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Analyzing snapshot diversity patterns with the Neutral Theory can show functional groups' effects on community assembly

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Abstract. A central question of community ecology is to understand how the interplay between processes of the Neutral Theory (e.g., immigration and ecological drift) and niche-based processes (e.g., environmental filtering, intra- and interspecific density dependence) shape species diversity in competitive communities. The articulation between these two categories of mechanisms can be studied through the lens of the intermediate organizational level of “functional groups” (FGs), defined as clusters of species with similar traits. Indeed, FGs stress ecological differences among species and are thus likely to unravel non-neutral interactions within communities. Here we presented a novel approach to explore how FGs affect species coexistence by comparing species and functional diversity patterns. Our framework considers the Neutral Theory as a mechanistic null hypothesis. It assesses how much the functional diversity deviates from species diversity in communities, and compares this deviation, called the “average functional deviation,” to a neutral baseline. We showed that the average functional deviation can indicate reduced negative density dependence or environmental filtering among FGs. We validated our framework using simulations illustrating the two situations. We further analyzed tropical tree communities in Western Ghats, India. Our analysis of the average functional deviation revealed environmental filtering between deciduous and evergreen FGs along a broad rainfall gradient. By contrast, we did not find clear evidence for reduced density dependence among FGs. We predict that applying our approach to new case studies where environmental gradients are milder and FGs are more clearly associated to resource partitioning should reveal the missing pattern of reduced density dependence among FGs.

Key words: beta-diversity index; community ecology; functional groups; neutral theory; Simpson diversity; spatially implicit; species coexistence; tropical forest.

INTRODUCTION

A central goal of community ecology is to understand the processes that underpin species diversity in space and time. Several theories have been proposed to explain how species coexist within a single trophic level. The Niche Theory has focused on how differences in per capita growth rate among species can or may not allow coexistence (Grinnell 1917, Hutchinson 1957). These differences can come from two “niche-based” processes: density dependence and environmental filtering. Density dependence refers to the fact that the per capita growth rate of some focal species depends on its own density (intraspecific density dependence) and on the density of other species in the community (interspecific density dependence). In competitive communities, these

relationships are thought to be negative. Resource partitioning in space and time (MacArthur and Levins 1967, Tilman 1981, Chesson 2000) leads to intraspecific negative density dependence being stronger than interspecific negative density dependence, which tends to generate stable coexistence among species. Environmental filtering refers to the fact that the per capita growth rate of a species depends on local environmental conditions. As a result, per capita growth rates of species may differ both in values and in ordination between two communities showing identical composition but different environmental conditions. Within communities, environmental filtering tends to erode coexistence among species with different environmental optima, which leads to spatial segregation of these species along environmental gradients, a phenomenon called “species sorting” (Leibold et al. 2004).

In contrast, the Neutral Theory (Caswell 1976, Bell 2001, Hubbell 2001, Alonso et al. 2006, Rosindell et al. 2011) makes the fundamental assumption that ecological

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differences among species do not play a significant role on community composition. Thus, individuals from distinct species are ecologically indiscernible. As a consequence, the dominant processes at work in the assembly of a community are immigration, ecological drift (i.e., random fluctuation of local population sizes) and “density dependence on the community level” (i.e., birth and death rates of individuals only depend on the total density of the community, pooling all species together; Haegeman and Etienne 2008). We will refer to these three processes as “neutral processes” below. More recent hybrid frameworks, such as the stochastic niche theory (Tilman 2004) or the niche neutrality continuum (Gravel et al. 2006), considered a joint influence of niche-based and neutral processes. As a result, an important part of empirical research is now dedicated to disentangling the contributions of niche-based and neutral processes in the field, using pattern-to-process approaches based on spatio-temporal surveys of communities (e.g., Münkemüller et al. 2012, Tucker et al. 2016, Clappe et al. 2018).

Assessing the contribution of environmental filtering and negative density dependence in communities can be achieved by controlled experiment: manipulating the density or frequency of species in communities, assessing impacts on individual growth, survival, or reproduction rate, and ultimately drawing qualitative conclusion about stabilization or parameterizing coexistence models (see Adler et al. 2007 and Broekman et al. 2019 for reviews). However, this type of approach is best suited to short-lived individuals in communities involving a small number of species, because it requires following each species individually in time under a variety of community contexts. For highly diverse communities and long-lived organisms (for example, communities of tropical trees), researchers rather resort to using “snapshot” observation of communities’ composition across space at a single time for the study of coexistence mechanisms. One can search for ecological processes underpinning snapshot data by fitting mechanistic models explicitly including or not the processes of interest (Volkov et al. 2005, Al Hammal et al. 2015, Janzen et al. 2015) and assessing models’ goodness of fit using statistical tests. An insightful first step in this direction consists in checking whether observed diversity patterns are consistent with the Neutral Theory (Condit et al. 2002, Volkov et al. 2003, Dornelas et al. 2006, Etienne 2007). Any departure from patterns predicted by neutral models suggests that some additional processes—environmental filtering of species or density dependence not occurring on the community level only—play a significant role in community assembly. In other words, the Neutral Theory provides a “null” reference model for assessing the contribution of environmental filtering and density dependence in snapshot diversity patterns (Alonso et al. 2006).

All species are not necessarily unique in terms of niche identity and interactions, and empirical studies repeatedly highlighted functional redundancy within communities (e.g., Moullot et al. 2014). Species functional traits allow delineating some species clusters (hereafter called “functional groups” or “FGs” in short; e.g., Diaz and Cabido 2001). The FG of some focal species may determine how environmental filtering affects its per capita growth rate. This should typically occur when traits involved in the clustering process are related to environmental tolerance (Jabot 2010, Munoz et al. 2017). The FG of a focal species may also determine how its per capita growth rate responds to the density of species belonging to the same or to a different FG. This should happen, for instance, when traits involved in clustering are related to specialization on distinct resources (MacArthur and Levins 1967, Saito et al. 2018). Then, one should observe reduced negative density dependence among FGs, making FGs analogous to “guilds,” where a guild is defined as a group of species exploiting the same array of resources in a similar way (see Simberloff and Dayan 1991 for a review).

Here, we explored whether the analysis of snapshot diversity patterns of species and FGs can contribute to clarify whether and how FGs contribute to species coexistence in communities. We showed that it is possible to assess if the diversity of FGs in communities is abnormally high or low compared to the prediction of the Neutral Theory. In order to interpret deviations, we built a niche-based framework where we added environmental filtering and reduced negative density dependence among FGs. Our rationale was that considering niche-based processes occurring at the FG level rather than at the species level constitutes a practical first step toward hybridizing the Niche and the Neutral Theory. We validated our interpretation framework using simulated data from a model including environmental filtering of FGs but no reduction of negative density dependence among FGs, and another model where FGs behave like ideal guilds (i.e., no negative density dependence among FGs). As a case study, we also applied our approach to tropical tree communities in Western Ghats, India. Tropical forests are a flagship example where the Neutral Theory has been successful in predicting species relative abundances in communities (Hubbell 2001, 2006, Volkov et al. 2003), and analyses of functional diversity also suggested the influence of non-neutral dynamics (Kraft et al. 2008, Paine et al. 2011). Tropical forests thus provide an ideal case to test our framework. We investigated the diversity of predefined FGs of trees based on either leaf-shedding phenology (deciduous or evergreen strategies) or canopy strata. In tropical forests, leaf-shedding phenology is tightly linked to drought resistance, and we expected phenology-based FGs to undergo environmental filtering along a rainfall gradient. By contrast, we expected that tree species with different potential strata have evolved very differently along trade-offs between light use efficiency and efficiency at using other

resources, and might therefore show reduced negative density dependence.

MATERIALS AND METHODS

All the simulations and analyses described in this section have been performed using the R software (R Development Core Team 2017). We made our scripts available in Data S1.

Neutral model

We used a broad family of neutral models leading to similar patterns (see Appendix S1: Section S1) as a reference to analyze species and FG diversity. In a neutral model, by definition, belonging to different FGs has no effect on species' per capita growth rates. The neutral models considered here include two spatial scales: the regional level is a pool of R species with constant relative abundance distribution through time, and the local level includes N local sites, each including one community. The vector of relative abundances of species in the regional pool is denoted by \mathbf{f} (all bold symbols stand for vectors). There are P distinct FGs in the regional pool and each species belongs to one FG. The vector of the relative abundances of FGs in the regional pool is denoted by \mathbf{g} . Note that \mathbf{g} can be deduced from \mathbf{f} : summing the relative abundances f_i over species i belonging to FG j yields the relative abundance of FG j in the regional pool, g_j .

Our approach considers neutral models where local community sizes can fluctuate in time. It applies to any kind of local dynamics as long as the following conditions are met. First, the dynamics must follow strict neutrality. This means that within a site, per capita rates of birth, death, and emigration are identical for all individuals, irrespective of their FG. It also means that these rates only depend on the community density (i.e., the total number of individuals in the community, irrespective of their species identity), a feature called “density dependence on the community level” (Haegeman and Etienne 2008). Second, immigration to a community occurs through random sampling of individuals from the regional pool. Third, immigration and per capita birth rate in communities depend in a similar way upon community density. The relative strength of immigration rate compared to per capita birth rate in site n is captured by a parameter I_n , called the “effective number of migrants” (Etienne and Olf 2004). More details about the set of neutral models compatible with our approach are provided in Appendix S1: Section S1.

We considered a random sample of s individuals in each site. The sample in site n was modeled as a random vector \mathbf{X}_n of integers, with dimension R and sum s , indicating the abundances of species. The vector X_n follows a Dirichlet-multinomial distribution (Bernardo and Smith 2009), which has also been called the “dispersal limited multinomial distribution (DLM)” by Etienne and Alonso (2005):

$$P(\mathbf{X}_n = \mathbf{x} | I_n, \mathbf{f}) = \binom{s}{\mathbf{x}} \frac{\prod_{i=1}^R \langle I_n f_i \rangle_{x_i}}{\langle I_n \rangle_s} \tag{1}$$

where $\binom{s}{\mathbf{x}} = \frac{s!}{\prod_{i=1}^R x_i!}$ is a multinomial coefficient and $\langle a \rangle_s = \prod_{l=0}^{s-1} (a + l)$ is a Pochhammer product. Equation 1 is valid irrespective of the particular specifications of birth, death, and immigration rates in sites as long as they match the hypotheses detailed above and in Appendix S1: Section S1. The hierarchical nature of Dirichlet-multinomial distribution, extensively discussed by Harris et al. (2017), yields a simple two-step simulation procedure detailed in Appendix S1: Section S1.

We considered the Simpson species diversity index of sample \mathbf{X}_n , denoted $D(\mathbf{X}_n)$. Equation 1 implies that the conditional expectation of $D(\mathbf{X}_n)$ equals (Munoz et al. 2008):

$$E[D(\mathbf{X}_n) | I_n, \mathbf{f}] = \frac{I_n}{1 + I_n} \left(1 - \sum_{i=1}^R f_i^2 \right) \tag{2}$$

where $E[\cdot | I_n, \mathbf{f}]$ is the conditional expectation for a given I_n value and the species composition of the regional pool \mathbf{f} . The quantity $1 - \sum_{i=1}^R f_i^2$ is the regional Simpson species diversity. In practice, we estimated the regional Simpson species diversity from a whole data set of community samples (all sites together), as proposed by Munoz et al. (2007, 2008).

A random vector \mathbf{Y}_n of integers with dimension P and sum s denotes the FG abundances in sample n . Because FGs are neutral, FG abundances also follow a DLM distribution:

$$P(\mathbf{Y}_n = \mathbf{y} | I_n, \mathbf{g}) = \binom{s}{\mathbf{y}} \frac{\prod_{l=1}^P \langle I_n g_l \rangle_{y_l}}{\langle I_n \rangle_s} \tag{3}$$

and the conditional expectation of $D(\mathbf{Y}_n)$ (the Simpson diversity of FGs, one facet of functional diversity—hereafter called “functional diversity” for simplicity) equals

$$E[D(\mathbf{Y}_n) | I_n, \mathbf{g}] = \frac{I_n}{1 + I_n} \left(1 - \sum_{l=1}^P g_l^2 \right). \tag{4}$$

The quantity $1 - \sum_{l=1}^P g_l^2$ is the regional Simpson functional diversity. We estimated the regional Simpson functional diversity from the whole data set (all sites together; Munoz et al. 2007, 2008).

Average functional deviation

For each site n , we considered the statistic

$$T_n = \frac{D(\mathbf{Y}_n)}{1 - \sum_{l=1}^P g_l^2} - \frac{D(\mathbf{X}_n)}{1 - \sum_{i=1}^R f_i^2}$$

which is a difference between the standardized Simpson functional diversity and the standardized Simpson

species diversity measured in site n . Equations 2 and 4 imply that $E[T_n] = 0$ in the neutral model, irrespective of the values of I_n , f , and g . Values of T_n depart from 0 under the influence of niche-based processes (in our framework, environmental filtering of FGs or reduced negative density dependence among FGs). We therefore called T_n the “functional deviation in site n .”

We considered the statistic $u = \sqrt{N}(\mu_T/\sigma_T)$, where μ_T and σ_T are the empirical mean and standard deviation of the T_n s among sites, respectively. The statistic u measures whether T_n tend to deviate from 0 on average across sites. We therefore called u the “average functional deviation.” The Neutral Theory predicts that, when the number of sites N is large, u follows a normal distribution with mean 0 and variance 1, noted $N(0, 1)$ below. We use this asymptotic property to test whether observed u values are consistent with the Neutral Theory. The test consists of measuring the quantile x of $N(0, 1)$ corresponding to the observed u value, and computing a P -value $p = 2 \min(x, 1 - x)$ associated with the departure of observed data from Neutral Theory prediction towards either positive or negative values. Finding $u < 0$ and $P < 0.05$ means that the average functional deviation is significantly negative: the functional diversity in sites is lower than predicted by the Neutral Theory. By contrast, $u > 0$ and $P < 0.05$ means that average functional deviation is significantly positive: the functional diversity in sites is higher than predicted by the Neutral Theory. We showed in Appendix S1: Section S2, that for number of sites and regional pool species diversity similar to the one we consider in our real example, the asymptotic approximation is not totally accurate, and the test tends to be slightly conservative for negative u and to harbor a moderately inflated type-I error rate for positive u (Appendix S1: Fig. S3). Consequently, one can safely reject neutral theory when $u < 0$ and $P < 0.05$, but should rather ask for $P < 0.01$ to reject Neutral Theory at a 5% threshold safely when $u > 0$ (Appendix S1: Fig. S4).

Exploring departure from neutrality in virtual data sets with non-neutral dynamics

We applied our framework to virtual data sets generated by two models of species coexistence deviating from neutrality. These models used the same implicit representation of space as the neutral model: one regional pool and N local communities. In all our simulations, we choose parameter values representative to the real data set analyzed below. This led us to set $N = 100$, $R = 100$, $s = 100$, $P = 4$. We made use of results about the multivariate Ewens distribution (Ewens and Tavaré 2004; see eq. [41.2], p. 233) to sample species abundances in the regional pool according to a distribution identical to that of the neutral model of Hubbell (2001). This distribution has a single parameter θ , which drives its skewness (low θ yielding highly unbalanced abundances of species; see Appendix S1: Fig. S1). In our real tropical

tree data set, using the estimation procedure for θ described in Munoz et al. (2007), we obtained that $\hat{\theta} = 48$. We therefore chose a similar value in our simulation ($\theta = 50$). Each species received a FG label randomly chosen in $1 \dots P$. If a FG did not occur in the regional species pool, we repeated the FG attribution until all FGs were present in the pool. We drew an effective number of migrant I_n for each site in a log-normal distribution with (log) mean 0 and (log) standard deviation 1.

The “environmental filtering model”.—We built an “environmental filtering model” that extends the framework proposed by Munoz et al. (2017). It modulates not only the immigration rate, but also the per capita birth and death rates of FGs according to environmental conditions within sites. Therefore, within a site, species belonging to distinct FGs did not have the same per capita growth rate and species belonging to the same FG had the same per capita growth rate. We implemented the modulation of individual rates as follows: for each FG, we sampled a trait in a Gaussian distribution with mean 0 and variance 1, and all species in a given FG had the same trait value. We sampled an optimal trait value t_{opt} for each site in a Gaussian distribution with mean 0 and variance 1. For a site with optimal value t_{opt} , individuals belonging to FG i had their per capita birth rate equal to a neutral birth rate, common to all FGs, multiplied by $\exp\left(-[\Omega_\beta(t_i - t_{\text{opt}})]^2\right)$, their per capita death rate equal to a neutral death rate multiplied by $\exp\left([\Omega_\delta(t_i - t_{\text{opt}})]^2\right)$, and their immigration rate equal to a neutral immigration rate multiplied by $\exp\left(-[\Omega_\mu(t_i - t_{\text{opt}})]^2\right)$. As a result, when FG i had a trait distant to the local optimum, its per capita birth rate and immigration rate decreased, while its per capita death rate increased. The positive parameters Ω_β , Ω_δ , Ω_μ quantify the intensity of the environmental filtering effect on per capita birth rate, per capita death rate, and immigration rate respectively, that is, how quickly these rates deteriorate when t_i deviates from the local optimum. In particular $\Omega = 0$ means that the corresponding rate is unaffected by environmental heterogeneity among sites. In Appendix S1: Section S3, we provide more details about the environmental filtering model, as well as a fast simulation algorithm based on a modified Dirichlet-multinomial distribution.

We focused on four scenarios of environmental filtering: (a) filtering with identical intensity on all rates $\Omega_\beta = \Omega_\delta = \Omega_\mu = \Omega$; (b) filtering with intensity $\Omega_\beta = \Omega$ on birth rate and no filtering on the other rates ($\Omega_\delta = \Omega_\mu = 0$); (c) filtering with intensity $\Omega_\mu = \Omega$ on immigration rate and no filtering on the other rates ($\Omega_\delta = \Omega_\beta = 0$); (d) filtering with intensity $\Omega_\delta = \Omega$ on death rate and no filtering on the other rates ($\Omega_\mu = \Omega_\beta = 0$). In each scenario, the Ω parameter varied from 10^{-1} (similar per capita growth rates among sites and among FGs) to 10 (marked differences in per capita growth rate among sites and among FGs) on a logarithmic scale. For each Ω value, we computed 30 replicates

of the model simulation. We sampled new regional pool relative abundances and site effective number of immigrants, FG traits and local trait optima for each replicate, following the procedures detailed earlier. For each simulated data set, we applied our asymptotic neutrality test on the average functional deviation u .

The “guild model”.—In the neutral models and the environmental filtering model described above, negative density dependence among species occur at the community level, meaning that the per capita growth rate of a focal species is affected by the total density of individuals in the community, irrespective of individual species densities. Here we considered a new model with a different structure of density dependence based on FGs. We considered that the per capita growth rate of a focal species could be affected by the densities species belonging to the same FG (including the species itself) but were unaffected by the densities of species belonging to other FGs. The absence of interspecific density dependence between species belonging to distinct FGs implements the idea that FGs based on traits inducing resource partitioning should delineate groups of species with reduced density-dependent effects among groups. In our model, FGs then constitute an ideal representation of guilds (Simberloff and Dayan 1991) where negative density dependence occurs within but not among FGs. We consequently called this model the “guild model.”

We further assumed that species are “neutral” within a FG, meaning that (a) all the individuals in a FG have equal birth and death and emigration rates at all times, and (b) the per capita growth rate of a focal species is affected by the total density of individuals of the same FG, irrespective of individual species densities. We called the latter assumption “density dependence on the FG level.” Density dependence on the FG level implies that the per capita growth rate of species within a FG are limited by the total FG density. Consequently, there exists some equilibrium density of the FG where species cannot grow anymore, which we called “carrying capacity” of the FG. Carrying capacities can differ among FGs within the same site, for example, if FGs depend on distinct resources with very different availability.

We modeled the dynamics of species abundances inside a FG with a zero-sum neutral dynamics with immigration (Hubbell 2001), setting the total FG size equal to its carrying capacity. FGs’ relative carrying capacities varied among sites, for example, because of variation in locally available resources. We did not explicitly model the mechanisms underpinning the variation in FGs’ relative carrying capacities, but rather considered random variation around the regional relative abundances of FGs (g) as a phenomenological description of changes in FGs relative carrying capacities among sites. To do this we drew relative carrying capacities from a Dirichlet distribution with parameters αg_i (see Appendix S1: Section S3: Eq. S14), which

modulate the variance of relative carrying capacities of FGs among sites. When $\alpha \rightarrow 0$, the variance was maximized, and sites tended to include only one FG, which changed among sites. When $\alpha \gg 1$, all the sites harbored the same relative capacities of FGs, equal to their regional relative abundance g . We thus called α the “similarity of functional composition” among communities. We varied α from $10^{-1.5}$ to $10^{1.5}$ on a logarithmic scale and computed 30 simulations of the model, resampling all the regional pool and site parameters each time. For each simulation, we applied our asymptotic neutrality test on the average functional deviation u . Additional details about the guild model are provided in Appendix S1: Section S3.

Application to rainforest tree communities in South India

We applied our approach to tropical forest communities of the Western Ghats, Karnataka State, South India. We used a data set including tree community composition in 96 1-ha plots spread across 22,000 km² (Ramesh et al. 2010). These sites cover a vegetation gradient from wet, evergreen to moist, deciduous forests, depending on a gradient of climatic conditions in terms of seasonality and annual rainfall (Pascal 1988). In each site, all trees above 10-cm diameter at breast height were identified, which yielded a global data set of 57,090 identified trees from 61 to 1,883 individuals per site. The complete data set is available in Ecological Archives [<http://esapubs.org/archive/ecol/E091/216/>], with accession number E091-216. The simplified data set used for this study is provided in Data S1.

In our analyses, we considered random subsample of 61 individuals (the minimum community size among the 96 plots) without replacement in each communities of the data set, in order to obtain a balanced design comparable to our simulations. We performed subsampling 100 times to get replicated data sets. We considered FGs based on the potential stratum position of species as documented by Ramesh et al. (2010): T5 (>34 m height), T4 (24–34 m), T3 (16–24 m), T2 (8–16 m), and T1 (<8 m). These potential strata were defined based on observations in various contexts (Pascal and Pelissier 1996). We also considered FGs based on leaf shedding phenology: deciduous (“D”) and evergreen (“E”) trees.

For each type of FGs, we used our asymptotic test to assess whether the average functional deviation (u) matched the prediction of the Neutral Theory. When we obtained a significant negative value of u , we explored the relationship between several abiotic factors (rainfall, elevation, longitude, latitude, soil type) and the community weighted means (CWM; Garnier et al. 2004) of phenology FGs and potential canopy stratum FGs. To do so, we converted FGs into a quantitative integer indices, arbitrarily setting “D” = 1 and “E” = 0 for phenology FGs and setting “T1” = 1, “T2” = 2 ... “T5” = 5 for potential canopy stratum FGs. Note that,

for phenology FGs, CWM simply corresponds to the proportion of deciduous trees in the community. We used the Spearman ρ correlation coefficients to quantify the relationship between CWMs and rainfall, elevation, longitude, and latitude. For soil type, which was a categorical variable, we reported the F statistics of an analysis of variance of CWMs as a function of soil type. For each environmental, we tested whether the statistical effect was significantly different from 0 by performing 10,000 permutation of FGs among species to generate a null distribution. This permutation procedure is known to control for the effects of ecological drift on species abundances better than full randomization of individuals (e.g., Laroche et al. 2016).

We also tested whether the average functional deviation of stratum FGs matched the neutral model predictions within evergreen and deciduous subcommunities separately. When finding a significant negative functional deviation of stratum FGs, we further explored whether the CWM of stratum FGs within evergreen and deciduous subcommunities was correlated to rainfall, elevation, longitude, latitude, soil type, and the density of individuals.

RESULTS

Analysis of non-neutral simulated data sets

We first assessed how the average functional deviation u deviated from neutral expectation in data sets simulated with the environmental filtering model, with a particular focus on the intensity of environmental filtering (Ω) in the four scenarios: filtering on birth, death, and immigration rate; filtering on birth rate only; filtering on immigration rate only; filtering on death rate only. We found that low Ω led to u being close to 0 and not deviating significantly from the prediction of the Neutral Theory in all the scenarios (Fig. 1). When Ω increased, u decreased and became significantly negative in all the scenarios, which indicated that functional diversity within sites was lower than predicted by the Neutral Theory. Filtering acting on the death rate of individuals led to the strongest decrease of u .

Second, we assessed how the average functional deviation u deviated from neutral expectation in data sets simulated with the guild model, with a particular focus on the effect of the similarity in functional composition (α). We found that when α was low (communities often harboring one single FG, changing from one site to another), u was significantly negative (Fig. 2), which indicated that functional diversity within sites was lower than predicted by the Neutral Theory. When α increased, u increased. For intermediate values of α (between 10^0 and $10^{0.5}$), u was not significantly different from 0, which indicated that functional diversity within sites was consistent with the prediction of the Neutral Theory. For higher values of α , u became significantly positive, which indicated that functional diversity within

sites became higher than predicted by the Neutral Theory.

Analysis of rainforest tree communities in South India

In the tropical tree communities of Karnataka, the average functional deviation of phenology FGs equaled -16 (mean over the 100 rarefied data sets) and strongly departed from neutral expectation (average $P = 1E-50$). We found a significant negative correlation between the community weighted mean (CWM) of phenology and rainfall (Spearman $\rho = -0.71$, $P = 8E-4$; Fig. 3). In other words, the proportion of deciduous trees in the community decreased in a non-neutral way as rainfall increased. Other abiotic variables showed no significant effect (Fig. 3; soil-type effect size $F = 3.0$, $P = 0.4$). The average functional deviation for stratum FGs equaled -1.7 (mean over the 100 rarefied data sets) and did not significantly deviate from neutral expectations (average $P = 0.1$).

We further analyzed the average functional deviation for stratum within deciduous and evergreen subcommunities separately. The average functional deviation equaled -0.55 for the potential stratum FGs in deciduous communities (averaged over the 100 rarefied data sets) and did not significantly deviate from neutral expectations (average $P = 0.6$). For potential stratum FGs in evergreen subcommunities, the average functional deviation equaled -2.1 (averaged over the 100 rarefied data sets) and was significant with respect to neutral expectation (average $P = 0.04$). The CWM of potential stratum FGs in evergreen subcommunities showed a significant negative relationship with deciduous individuals density (Spearman $\rho = -0.67$, $P = 0.001$) and a significant positive relationship with rainfall (Spearman $\rho = 0.55$, $P = 0.01$; Fig. 4). It indicated that evergreen subcommunities contained a higher proportion of understory species in dry deciduous-dominated forests. Finding opposite effects of rainfall and deciduous tree density upon low-stratum evergreen trees stemmed from the fact that these two covariates were negatively correlated across sites. We found no effect of soil type on the stratum CWM in evergreen subcommunities ($F = 1.8$, $P = 1.0$).

DISCUSSION

We have presented a novel approach to explore how functional groups (FGs) affect species coexistence by comparing species and functional diversity patterns. Our framework considers the Neutral Theory (Caswell 1976, Bell 2001, Hubbell 2001) as a mechanistic null hypothesis, in line with Alonso et al. (2006). It assesses how much the average difference between functional diversity and species diversity in communities, called the average functional deviation (u), departs from the prediction from the Neutral Theory $u = 0$. Importantly, functional and species diversity measures within local communities

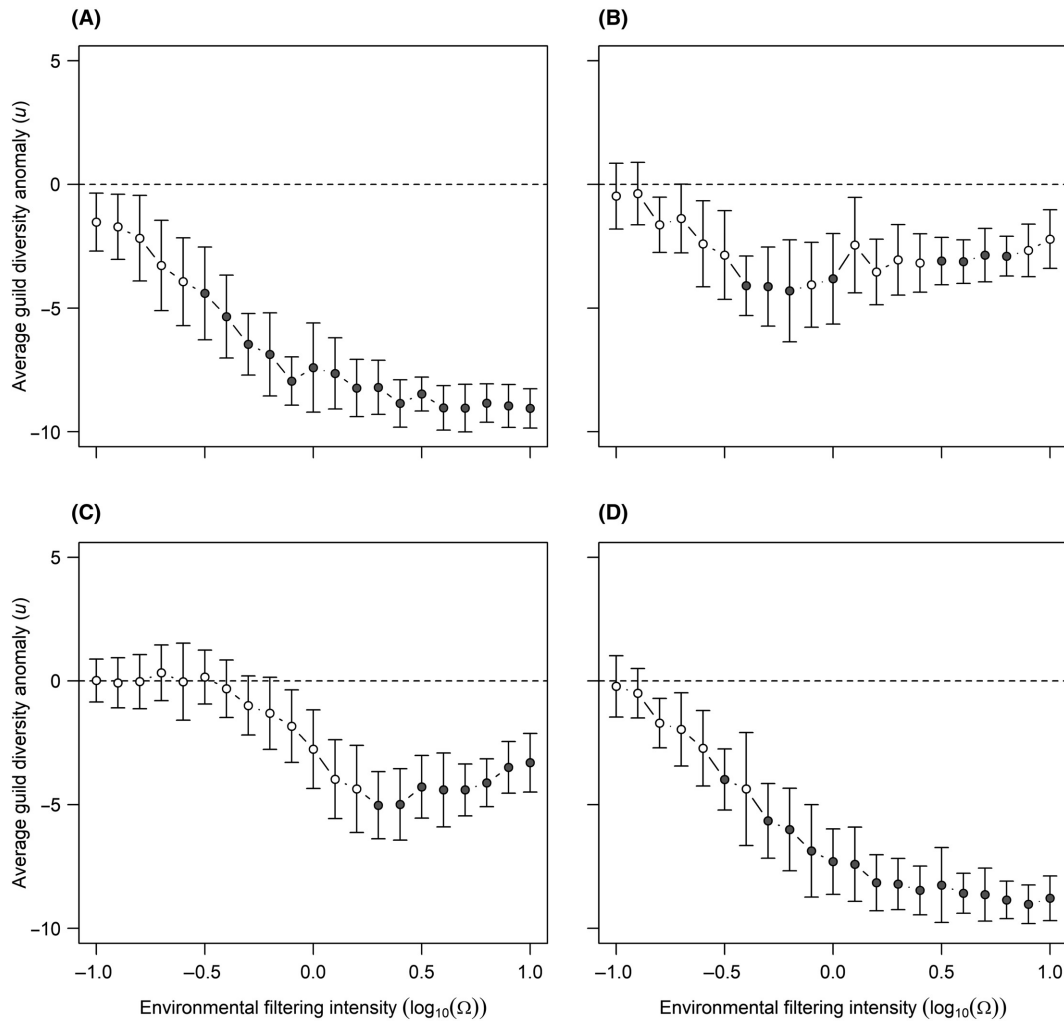


FIG. 1. Effect of environmental filtering intensity (Ω) upon the average functional deviation (u). Each panel corresponds to a distinct effect of environmental filtering: (A) filtering on birth, death, and immigration rate of functional groups (FGs); (B) filtering on birth rate of FGs only; (C) filtering on immigration rate of FGs only; (D) filtering on death rate of FGs only. For each value of Ω , we performed 30 simulations of the environmental filtering model with distinct site, species, and FG parameters (sampled as described in methods). This yielded 30 values of u and 30 corresponding P values of the departure from the neutral expectation $u = 0$. Dots correspond to the mean of the 30 values of u . Error bars indicate standard deviation of the 30 values of u . When the mean of the corresponding P value was below 0.05, we set the dot color to gray, indicating significant departure from the neutral expectation $u = 0$ across replicates; otherwise we set the dot color to white. As environmental filtering intensity increases, the average functional deviation decreases and becomes significantly negative compared to values predicted by the Neutral Theory.

are standardized with respect to corresponding regional diversity levels. This implies that the average functional deviation u also corresponds to a difference between the species β diversity and the FGs' β diversity (Appendix S1: Section S4), where β diversity is the part of the total diversity in all the communities (γ diversity) that comes from dissimilarities among communities (Whittaker 1972, Jost 2007). A significantly positive average functional deviation thus indicates that (a) the functional diversity within communities is higher than expected under the Neutral Theory given the level of species diversity within communities; and (b) the dissimilarity of FGs relative abundances among communities

is smaller than expected under the Neutral Theory, given the level of dissimilarity of species relative abundances among communities. Similarly, a significantly negative average functional deviation means that the functional diversity within sites is lower and the dissimilarity of FGs relative abundances among communities is larger than expected under the Neutral Theory given the species diversity and dissimilarity patterns.

Our simulation work showed how environmental filtering of FGs and reduced negative density dependence among FGs should affect the average functional deviation—as summarized in Fig. 5—and reciprocally how the sign of the average functional deviation may provide

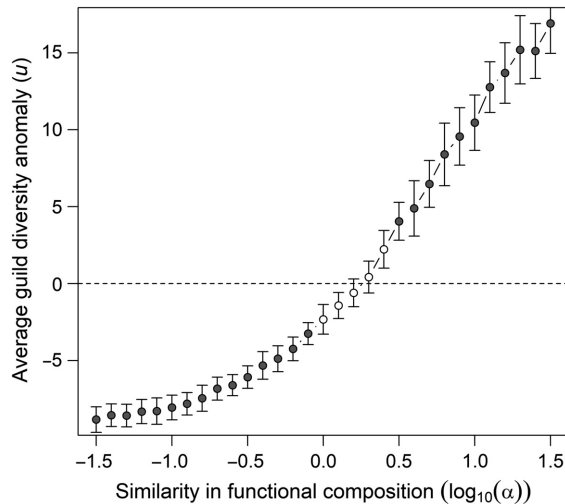


FIG. 2. Effect of similarity in functional composition (α) on the average functional deviation (u). For each value of α , we performed 30 simulations of the guild model resampling site, species, and FGs parameters. This yielded 30 values of u and 30 corresponding P values of the departure from the neutral expectation $u = 0$. Dots corresponds to the mean of the 30 values of u . Error bars indicate standard deviation of the 30 values of u . When the mean of the corresponding P value was below 0.05 for negative u values and below 0.01 for positive u values (hence controlling for the slight inflated type-I error rate; see main text), we set the dot color to gray, indicating significant departure from the neutral expectation $u = 0$ across replicates at a 5% level. Otherwise, we set the dot color to white. As similarities in functional composition increases, the average functional deviation increases. It is significantly negative compared to values predicted by the Neutral Theory for low similarity in functional composition values, not significantly different from values predicted by the Neutral Theory for intermediate similarity values and significantly positive compared to values predicted by the Neutral Theory for large similarity values.

insights about ecological processes. Environmental filtering always generated negative values of the average functional deviation u compared to neutral expectations (i.e., $u < 0$ and $P < 0.05$). This came from the fact that differences in per capita growth rate among FGs within communities entailed greater abundance of more adapted FG and lesser abundance of other FGs, leading to dominance and low functional diversity. In the meantime, variation of the environmental optimum generates changes of dominant FGs across sites, hence leading to FG segregation in space and high FG β diversity.

However, a negative average functional deviation did not necessarily indicate environmental filtering: the guild model could also generate significantly negative average functional deviation values, reflecting imbalanced local abundances of FGs and their segregation in space. This pattern emerged when the similarity in functional composition (α) was set to low values. The guild model does not explicitly model the mechanisms that underpin low α and marked differences in FG composition among sites, but simply states that these differences stem from

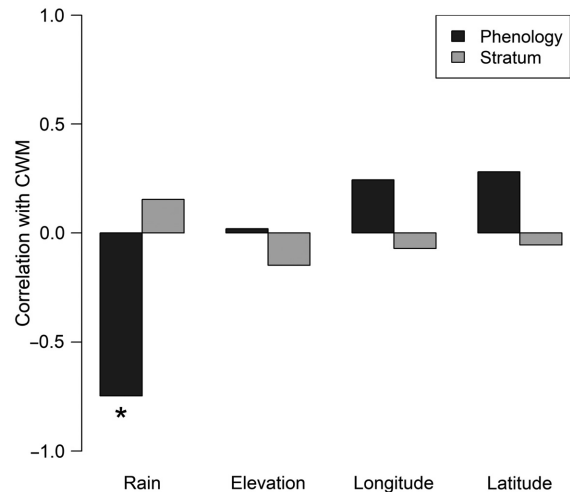


FIG. 3. Correlation between site abiotic factors and the community weighted means (CWM) of phenology and potential stratum in Karnataka tropical tree communities. Correlations are measured as Spearman ρ . Stars indicate correlations that significantly deviate from 0 compared to neutral expectations ($P < 0.05$; P values are determined using 10,000 permutations; see methods). Rainfall is the only abiotic variable that is significantly correlated with phenology community weighted mean compared to the neutral expectation (recalling that high-phenology community weighted mean implies high proportion of deciduous species). The correlation is negative, meaning that higher rainfall comes along with higher proportion of evergreen species in the communities.

contrasted variation of FGs' relative carrying capacities among sites. The carrying capacity of a FG may vary across sites for a wide array of reasons such as resources, predators, or parasite heterogeneous distribution in space.

A negative u statistic thus does not allow discriminating between the two following hypotheses: (a) environmental filtering of FGs without reduction of negative density dependence among FGs; (b) reduction of negative density dependence among FGs with FG carrying capacities showing antagonistic variation in space. In scenario (a), FGs do not behave like distinct guilds, because they do not show no reduced competition among species groups compared to within-group competition. In scenario (b), FGs behave like distinct guilds. Teasing apart these two scenarios require more than one snapshot pattern of diversity. Temporal survey within sites may, for instance, allow exploring whether the per capita growth rate of some FG is related to its own density only, or also depends on the densities of other FGs, and thus discriminating between the two scenarios (e.g., Adler et al. 2007).

By contrast, only the guild model with high similarity in functional composition among sites (α) could lead to significantly positive average functional deviation u . High similarity in functional composition means that carrying capacities of FGs are very similar among sites.

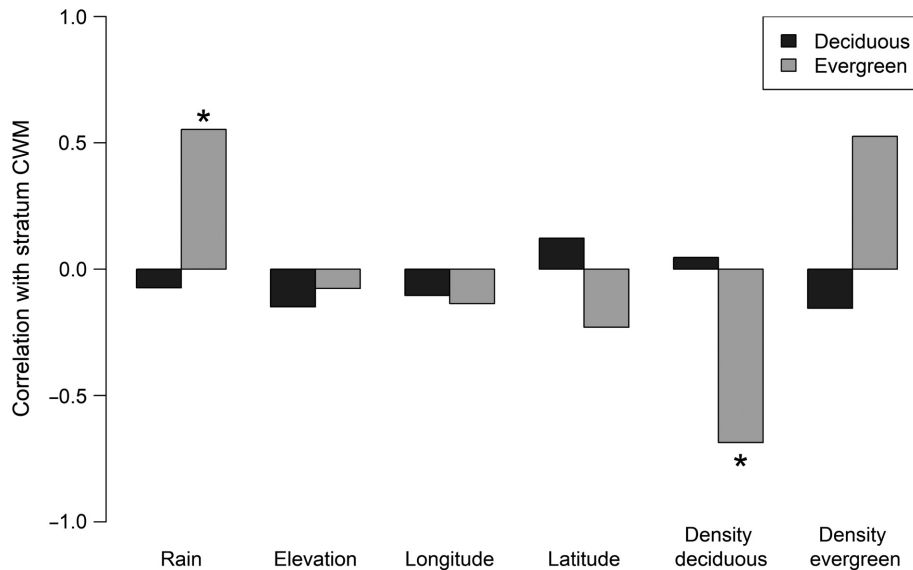


FIG. 4. Correlation between site factors (abiotic and biotic) and the community weighted mean (CWM) of potential stratum considering deciduous and evergreen subcommunities separately. Correlations are measured as Spearman ρ . Stars indicate correlations that significantly deviate from 0 compared to neutral expectations ($P < 0.05$; P values are determined using 10,000 permutations; see methods). Higher rainfall or lower density of deciduous trees leads to higher stratum community weighted mean in evergreen subcommunities than predicted by neutral theory.

This may occur if resources, predators, or parasites are homogeneously distributed in space at the scale of study, for example, when some predators with high dispersal abilities exert a top-down control on FGs of the focal trophic level. Very similar FG composition of communities (hence of samples) is unlikely in the neutral model because of ecological drift affecting species and FGs densities. u values less than or equal to 0 lead to ambiguous interpretation, so we suggest that significantly positive values of u univocally indicate that considered FGs behave like guilds.

Chisholm and Pacala (2010) developed a model of niche and neutral processes in a local community, which turns out to be a particular case of the guild model presented here, where the similarity in functional composition parameter (α) would be infinite, leading to exactly the same FG composition in every site. Their model predicts that, in speciose communities, the species abundance distribution (pooling all FGs together) within a community should not be discernable from that of a neutral model. By contrast, we evidenced that, under the same conditions, the average functional deviation (u) should be significantly positive, and thus should clearly deviate from neutral patterns. The better performance of u compared to analyses based on species composition of a single community comes from two essential features. First, it makes use of the additional information of FGs, which constitute a biologically informed decomposition of the community maximizing chances to observe non-neutral phenomena. Second, it makes use of dissimilarities among communities (i.e., functional and species β -diversity indices; Appendix S1: Section S4), which are

more informative to detect non-neutral processes than purely local species diversity patterns (Condit et al. 2002).

The guild model can also generate values of the average functional deviation (u) compatible with the Neutral Theory, which suggests that u can sometimes fail to detect reduced density dependence among FGs. This occurs when fluctuations of FGs' carrying capacity among sites happen to resemble the outcome of ecological drift induced by neutral processes. The most extreme example of this phenomenon arises when the similarity in functional composition (α) is exactly equal to the effective number of migrants in sites (i.e., $I_n = \alpha$ for all site n). Then, the FG composition of communities predicted by the guild model is identical to the FG composition predicted by a neutral model (Eq. 3). As a result, in this very particular case, it is not possible to tease the guild and the neutral model apart on the sole basis of a snapshot analysis. However, here again, a temporal survey should allow revealing whether there is reduced density dependence among FGs at play or not, and thus clarify whether FGs behave like guilds.

The particular case mentioned above—FGs behaving like guilds but showing abundance patterns exactly resembling the outcome of ecological drift, in sites having identical immigration rates—is a rather unlikely scenario. However, undistinguishable patterns between non-neutral and neutral models can emerge under a broader variety of contexts: low filtering intensity (Ω) in the environmental filtering or similarity in functional composition (α) larger but close to the average of immigration rates in sites. Discriminating between neutral

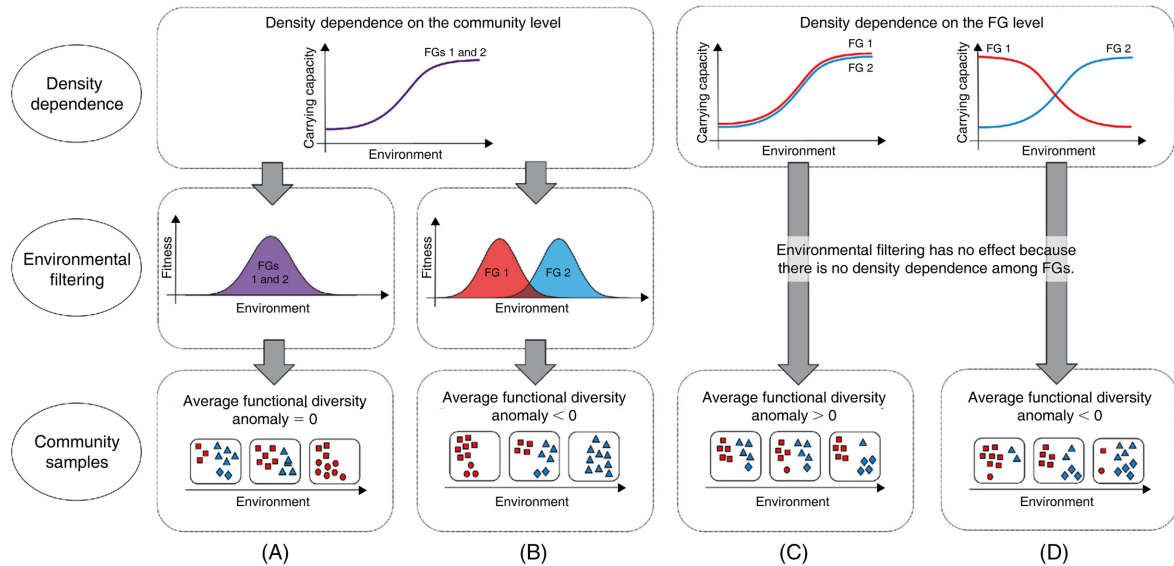


FIG. 5. Effect of environmental filtering and reduced negative density dependence among functional groups on community samples and average functional deviation (u). In our framework, negative density dependence among species can occur either at the community level (i.e., the per capita growth rates of species depends on the total density of the community) or at the functional group (FG) level (i.e., the per capita growth rates of species depends on the density of individuals belonging to the same FG). This leads to defining carrying capacity at the community or the FG level, respectively. Carrying capacities may vary among sites, for example, because of some environmental gradient. All species in the same FG have the same per capita growth rate. Environmental filtering of FGs can occur along some environmental gradient. Variation in per capita growth rates among FGs has no effect on metacommunity assembly when FGs behave as guilds (i.e., no negative density dependence among FGs). Our framework thus leads to four distinct scenarios. When density dependence occurs at the community level (i.e., no reduction of density dependence among FGs) and FGs have similar per capita growth rates, one retrieves the neutral model (A). Average functional deviation (u) should not differ significantly from 0 then. When negative density dependence among FGs is not reduced, but per capita growth rates of FGs are heterogeneous and ordered differently among sites because of some environmental gradient, one retrieves the environmental filtering model (B). u should then be significantly negative. When FGs behave as ideal guilds (i.e., no density dependence among FGs), one retrieves the guild model. FG composition can be strongly similar among sites (C) or strongly dissimilar among sites (D), which should lead to significantly positive or negative u , respectively. Example of community samples are drawn for each scenario with colors corresponding to FGs and shapes corresponding to species. Size of samples is assumed to be controlled to 10 individuals.

and non-neutral models using snapshot data in these situations may require a large amount of data, and the average functional deviation may not be a powerful statistic to do so. Including other statistics in the analysis would probably contribute to increase the ability to detect non-neutral dynamics in those ambiguous situations (McGill et al. 2006). However, additional statistics have to meet the following two conditions: one must be able (a) to derive their distribution under the Neutral Theory and (b) to interpret departures from the prediction of the Neutral Theory in terms of reduced density dependence among FGs or environmental filtering of FGs.

In our study of rainforest tree communities in Karnataka, South India, we found a negative average functional deviation of phenology FGs (deciduous vs. evergreen species). Rainfall drove changing functional composition of tropical tree communities, separating evergreen (at high rainfall) and deciduous (at low rainfall) dominated forests. This validates our prediction and confirms that the previously observed shift from deciduous-dominated to evergreen-dominated forests (Pascal 1988) is not consistent with neutral theory. As mentioned

earlier, a significant negative average functional deviation of phenology FGs does not indicate whether spatial segregation of phenology along the rainfall gradient stems from differences in per capita (population) growth rates between competing FGs or differences in carrying capacities among noncompeting FGs. However, biological knowledge about the effect of water availability and drought in tropical tree communities suggested an influence of environmental filtering on mortality: evergreen trees undergo an increased per capita death rate associated with embolism in drier contexts, and deciduousness constitutes a stress-avoidance strategy that limits the deleterious effect of long dry seasons (Corlett 2016). This interpretation is consistent with the fact that, in our simulations of the environmental filtering model, values of the average functional deviation as negative as the one observed for phenology in the field occurred only when environment affected the death rate of FGs.

The diversity of vertical strata did not deviate from neutrality either in full communities or in deciduous species. By contrast, we found a significant and negative average functional deviation of stratum FGs among evergreen subcommunities, and lower rainfall level was

related to greater frequency of understory species among evergreen trees. This result is consistent with the idea that greater drought stress and embolism risk constrain taller evergreen trees in drier ecosystems (Corlett 2016), whereas in wetter forests, lack of such constraints allow evergreen trees to dominate upper strata as well. Conversely, leaf shedding allows avoiding embolism risk during driest periods and does not constrain the survival of taller deciduous trees in driest ecosystems, which may explain why we found no signature of environmental filtering on vertical stratum diversity of deciduous subcommunities. Consequently, we were not able to validate our prediction that differences in potential canopy stratum drive reduced negative density dependence.

Our study provides a simple way of testing how the distribution of functional and species diversity across communities deviate from a neutral situation, against two alternative hypotheses: (a) environmental filtering of FGs or (b) reduced negative density dependence among FGs. We have shown that hypotheses (a) and (b) are often impossible to discriminate with a snapshot pattern, which advocates for the acquisition and use of temporal community data where possible. Time series indeed allow us to unravel complex non-neutral dynamics at species (Adler et al. 2007) and FG levels (Alonso et al. 2015). However, we have illustrated that snapshot data of species and FGs distribution is often sufficient for rejecting the Neutral Theory. Our use of FGs and spatial data allows us to do so with more statistical power than approaches based on species abundance distribution in a single community (Chisholm and Pacala 2010, Al Hammal et al. 2015). We have illustrated the potential of our approach to reject neutrality in a tropical tree metacommunity, and retrieved that changing constraints along a major rainfall gradients shape the diversity of FGs of trees, probably through an environmental filtering effect upon death rate of trees. This example provided a first proof of concept of our approach. We also identified one particular type of situation where snapshot data are sufficient to conclude that FGs behave like guilds (i.e., reduced negative density dependence among FGs): when the average functional deviation is positive. Data sets showing a positive average functional deviation would bring strong empirical support to this finding. We predicted that pattern should arise for FGs based on traits that are likely to drive resource partitioning. We expected the potential canopy-height FGs to play that role, by differentiating species with clearly distinct position along some trade-off between light use and the use of other resources. We did not find such a pattern here, probably because constraints associated with water availability have a dominant imprint in our study system. Such patterns may have more chance to emerge at finer scale where environmental gradient is narrower. For instance, in a 25-ha study, Kraft et al. (2008) found several leaf and size-related traits to show nonrandom distribution within subplots, with very distinct strategies co-occurring more often than expected. Although this pattern was not tested against a neutral

model in their study, we speculate that average functional deviation is positive in this type of context.

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