.3e-5	0.002	-0.027	0.98

Finally, we examined whether the inclusion of transient species impacted four fundamental ecological patterns. Species abundance distributions for full assemblages were generally best fit by a logseries distribution, although there was some support for the lognormal, whereas assemblages excluding transient species were universally better fit by a lognormal distribution (Figure 5A). The strength of species richness drivers varied depending on whether transient species were included or not, because transient species exhibited environmental correlations of opposite sign to non-transient species (Figure 5B). As such, excluding transient species led to a stronger positive correlation between richness and the vegetation index NDVI, (0.53 versus 0.48), and a stronger negative correlation with mean elevation (-0.46 versus -0.37). Species turnover was always higher when transient species were included than when they were excluded, with an average deviation of 0.11 (Figure 5C). Finally, the exponent of the species-area relationship was typically higher when excluding transients (average deviation = 0.07; Figure 5D). All results were similar using alternative occupancy thresholds to define transient species (Figures A2-6).



**Figure 5.** Comparison of common ecological patterns between full communities and communities excluding transient species. (A) Histogram of Akaike weights for the logseries model of the species abundance distribution for all species (orange) and excluding transients (yellow). Because only two models were compared, Akaike weights close to 0 imply strong support for the lognormal model. (B) Environmental correlates of species richness (NDVI and elevation) including transients (orange), excluding transients (yellow), and transients only (pink). (C) Comparison of temporal turnover estimates when including or excluding transient species. Temporal turnover was quantified using the Jaccard dissimilarity index. Points are color coded by taxa and small blue circles represent the North American Breeding Bird Survey. (D) Comparison of species-area relationship exponents when including or excluding transient species. Points are the same as in (C).

## Discussion

We quantified the prevalence and impact of transient species in ecological communities using data on over 17,000 community time series spanning multiple ecosystems, taxonomic groups, and spatial scales. Transient species were a common element of communities in all taxa



and ecosystems examined, demonstrating that these species are a general feature of ecological systems. Transient species interact with their abiotic and biotic environment in distinct ways (Magurran and Henderson 2003; Ulrich and Ollik 2004; Coyle et al. 2013; Umaña et al. 2017), which highlights the need to better understand the contexts in which transient species are expected to be prevalent and the potential impact transient species may have on ecological inferences.

The largest source of variation in the proportion of transient species observed in a community is related to spatial scale. For communities sampled at multiple spatial scales, the proportion of transient species decreased with increasing scale, as species were more likely to be observed and actually persist over larger sampling areas. As a result, comparisons of the prevalence of transient species between studies should account for scale. However, area per se may not be directly comparable between communities that differ substantially in body size or otherwise use space differently. An alternative measure of scale, community size, effectively controls for differences in area usage between taxonomic groups by integrating the influence of each species' distinct life history traits and home range sizes. Correcting for scale in this way, we found that the proportion of transient species did not vary with ecosystem type, whereas ignoring scale would have led to the conclusion that transient species were much more common in freshwater than terrestrial ecosystems. Similarly, correcting for scale led to a more even distribution of the proportion of transient species across taxonomic groups, and some groups that would otherwise have been inferred to differ substantially in the prevalence of transients were actually found to be comparable.

Differences in the prevalence of transient species were evident among taxonomic groups even when controlling for spatial scale. Invertebrate, plant, and bird communities had the highest proportion of transient species while plankton and mammal communities had the lowest. These

taxonomic groups differ in many respects precluding a rigorous analysis, but we speculate that traits such as dispersal ability and habitat specialization may increase the likelihood of species being temporarily observed in areas where they are not well adapted and hence being recorded as transients. For example, birds have strong dispersal ability relative to the other taxonomic groups and there are numerous records of individuals spotted far outside their geographic range and in unexpected habitats (Grinnell 1922). Similarly, plants with passive seed dispersal may be transported great distances and may consequently be more likely to be observed in unsuitable habitat (Willson 1993). Small mammals have more limited dispersal, which may explain why mammal communities (dominated in our dataset by small mammal communities) have a lower proportion of transient species on average. The plankton datasets examined in this study came primarily from lakes, and low rates of dispersal between lakes could explain the low proportion of transient species for this group.

In addition to dispersal, groups composed of more generalist species might be expected to have a lower proportion of transient species because most species can maintain viable populations in most locations. The low prevalence of transient species in plankton communities may also be explained by this phenomenon, as Hutchinson (1961) noted "paradoxically" that most plankton species are generalists that compete for the same limited resources. Specialist species, on the other hand, will only maintain populations in select locations with suitable conditions, allowing mass effects (Shmida and Wilson 1985) or accidental dispersal to result in transient occurrences in other areas.

In addition to trait differences among taxa, variability in the prevalence of transient species was related to environmental heterogeneity. Transient species were more prevalent in communities with higher elevational heterogeneity, which extends the findings of Coyle et al. (2013) for birds

to a broader range of taxa. Homogeneous landscapes tend to have homogeneous communities (Stegen et al. 2013; Stein et al. 2014) and a site within such a landscape is unlikely to receive immigrants from poorly adapted species compared to a site in a heterogeneous landscape with a more diverse species pool from more diverse habitats. Indeed, environmental heterogeneity and species richness are frequently positively related (Stein et al. 2014), and our results indicate this may be due in part to an increase in transient species rather than an increase in habitat specialists (Gaston et al. 2007; Stein et al. 2014).

### *Impacts of Transient Species on Ecological Inference*

The presence of transient species in ecological communities influenced all of the ecological patterns we examined, from measures of local community structure, to spatial and temporal turnover, to richness gradients at continental scales. This highlights the importance of considering transients when trying to manage and understand ecological communities. The species abundance distribution (SAD) characterizes the relative abundance of common and rare species in communities and different distributions have been associated with different processes structuring the community (McGill et al. 2007; Connolly et al. 2014). Building on the results of Magurran and Henderson (2003), we show that including transient species in an analysis results in more logseries-like SADs while excluding them results in more lognormal distributions. This result is consistent with the idea that different processes influence the community assembly of transient versus core species (Henderson and Magurran 2014; Supp et al. 2015). Based on theoretical grounds, many SAD models may be more appropriately applied to all species observed, or only to the set of species that strongly interact and maintain viable populations. For example, neutral theory applies to all species, as it explicitly allows for rare immigration or speciation events

(Hubbell 2001), whereas resource allocation based niche apportionment models (MacArthur 1957; Tokeshi 1990) are likely more appropriately applied only to non-transient species. While the SAD may not be sufficient on its own to infer community structuring processes (Cohen 1968; Volkov et al. 2005; Baldrige et al. 2016; but see Connolly et al. 2014), it is one of several ecological patterns that may collectively shed light on such mechanisms (McGill et al. 2007; Blonder et al. 2014). As such, consideration of transient species has the potential to influence our understanding of local community structure.

In addition to influencing measures of local community structure, the inclusion of transient species also affected measures of how ecological systems turnover and change with scale. Estimates of temporal turnover were always higher when transients were included in assemblages. This occurs because transient species are only present over a small fraction of a time series, resulting in higher turnover in species composition within a community over time (see also Magurran and Henderson 2010). Conversely, the inclusion of transient species led to lower estimates of spatial turnover as reflected in the slope of species-area relationships. This is because a greater proportion of the species list at small spatial scales is identified as transient compared to at a larger scale. As such, including transient species increases richness more at small scales than large, resulting in a shallower species-area relationship and lower spatial turnover (Figure 1D). Turnover and associated scaling relationships have implications for assessment of community responses to global change (Brown et al. 1997; Suding et al. 2008), understanding processes structuring spatiotemporal variation in communities (Adler et al. 2005; McGlinn and Palmer 2009), and up and downscaling biodiversity estimates for conservation (Shen and He 2008; Azaele et al. 2015; Kitze and Harte 2015), further indicating that consideration of transients is important for understanding local to regional scale ecological systems.

Finally, inclusion of transient species also influenced the strength of continental scale correlates of species richness. Excluding transient species increased the explanatory power of both NDVI and elevational heterogeneity. Transient species correlations were opposite of those observed for core species, consistent with our general findings on the relationships between environment and heterogeneity (Coyle et al. 2013). Because the proportion of transient species varies along environmental gradients, analyses at large scales will potentially weight core and transient species differently in different locations and the perceived importance of environmental associations with ecological patterns may often change when excluding transient species. In this example, the inclusion of transients weakens the perceived support for a species-energy relationship (Wright 1983; Hurlbert 2004) compared to when only non-transients were considered. Given the impact on a wide range of ecological patterns, the decision to include or exclude transient species in a community analysis is an important one that should be made by explicitly considering the nature of the conceptual framework or theory being investigated. In some cases, it will be necessary to remove these species from analyses or risk making improper inferences.

### *Considerations*

Conceptually, transient species are those that do not maintain persistent populations over time and therefore only appear infrequently during surveys. The bimodality of temporal occupancy distributions (e.g., Figure 1A) has led many authors to suggest that temporal occupancy can be used to distinguish these transient species from more core members of a community. However, it can be difficult to tease apart whether species of low occupancy are truly transient or simply have low density or detectability (Henderson and Magurran 2014). We followed Coyle et al. (2013) in using a maximum occupancy threshold of 33% as our operational definition of transient species,

but all of the results we report here were similar using stricter thresholds of 10% or 25% (Figures A2-A6). If the focus were on a single community, then the accuracy of identifying transient species might be improved by a combination of assessing the shape and natural break points of each community's particular occupancy distribution, and incorporating information on species habitat preference as done by Belmaker (2009) for coral reef fish. Alternatively, when the sampling design allows for the estimation of detection probabilities it should be possible to correct for these issues using occupancy modeling (MacKenzie et al. 2006). Independent validation of transient status (e.g., by evidence of breeding, or knowledge of habitat affinities) or occupancy modeling based approaches are always desirable when possible, and analyses along environmental gradients should carefully consider how detectability might vary along such gradients (Coyle et al. 2013). However, for many groups detailed information on habitat preferences or estimates of true population persistence is not readily available, and a definition based on a universal occupancy threshold is currently the most feasible option for analyzing hundreds or thousands of assemblages for cross-taxon comparisons like those presented here.

As described in the *Methods*, there is evidence that occupancy based thresholds provide reasonable identifications of transient species (Magurran and Henderson 2003; Belmaker 2009; Coyle et al. 2013). There is additional evidence from our results that using this raw occupancy based approach provides a reasonable approximate classification. First, the misclassification rate should presumably be lower when defining transient species using stricter occupancy thresholds, and so the consistency of our results across multiple thresholds lends some confidence to this approach. Second, for certain communities the taxonomic group and mode of data collection provide nearly complete censuses of all individuals within a static sample (e.g. plant stems within a quadrat or fish in a seine net). In these communities, imperfect detection should have little

influence on estimates of occupancy (at the scale of sampling). The similarity of results in this study across groups that tend to be thoroughly surveyed (e.g., plants and fish) and those that are less intensively sampled (e.g., birds and butterflies) suggests that our results are not driven heavily by misclassifying imperfectly detected species. A detailed understanding of when and to what extent imperfect detection probabilities influence the assessment of the prevalence and impact of transient species will require simulation based approaches (Hurlbert unpublished data).

## *Conclusions*

Our results show that transient species are prevalent in ecological communities across all taxa, scales, and ecosystems examined. Despite the ubiquity of these species, most studies in community ecology have implicitly ignored this concept by characterizing communities using surveys that provide a snapshot of community composition in time. Because transient species interact with their biotic and abiotic environment differently—in most cases, more weakly—than non-transient species, their inclusion in community analyses impacts a wide range of ecological patterns including estimates of community structure, turnover, and biodiversity. Ecologists should explicitly consider whether to include or exclude transient species in analyses by determining whether the theories, conceptual frameworks, and conservation interests of their research are best aligned with entire communities including transient species or with only core species that maintain sustained populations at a site. A failure to do so may result in inappropriate tests of models, incorrect inferences regarding processes, and imperfect conservation efforts. When data are unavailable for distinguishing species in a community as transient or not, researchers should be aware of how this uncertainty may bias their results. While some methodological challenges remain, future studies will benefit from considering when and how the inclusion of transient

species impacts our understanding of how communities respond to environmental gradients, habitat fragmentation, climatic shifts, and other disturbances.

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record of bird species observed on Konza Prairie, and Fish population on selected watersheds at Konza Prairie was supported by the NSF Long Term Ecological Research Program at Konza Prairie Biological Station. Hubbard Brook: Data on the Bird Abundances at the Hubbard Brook Experimental Forest (1969-present) and on three replicate plots (1986-2000) in the White Mountain National Forest were provided by Richard Holmes on 6/16/2016. These data were gathered as part of the Hubbard Brook Ecosystem Study (HBES). The HBES is a collaborative effort at the Hubbard Brook Experimental Forest, which is operated and maintained by the USDA Forest Service, Northern Research Station, Newtown Square, PA. Significant funding for collection of these data was provided by DEB 0423259 (Hubbard Brook Long Term Ecological Research). Sevilleta LTER: Sevilleta LTER mammals data set was provided by the Sevilleta Long Term Ecological Research (LTER) Program. Significant funding for collection of these data was provided by the National Science Foundation Long Term Ecological Research program (NSF Grant numbers BSR 88-11906, DEB 9411976, DEB 0080529 and DEB 0217774). Maryland Biological Stream Survey: Data included in this document were provided by the Maryland Department of Natural Resources Monitoring and Non-tidal Assessment Division. Lake Kasumigaura: The Lake Kasumigaura database, Table 10 Phytoplankton density, Lake Kasumigaura database, Table 12-1 Density of Rotifer, Cladocera and Copepoda, Lake Kasumigaura database, Table 14-1 Benthos data, and Lake Kasumigaura database, Table 15-2 Fish density data are those of the Lake Kasumigaura Long-term Environmental Monitoring Program of the National Institute for Environmental Studies, Japan. Data collection for the ichthyoplankton time series northeast of Taiwan was supported by the Council of Agriculture and the Ministry of Science and Technology, Taiwan (to CHH). We are grateful to the thousands of scientists and volunteers who have helped to collect and share all of the data analyzed herein.

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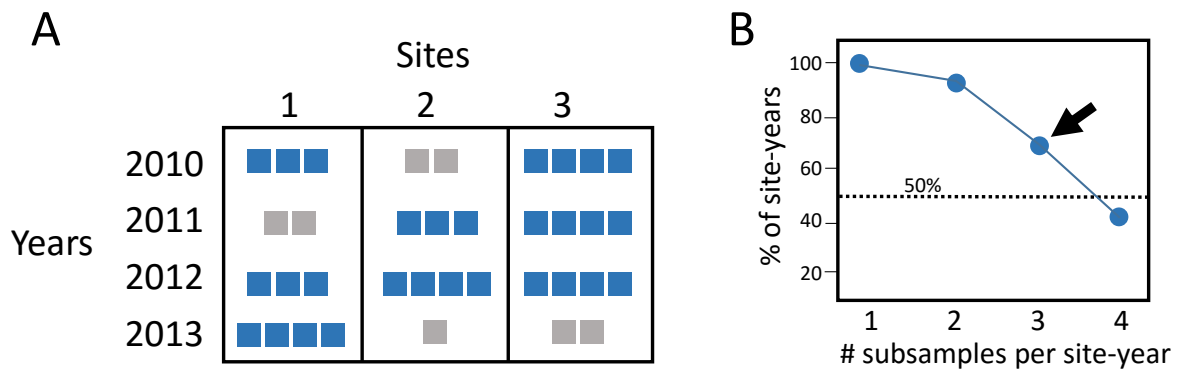
## Appendix

### *Sampling standardization of community time series datasets*

For the most accurate estimates of temporal occupancy, the sampling intensity used to characterize the assemblage in question should be identical every year. However, for some datasets, sampling intensity was not uniform in space or in time. In some cases, the number of spatial units (e.g. plant quadrats) censused varied by sampling date, in other cases, the number of sampling dates per year with which an assemblage could be characterized varied between years, and occasionally both spatial and temporal subsampling levels varied.

We used a sample-based rarefaction approach (Gotelli 2008) to standardize the effort with which an assemblage is characterized over its time series. Choosing the number of spatial or temporal subsamples to use for rarefaction is a non-trivial problem, however. On the one hand, the lowest common level of subsampling across years or sites might be chosen which will enable the inclusion of all years or sites available in the dataset. In this case, data from the best sampled sites or years will be thrown out during rarefaction in order to compare those sites or years with the less well sampled ones. On the other hand, one might choose a high level of subsampling which will provide a more thorough characterization of those well sampled assemblages. In this case, data will be lost as many sites or years will not meet this high threshold and so will not be included in the analysis.

For each dataset, we attempted to maximize both the number of assemblages that would be available for analysis as well as the thoroughness with which an assemblage was characterized by choosing the lowest level of subsampling that was met by at least 50% of possible site-years (Figure A1).



**Figure A1.** (A) A hypothetical dataset with 3 sites that have been sampled with variable intensity over time (squares). Site-years exceeding the threshold of 3 subsamples are highlighted in blue. Only data from these site-years would be used in an analysis, and where the total number of subsamples exceeds the threshold, only 3 would be chosen at random to characterize an assemblage. (B) The subsampling threshold is the smallest value for which the % of available site-years exceeds 50% (dotted line).

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**Table A1.** Table of datasets, sources, and citations used for analyses.

Dataset Name	Link	System	Taxa	Number of Sites	Years of Study	Number of Species	Multi-scale	Citation
A multi-decade time series of kelp forest community structure at the California Channel Islands	<a href="http://esapubs.org/archive/ecol/E094/245/">http://esapubs.org/archive/ecol/E094/245/</a>	Marine	Benthos	33	30	28	N	Kushner et al. 2013
2003 Prescribed Burn Effect on Chihuahuan Desert Grasses and Shrubs at the Sevilleta National Wildlife Refuge, New Mexico: Species Composition Study (2004 - present)	<a href="http://sev.lternet.edu/data/sev-166">http://sev.lternet.edu/data/sev-166</a>	Terrestrial	Plant	16	9	147	Y	Muldavin and Collins 2016
A 12-year study on the scaling of vascular plant composition in an Oklahoma tallgrass prairie	<a href="http://esapubs.org/Archive/ecol/E091/124/default.htm#data">http://esapubs.org/Archive/ecol/E091/124/default.htm#data</a>	Terrestrial	Plant	20	12	318	Y	McGlinn et al. 2010
A long-term bird population study in an Appalachian spruce forest	<a href="http://www.jstor.org/stable/4161914">http://www.jstor.org/stable/4161914</a>	Terrestrial	Bird	1	22	20	N	Hall 1984

A multi-decade time series of kelp forest community structure at San Nicolas Island, California (USA): benthic cover	<a href="http://esapubs.org/archive/ecol/E094/244/#data">http://esapubs.org/archive/ecol/E094/244/#data</a>	Marine	Benthos	7	27	128	Y	Kenner et al. 2013
A multi-decade time series of kelp forest community structure at San Nicolas Island, California (USA): benthic fish	<a href="http://esapubs.org/archive/ecol/E094/244/#data">http://esapubs.org/archive/ecol/E094/244/#data</a>	Marine	Fish	7	26	36	Y	Kenner et al. 2013
A multi-decade time series of kelp forest community structure at San Nicolas Island, California (USA): midwater fish	<a href="http://esapubs.org/archive/ecol/E094/244/#data">http://esapubs.org/archive/ecol/E094/244/#data</a>	Marine	Fish	1	17	57	Y	Kenner et al. 2013
A multi-decade time series of kelp forest community structure at the California Channel Islands	<a href="http://esapubs.org/archive/ecol/E094/245/">http://esapubs.org/archive/ecol/E094/245/</a>	Marine	Fish	32	16	86	N	Kushner et al. 2013
Above ground plant biomass in a mesic acidic tussock tundra experimental site from 1982 to	<a href="http://arc-lter.ecosystems.mbl.edu/19822000gs81tusbm">http://arc-lter.ecosystems.mbl.edu/19822000gs81tusbm</a>	Terrestrial	Plant	4	6	24	Y	Shaver 2006

2000 Arctic LTER, Toolik Lake, Alaska								
An efficient light-trap for catching insects. Acta Entomologica	<a href="http://www3.imperial.ac.uk/cpb/databases/gpdd">http://www3.imperial.ac.uk/cpb/databases/gpdd</a>	Terrestrial	Invertebrate	1	26	133	N	Novak 1983
Arthropod Pitfall Traps at LTER II NPP sites. Jornada LTER	<a href="http://jornada.nmsu.edu/lter/project/49395/view">http://jornada.nmsu.edu/lter/project/49395/view</a>	Terrestrial	Invertebrate	10	6	157	Y	Lightfoot et al. 2008
Belgian Migrating Lepidoptera Survey	<a href="https://web.archive.org/web/19990220041409/http://users.skynet.be/bs663526/">https://web.archive.org/web/19990220041409/http://users.skynet.be/bs663526/</a>	Terrestrial	Invertebrate	1	14	25	N	Vanholder 1997
Bialowieza National Park bird assemblage	<a href="http://www.bioone.org/doi/abs/10.3161/000164510X551354">http://www.bioone.org/doi/abs/10.3161/000164510X551354</a>	Terrestrial	Bird	7	40	84	N	Wesołowski et al. 2010
Breeding Bird Populations at William Trelease Woods	<a href="http://hdl.handle.net/2142/25182">http://hdl.handle.net/2142/25182</a>	Terrestrial	Bird	1	44	60	N	Kendeigh 1982
Breeding Bird Populations on Abandoned Farmland in Robert Allerton Park	<a href="http://hdl.handle.net/2142/25182">http://hdl.handle.net/2142/25182</a>	Terrestrial	Bird	1	6	34	N	Kendeigh 1982

Breeding Bird Populations on Abandoned Farmland in Robert Allerton Park	<a href="http://hdl.handle.net/2142/25182">http://hdl.handle.net/2142/25182</a>	Terrestrial	Bird	1	25	53	N	Kendeigh 1982
Breeding Bird Populations wintering in William Trelease Woods	<a href="http://hdl.handle.net/2142/25182">http://hdl.handle.net/2142/25182</a>	Terrestrial	Bird	1	48	48	N	Kendeigh 1982
Breeding Bird Censuses, Neotoma	<a href="http://www.jstor.org/stable/1931793">http://www.jstor.org/stable/1931793</a>	Terrestrial	Bird	1	10	56	N	Preston 1960
Canadian duck censuses	<a href="http://ecologicaldata.org/wiki/redvers-waterfowl-census">http://ecologicaldata.org/wiki/redvers-waterfowl-census</a>	Terrestrial	Bird	2	26	13	N	Vickery et al. 1984
Central California Butterfly Population Monitoring	<a href="http://butterfly.ucdavis.edu/">http://butterfly.ucdavis.edu/</a>	Terrestrial	Invertebrate	8	41	148	N	Thorne et al. 2006
Eastern Wood Breeding Bird Data	<a href="http://onlinelibrary.wiley.com/doi/10.1002/9780470999592.app2/summary">http://onlinelibrary.wiley.com/doi/10.1002/9780470999592.app2/summary</a>	Terrestrial	Bird	1	29	45	N	Gaston et al. 2000
El Verde Grid long-term invertebrate data	<a href="http://luq2.lternet.edu/data/luqmetadata107">http://luq2.lternet.edu/data/luqmetadata107</a>	Terrestrial	Invertebrate	33	22	19	Y	Willig et al. 2007

Farne Island birds	<a href="http://www.jstor.org/stable/1744518">http://www.jstor.org/stable/1744518</a>	Terrestrial	Bird	1	29	16	N	Diamond and May 1977
Fish populations on selected watersheds at Konza Prairie	<a href="http://lter.konza.ksu.edu/content/cfp01-fish-population-selected-watersheds-konza-prairie">http://lter.konza.ksu.edu/content/cfp01-fish-population-selected-watersheds-konza-prairie</a>	Freshwater	Fish	1	7	17	Y	Whitney et al. 2015
Fourteen years of mapped, permanent quadrats in a northern mixed prairie, USA	<a href="http://esapubs.org/archive/ecol/E092/143/metadata.htm">http://esapubs.org/archive/ecol/E092/143/metadata.htm</a>	Terrestrial	Plant	1	7	52	Y	Anderson et al. 2011
Hinkley Point fish	<a href="http://www.nature.com/nature/journal/v422/n6933/full/nature01547.html">http://www.nature.com/nature/journal/v422/n6933/full/nature01547.html</a>	Marine	Fish	1	21	80	N	Magurran and Henderson 2003
Hubbard Brook LTER birds	<a href="https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-hbr.81.5">https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-hbr.81.5</a>	Terrestrial	Bird	4	14	37	N	Holmes 2016
Indiana stream fish assemblage	<a href="http://www.jstor.org/stable/2461070">http://www.jstor.org/stable/2461070</a>	Freshwater	Fish	1	12	49	N	Grossman et al. 1982
Insect Populations via Sticky Traps at KBS-LTER	<a href="http://lter.kbs.msu.edu/datatables/67">http://lter.kbs.msu.edu/datatables/67</a>	Terrestrial	Invertebrate	10	23	20	Y	Landis and Gage 2015
Ireland amphipods	<a href="http://www.sciencedirect.com/science/article/pii/0022098196000305">http://www.sciencedirect.com/science/article/pii/0022098196000305</a>	Marine	Invertebrate	1	12*	27	N	Costello and Myers 1996

Konza LTER grasshopper monitoring	<a href="http://lter.konza.ksu.edu/content/cgr02-sweep-sampling-grasshoppers-konza-prairie-lter-watersheds-1982-present">http://lter.konza.ksu.edu/content/cgr02-sweep-sampling-grasshoppers-konza-prairie-lter-watersheds-1982-present</a>	Terrestrial	Invertebrate	16	24	37	Y	Rode et al. 2017
Konza LTER small mammals	<a href="http://lter.konza.ksu.edu/content/csm01-seasonal-summary-numbers-small-mammals-14-lter-traplines-prairie-habitats-konza">http://lter.konza.ksu.edu/content/csm01-seasonal-summary-numbers-small-mammals-14-lter-traplines-prairie-habitats-konza</a>	Terrestrial	Mammal	14	33	15	Y	Ricketts and Sandercock 2016
Lac Croche understory vegetation	<a href="http://www.esapubs.org/archive/ecol/E088/197/default.htm">http://www.esapubs.org/archive/ecol/E088/197/default.htm</a>	Terrestrial	Plant	43	8	83	Y	Paquette et al. 2007
Yanliao Bay, Taiwan, Ichthyoplankton	NA	Marine	Plankton	3	6	137	N	Hsieh unpublished
Lake Kasumigaura database, Table 10 Phytoplankton density	<a href="http://db.cger.nies.go.jp/gem/monite/inter/GEMS/database/kasumi/contents/datalist.html">http://db.cger.nies.go.jp/gem/monite/inter/GEMS/database/kasumi/contents/datalist.html</a>	Freshwater	Plankton	2	33	172	N	Takamura and Nakagawa 2012
Lake Kasumigaura database, Table 12-1 Density of Rotifer, Cladocera and Copepoda	<a href="http://db.cger.nies.go.jp/gem/monite/inter/GEMS/database/kasumi/contents/datalist.html">http://db.cger.nies.go.jp/gem/monite/inter/GEMS/database/kasumi/contents/datalist.html</a>	Freshwater	Plankton	2	21	62	N	Takamura et al. 2015

Lake Kasumigaura database , Table 14-1 Benthos data	<a href="http://db.cger.nies.go.jp/gem/monie/inter/GEMS/database/kasumi/contents/datalist.html">http://db.cger.nies.go.jp/gem/monie/inter/GEMS/database/kasumi/contents/datalist.html</a>	Freshwater	Benthos	4	22	10	N	Iwakuma and Ueno 2010
Lake Kasumigaura database , Table 15-2 Fish density data	<a href="http://db.cger.nies.go.jp/gem/monie/inter/GEMS/database/kasumi/contents/datalist.html">http://db.cger.nies.go.jp/gem/monie/inter/GEMS/database/kasumi/contents/datalist.html</a>	Freshwater	Fish	1	9	45	N	Matsuzaki and Nohara 2017
Long-Term Community Dynamics of Small Landbirds with and Without Exposure to Extensive Disturbance from Military Training Activities - Konza prairie site	<a href="http://link.springer.com/article/10.1007%2Fs00267-009-9421-6">http://link.springer.com/article/10.1007%2Fs00267-009-9421-6</a>	Terrestrial	Bird	1	11	62	N	Rivers et al. 2010
Long-term dynamics of breeding birds in broad-leaved deciduous forest on Hanikatsi Island in the West-Estonian archipelago	<a href="https://www.researchgate.net/publication/253704570_Long-term_dynamics_of_breeding_birds_in_broad-leaved_deciduous_forest_on_Hanikatsi_Island_in_the_West-Estonian_archipelago">https://www.researchgate.net/publication/253704570_Long-term_dynamics_of_breeding_birds_in_broad-leaved_deciduous_forest_on_Hanikatsi_Island_in_the_West-Estonian_archipelago</a>	Terrestrial	Bird	1	27	33	N	Leito et al. 2006

Long-term mapped quadrats from Kansas prairie: demographic information for herbaceous plants	<a href="http://esapubs.org/archive/ecol/E088/161/">http://esapubs.org/archive/ecol/E088/161/</a>	Terrestrial	Plant	51	41	137	Y	Adler et al. 2007
Long-term monitoring of mammals in the face of biotic and abiotic influences at a semiarid site in north-central Chile: shrubs and herbaceous plants	<a href="http://esapubs.org/archive/ecol/E094/084/metadata.php">http://esapubs.org/archive/ecol/E094/084/metadata.php</a>	Terrestrial	Plant	16	16	85	N	Kelt et al. 2013
Long-term monitoring of Mammals in the face of biotic and abiotic influences at a semiarid site in north-central Chile: mammals	<a href="http://esapubs.org/archive/ecol/E094/084/metadata.php">http://esapubs.org/archive/ecol/E094/084/metadata.php</a>	Terrestrial	Mammal	4	12	12	Y	Kelt et al. 2013



Long-Term Nitrogen Deposition: Population, Community, and Ecosystem Consequences - Experiment 001	<a href="https://www.cedarcreek.umn.edu/research/data/dataset?ple001">https://www.cedarcreek.umn.edu/research/data/dataset?ple001</a>	Terrestrial	Plant	3	30	148	Y	Tilman 2012
Long-term stem inventory data from tropical rain forest plots in Australia: trees >10cm dbh	<a href="http://esapubs.org/archive/ecol/E095/209/">http://esapubs.org/archive/ecol/E095/209/</a>	Terrestrial	Plant	20	34	488	Y	Bradford et al. 2014
Luquillo LTER bird point counts	<a href="http://luq.lternet.edu/data/luqmetadata23">http://luq.lternet.edu/data/luqmetadata23</a>	Terrestrial	Bird	1	19	39	Y	Willig et al.2007
Mapped quadrats in sagebrush steppe: long-term data for analyzing demographic rates and plant–plant interactions	<a href="http://onlinelibrary.wiley.com/doi/10.1890/10-0404.1/abstract">http://onlinelibrary.wiley.com/doi/10.1890/10-0404.1/abstract</a>	Terrestrial	Plant	1	17	18	Y	Zachmann et al. 2016
Maryland Biological Stream Survey Fish Data	<a href="http://dnr2.maryland.gov/streams/Pages/mbss.aspx">http://dnr2.maryland.gov/streams/Pages/mbss.aspx</a>	Freshwater	Fish	48	17	86	Y	Roth et al. 2005

Maryland Biological Stream Survey Macroinvertebrate Data	<a href="http://dnr2.maryland.gov/streams/Pages/mbss.aspx">http://dnr2.maryland.gov/streams/Pages/mbss.aspx</a>	Freshwater	Benthos	52	17	364	Y	Roth et al. 2005
Mediterranean tintinnid ciliates	<a href="http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2699.2008.02046.x/abstract">http://onlinelibrary.wiley.com/doi/10.1111/j.1365-2699.2008.02046.x/abstract</a>	Marine	Plankton	1	18*	49	N	Dolan et al. 2009
Monitoring the Abundance of Butterflies 1976-1985	<a href="http://jncc.defra.gov.uk/page-2614">http://jncc.defra.gov.uk/page-2614</a>	Terrestrial	Invertebrate	35	10	44	N	Pollard et al. 1986
Mosquitoes of North America with emphasis in the midwestern United States: long-term occurrence patterns	<a href="http://esapubs.org/archive/ecol/E094/126/">http://esapubs.org/archive/ecol/E094/126/</a>	Terrestrial	Invertebrate	13	37	28	N	Hellmann et al. 2013
Mountain Birdwatch	<a href="https://knb.ecoinformatics.org/#view/doi:10.5063/F1DN430G">https://knb.ecoinformatics.org/#view/doi:10.5063/F1DN430G</a>	Terrestrial	Bird	35	11	72	N	Lambert and Hart 2015
North American Breeding Bird Survey	<a href="https://www.pwrc.usgs.gov/bbs/">https://www.pwrc.usgs.gov/bbs/</a>	Terrestrial	Bird	1000+	15	405	Y	Pardieck et al. 2016

North Temperate Lakes LTER: Fish Abundance 1981-current, ELECTRO FISH	<a href="https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-ntl.7.10">https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-ntl.7.10</a>	Freshwater	Fish	8	21	61	N	De Stasio et al. 1996
North Temperate Lakes LTER: Fish Abundance 1981-current, FYKE NET	<a href="https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-ntl.7.10">https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-ntl.7.10</a>	Freshwater	Fish	9	31	53	N	De Stasio et al. 1996
North Temperate Lakes LTER: Fish Abundance 1981-current, SEINE	<a href="https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-ntl.7.10">https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-ntl.7.10</a>	Freshwater	Fish	9	15	57	N	De Stasio et al. 1996
North Temperate Lakes LTER: Macrophyte Species at Quadrat Level - Trout Lake 1993 - current	<a href="https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-macrophyte-species-quadrat-level-trout-lake-1993-current">https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-macrophyte-species-quadrat-level-trout-lake-1993-current</a>	Freshwater	Plant	2	20	28	Y	Magnuson et al. 2010
North Temperate Lakes LTER: Macrophyte Transects - Trout Lake 1982 - current	<a href="https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-macrophyte-transects-trout-lake-1982-current">https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-macrophyte-transects-trout-lake-1982-current</a>	Freshwater	Plant	2	22	29	Y	Magnuson et al. 2010
North Temperate Lakes LTER: Phytoplankton - Madison Lakes Area 1995 - current	<a href="https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-phytoplankton-madison-lakes-area-1995-current">https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-phytoplankton-madison-lakes-area-1995-current</a>	Freshwater	Plankton	2	18	315	Y	Magnuson et al. 2011

North Temperate Lakes LTER: Phytoplankton - Trout Lake Area 1984 - current	<a href="https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-phytoplankton-trout-lake-area-1984-current">https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-phytoplankton-trout-lake-area-1984-current</a>	Freshwater	Plankton	2	10	135	N	Magnuson et al. 2007
North Temperate Lakes LTER: Zooplankton - Madison Lakes Area 1997 - current	<a href="https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-zooplankton-madison-lakes-area-1997-current">https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-zooplankton-madison-lakes-area-1997-current</a>	Freshwater	Plankton	2	19	26	Y	Magnuson et al. 2011
North Temperate Lakes LTER: Zooplankton - Trout Lake Area 1982 - current	<a href="https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-zooplankton-trout-lake-area-1982-current">https://lter.limnology.wisc.edu/dataset/north-temperate-lakes-lter-zooplankton-trout-lake-area-1982-current</a>	Freshwater	Plankton	7	29	100	Y	Magnuson et al. 1983
One hundred and six years of population and community dynamics of Sonoran Desert Laboratory perennials	<a href="http://esapubs.org/archive/ecol/E094/083/">http://esapubs.org/archive/ecol/E094/083/</a>	Terrestrial	Plant	2	28	58	N	Rodriguez-Buritica et al. 2013
Plant species composition on selected watersheds at Konza Prairie	<a href="http://lter.konza.ksu.edu/content/pvc02-plant-species-composition-selected-watersheds-konza-prairie">http://lter.konza.ksu.edu/content/pvc02-plant-species-composition-selected-watersheds-konza-prairie</a>	Terrestrial	Plant	4	18	294	Y	Briggs et al. 2002

Portal Plants, summer	<a href="http://esapubs.org/archive/ecol/E090/118/metadat&lt;br/&gt;a.htm">http://esapubs.org/archive/ecol/E090/118/metadat a.htm</a>	Terrestrial	Plant	24	14	105	Y	Ernest et al. 2009
Portal Plants, winter	<a href="http://esapubs.org/archive/ecol/E090/118/metadat&lt;br/&gt;a.htm">http://esapubs.org/archive/ecol/E090/118/metadat a.htm</a>	Terrestrial	Plant	1	14	95	Y	Ernest et al. 2009
Portal Rodents	<a href="http://esapubs.org/archive/ecol/E090/118/metadat&lt;br/&gt;a.htm">http://esapubs.org/archive/ecol/E090/118/metadat a.htm</a>	Terrestrial	Mammal	1	15	21	Y	Ernest et al. 2009
Powdermill Biological Station Small Mammal Database	<a href="http://ecologicaldata.org/wiki/powdermill-&lt;br/&gt;biological-station-small-mammal-database">http://ecologicaldata.org/wiki/powdermill- biological-station-small-mammal-database</a>	Terrestrial	Mammal	1	11	16	N	Merritt 1999
Preston 1948 moths	<a href="https://www.jstor.org/stable/1930989">https://www.jstor.org/stable/1930989</a>	Terrestrial	Invertebrate	2	22	291	N	Preston 1948
SBC LTER: Reef: Kelp Forest Community Dynamics: Fish abundance	<a href="https://portal.lternet.edu/nis/mapbrowse?packagei&lt;br/&gt;d=knb-lter-sbc.17.27">https://portal.lternet.edu/nis/mapbrowse?packagei d=knb-lter-sbc.17.27</a>	Marine	Fish	39	13	58	Y	Reed 2013

Sevilleta LTER arthropods	<a href="https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sev.29.175390">https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-sev.29.175390</a>	Terrestrial	Invertebrate	42	12	365	Y	Lightfoot 2010
Sevilleta LTER mammals	<a href="http://sev.lternet.edu/content/small-mammal-exclosure-study-smes-0">http://sev.lternet.edu/content/small-mammal-exclosure-study-smes-0</a>	Terrestrial	Mammal	1	16	24	Y	Baéz et al. 2006
Skokholm birds	<a href="http://ecologicaldata.org/wiki/skokholm-bird-observatory">http://ecologicaldata.org/wiki/skokholm-bird-observatory</a>	Terrestrial	Bird	1	47	29	N	Williamson 1983
Small Mammal Exclosure Study (SMES) Vegetation Data from the Chihuahuan Desert Grassland and Shrubland at the Sevilleta National Wildlife Refuge, New Mexico (2006-2009)	<a href="http://repository.unm.edu/handle/1928/29843">http://repository.unm.edu/handle/1928/29843</a>	Terrestrial	Plant	7	15	101	Y	Lightfoot 2010
Small Mammal Exclosure Study. Jornada LTER	<a href="http://jornada.nmsu.edu/lter/project/49356/view">http://jornada.nmsu.edu/lter/project/49356/view</a>	Terrestrial	Mammal	1	7	15	Y	Lightfoot 1995

Species composition and population fluctuations of alpine bird communities during 38 years in the Scandinavian mountain range	<a href="http://portal.research.lu.se/portal/en/publications/species-composition-and-population-fluctuations-of-alpine-bird-communities-during-38-years-in-the-scandinavian-mountain-range(94d93170-8b5a-4d80-a72b-c06fd0149dcb).html">http://portal.research.lu.se/portal/en/publications/species-composition-and-population-fluctuations-of-alpine-bird-communities-during-38-years-in-the-scandinavian-mountain-range(94d93170-8b5a-4d80-a72b-c06fd0149dcb).html</a>	Terrestrial	Bird	4	38	47	N	Svensson 2006
Species trends, turnover and composition of a woodland bird community in southern Sweden during a period of 57 years	<a href="http://birdlife.se/1020.0.1.0/274/download_24762.php">http://birdlife.se/1020.0.1.0/274/download_24762.php</a>	Terrestrial	Bird	1	57	41	N	Svensson et al. 2010
Stream fish assemblage stability in a southern Appalachian stream at the Coweeta Hydrologic Laboratory from 1984 to 1995	<a href="https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-cwt.3047.13">https://portal.lternet.edu/nis/mapbrowse?packageid=knb-lter-cwt.3047.13</a>	Freshwater	Fish	2	10	14	N	Grossman 2007
Structure and dynamics of a passerine bird community in a spruce-dominated boreal forest	<a href="http://www.jstor.org/stable/23735355?seq=1#page_scan_tab_contents">http://www.jstor.org/stable/23735355?seq=1#page_scan_tab_contents</a>	Terrestrial	Bird	1	12	33	N	Hogstad 1993

Temporal variation in richness and composition of recruits in a diverse cnidarian assemblage of subtropical Brazil	<a href="http://www.sciencedirect.com/science/article/pii/S0022098114001877">http://www.sciencedirect.com/science/article/pii/S0022098114001877</a>	Marine	Invertebrate	1	8	34	N	Fernandez et al. 2014
The 37-year dynamics of a subalpine passerine bird community, with special emphasis on the influence of environmental temperature and <i>Epirrita autumnata</i> cycles	<a href="http://birdlife.se//1020.0.1.0/40/download_18564.php">http://birdlife.se//1020.0.1.0/40/download_18564.php</a>	Terrestrial	Bird	1	37	35	N	Enemar et al. 2004
Vegetation surveys in large-herbivore exclusion in an African savanna: five years of the UHURU experiment	<a href="http://www.esapubs.org/archive/ecol/E095/064/metadata.php">http://www.esapubs.org/archive/ecol/E095/064/metadata.php</a>	Terrestrial	Plant	7	6	90	Y	Kartzinel et al. 2014
Weekly record of bird species observed on Konza Prairie	<a href="http://lter.konza.ksu.edu/content/cbp01-variable-distance-line-transect-sampling-bird-population-numbers-different-habitats">http://lter.konza.ksu.edu/content/cbp01-variable-distance-line-transect-sampling-bird-population-numbers-different-habitats</a>	Terrestrial	Bird	16	26	221	Y	Verheijen et al. 2017
Western English Channel phytoplankton	<a href="http://plankt.oxfordjournals.org/content/32/5/643.full#sec-5">http://plankt.oxfordjournals.org/content/32/5/643.full#sec-5</a>	Marine	Plankton	1	18	157	N	Widdicombe et al. 2010



Zooplankton survey of Oneida Lake	<a href="https://knb.ecoinformatics.org/#view/kgordon.17.56">https://knb.ecoinformatics.org/#view/kgordon.17.56</a>	Freshwater	Plankton	5	37	30	Y	Rudstam 2008
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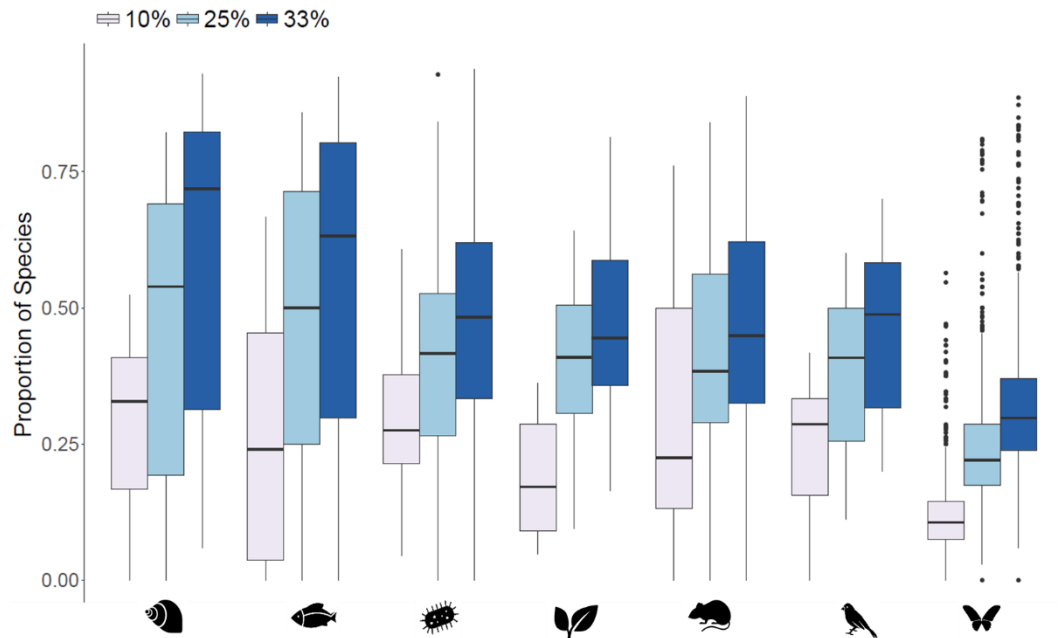


Figure A2. The impact of different thresholds on the proportion of transient species in assemblages from different taxonomic groups. Taxon symbols as in Figure 2.

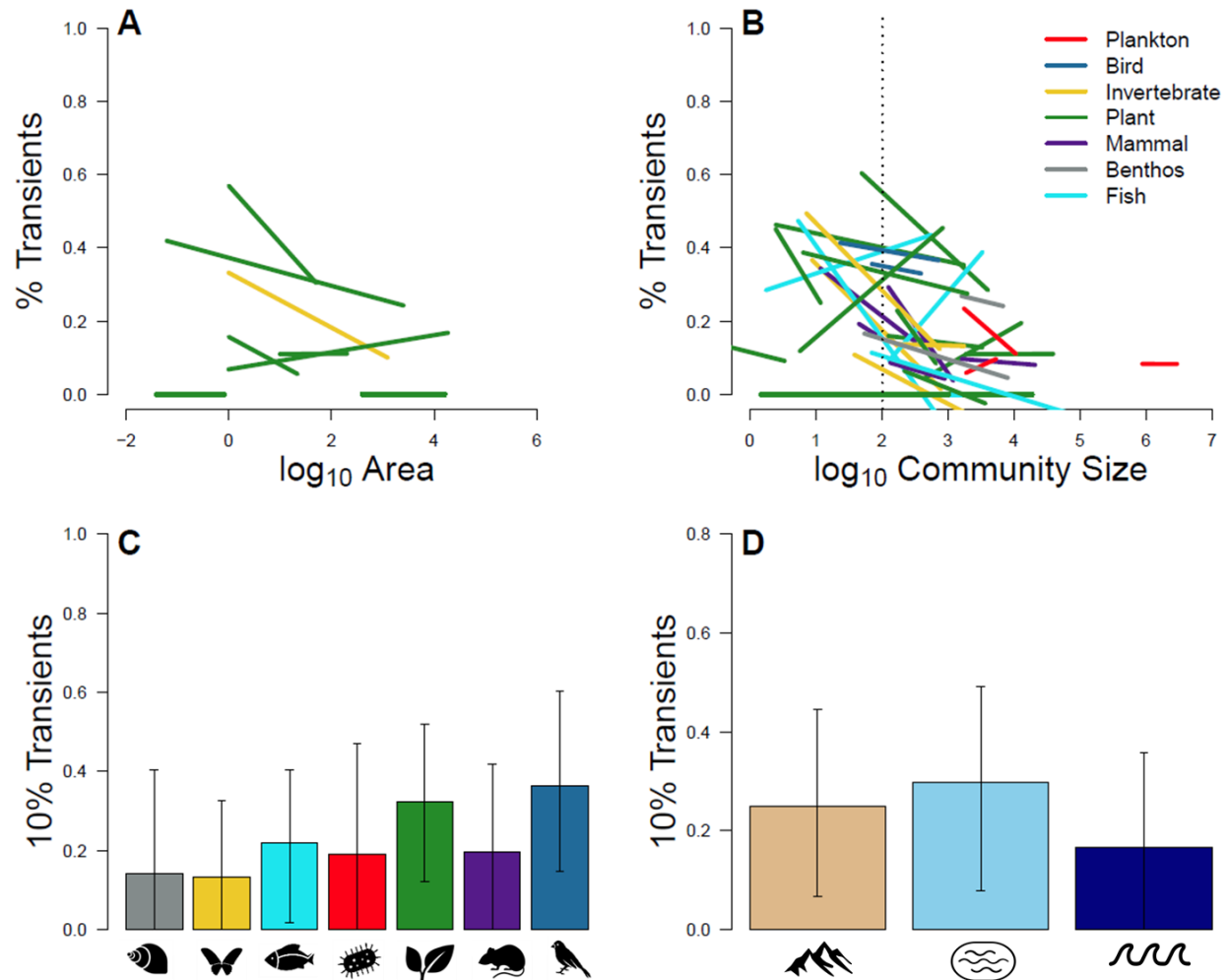


Figure A3. The impact of scale on the proportion of transient species as displayed in Figure 4 in the main text, but where transient species are defined as those with temporal occupancy  $\leq 10\%$ .

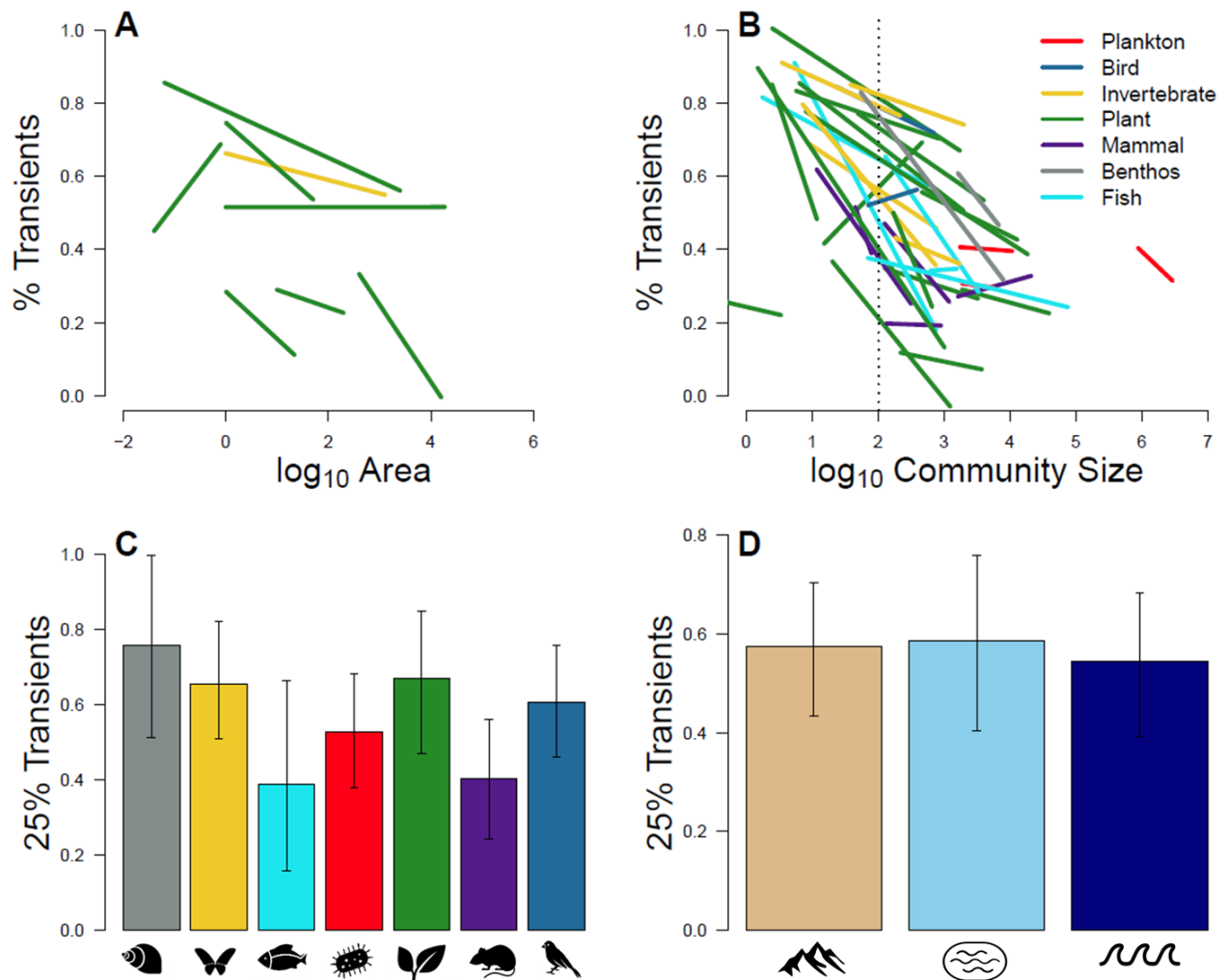


Figure A4. The impact of scale on the proportion of transient species as displayed in Figure 4 in the main text, but where transient species are defined as those with temporal occupancy  $\leq 25\%$ .

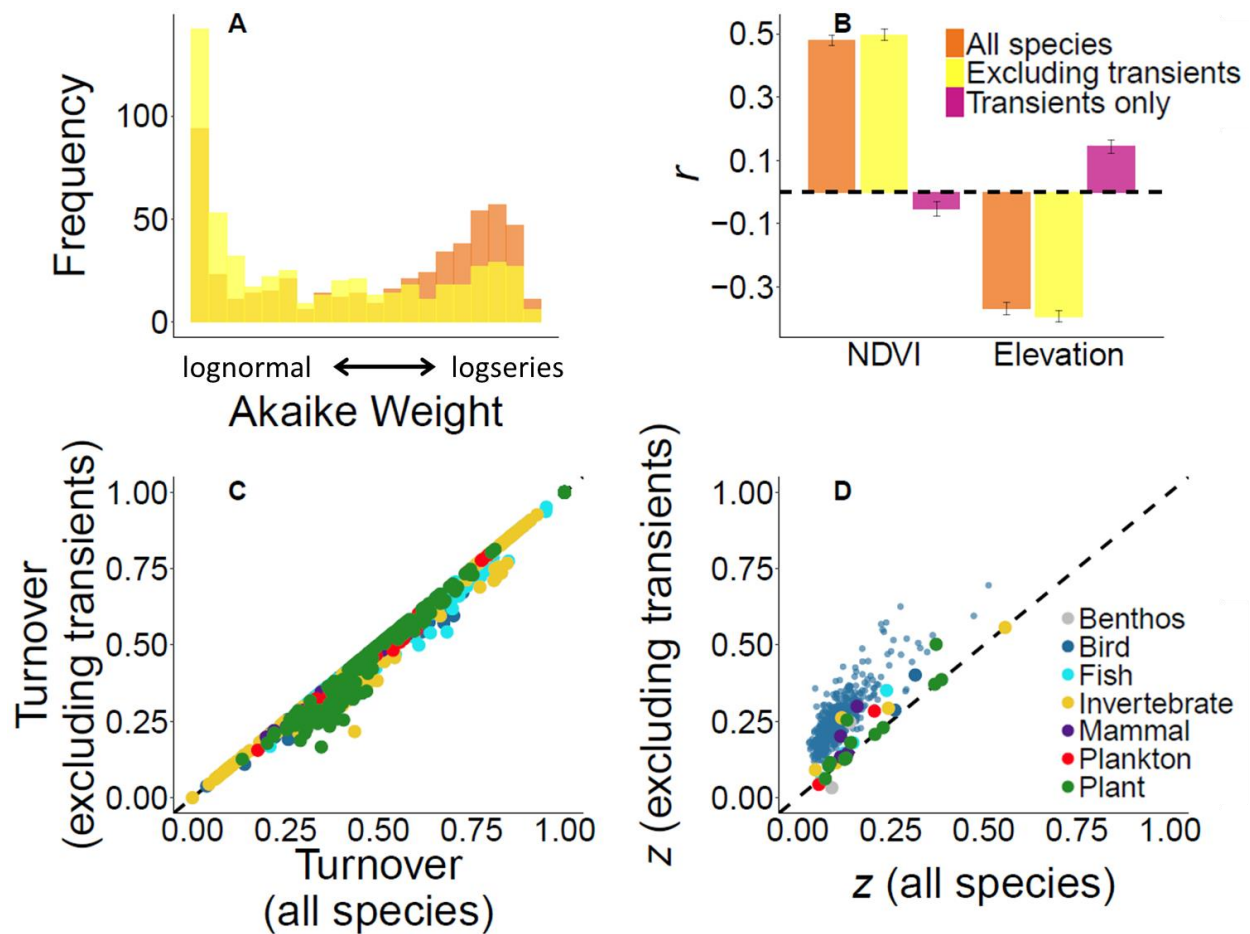


Figure A5. Impact of excluding transient species on four ecological patterns as displayed in Figure 5 in the main text, but where transient species are defined as those with temporal occupancy  $\leq 10\%$ .

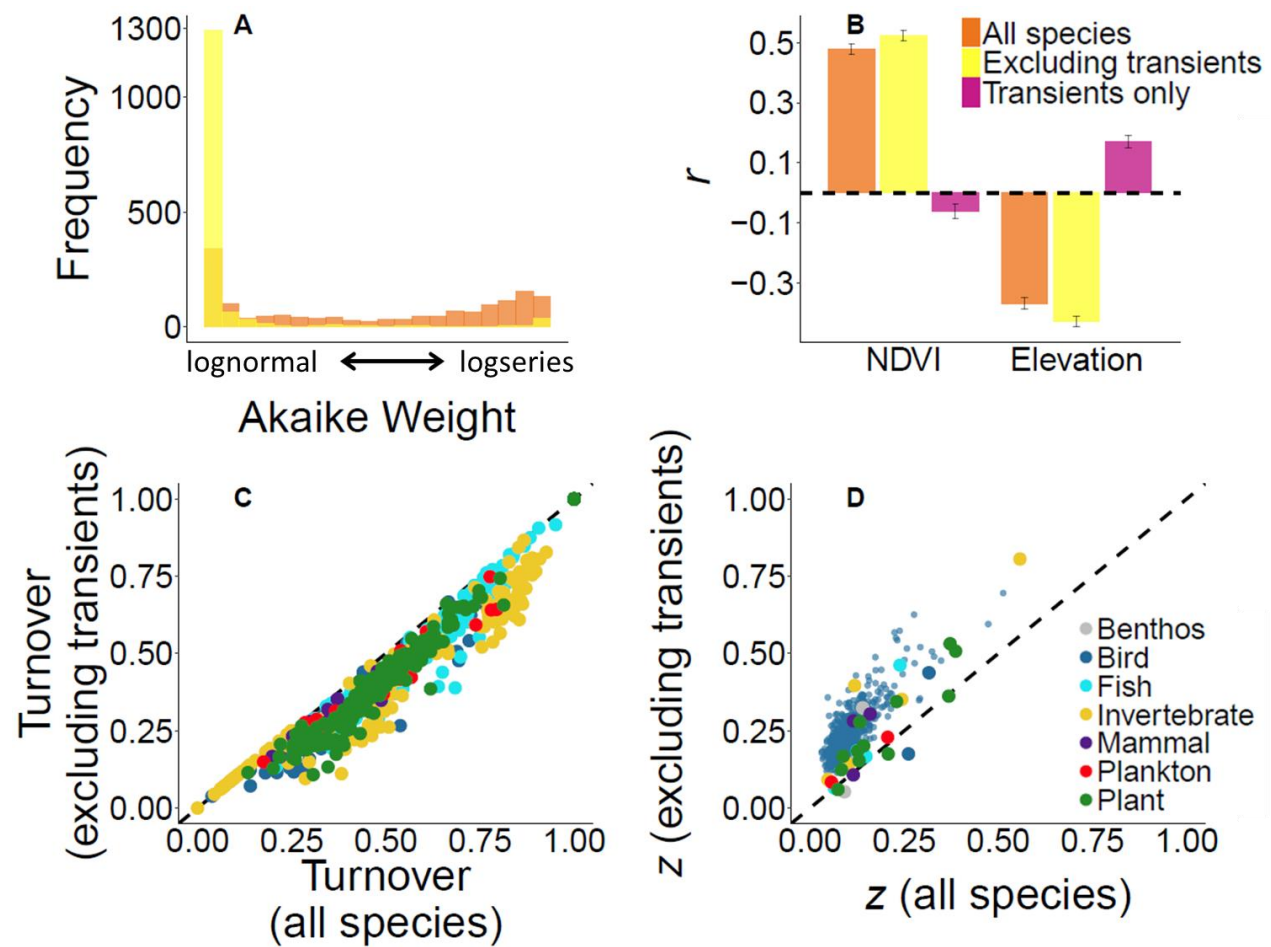


Figure A6. Impact of excluding transient species on four ecological patterns as displayed in Figure 5 in the main text, but where transient species are defined as those with temporal occupancy  $\leq 25\%$ .