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Community size affects the signals of selection and ecological drift on biodiversity

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Abstract. Ecological drift can override or interact with the effects of deterministic niche selection on small populations to drive the assembly of small communities. We tested the hypothesis that small communities are more dissimilar among each other because of ecological drift than large communities, which are mainly structured by niche selection. We used a unique dataset on insect communities sampled identically in a total of 200 streams in climatically different regions (Brazil and Finland) that differ in community size by fivefold. Null models allowed us to estimate the magnitude to which beta diversity deviates from the null expectation under a random assembly process while taking differences in species richness and relative abundance into account. Beta diversity of small communities was consistently closer to null expectations than beta diversity of large communities. However, although beta diversity and community size were strongly related in both regions, the type of relationship varied according to the type of dissimilarity coefficient. While incidence-based beta diversity was lower than expected and negatively related to community size only in Brazil, abundance-based beta diversity was higher than expected and positively related to community size in both regions. We suggest that ecological drift plays an important role in small communities by increasing the chances of species with low competitive ability to occur within the metacommunity. Also, while weak niche selection and high dispersal rates likely reduced variation in community composition among large tropical streams, niche selection was likely sufficient to cause non-random variations in genera relative abundances among large communities in both regions. Habitat destruction, overexploitation, pollution, and reductions in connectivity have been reducing the size of biological communities; these environmental pressures will make smaller communities more vulnerable to novel conditions and community dynamics more unpredictable, as random demographic processes should prevail under these conditions. Incorporation of community size into ecological models should provide conceptual, empirical and applied insights into a better understanding of the processes driving changes in biodiversity.

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Introduction

Recent conceptual syntheses in community ecology propose that interactions among 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 rates and colonization history interact with spatial heterogeneity to produce major biodiversity patterns (Winegardner et al. 2012, Leibold and Chase 2018), while speciation also 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 and their different utilization of resources (Leibold and Chase 2018). However, stochasticity may also play an important role in driving local community dynamics, for example when demographic events occur at random with respect to species identities (Vellend et al. 2014). Indeed, theory (Orrock and Watling 2010) and recent empirical evidence (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.

Small communities have few individuals per unit area (Orrock and Watling 2010), and thus random birth and death events are likely to have a high impact on their structure (species composition and relative abundances). 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 among small populations or on those large populations in which only a reduced fraction of adults successfully reproduce (Bunn and Hughes 1997). Theoretical models suggest 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

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(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 theoretical models 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 this should help us reaching better understanding of the relative importance of deterministic and stochastic processes on beta diversity, as environmentally similar local communities may differ in species composition due to distinct legacies of demographic stochasticity. This 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, Petsch et al. 2015).

Most methods commonly used to estimate beta diversity are affected by differences in species richness or species abundance distributions (Chase and Myers 2011). This is undesirable for understanding a beta diversity-community size relationship for two main reasons. First, estimates of beta 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 the species composition of 10 local communities embedded in a larger metacommunity represents each a random subset (say 5 species) of the regional species pool with, for instance, 100 species. This would likely result in high beta diversity as, by chance, many pairs of local communities would not share species. Second, many if not most studies employ incidence-based estimates of beta diversity (e.g., Jaccard or Sørensen dissimilarity indices) that do not capture variation in species relative abundances (Anderson et al. 2006, Siqueira et al. 2015). In this case, if the same species occur in two sites but with different relative abundances, beta diversity should not be equal. Thus, to properly analyze the relationship between beta diversity and community size, we need estimates of beta diversity that account for differences both in species richness and species relative abundance. A solution is to use a null model to produce expected values, contrast observed and expected values and use the difference between them as estimates of beta diversity; called beta deviations hereafter

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(Kraft et al. 2011, Myers et al. 2013, 2015, Catano et al. 2017). In this case, positive and negative values of beta deviation indicate that communities are more dissimilar and less dissimilar than expected by chance, respectively. Beta deviation values close to zero indicate communities are as dissimilar as expected by chance (Kraft et al. 2011, Chase et al. 2011, Catano et al. 2017, Petsch et al. 2017).

In this study, we tested the hypothesis that ecological drift is a major process causing variation among small communities. We expected that ecological drift would play a smaller role in large communities where deterministic niche selection should drive spatial variation in community structure. To reach our goals we used a unique dataset on insect communities sampled identically in a total of 200 streams in climatically highly different regions (100 in Brazil and 100 in Finland). The sampling design included 5 streams (communities) per watershed and provided us replicates of metacommunities (watersheds). This allowed us to make specific predictions considering a community size gradient that includes both regions (countries). First, because our previous study showed that local community sizes are, on average, five-fold larger in boreal than in tropical streams (Heino et al. 2018), we expected that beta diversity would be high and beta deviations would be close to zero in watersheds with the smallest communities (some watersheds in Brazil only). This would indicate that ecological drift plays a major role in structuring these small subtropical communities. Second, we expected that watersheds with larger communities in Brazil would have lower values of beta diversity compared to smaller communities, but high positive values of beta deviation. This would indicate that niche selection and sufficient dispersal rates are the main processes resulting in large communities to be more dissimilar than expected by chance. Together, these two predictions would lead to a negative relationship between beta diversity (before controlling for sampling effects) and community size, but a positive relationship between beta deviation and community size. Finally, because the smallest boreal stream communities are as large as the largest tropical communities (Heino et al. 2018), we expected that boreal communities would show a weak or lack of relationship between (positive) values of beta deviation and community

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size. This would indicate that deterministic niche selection is the main processes determining the structure of boreal communities because boreal stream insect communities are usually large enough and not subject to strong demographic stochastic effects.

Material and methods

Study area and sampling

In Brazil, we sampled 100 streams distributed among 20 watersheds located in the southeastern region of the country – i.e., five streams per watershed. These streams drain through three major Atlantic Forest protected areas ('Carlos Botelho', 'Intervales' and 'Alto Ribeira' State Parks) and watersheds dominated by agriculture (mainly pastures, and *Eucalyptus* and *Pinus* plantations). The region has a dry season from April to August (average rainfall from 45 to 80 mm per month; average temperature from 16 to 20 ^{o}C) and a wet season from September to March (average rainfall from 105 mm to 180 mm per month; average temperature from 20 to 23 ^{o}C). 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 among 20 watersheds, as described above. The streams drain within 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. A more detailed description of both regions, including a map with the location of sampling sites, can be found in Heino et al. (2018).

At each of the 100 stream sites 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

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from debris and the following taxonomic orders were identified to genus level: Ephemeroptera, Odonata, Plecoptera, Megaloptera, Trichoptera and Coleoptera.

We adopted a modified definition of community size provided by Orrock and Watling (2010) and estimated local community size as the mean number of individuals sampled in a watershed. Because streams within and among regions differ in width and this could be viewed as measure of habitat size, we multiplied local community size by stream width, averaged it within watersheds, and defined it as an alternative measure of community size. Also, we estimated the median population size per stream, average it within watersheds, and defined it as another measure of community size. Fitted models provided similar results with all measures of community size and, thus, we show here results based on the former measure.

Beta diversity and beta deviations

We first estimated beta diversity by using the Sørensen incidence-based coefficient and the Bray-Curtis abundance-based coefficient. To do that, we calculated pairwise dissimilarity values among all five streams within each of the 20 watersheds, separately for the tropical and boreal datasets. Estimates of beta diversity represented the mean of these values in each watershed.

We estimated beta-deviations by using two procedures based on null models. To estimate incidence-based beta deviations that accounted for random sampling effects, we used a modified version of the Raup-Crick coefficient following Chase et al. (2011) : (i) we defined the species pool as all species occurring in each region; (ii) an algorithm assembled local communities by randomly sampling species from the species pool until reaching the local (observed) species richness and by using the observed species' occupancy frequency to determine the probability to sample a species; (iii) step (ii) was repeated 10000 times to generate a null distribution of species composition and, posteriorly, the number of shared species between each pairwise stream within each watershed assuming random sampling; (iv) beta-deviations were calculated as an index rescaled to range between -1 and 1, "indicating whether local communities are more dissimilar (approaching 1), as

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dissimilar (approaching 0), or less dissimilar (approaching -1), than expected by random chance" (Chase et al. 2011).

To estimate abundance-based beta deviations, we followed the procedure described by Kraft et al. (2011): (i) we defined the species pool as all species occurring in each region; (ii) the algorithm assembled local communities by randomly sampling individuals from the pool until reaching the (local) total abundance and species richness; (iii) step (ii) was repeated 10000 to generate a null distribution of pairwise dissimilarities within each watershed; (iv) beta-deviations were calculated as the difference between the observed Bray-Curtis dissimilarity and the mean expected dissimilarity, divided by the standard deviation of the (null) simulated distribution. Positive and negative values indicate greater and lower dissimilarity than expected from changes in community size or species pools, respectively. This null model allows one to analyze how beta diversity differs from patterns generated without processes that cause clumping of species across the landscape (Kraft et al. 2011, Myers et al. 2015). We repeated the procedures described above but changing the definition of species pool to the watershed scale (not the entire region; step (ii)). Results were similar with both definitions of species pools, and thus we only show results based on the former definition.

We tested whether beta deviation was related with community size by using ordinary-least-squares regression models. Because environmental heterogeneity and spatial extent are usually predicted to be associated with beta diversity (Heino et al. 2015), we also included them as co-variates in our models. Environmental heterogeneity within watersheds was estimated as the average distance of streams to the watershed spatial median in a multivariate Euclidean ordination space using environmental data (Anderson et al. 2006). We used standardized values (zero mean and unit variance) of the following variables to estimate within-watershed environmental heterogeneity: 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. These were all

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measured at the stream riffle scale (for details, see Heino *et al.* 2018). 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. Geographical coordinates of the sampling sites were transformed to a Euclidean distance matrix and then submitted to a PERMDISP procedure (Anderson et al. 2006), using watershed as a grouping variable, to estimate mean spatial extent. We used the *vegan* package (Oksanen *et al.* 2018) in R (version 3.5.0; R Core Team 2018) to estimate beta diversity, Raup-Crick beta deviation, environmental heterogeneity, and spatial extent. Code and data are available as Supplementary Material (Siqueira et al. 2019).

Results

There was a strong negative relationship between beta diversity (both incidence- and abundance-based data) and community size in Brazil (b = -0.87, t = -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. 1), indicating that small communities were more dissimilar among each other than larger communities, as we predicted. Neither incidence-based (Sørensen) nor abundance-based (Bray-Curtis) beta diversity were related to community size in Finland (b = -0.14, t = -0.59, p = 0.563; and b = -0.22, t = -0.94, p = 0.357, respectively).

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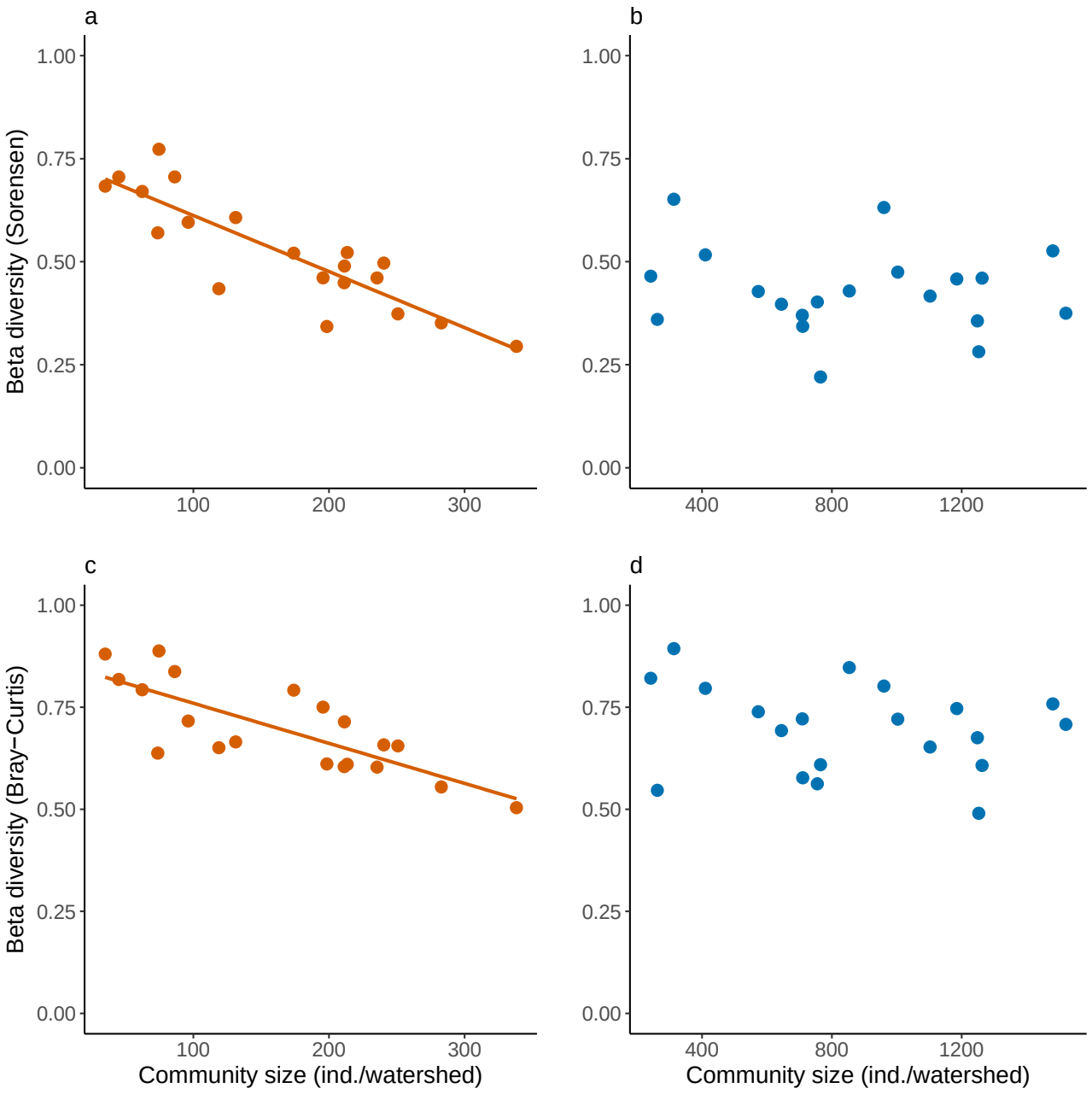

Figure 1. (a, b) Incidence-based (Sørensen) and (c, d) abundance-based (Bray-Curtis) beta diversity-community size (average abundance in 5 streams) relationships within tropical (vermilion) and boreal (blue) stream watersheds.

We found strong relationships between beta deviation (i.e., beta 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) and type of relationship (negative and

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positive; Table 1, Fig. 2). Raup-Crick (incidence-based) beta deviation was negatively related to community size in Brazil (Table 1). Beta diversity of tropical smaller communities were closer to null expectations than those of larger communities (Fig. 2). Mean Raup-Crick beta deviation varied from -0.98 to -0.02 in Brazil, indicating that tropical communities were less dissimilar in the composition of genera than expected by random sampling from the species pool. Neither environmental heterogeneity nor spatial extent were significant predictors of Raup-Crick beta deviation in Brazil. Raup-Crick beta deviation in boreal watersheds (ranging from -0.99 to 0.30) was not related to community size but it was to environmental heterogeneity (Table 1), supporting our prediction.

Table 1. Relationship between beta deviation (abundance-based [Bray-Curtis] and incidence-based [Raup-Crick]) and community size, environmental heterogeneity and spatial extent (n = 20 watersheds in each region). Size = Community size; Env. Het. = Environmental heterogeneity; Spa. Ext. = Spatial extent. R^2 and adj. R^2 = coefficient of determination and adjusted coefficient of determination of the full model, respectively. b = standardized slope.

			b	*se*	*t*	*p*	R^2	adj. R^2
Brazil	Raup-Crick	Size	**-0.737**	**0.164**	**-4.505**	**<0.001**	0.510	0.419
		Env. Het.	-0.114	0.200	-0.572	0.575		
		Spa. Ext.	0.057	0.200	0.289	0.776		
	Bray-Curtis	Size	**0.777**	**0.147**	**5.279**	**<0.001**	0.658	0.594
		Env. Het.	0.211	0.167	1.267	0.223		
		Spa. Ext.	-0.087	0.167	-0.522	0.609		
Finland	Raup-Crick	Size	-0.252	0.221	-1.137	0.271	0.319	0.192
		Env. Het.	**0.461**	**0.207**	**2.229**	**0.040**		
		Spa. Ext.	0.338	0.222	1.527	0.146		
	Bray-Curtis	Size	**0.728**	**0.168**	**4.328**	**<0.001**	0.607	0.534
		Env. Het.	-0.115	0.157	-0.731	0.475		
		Spa. Ext.	0.087	0.168	0.518	0.611		

Bray-Curtis (abundance-based) beta deviation was positively related to community size in both regions (Table 1; Fig. 2). In tropical watersheds, mean Bray-Curtis beta deviations varied from 3.08 to 16.66, indicating that communities were more dissimilar than expected by random changes

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in species abundances or in the species pool. Again, beta deviations of smaller communities were closer to zero than those of larger tropical communities, supporting our predictions. In boreal watersheds, mean Bray-Curtis beta deviation varied from 17.40 to 102.51, also indicating that communities were more dissimilar than expected by random changes in species abundances or in the species pool. Neither environmental heterogeneity nor spatial extent were significant predictors of Bray-Curtis beta deviation in any region.

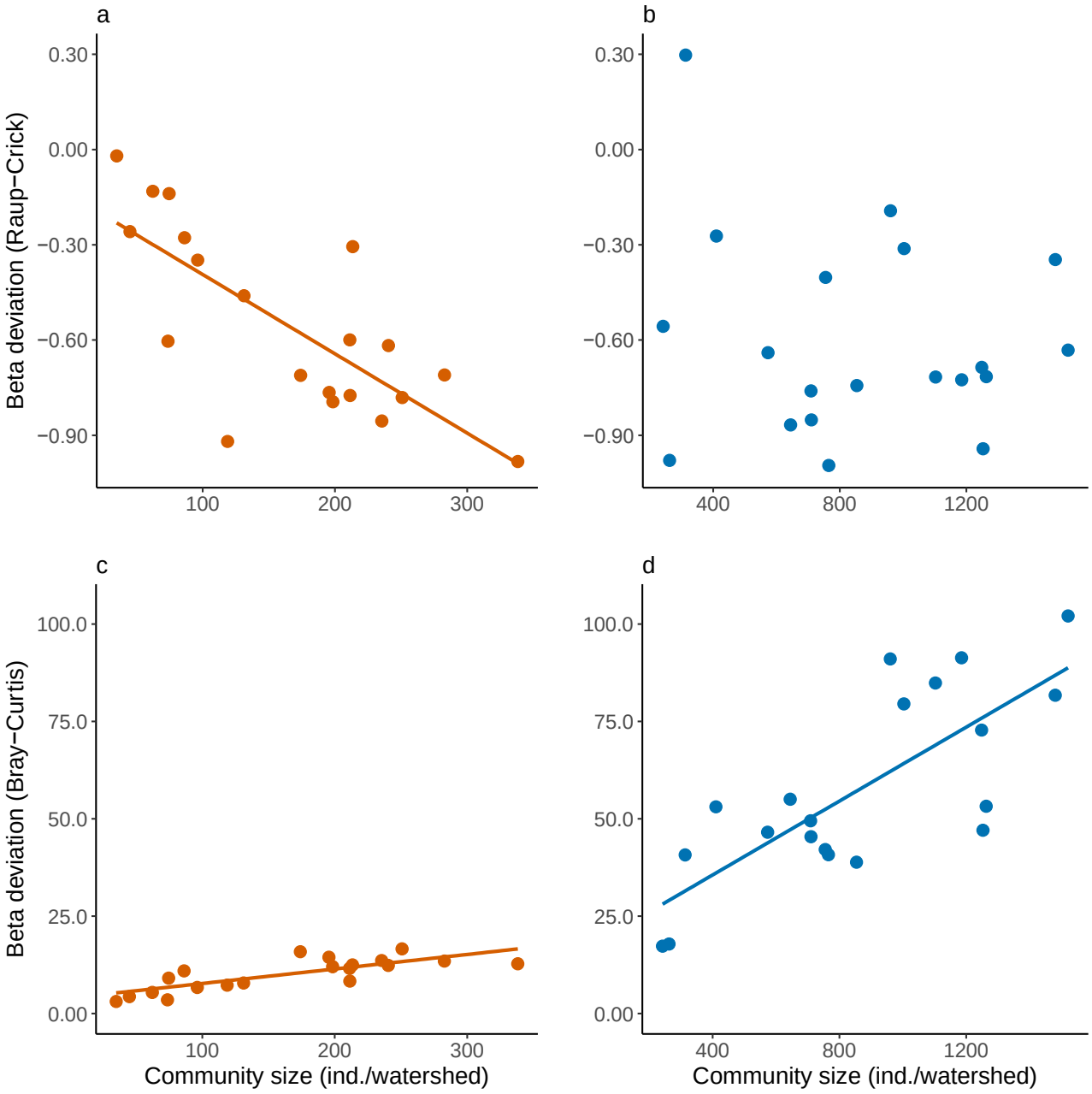

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Figure 2. (a, b) Incidence-based (Raup-Crick) and (c, d) abundance-based (Bray-Curtis) beta deviation-community size (average abundance in 5 streams) relationships within tropical (vermilion) and boreal (blue) stream watersheds.

Although there was a negative relationship between Raup-Crick beta deviation and community size in tropical watersheds only, mean incidence-based beta deviation in Brazil was not different from mean incidence-based beta deviation in Finland (Fig. 2). This suggests that variation in genus composition (pure compositional change) among streams is similar in tropical and boreal regions. On the other hand, mean abundance-based beta deviation was five times higher in Finland than in Brazil, suggesting that departures from null expectations are much higher in boreal than in tropical streams (Fig. 2).

Discussion

The importance 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 field data (Cottenie 2005, Lancaster and Downes 2017, Germain et al. 2017, Swan and Brown 2017, Valente-Neto et al. 2017). Here, we provide empirical evidence that community size (i.e., the total number of individuals in a local community average within watersheds), a simple characteristic of ecological communities, may mediate the interplay between deterministic niche selection and ecological drift as drivers of beta diversity in tropical and boreal metacommunities. Based on null models, we obtained estimates of beta diversity that accounted for both differences in species richness and species relative abundance that deviate from random assembly (i.e., beta deviations). We found that beta diversity of smaller communities deviates less from null expectations than larger communities. This means that the high beta diversity we observed among smaller communities was, to some extent, indistinguishable from patterns generated via random assembly processes. As findings generated by null models are our

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best approximation of patterns generated by stochastic processes (Kraft et al. 2011, Chase et al. 2011), our results indicate that ecological drift plays an important role in small communities (Orrock and Watling 2010, Gilbert and Levine 2017), probably together with deterministic assembly processes, as beta deviation values were different from zero.

Mechanistic explanations for the major role of ecological drift in small communities involve the alteration of competitive outcomes of species with different fitness (Orrock and Watling 2010). When local communities are small, even species with high fitness are at a high risk of extinction due to demographic stochasticity in comparison to a situation when communities harbor large populations. Consequently, species with low competitive ability have a chance to increase in relative abundance in small communities (Orrock and Watling 2010, Gilbert and Levine 2017). If these inferior competitors have high dispersal rates, a trade-off suggested by theoretical models (Cadotte et al. 2006), then they would have a higher chance to occur in some small communities within the metacommunity. As this would be the result of a local demographic random process, and because dispersal ability is highly variable among species (Tonkin et al. 2018a), the outcome of the assembly would likely differ among local communities, increasing beta diversity within metacommunities. Indeed, in Brazil, the three most abundant and widespread genera (Heino et al. 2018) did not dominate the abundance of 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 were dominant in four of the five largest communities in Brazil. The smaller communities in Brazil were dominated by genera with intermediate regional abundance and occupancy, such as *Gripopteryx* (stonefly), the sixth most abundant genera, *Cloeodes* (mayfly), the eleventh most abundant genera, and *Callibaetis* (mayfly), the sixteenth most abundant genera. In Finland, these differences were less evident, as the three most abundant and widespread genera dominated the abundance of similar numbers of smaller and larger communities: the beetle *Elmis* (two of the smallest vs. three of the largest communities); the

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mayfly *Baetis* (three vs. three); and stonefly *Nemoura* (one vs. one). This is likely because the smallest boreal stream communities were as large as the largest tropical communities (Heino et al. 2018). Also, in general, these results are in line with our predictions, as the relationship between abundance-based (Bray-Curtis) beta deviation and community size was positive in both regions. This indicates that the patterns of abundance distribution among genera in large communities were more dissimilar (positive values of beta deviation) than patterns predicted by random assembly – i.e., in terms of which genera were more abundant and rarer, communities within the same watershed differed from each other more than expected by chance. Thus, niche selection was likely sufficient to cause non-random variations in genera relative abundances among large communities.

Although small communities had beta diversity values close to random assembly expectations (i.e. low beta deviations), the relationship between incidence-based (Raup-Crick) beta deviation and community size was negative in Brazil. This result indicates that the genera composition of streams harboring large communities in tropical watersheds is less dissimilar (negative values of beta deviation) than patterns predicted by random assembly – i.e., these communities share more genera than expected. In general, ecological communities can be less dissimilar than random expectations in at least two cases. First, dissimilarity should be low when niche selection is spatially constant (e.g., harsh conditions within the metacommunity, Chase 2010) as the environment maximizes the fitness of a few species (Vellend 2016). The streams sampled in Brazil and Finland were distributed along a strong gradient of land cover among watersheds. 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). Environmental heterogeneity within watersheds was not a significant predictor of variation in Raup-Crick beta deviation in Brazil, but it was weakly and positively correlated with beta deviation in Finland, where community sizes are on average five-fold larger than in tropical streams (Heino et al. 2018). Thus, it is likely that the large size of boreal communities allowed niche selection to be strong enough to drive spatial variation in genus composition among communities.

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A second reason for communities to be less dissimilar than random expectations is when dispersal rates are high within the metacommunity (Mouquet and Loreau 2003, Leibold and Chase 2018). As the process distributing organisms among communities, dispersal can reduce beta 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). Although contemporary dispersal across watersheds tends to be limited for many aquatic species, those with an adult flight 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. Also, while Macneale et al. (2005) found that the stonefly *Leuctra ferruginea* was able to fly across headwater forested catchments, Flenner and Sahln (2008) estimated annual rage expansions of up to 88 km in non-migratory dragonflies in a boreal region of Sweden. The northern faunas of Europe should be composed of species with good dispersal ability, as they have reached these areas since the Last Glacial Period. On the other hand, many tropical aquatic insects have multiple reproduction events per year, i.e., many are multivoltine species (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 sites distant more than one kilometer per year. Thus, we suggest that long-term availability for colonization and multivoltinism allowed some genera to reach widespread distribution within tropical watersheds (Saito et al. 2016). Similarly, good dispersal abilities of northern species also tended to homogenize genus composition within boreal watersheds, making these communities less dissimilar than expected. Our results reinforce previous

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ideas that dispersal should be viewed as a process occurring over time and not only considering the distance individuals can move in one dispersal event (Saito et al. 2015).

Understanding the extent to which community assembly dynamics can be predicted 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, while Hallmann et al. (2017) estimated a decline of more than 70% in insect biomass between 1989 and 2016 in Germany, 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 beta diversity with environmental changes were related to small communities being more variable. For example, Hawkins et al. (2015) showed that disturbed sites had high beta 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 as 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 should be small at the earlier stages of community assembly and, thus, more prone to ecological drift.

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Our study provides empirical 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, providing a solution to a long-standing debate on why some communities are apparently more influenced by stochastic processes than others. This evidence complements previous empirical and conceptual efforts that indicated that ecological drift can have a major role in driving biodiversity patterns even in communities where species have clear differences in life-history traits, resource use, and competitive abilities (i.e., those communities assumed to be non-neutral). 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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Author contributions. TS conceived the idea, ran the analyses, and wrote the manuscript with substantial support from VSS, LMB, ASM, and JH. TS, LMB, VLL, ASM, JS, and JH planned the sampling design. DKP and JJ-M sampled the data. DKP, VSS and KTT identified the insects. DKP, JJ-M, KT, VLL and JS commented on the manuscript.

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