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Community size can affect the signals of ecological drift and niche selection on biodiversity

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Abstract. Ecological drift can override the effects of deterministic niche selection on small populations and drive the assembly of some ecological communities. We tested this hypothesis with a unique dataset sampled identically in 200 streams in two regions (tropical Brazil and boreal Finland) that differ in macroinvertebrate community size by five-fold. Null models allowed us to estimate the magnitude to which beta diversity deviates from the expectation under a random assembly process while taking differences in richness and relative abundance into account, i.e., beta deviation. We found that while incidence-based β-diversity was negatively related to community size only in Brazil, abundance-based β-diversity was negatively related to community size in both Brazil and Finland. β-diversity of small tropical communities was closer to stochastic expectations compared with β-diversity of large communities. We suggest that ecological drift may drive variation in some small communities by changing the expected outcome of niche selection, increasing the chances of species with low abundance and narrow distribution to occur in some communities. Habitat destruction, overexploitation, pollution, and reductions in connectivity have been reducing the size of biological communities. These environmental pressures might make smaller communities more vulnerable to novel conditions and render community dynamics more unpredictable. Incorporation of community size into ecological models should provide conceptual and applied insights into a better understanding of the processes driving biodiversity.

Key words: aquatic insects; beta diversity deviation; community assembly; demographic stochasticity; dispersal; metacommunities; null models

Introduction

Recent syntheses in community ecology propose that four main processes drive the dynamics of metacommunities – deterministic niche selection, ecological drift, dispersal and speciation (Vellend 2010, 2016, Leibold and Chase 2018). At broad spatial scales, dispersal, colonization

history, and spatial heterogeneity are thought to produce major biodiversity patterns (Leibold and Chase 2018), while speciation plays a role by altering the composition of regional species pools at longer time frames (Vellend 2010). Within localities, niche selection determines community structure mainly through species interactions, differential use of resources and species responses to environmental gradients (Leibold and Chase 2018). However, stochasticity may also play a role in driving local community dynamics, for example, when demographic events occur at random with respect to species identities (Vellend et al. 2014). Indeed, mechanistic models (Orrock and Fletcher 2005, Orrock and Watling 2010), observational studies (Bosc et al. 2019) and controlled experiments (Gilbert and Levine 2017) suggest that ecological drift can even override the effects of niche selection under certain circumstances, such as when species' populations in local communities are small and isolated from other populations. However, the extent to which these findings apply to natural situations is still uncertain, as tests based on field data in regions where community size differs naturally are scarce (Liu et al. 2018).

Small communities have few individuals per unit area, and thus random birth and death events are likely to have a high impact on their structure. For example, the species composition of a local community would change if all individuals of a species die before reproducing. This is likely to happen in nature especially in small populations or in those large populations in which only a reduced fraction of adults successfully reproduces, such as populations of insects in tropical streams (Bunn and Hughes 1997). Some models indicate that ecological drift can even reduce competition asymmetries in small communities to a level that strong and weak competitors become effectively neutral (Orrock and Watling 2010) – i.e., the negative effect of a superior competitor on other species is relatively small compared to the effects of demographic stochasticity. Indeed, in an experiment with annual plants, Gilbert and Levine (2017) found that larger communities converged to a state in which a strong competitor dominated after three years, whereas in smaller communities the strong competitor co-occurred with other species at different densities. Thus, both theory and experimental evidence suggest that ecological drift can change the structure of local communities by altering species relative abundances as well as species occurrences. Investigating the relationship between variation in community structure and community size would help us better understanding the relative effects of deterministic and stochastic processes on biodiversity. If this relationship occurs in different

environmental contexts, it should also be relevant from an applied perspective, as many types of environmental disturbances, such as deforestation and floods, tend to reduce the size of local communities (Barnes et al. 2014).

Most methods commonly used to estimate variation in the identities of species among sites (β-diversity) are affected by differences in species richness or species abundance distributions (Chase and Myers 2011). This is undesirable for understanding the β-diversity–community size relationship, as estimates of β-diversity can be influenced by random sampling effects that are neutral with respect to species identity (Chase and Myers 2011, Myers et al. 2013, 2015). For example, let us assume that 10 local communities, embedded in a larger metacommunity, contain each a random subset (say five species) of a regional species pool with, for instance, 100 species. This would likely result in high β-diversity as, by chance, many pairs of local communities would not even share species. Second, studies only using incidence-based estimates of β-diversity (e.g., Jaccard or Sørensen dissimilarity indices) do not capture variation in species relative abundances (Anderson et al. 2011). In this case, if the same species occur at two sites but with different relative abundance, β-diversity should not be equal. A solution to the first issue is to use a null model to produce expected values under random assembly from a large species pool, contrast observed and expected values, and use the difference between them as estimates of β-deviation, i.e., the extent to which β-diversity differs from null expectations (Kraft et al. 2011, Myers et al. 2013, 2015, Catano et al. 2017). According to this approach, positive and negative values of β-deviation indicate that communities are more dissimilar and less dissimilar than expected by random sampling, respectively. β-deviation values close to zero indicate that communities are as dissimilar as expected by chance (Kraft et al. 2011, Chase et al. 2011, Catano et al. 2017). Thus, β-deviation provides a means to determine whether β-diversity deviates from the expectations of stochastic assembly and if the magnitude of the deviation is related to community size. A solution to the second issue is to also analyze the data with dissimilarity coefficients that take into account species composition and species relative abundances (e.g., Bray-Curtis; Anderson et al. 2011). Such dissimilarity coefficients provide complementary information regarding the main mechanisms responsible for β-diversity patterns (e.g., Siqueira et al. 2015). Subtle changes in community structure due to processes that affect species' relative abundances would be only captured by abundance-based coefficients. On the other hand, profound alterations in community

composition, such as the loss of rare species are expected to be detected even with presence/absence data and incidence-based coefficients.

In this study, we tested the hypothesis that ecological drift can cause variation in species composition among small communities. Although the theory about how drift affects β-diversity is not completely developed, by using conceptual (Vellend 2016) and simulation (Orrock and Watling 2010) models about the role of drift as an assembly process, one can make specific predictions about β-diversity patterns and underlying mechanisms. For example, assuming that communities are subject to drift when demographic stochastic events (such as births and deaths) overcome the role of fitness differences (Orrock and Watling 2010), one could expect that the species composition in a local community would be different from what would be expected by deterministic niche selection alone. Furthermore, if local communities within a metacommunity also are subject to drift, and assuming that drift in each one of them would produce a different local species composition, then one should expect high beta diversity within a metacommunity.

To reach our goal, we used a unique, comprehensive dataset on aquatic insect communities sampled using identical methods in a total of 200 streams in two regions with highly different climates (100 in tropical Brazil and 100 in boreal Finland). The sampling design included five streams (communities) per watershed (20 in each region) and provided us replicates of metacommunities (watersheds; Appendix S1: Fig. S1). This allowed us to make specific predictions along a community size gradient. Our previous study showed that local community size is, on average, five-fold larger in boreal than in tropical streams, with the watersheds with the smallest boreal communities being as large as the largest tropical ones (Heino et al. 2018). Thus, we predicted that β-diversity would be high (E1) and close (E2) to what would be expected due to random assembly from the regional pool in watersheds with the smallest communities (some watersheds in Brazil only; Fig. 1). This would be consistent with the hypothesis that ecological drift plays a role in structuring these small tropical communities. However, ecological drift can leave different signals on communities. If drift was strong enough to cause variation in species identities among communities, both incidence- and abundance-based β-deviation of small communities would be close to zero. On the other hand, if drift only caused variation in species relative abundances among communities, then only abundance-based β-deviation of small communities would be close to zero. In this case, incidence-based β-deviation

would not be related to community size. Second, all else being equal, we expected that (E2a) β-deviation would be positive in all watersheds, but higher in the largest communities (Fig. 1). This would suggest that niche selection and sufficient dispersal rates are the main processes driving β-diversity of large communities. These communities would then be more dissimilar than expected by chance, as species sorting occurs when dispersal is sufficient to allow individuals to reach sites that match their ecological requirements (Winegardner et al. 2012, Leibold and Chase 2018). Taken together, these expectations would lead to a negative relationship between β-diversity (before controlling for sampling effects) and community size, but to a positive relationship between β-deviation and community size (Fig. 1). Finally, because environmental heterogeneity and spatial extent are also expected to increase β-diversity (Heino et al. 2015a), we included them as co-variates in our models (Appendix S1: Fig. S1).

Material and methods

Study area and sampling

The streams sampled in Brazil and Finland were distributed across a strong gradient of land cover among watersheds. In Brazil, we sampled 100 streams distributed in 20 watersheds located in the southeastern part of the country – i.e., five streams per watershed, with spatial extent of 70 km in north-south and 120 km in east-west directions (Appendix S1: Fig. S2). These streams run through three major Atlantic Forest protected areas ('Carlos Botelho', 'Intervales' and 'Alto Ribeira' State Parks; São Paulo State). The watersheds are mainly dominated by pastures and planted forests (*Eucalyptus* and *Pinus*). The region has a dry season from April to August and a wet season from September to March. Sampling was done between September and November in 2015.

The study sites in Finland were situated in the western part of the country. We sampled 100 streams that were distributed in 20 watersheds (as described above) with spatial extents of ca. 500 km and 300 km in north-south and in east-west directions (Appendix S1: Fig. S2). The streams drain watersheds covered with agriculture and boreal forests. Western Finland has four typical seasons: a long winter that lasts from November to March, a short spring from April to May, a short summer from June to August, and an autumn period from September to October. Sampling was done in September 2014.

Streams were generally of the same order within each watershed, but varied among watersheds, including 2nd and 3rd order streams in Brazil, and a few 4th order streams in Finland. In Brazil, maximum distances between pairs of streams within watersheds varied from 2.48 to 8.86 km, whereas in Finland it varied from 12.77 to 109.5 km. Most local (in-stream) abiotic variables varied within a similar range and had similar mean values between regions (Heino et al. 2018).

At each site in both regions, we took a 2-minute kick-net sample (net mesh size: 0.5 mm), which was composed of four 30-seconds sample units obtained in the main microhabitats at a riffle site (e.g., which considered differences in current velocity, depth, benthic particle size and macrophyte cover). The four sample units were pooled, preserved in alcohol in the field and taken to the laboratory for further processing and identification. All insects were separated from debris and the following taxonomic orders were identified to genus level: Ephemeroptera, Odonata, Plecoptera, Megaloptera, Trichoptera and Coleoptera. We found 16,113 individuals, distributed among 83 genera in Brazil, and 86,048 individuals distributed among 77 genera in Finland. The mean number of genera per stream was 17.84 (standard deviation = 7.46) in Brazil and 14.01 (sd = 5.07) in Finland, while the mean number of individuals per stream was 181.50 (sd = 111.38) and 886.57 (sd = 700.73), respectively (Heino et al. 2018).

We adopted the definition of community size proposed by Orrock and Watling (2010) and estimated local community size as the number of individuals sampled in a stream site. However, as β-diversity was estimated for each watershed (i.e., considering five stream sites; see below), we averaged the number of individuals across five streams within each watershed. This resulted in 20 values of community size, one per watershed (Appendix S1: Fig. S1). We excluded streams with less that 10 individuals from analyses. Thus, three watersheds from Brazil had four streams and one watershed had three streams, while one watershed from Finland had four streams.

Beta diversity and beta deviations

We first estimated β-diversity by using the Sørensen incidence-based coefficient and the Bray-Curtis abundance-based coefficient. To do that, we calculated dissimilarity values between all pairs of five streams within each of the 20 watersheds, separately for the tropical and boreal datasets. Our measure of β-diversity was represented by the mean of these values in each watershed. Thus, we

estimated 20 values of Sørensen β-diversity and 20 values of Bray-Curtis β-diversity per region (Appendix S1: Fig. S1).

We estimated β-deviations, within each region, by using a null model developed by Kraft et al. (2011). Our null models were generated for each region separately because absolute values estimated from different metacommunities might reflect different assembly processes (Tucker et al. 2016). Thus, (i) we defined the genus pool as all genera found at all sampled streams in each region; (ii) an algorithm then randomly assigned individuals to stream sites while preserving the overall genus-abundance distribution in the region and the total number of individuals in each stream site (local community size); (iii) using the resulting genera matrix, we calculated a pairwise beta diversity matrix; (iv) steps (ii) and (iii) were repeated 10,000 and an average dissimilarity value was calculated for each pair of streams; (v) for each pair of streams within a watershed, we calculated the difference between the observed dissimilarity value and the averaged dissimilarity value generated by the simulations, and divided this value by the standard deviation of the simulated values. These standardized effect sizes were then averaged within each watershed; i.e., considering only the pairs of streams that were inside a given watershed. Positive values and negative values indicate greater and lower dissimilarity than expected from random assembly, respectively. This null model allows one to analyze how β-diversity differs from patterns generated by processes that cause clumping of species across the landscape (Kraft et al. 2011, Myers et al. 2015). These procedures also resulted in 20 values of abundance-based β-deviation per region, one value per watershed (Appendix S1: Fig. S1).

Our basic multiple regression model, relating β-diversity (and β-deviation) to community size, environmental heterogeneity and spatial extent, was tested separately using the two independent datasets (Appendix S1: Fig. S1). Similar results for both regions would suggest that the effect of community size is not contingent on regional or historical processes (e.g., dispersal, diversification rates). Environmental heterogeneity within watersheds was estimated using environmental data and a Permutational analysis of multivariate dispersions (PERMDISP), as described by Anderson et al. (2006). This analysis was based on a Euclidean distance calculated with the standardized values (zero mean and unit variance) of the following variables: current velocity (m/s), depth (cm), stream width (cm), % of sand (0.25-2 mm), gravel (2-16 mm), pebble (16-64 mm), cobble (64-256 mm), and boulder (256-1024 mm), % of canopy cover by riparian vegetation, pH, conductivity, total nitrogen,

and total phosphorus. In PERMDISP, we also included the following watershed-scale variables estimated through satellite images within a 400-m buffer along tracts of the sampled streams: average slope, % of native forest cover, pasture, agriculture, planted forests, urban areas, mining, water bodies, bare soil, secondary forest cover, and mixed land uses. We mapped land use and land cover of Brazilian and Finnish watersheds using 5-m resolution RapidEye multispectral imagery and the CORINE database (https://land.copernicus.eu/pan-european/corine-land-cover), respectively. Geographic coordinates of the sampling sites were transformed to a Euclidean distance matrix and then submitted to the PERMDISP procedure (Anderson et al. 2006), using watershed as a grouping variable, to estimate mean spatial extent. In the tropical data, the strongest correlation between explanatory variables was between environmental heterogeneity and spatial extent ($r = 0.47$), whereas in the boreal data, it was between community size and spatial extent ($r = 0.36$). All other correlations were lower than 0.07. Thus, multicollinearity was not an issue in our study. We used the vegan package (Oksanen et al. 2018) in R (version 3.5.0; R Core Team 2018) to estimate β-diversity, environmental heterogeneity, and spatial extent.

Results

There was a strong negative relationship between β-diversity (both with incidence- and abundance-based data) and community size in Brazil ($b = -0.87$, $t(18) = -7.47$, $p < 0.001$, $R^2 = 0.74$; and $b = -0.78$, $t = -5.32$, $p < 0.001$, $R^2 = 0.59$, respectively; Fig. 2), indicating that small communities were more dissimilar among each other than larger communities, as we expected (E1). However, we found that neither incidence-based (Sørensen) nor abundance-based (Bray-Curtis) β-diversity were related to community size in Finland ($b = -0.14$, $t(18) = -0.59$, $p = 0.563$; and $b = -0.22$, $t = -0.94$, $p = 0.357$, respectively).

We found strong relationships between β-deviation (i.e., β-diversity apart from null expectations) and community size in both regions, but they varied according to the type of dissimilarity coefficient (incidence- and abundance-based; Table 1, Fig. 3). As we expected (E2), β-diversity of tropical smaller communities was closer to null expectations than those of larger communities – i.e., β-deviation was close to zero and the relationship was positive (Fig. 3). However, differently from what we expected, mean Sørensen β-deviations were positively related to community

size only in Brazil (Fig. 3A), ranging from 0.91 to 7.35. Neither environmental heterogeneity nor spatial extent were related to Sørensen β-deviation in Brazil and in Finland (Table 1).

Bray-Curtis (abundance-based) β-deviation was positively related to community size in both regions (Table 1; Fig. 3B), supporting our expectations (E2a). In tropical and boreal watersheds, mean Bray-Curtis β-deviations ranged, respectively, from 3.08 to 16.66 and from 17.40 to 102.51, indicating that communities were more dissimilar than expected by random changes in species abundances and genus composition. Again, β-deviations of smaller communities were closer to zero than those of larger tropical communities, supporting our expectation E2. Neither environmental heterogeneity nor spatial extent were related to Bray-Curtis β-deviation in either region.

Discussion

The role of stochastic community assembly processes in arranging species within and among communities has gained support from theoretical models (Mouquet and Loreau 2003, Orrock and Fletcher 2005, Durães et al. 2016) and empirical data (Cottenie 2005, Lancaster and Downes 2017, Germain et al. 2017, Swan and Brown 2017, Valente-Neto et al. 2017, Bosc et al. 2019). Here, we provide empirical observational evidence that community size, a simple characteristic of communities, can mediate the interplay between niche selection and ecological drift as drivers of β-diversity in tropical and boreal stream metacommunities. Our estimates of variation in community structure accounted for both differences in local species richness and species relative abundance that deviate from random assembly (i.e., β-deviations). We showed that β-diversity of smaller tropical communities deviated less from null expectations than of larger communities. This means that the high β-diversity we observed among smaller communities was less distinguishable from patterns expected given changes in richness that are random with respect to identity (Sørensen β-deviations) and from patterns expected under a random spatial distribution of individuals (Bray-Curtis β-deviations). As findings based on the null models we used are our best approximation of β-diversity generated by random stochastic processes (Kraft et al. 2011, Chase et al. 2011), we suggest that demographic stochasticity may play role in structuring some small ecological communities (Orrock and Fletcher 2005, Orrock and Watling 2010, Gilbert and Levine 2017).

Explanations for the role of demographic stochasticity in small communities involve the alteration of the occupancy frequency and relative abundance of species with different fitness (Orrock and Watling 2010). In small local communities, even species with high fitness are at a high risk of extinction due to demographic stochasticity in comparison to a situation when communities have large populations. Consequently, species with low relative abundances have a higher chance to increase their populations in small communities due to a reduced role of density dependent selection (Orrock and Watling 2010, Gilbert and Levine 2017). As this would be the result of a local demographic random process, and because (i) small communities are usually associated with reduced α-diversity (Vellend 2016) and (ii) dispersal ability is highly variable among species in riverine systems (Heino et al. 2015b, Tonkin et al. 2018a), the outcome of the assembly process would very likely differ among local communities, thus, increasing β-diversity within metacommunities. Indeed, in Brazil, the three regionally most abundant and widespread genera (Heino et al. 2018) were not dominant in smaller communities: the mayfly *Farrodes* was not among the most abundant in any of the smallest communities; the beetle *Heterelmis* was among the most abundant in two communities only; and the caddisfly *Smicridea* was among the most abundant in three of the five smallest communities. These three genera, on the other hand, were dominant in four of the five largest communities in Brazil. The smallest communities in Brazil were dominated by genera with intermediate regional abundance and occupancy. For example, *Gripopteryx* (stonefly), *Cloeodes* (mayfly) and *Callibaetis* (mayfly) were the 6th, 11th and 16th most abundant genera in Brazil, respectively. In Finland, these differences were less evident, as the three regionally most abundant and widespread genera dominated small and large communities: the beetle *Elmis* (two of the smallest vs. three of the largest communities); the mayfly *Baetis* (three vs. three); and stonefly *Nemoura* (one vs. one). This difference is likely because the smallest boreal stream communities were as large as the largest tropical communities (Heino et al. 2018).

The positive relationship between abundance-based β-deviation and community size in both regions, and between incidence-based β-deviation and community size in Brazil is generally in line with our expectations. Positive values of β-deviation and slopes indicate that variation in community structure among streams was higher than what would be expected by random assembly and that this was more so with increasing community size. As dispersal within watersheds was likely not limited,

this positive relationship indicates that niche selection was sufficient to cause non-random variations in genera relative abundance and aggregation patterns among large communities in both regions. Thus, we suggest that as community size increases in streams, demographic stochasticity plays a minor role and niche selection and dispersal rates mostly determine which species are more abundant locally and widely distributed within the metacommunity. However, incidence-based β-deviation was related to community size in Brazil only, suggesting that the large size of boreal communities was sufficient to make variation in genus identity among communities to be higher than expected by chance, independently of community size.

Even though β-deviation was higher than zero in both regions, β-diversity was negatively related with community size only in Brazil, indicating that variation in community composition was lower in large communities compared to small ones. Low β-diversity can be the result of high dispersal rates within the metacommunity (Mouquet and Loreau 2003, Leibold and Chase 2018). By distributing organisms among communities, dispersal can reduce β-diversity if it is excessive and is combined with a source-sink system, where populations with high growth rates supply individuals to other localities where they would otherwise be excluded by niche selection (Mouquet and Loreau 2003, Siqueira et al. 2014). This type of source-sink dynamic was hypothesized to maintain coexistence of species even in sites with low local environmental suitability if species have their niche requirements contemplated at the regional scale (Mouquet and Loreau 2002), which could be the case in the metacommunities we studied. Although dispersal across watersheds tends to be limited for many aquatic species, those with a flying adult stage may have higher dispersal rates especially along the stream channel (Hughes 2007, Lancaster and Downes 2017). A meta-analysis by Muehlbauer et al. (2014) showed that most adult aquatic insects tend to fly ca. 1.5 m around their natal stream, but that a few individuals can fly 550 m away from the stream, with some caddisflies being able to reach sites distant more than 650 m. Many tropical aquatic insects are multivoltine (Wallace and Anderson 1996, Vásquez et al. 2009). Unless local population growth rate is low, multivoltine species should have many opportunities per year to disperse from their natal streams. If a few of these multivoltine species can fly 250 m (a conservative estimate considering the results by Muehlbauer et al. 2014), after some generations, some individuals of these species could reach distant sites, at a velocity of one kilometer per year. We thus suggest that long-term availability for colonization of tropical streams

and multivoltinism allowed some stream insects to reach widespread distribution within tropical watersheds (Saito et al. 2015, 2016). In this scenario, with sufficient dispersal, niche selection should have favored species with the highest fitness to dominate large communities in Brazil. However, this idea should be scale dependent (Chase et al. 2018). If our watersheds were larger in spatial extent, dispersal limitation would likely have been the major driver of community structure (Heino et al. 2015b).

As our study was based on empirical observational data, there are potential caveats that deserve consideration. First, the relationship between β-diversity and community size may be due to an unseen indirect path, where other variables play an unknown role. This is unlikely in our study because even though the streams sampled in Brazil and Finland were distributed along a strong gradient of land cover among watersheds – and it is well established that watershed land cover influences the structure of stream communities (Hynes 1975, Allan 2004, Roque et al. 2010, Siqueira et al. 2015), we found that neither environmental heterogeneity nor spatial extent were major drivers of β-deviation. Also, community size was weakly correlated with all environmental variables we measured (the highest Pearson was $r = 0.41$; Appendix S1: Table S1). Second, previous research has suggested that the β-deviation approach may suffer from undesirable biases that prevents finding correct association between patterns and processes. Bennett and Gilbert (2016) showed that comparisons across regions using β-deviations can be biased by both differences in sampling effort and in gamma diversity. As sampling effort was identical in Brazil and Finland, and regional genus richness was only slightly higher in Brazil (83) than in Finland (77), our estimates of β-deviation are unlikely to be affected by these problems. However, Tucker et al. (2016) suggested that only abundance-based β-deviations could distinguish between assembly mechanisms in simulated metacommunities. We thus suggest some caution when interpreting incidence-based β-deviations, as the functioning of such null models is still under debate (Bennett and Gilbert 2016, Tucker et al. 2016). Finally, one could suggest that even if tropical streams have fewer organisms, the true population sizes may be large enough to avoid demographic stochasticity. However, as it is common for stream insects, only a few immatures become adults that reproduce successfully. For instance, high local densities of some species may be due to a few successful females from the previous generation (Bunn and Hughes 1997). Thus, demographic stochasticity may indeed play a role as in

some locations and some years adults of some species may fail to reproduce. We tried to minimize these problems, that usually affect observational empirical studies, by combining standardized field sampling in the two regions with complementary use of β-diversity metrics and a cautionary interpretation of results.

Predicting community assembly dynamics has been a major challenge for ecology in a changing world (Mouquet et al. 2015). Many drivers of environmental change, such as habitat destruction, overexploitation, pollution, and reductions in landscape connectivity, are likely to cause reductions in community size. For example, Hallmann et al. (2017) estimated a decline of more than 70% in insect biomass between 1989 and 2016 in Germany, and Lister and Garcia (2018) found that arthropod biomass has fallen 10 to 60 times since 1970 in Puerto Rico. It is possible, then, that results from previous studies associating high β-diversity with environmental changes were related to small communities being more variable. For example, Hawkins et al. (2015) showed that disturbed sites had high β-diversity due to a decreased prevalence of more common taxa. Although they did not analyze community size per se, the mechanism they evoked to explain this pattern – i.e., the relative abundance of species with lower fitness become progressively higher – is what has been suggested to be the reason for a major role of ecological drift in small communities (Orrock and Watling 2010, Gilbert and Levine 2017). Additionally, the effects of environmental changes on naturally small communities might be combined with the effects of ecological drift in non-obvious ways, making community dynamics even harder to predict (e.g., Bini et al. 2014) and smaller communities more vulnerable to novel environmental conditions, such as altered flow regimes (Tonkin et al. 2018b, Ruhi et al. 2018). This should also be relevant for the conservation and management of ecosystems. For example, stream restoration efforts tend to be directed towards sites with low habitat quality and with reduced number of species and low-density populations. Even if restoration efforts overcome dispersal constraints and barriers to recolonization, which are a major cause for unsuccessful stream restoration (Bond and Lake 2003, Sundermann et al. 2011, Tonkin et al. 2014), restored communities will likely be small at the earlier stages of community assembly and, thus, more prone to ecological drift.

Our study provides empirical field-based evidence of the role that community size can play in mediating stochastic and deterministic process as drivers of metacommunity dynamics in tropical and

boreal streams, suggesting one possible solution to a long-standing debate about why some communities are apparently more influenced by stochastic processes than others. Our findings complement previous empirical and conceptual efforts indicating that, in certain conditions such as when community size is small, ecological drift can also drive variation in biodiversity even in communities where species have clear differences in life-history traits, resource use and competitive abilities. Incorporation of community size into ecological models should provide conceptual, empirical and applied insights towards better understanding of the processes driving changes in biodiversity.

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Data availability

Code and data that fully reproduce the analyses are archived on Zenodo: https://doi.org/10.5281/zenodo.2620550

Table 1. Relationship between beta deviation (incidence-based [Sørensen] and abundance-based [Bray-Curtis]) and community size, environmental heterogeneity and spatial extent (n = 20 watersheds in each region). CS = Community size; EH = Environmental heterogeneity; SE = Spatial extent. R^2 and adj. R^2 = coefficient of determination and adjusted coefficient of determination of the full model, respectively. b = standardized regression coefficient. t(df) = t statistic and degrees of freedom.

|			b	se	t(16)	P	R^2	adj. R^2
Brazil	Sørensen	CS	0.428	0.190	2.251	0.038	0.430	0.323
		EH	0.291	0.215	1.353	0.195		
		SE	0.310	0.216	1.434	0.171		
	Bray-Curtis	CS	0.777	0.147	5.279	<0.001	0.658	0.594
		EH	0.211	0.167	1.267	0.223		
		SE	-0.087	0.167	-0.522	0.609		
Finland	Sørensen	CS	0.179	0.257	0.70	0.494	0.083	0.0
		EH	0.211	0.240	0.879	0.393		
		SE	0.061	0.258	0.238	0.815		
	Bray-Curtis	CS	0.728	0.168	4.328	<0.001	0.607	0.534
		EH	-0.115	0.157	-0.731	0.475		
		SE	0.087	0.168	0.518	0.611		

Figure captions

Figure 1. A graphical representation describing a priori expectations (E) about the relationship between beta diversity or beta deviation and community size in tropical (Brazil, vermilion) and boreal (Finland, blue) streams.
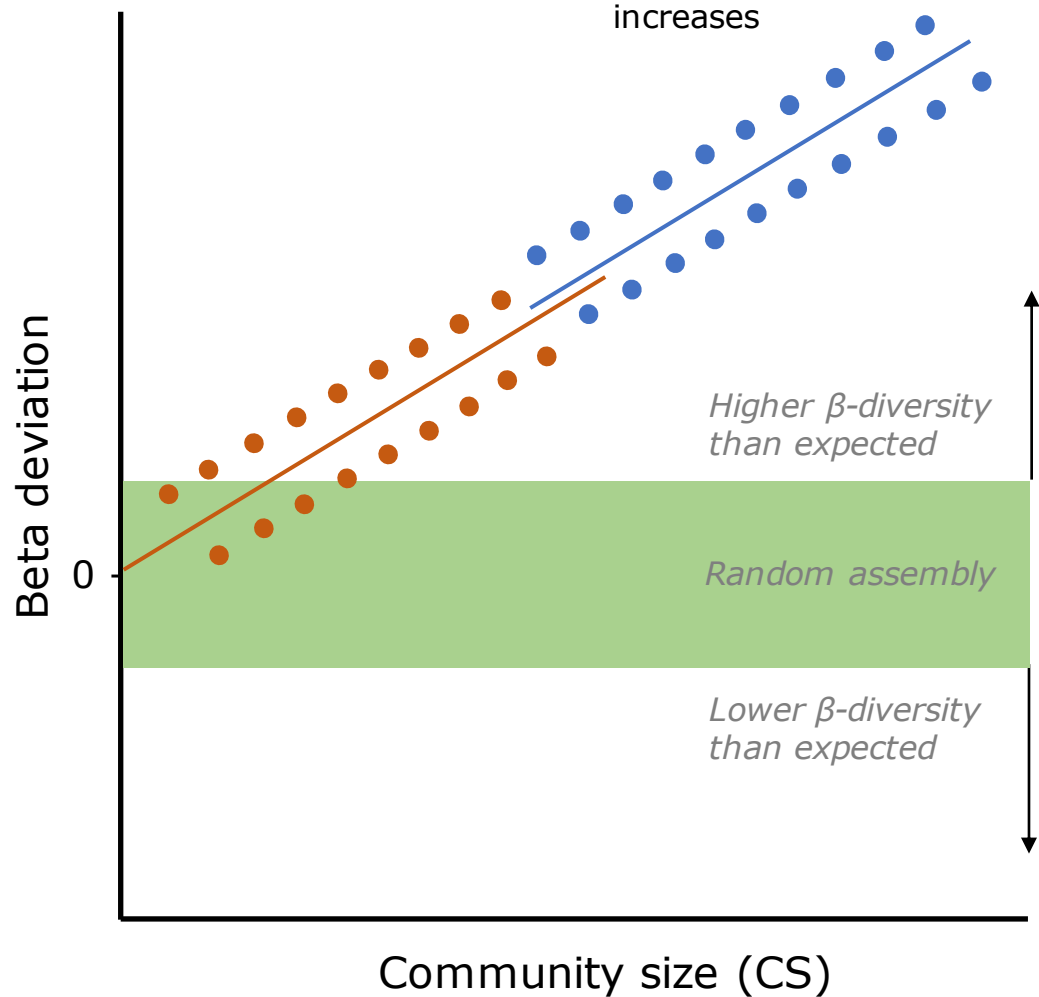
Figure 2. (A) Incidence-based (Sørensen) and (B) abundance-based (Bray-Curtis) beta diversity-community size (average number of individuals per watershed) relationships within tropical (vermilion) and boreal (blue) stream watersheds (n = 20 watersheds for each region). The average number of individuals per watershed was calculated with a sample size of five streams.

Figure 3. (A) Incidence-based (Sørensen) and (B) abundance-based (Bray-Curtis) beta deviation-community size (average number of individuals per watershed) relationships within tropical (vermilion) and boreal (blue) stream watersheds (n = 20 watersheds for each region). The average number of individuals per watershed was calculated with a sample size of five streams. The dashed grey line indicates expected beta diversity under null assembly.

E1: high β-diversity in the smallest communities
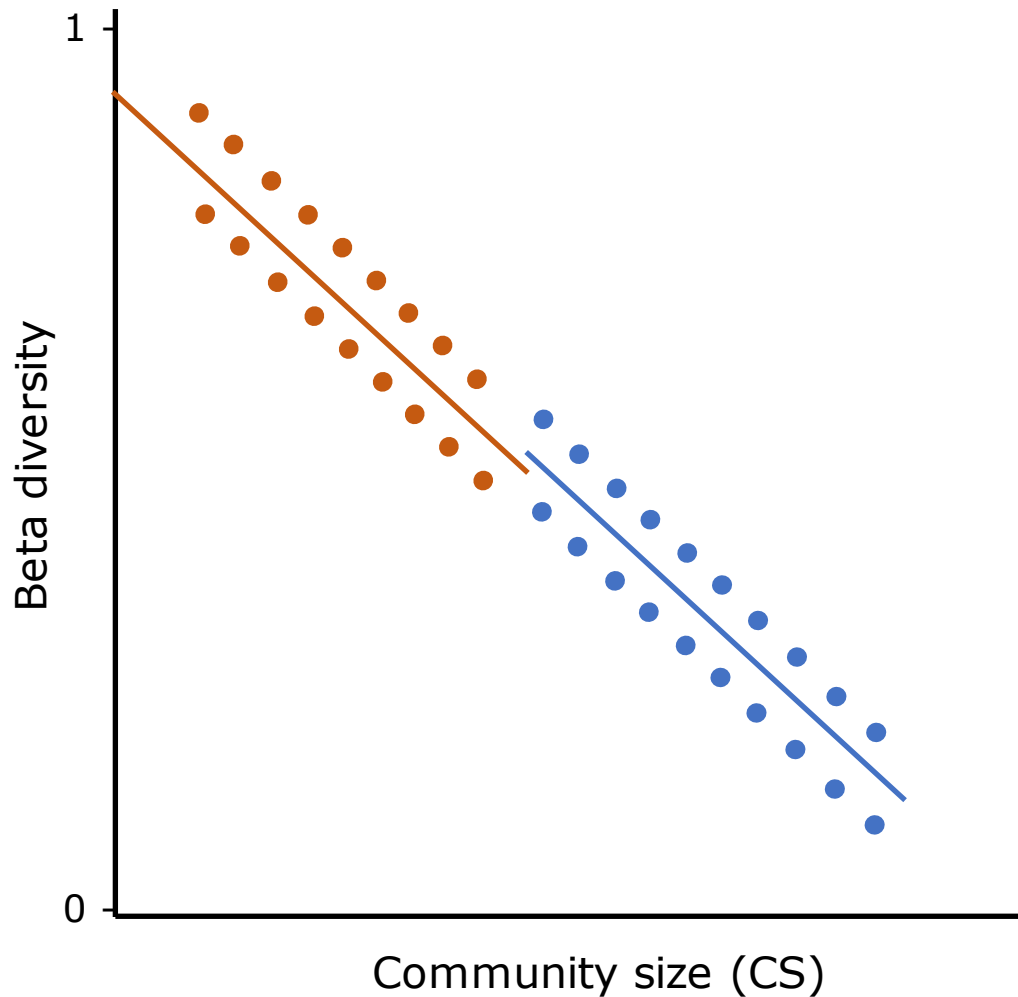
E2: β-diversity is close to null expectations in small communities

E2a: β-deviation is positive in all watersheds and more so when CS increases

Beta diversity

Community size (CS)

Beta deviation

Higher β-diversity than expected

Random assembly

Lower β-diversity than expected

Community size (CS)