Clumpy coexistence in phytoplankton: The role of functional similarity in community assembly

Caio Graco-Roza[1,4]*, Angel M Segura[2], Carla Kruk[3], Patrícia Domingos[1], Janne Soininen[4], Marcelo Manzi Marinho[1]

[1]Laboratory of Phytoplankton of Ecology and Physiology, Department of Plant Biology, University of Rio de Janeiro State, Rua São Francisco Xavier 524—PHLC Sala 511a, 20550-900, Rio de Janeiro, Brazil. Telephone: +552123340822

[2]Modelización y Análisis de Recursos Naturales, CURE-Rocha, Universidad de la República, Uruguay.

[3]Sección Limnología, IECA, Facultad de Ciencias, Universidad de la República, Uruguay.

[4] University of Helsinki, Department of Geosciences and Geography, PO Box 64, FI-00014, Helsinki, Finland.

***correspondence author: caiogracor@gmail.com**

Abstract

Emergent neutrality (EN) suggests that species must be sufficiently similar or sufficiently different in their niches to avoid interspecific competition. Such a scenario results in species-rich aggregation patterns termed clumps. Plankton has been a popular model system in developing and testing ecological theories, especially size structure and species coexistence. We tested EN predictions for the phytoplankton community along

the course of a tropical river considering body size structure and multidimensional trait similarity in terms of morphology-based functional groups (MBFG). We found two stable main clumps in body size with species pertaining to three MBFGs. Among-species differences in biovolume were driven by their functional redundancy at the clump level but not at the whole community level. Furthermore, the dominance of functionally redundant species at the clump level varied stochastically as expected under EN. The relative biovolume of species was related to species functional distinctiveness at the clump level. Our findings suggest that species with similar traits are selected under given environmental conditions, but even minor shifts in trait combination may lead to reproductive success.

Keywords: *species coexistence; emergent neutrality; functional distinctiveness; functional differences*

Introduction

Understanding the mechanisms promoting species coexistence and shaping community structure has been a long-standing goal in community ecology. The former idea that the number of coexisting species will be limited by the number of growth-limiting resources or niche dimensions (Gause 1936; Hardin 1960), and its derivate idea, “the paradox of the plankton” (Hutchinson 1957) , have been widely explained in terms of endogenous and exogenous spatio-temporal mechanisms (Roy & Chattopadhyay 2007). In contrast, the neutral theory suggests that diversity results from random dispersal, speciation and extinction rates with no role of niche differences in species coexistence (Hubbell 2001).

More recently, it was shown that community organization is driven by eco-evolutionary processes such as speciation and nutrient uptake kinetics resulting in groups comprising different species with similar ecological requirements (Gravel *et al.* 2006; Hubbell 2006; Scheffer & van Nes 2006). This finding led to the 'emergent neutrality hypothesis' (EN) (Holt 2006) and has been supported by a limited number of observational studies from a wide range of ecosystems (Segura *et al.* 2011; Thibault *et al.* 2011; Scheffer *et al.* 2015). EN suggests that species must be sufficiently similar, and thus, behave neutrally, or different enough in their niches to avoid competition. Such a scenario would result in species-rich aggregations or clumps along the niche axis (Scheffer & van Nes 2006; Vergnon *et al.* 2009; Fort *et al.* 2010). These predictions were tested theoretically at both steady (Fort *et al.* 2010) and fluctuating resource conditions (Sakavara *et al.* 2018), but beyond robust theoretical results, empirical evidence of EN is still scarce.

EN states that the clumpy species pattern arises from the species niche preferences and species within clumps would behave quite neutral (Scheffer *et al.* 2018). However, even small differences in organismal traits are linked to species performance in the niche space (McGill *et al.* 2006; Violle *et al.* 2007). Zooming in on the uniqueness of trait combinations of species, i.e. functional distinctiveness, within clumps may advance our comprehension of competitive interactions and disclose the trigger of stochasticity driving the species coexistence. Functional distinctiveness reflects the non-shared functions among species within a given species pool (Violle *et al.* 2007), mirroring the concept of functional redundancy (Pavoine *et al.* 2017). However, although two functionally redundant species most likely show high similarity in trait combination, functional distinctiveness is not directly linked to redundancy. One could expect two

equally distinct species to be non-redundant if such species show different niche preferences (Violle *et al.* 2017). This suggests that both functional differences and distinctiveness are good metrics to assess the role of trait combination in community assembly. Planktonic communities offer a highly interesting model for biodiversity theory testing due to their highly speciose communities and their known relationship between morphological traits and function.

Body size is considered as a master ecological trait and it is highly useful to characterize species niche (Downing *et al.* 2014). In phytoplankton, the body size is related to physiology and life-history (Litchman & Klausmeier 2008), photosynthetic processes (Marañón 2008), nutrient uptake kinetics (Litchman *et al.* 2010) and other eco-evolutionary processes (Sauterey *et al.* 2017). Despite the importance of body size, considering only a single trait as a proxy for the niche might obscure clumpy patterns (D ’andrea *et al.* 2018). The use of multiple traits emerges as a powerful tool to disentangle plankton functional structure and evaluate competing hypotheses (Reynolds *et al.* 2014; Chen *et al.* 2015; Bortolini & Bueno 2017). Morphology-based functional groups (MBFG) classification of phytoplankton species (Kruk *et al.* 2010) uses a combination of morphological traits to define taxa with similar physiology and ecological responses (Kruk *et al.* 2011), potentially overcoming the limitations of a single trait dimension only. Most importantly, specific combinations of traits within the MBFG could make two species of the same MBFG not redundant. Overall, the functional distance among species is a useful tool to compare species in a multidimensional space by comparing species' functional differences in high resolution (Mouillot *et al.* 2013).

Riverine ecosystems are highly heterogeneous systems characterized by a continuous water flow that affects the morphology, sedimentation patterns, dispersal, and phytoplankton diversity (Reynolds & Descy 1996; Wetzel 2001). Several theories explain the specific features of river phytoplankton communities, such as River Continuum (Vannote *et al.* 1980) and Flood Pulse (Junk *et al.* 1989) concepts. However, an explicit study of community size structure and phytoplankton species coexistence under EN in riverine ecosystems is lacking. Under the EN hypothesis, we expect that there is a stable clumpy distribution of species abundance (i.e. total biovolume) along the body size axis across space and time as a result of eco-evolutionary processes. We hypothesize that: H_1 – differences in species biovolume are linked to their functional differences at the clump (i.e. peak aggregation in body size) but not at the community level, because competition should be stronger within clumps rather than among clumps. However, the dominance within clump will vary stochastically between the redundant species because the interspecific competition rates would be similar to the intraspecific level; H_2 - Species with higher distinctiveness will show higher relative biovolume within clump because higher distinctiveness reduces the competition rates and increases reproductive success. Here, we evaluate these predictions in a tropical river by investigating phytoplankton community size structure both seasonally and spatially.

Methods

Study area

Piabanha river is in the tropical region of Brazil and has a drainage basin of approximately 4500 km² . The headwater is on Petrópolis at 1546m altitude and drains

to the medium valley of Paraíba do Sul river crossing three cities and with agricultural activities in their watershed. Monthly samples were taken in nine stations approximately every 6 km from headwaters to the mouth of Piabanha River between May-2012 and April-2013. A dry season and wet season were observed based on the rainfall data from two meterological stations close to the sampling sites. We set three river stretches (upper, medium, and lower courses) based on the sharp slopes at the river elevation profile. A detailed description of the biological and physico-chemcial sampling methodology as well as the dynamics of Piabanha river can be found in Graco-Roza et al. 2019.

Phytoplankton functional traits

Here, we measured species individual volume (V, μm^3), surface to volume ratio (sv^{-1}), maximum linear dimension (MLD, µm), and the presence of aerotopes, mucilage, flagella, silica. Functional traits were used to classify the species into MBFG (Kruk *et al.* 2010). This classification included the following seven groups: (I) small organisms with high surface volume ratio, (II) small flagellated organisms with siliceous exoskeletal structures, (III) large filaments with aerotopes, (IV) organisms of medium size lacking specialized traits, (V) flagellated unicells with medium to large size, (VI) non-flagellated organisms with siliceous exoskeletons and (VII) large mucilaginous colonies. A detailed description of the MBFGs can be found elsewhere (Kruk *et al.* 2010).

Clumpy pattern

The individual biovolume of species was used as the main niche axis (X= log2 volume) and Shannon entropy (S) was used to detect aggregation patterns of species along the niche axis (Fort *et al.* 2010; Segura *et al.* 2011) along the river and across seasons. The entropy index was defined as $S = \sum_1^n p_i \log2 (p_i)$ where p_i is the fraction of biovolume of species *i* in the community of *n* species. The niche axis was divided into equally spaced fractions. We determined the significance of entropy (*S*) peaks by comparing observed entropy against an expected uniform distribution under the null hypothesis of homogeneous entropy (Segura *et al.* 2011). One thousand comunities were created by sampling the volumes of species from a random uniform distribution bounded by observed individual volumes. Then, each species had a biovolume assigned to it, which was taken from a randomization of the observed biovolume matrix, keeping both the empirical species rank-abundance pattern and total biovolume in the sample. Subsequently, entropy was estimated for each segment of the niche as described in methods. For each segment, the observed S value was compared with the distributions of *S* generated under the null hyphothesis, with significance defined according to standard 5% criterion.

Hence, we computed species functional distances using a Gower's general similarity coefficient (Gower 1971) on six (sv^{-1}, MLD, aerotopes, mucilage, flagella, and silica) out of the seven functional traits included in MBFG classification to estimate the differences amongst species from significant clumps. Individual volume was excluded to avoid overweighting once it was used to define the clumps. We used Gower's dissimilarity (Gd) measure as it can handle mixed variable types (continuous and binary traits). Gd defines a distance value d_{jk} between two species as $d_{jk} = 1/N \sum_{i=1}^{n} | ((x_{ij}-x_{ik})/$

$(\max(x_i) - (\min(x_i)))$ | where, N is the number of functional traits considered, xij the value of trait i for species j and xik the value of the trait i for species k.

Functional differences (F_{Diff})

We tested our H_1 - differences in species biovolume are linked to their functional differences at the clump but not at the community level - by conducting Mantel tests with 1000 randomizations on pairwise functional differences (F_{Diff}) and differences in biovolume ($Diff_{Biov}$) at clump and community levels along the seasons and river stretches. Here, functional differences (F_{Diff}) were calculated as the pairwise difference between species based on their functional traits.

Functional distinctiveness (F_{Dist})

To test our H_2 - species with higher distinctiveness will show higher relative biovolume within the clump we applied linear regressions between species functional distinctiveness (F_{Dist}) and relative biovolume (R_{Biov}) standardized to range between zero and one at clump-level. F_{Dist} was calculated as the distance of a species from the centroid of its clump in the functional space. If centroids are weighted by the species abundances, F_{Dist} values are site-based and vary among samples. On the contrary, non-weighted values give a community-based measure of distinctiveness that reflects the number of species (not individuals) sharing similar trait combinations. Here, we consider the latter over the former to compare the relationship between R_{Biov} and F_{Dist} at clump-level across river stretches and seasons.

All the analyses were run in the R software, version 3.5.1 (R Development Core Team *et al.* 2016) using the packages *FD* (Laliberté *et al.* 2015), *vegan* (Oksanen 2017) and *ape* (Bolker *et al.* 2014).

Results

Three out of seven MBFGs (MBFG IV, V and VI) accounted for 95% of the mean biovolume of total phytoplankton in dry and wet seasons and 96.6% across the stretches (upper, medium, lower stretches). MBFG IV species size ranged from 21 μm^3 to 8181 μm^3 lacking specialized traits. MBFG V comprised unicellular flagellated species ranging in size from 31μm^3 to 31864μm^3 while MBFG VI included unicellular and chain-forming diatoms (48μm^3 to 19045μm^3). The three groups comprised 87% of a total of 150 recorded species. MBFG VI dominated in almost all river stretches and both seasons, except for the upper course during dry season that showed a dominance of group IV (Figure 1). The entire list of species, functional traits, and assigned MBFG can be found in the supplementary material - Table S1.

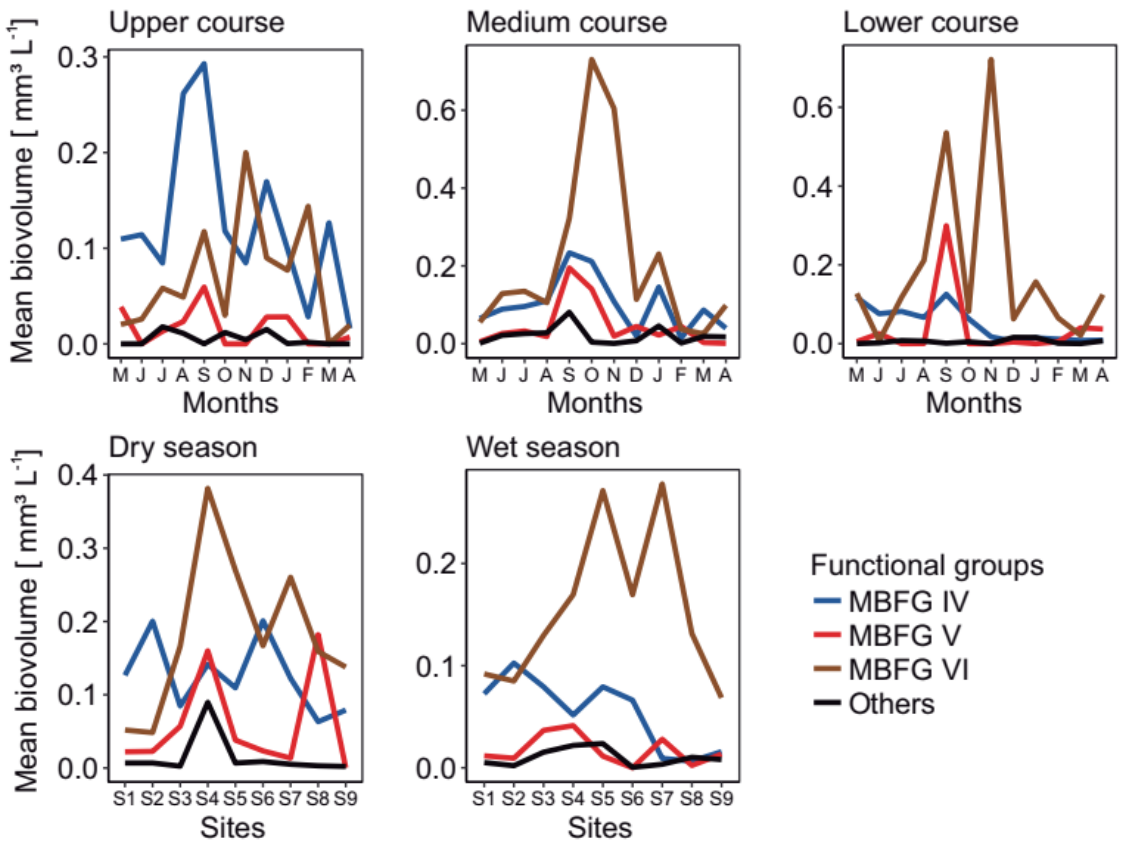

Figure 1. Mean biovolume of morphologic based functional groups (MBFG) along river stretches (upper, medium and lower course) and seasons (dry and wet).

There were two significant (randomization test, $p<0.05$, Figure 2) clumps along the niche axis in most of the samples. The first aggregation (clump I, 24 species) comprises species ranging from 9 to 10 in log2 volume mainly from MBFG IV. A second aggregation (clump II, 6 species) occurred in the range from 14 to 15 log2 volume, which was mainly dominated by species from MBFG VI (Figure 2). The remaining results are presented at the temporal (dry and wet seasons) and spatial (upper, medium and lower courses) levels.

The mean biovolume of species within clumps differed across seasons and river stretches even if the identity of dominant species did not vary. Within clump I, the

dominance was shared between *Pseudanabaena* sp. 4 (spp. 28) and *Pseudanabaena catenata* (spp. 12), whereas *Synedra* sp. (spp. 80) was showing the highest biovolume within clump II with alternating dominance among *Melosira* sp. (spp. 43; 1.5%), *Pinnularia* sp. 6 and *Pinnularia* sp.7 (Figure 2). Dominant species within clumps were not the dominant species at the whole river level (except for the upper course, P. *catenata*) though.

According to the Mantel tests, the relationship between F_{Diff} and $Diff_{Biov}$ was non-significant at the overall community level, except for the dry season. However, there was a significant ($p< 0.05$) relationship within clump I for the dry season and all the river stretches. Within clump II, the relationship was non-significant probably due to the small community size (18 pairs of species). Regarding F_{Dist} , we found a positive relationship ($p < 0.05$) with R_{Biov} at clump I for both seasons and also the upper course. However, we did not find any significant relationship at clump II (Figure S1).

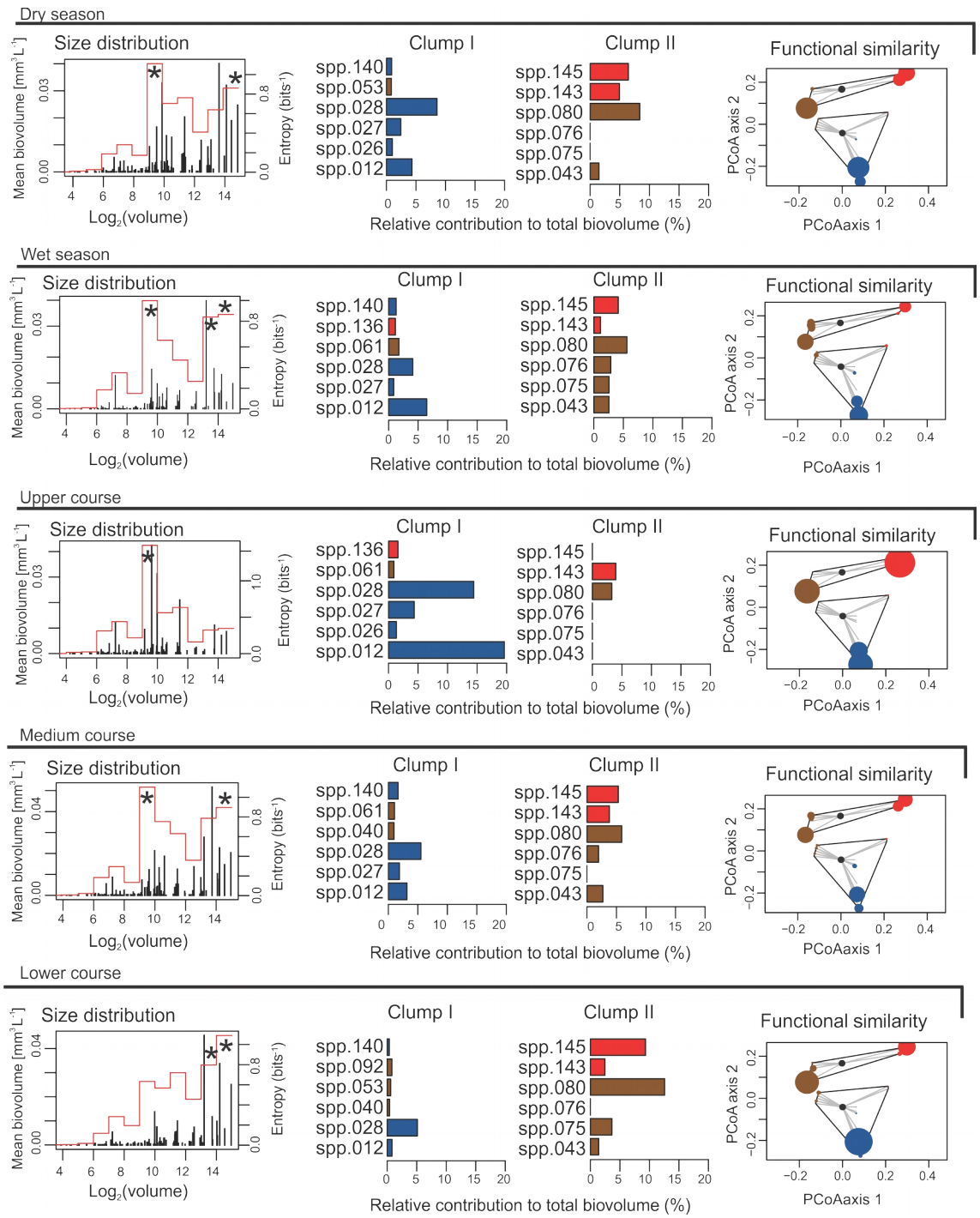

Figure 2. Phytoplankton size structure, the relative contribution of the six species with the highest biovolume, and functional similarity among species within the two main clumps. The sizes of circles in functional similarity panels were scaled by the relative contribution in biovolume of species at the clump level. The group colors legend can be found in Figure 1. * Significant clumps (randomization test; $p<0.05$).

Discussion

Present results showed that the clumps in body size are a conspicuous feature of phytoplankton community structure in riverine systems across seasons and river stretches. In fact, the observation of multimodal aggregation of species biovolume along body size axis alone does not imply that EN is the mechanism behind phytoplankton coexistence. Yet, it points to the integration of niche-based processes and neutrality driving community assembly (Vergnon *et al.* 2009). Our results does not support alternative explanations as pure Neutrality (Hubbell 2001) or High Dimensional hypothesis (Clark *et al.* 2007). This is simply because Pure neutrality predicts a uniform distribution of species biovolume along the niche axis (Hubbell 2001) and, although we are using multiple traits to expand our vision on species coexistence, the HDH does not predicts any particular trait distribution and (Vergnon *et al.* 2009; Ingram *et al.* 2018).

One alternative theory that are likely to explain clumpy aggregations is the Holling's Textural hypothesis (Holling 1992). The textural hypothesis explains multimodal species size distribution with environmental constraints. However, note that the clumps in our data were in the same size range found in previous studies (Segura *et al.* 2011, 2013), even though the earlier studies were not conducted in freshwaters. Furthermore, similar MBFG were found in both types of ecosystems, mainly V and VI, reflecting adaptations to survive in turbulent and mixed conditions (Margalef 1978; Soares *et al.* 2007; Bortolini & Bueno 2017). This suggests that the coexistence of these MBFGs tends to generate clumpy distributions that are eroded when the ecosystem properties favor the dominance of other MBFGs. This is because, in natural systems EN is not expected to be the only process shaping species biovolume, but will always interact with

environmental constraints (Vergnon *et al.* 2012). Studies evidencing EN using phytoplankton as the model community in coastal, estuarine, and here, riverine ecosystems presented fluctuations in environmental conditions (Segura *et al.* 2011, 2013), which is in agreement with recent modeling results (Sakavara *et al.* 2018).

Here we expanded the level of analysis from mere size structure towards the inclusion of new trait dimensions by analyzing the functional similarity at MBFG classification level and within clump functional differences. We found that the species from the same clump represent a selection of all the possibilities amongst MBGFs, reinforcing that body size is a good proxy for niche preferences of the species (Blanckenhorn 2000). This is in line with the idea that considering only a single trait could obscure the patterns behind community assembly (D'Andrea *et al.* 2018). Species within the same MBFG are expected to share ecological strategy (Kruk *et al.* 2010; Kruk & Segura 2012) and, accordingly to EN, would also perform similarly (Scheffer *et al.* 2018). Not surprisingly, we in fact observed that species within clumps represented mostly the same MBFG. EN hypothesizes a quasi-neutral coexistence of species at a clump level, but contrarily, we observed here a niche-based driven assembly process at clump I. It has been suggested that functional multidimensional space describes better community assembly processes (Bonser 2006) and the outcome of competition (Kraft *et al.* 2015) than a single trait framework because some traits would reflect better fitness differences or stabilizing niche differences than the others. Our results suggest a strong effect of stabilizing mechanisms at the overall community level as size differences increase and, at a clump level, equalizing forces take place because fitness differences are not large enough to avoid competition (Chesson 2000). Small trait differences eventually change species responses to multiple environmental factors (Elmqvist *et al.* 2003) resulting in

the coexistence of species with similar body size (Gallego *et al.* 2019). Here, we suggest that the lack of relationship between species biovolume and functional differences at a clump II results from the small number of species within the clump. Larger species generally show lower growth rates and nutrient-uptake, and thus, their effect in resource availability is low and favors the invasion of species with smaller body size (Gallego *et al.* 2019), resulting in the higher richness at clump I as observed here and in other studies (Vergnon *et al.* 2009; Segura *et al.* 2011, 2013). In addition, the rarity of large-bodied species reduces the probability that two individuals occupy the same niche simultaneously especially in open systems such as rivers. Such mechanism helps to maintain the lower fluctuation on individual biovolume as observed at clump II. On the contrary, higher number of species under the same size range impose trait variability and highlight the relationship between functional distinctiveness and species biovolume at clump I rather than at clump II. Our results thus support H_1 and show that, at the clump level, differences in species biovolume are driven by species functional differences but species dominance fluctuates stochastically.

The role of functional similarity in community assembly is even clearer when taking into account functional distinctiveness and its effects on species biovolume. The clustered pattern of species biovolume within clump I arise with the dominance of species with rare trait combination, whereas the dominant species within clump II showed a common trait combination. Despite larger species showing lower growth rates (Kruk *et al.* 2010), the elongated shape provides advantage under turbulent conditions (Reynolds *et al.* 1994) favoring these species under high flow conditions on nutrient-rich environments (Irwin *et al.* 2006). Furthermore, nutrients are hardly limiting phytoplankton growth especially in meso- or eutrophic rivers (Reynolds 2006), and

large-bodied species are mostly randomly introduced from different habitats (e.g. sediment or epiphyton) (Wang *et al.* 2014; Descy *et al.* 2017; Graco-Roza *et al.* 2019), which brings some uncertainty to the assumption of niche overlap due to size similarity. Thus, one cannot be sure if species within clump II are truly occupying same niche. Therefore, this may be the main reason for the lack of a relationship between functional distinctiveness and relative biovolume within clump II.

Emergent neutrality results from an eco-evolutionary process of which species evolve towards having only a limited number of functional groups (Scheffer & van Nes 2006). This implies that the self-organized aggregation patterns observed here are not likely a result of competitive exclusion within the Piabanha river, but a convergent evolution of competing species over time as already suggested in the seminal paper by Macarthur & Levins 1967, observed by Scheffer et al. 2015 and now corroborated by the observation of same size structure in same organisms across different environments (Segura *et al.* 2011, 2013). Note that even when the competition rates are relaxed due to sufficient nutrient supply, some other limiting factors that are not consumed by biotic organisms such as heat energy or turbulence determine species biovolume and in such a scenario, minor shifts in species trait combination might provide reproductive success. Our results show that functional distinctiveness plays an important role in species biovolume within clumps. Thus, we partially corroborated our H_2 - species with higher distinctiveness show higher relative biovolume within clump, but the mechanism that delimits clumps should be considered. In addition, we encourage future studies to investigate how functional distinctiveness modulates species abundances in species rich and poor communities.

In summary, we provided evidence of both neutral and niche perspective driving planktonic community assembly and support the view that emergent neutrality is a likely mechanism to explain species coexistence in an open and environmentally heterogeneous ecosystem. The use of MBFG classification and functional space to describe species within clumps revealed that under the same size range, species with a greater degree of redundancy alternate their dominance in an unpredictable way. Moreover, niche-based mechanisms within clumps were related to the environmental conditions and favored the most functionally distinct species. Finally, it is difficult to avoid the ghost of hidden niches (Barabás *et al.* 2013), but present results provide evidence from multiple angles that point to EN as a plausible mechanism in shaping species coexistence.

References

Barabás, G., D'Andrea, R., Rael, R., Meszéna, G. & Ostling, A. (2013). Emergent neutrality or hidden niches? *Oikos*.

Blanckenhorn, W.U. (2000). The Evolution of Body Size: What Keeps Organisms Small? *Q. Rev. Biol.*, 75, 385–407.

Bolker, B., Claude, J., Sien, H., Des-, R., Durand, B., Dutheil, J., *et al.* (2014). Package "ape." *Anal. Phylogenetics Evol.*

Bonser, S.P. (2006). Form defining function: interpreting leaf functional variability in integrated plant phenotypes. *Oikos*.

Bortolini, J.C. & Bueno, N.C. (2017). Temporal dynamics of phytoplankton using the morphology-based functional approach in a subtropical river. *Rev. Bras. Bot.*, 40, 741–748.

Chen, N., Liu, L., Li, Y.Y., Qiao, D., Li, Y.Y., Zhang, Y., *et al.* (2015). Morphology-based classification of functional groups for potamoplankton. *J. Limnol.*, 74, 559–571.

Chesson, P. (2000). Mechanisms of Maintenance of Species Diversity. *Annu. Rev. Ecol. Syst.*, 31, 343–366.

Clark, J.S., Dietze, M., Chakraborty, S., Agarwal, P.K., Ibanez, I., LaDeau, S., *et al.* (2007). Resolving the biodiversity paradox. *Ecol. Lett.*, 10, 647–659.

D'Andrea, R., Ostling, A. & O'Dwyer, J.P. (2018). Translucent windows: how uncertainty in competitive interactions impacts detection of community pattern. *Ecol. Lett.*, 21, 826–835.

D 'andrea, R., Ostling, A. & O 'dwyer, J.P. (2018). Translucent windows: how uncertainty in competitive interactions impacts detection of community pattern. *Ecol. Lett.*, 21, 826–835.

Descy, J.P., Darchambeau, F., Lambert, T., Stoyneva-Gaertner, M.P., Bouillon, S. & Borges, A. V. (2017). Phytoplankton dynamics in the Congo River. *Freshw. Biol.*, 62, 87–101.

Downing, A.S., Hajdu, S., Hjerne, O., Otto, S.A., Blenckner, T., Larsson, U., *et al.* (2014). Zooming in on size distribution patterns underlying species coexistence in Baltic Sea phytoplankton. *Ecol. Lett.*, 17, 1219–1227.

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B., *et al.* (2003). Response diversity, ecosystem change, and resilience. *Front. Ecol. Environ.*, 1, 488–494.

Fort, H., Scheffer, M. & Van Nes, E. (2010). The clumping transition in niche competition: A robust critical phenomenon. *J. Stat. Mech. Theory Exp.*, 2010.

Gallego, I., Venail, P. & Ibelings, B.W. (2019). Size differences predict niche and relative fitness differences between phytoplankton species but not their coexistence. *ISME J.*, 13, 1133–1143.

Gause, G.F. (1936). The Struggle for Existence. *Soil Sci.*, 41, 159.

Gower, J.C. (1971). A General Coefficient of Similarity and Some of Its Properties. *Biometrics*, 27, 857.

Graco-Roza, C., Santos, J.B.O., Huszar, V.L.M., Domingos, P., Soininen, J. & Marinho, M.M. (2019). Downstream transport processes modulate the effects of environmental heterogeneity on riverine phytoplankton. *Sci. Total Environ.*, 135519.

Gravel, D., Canham, C.D., Beaudet, M. & Messier, C. (2006). Reconciling niche and neutrality: The continuum hypothesis. *Ecol. Lett.*

Hardin, G. (1960). The Competitive Exclusion Principle. *Science (80-.).*

Holling, C.S. (1992). Cross-Scale Morphology, Geometry, and Dynamics of Ecosystems. *Ecol. Monogr.*, 62, 447–502.

Holt, R.D. (2006). Emergent neutrality. *Trends Ecol. Evol.*, 21, 531–533.

Hubbell, S.P. (2001). *The Unified Neutral Theory of Biodiversity and Biogeography*. *Monogr. Popul. Biol.*

Hubbell, S.P. (2006). Neutral theory and the evolution of ecological equivalence. *Ecology*.

Hutchinson, G.E. (1957). Concluding Remarks. *Cold Spring Harb. Symp. Quant. Biol.*

Ingram, T., Costa-Pereira, R. & Araújo, M.S. (2018). The dimensionality of individual niche variation. *Ecology*, 99, 536–549.

Irwin, A.J., Finkel, Z. V., Schofield, O.M.E. & Falkowski, P.G. (2006). Scaling-up from nutrient physiology to the size-structure of phytoplankton communities. *J. Plankton Res.*

Junk, W.J., Bayley, P.B. & Sparks, R.E. (1989). The flood pulse concept in river-floodplain systems. *Can. Spec. Publ. Fish. Aquat. Sci.*, 106, 110–127.

Kraft, N.J.B., Godoy, O. & Levine, J.M. (2015). Plant functional traits and the multidimensional nature of species coexistence. *Proc. Natl. Acad. Sci.*, 112, 797–802.

Kruk, C., Huszar, V.L.M.M., Peeters, E.T.H.M.H.M., Bonilla, S., Costa, L., LüRling, M., *et al.* (2010). A morphological classification capturing functional variation in phytoplankton. *Freshw. Biol.*, 55, 614–627.

Kruk, C., Peeters, E.T.H.M., Van Nes, E.H., Huszar, V.L.M., Costa, L.S. & Scheffer, M. (2011). Phytoplankton community composition can be predicted best in terms of morphological groups. *Limnol. Oceanogr.*, 56, 110–118.

Kruk, C. & Segura, A.M. (2012). The habitat template of phytoplankton morphology-based functional groups. *Hydrobiologia*, 698, 191–202.

Laliberté, E., Legendre, P. & Shipley, B. (2015). FD: measuring functional diversity from multiple traits, and other tools for functional ecology. *R Packag.*

Litchman, E. & Klausmeier, C. a. (2008). Trait-Based Community Ecology of Phytoplankton. *Annu. Rev. Ecol. Evol. Syst.*, 39, 615–639.

Litchman, E., de Tezanos Pinto, P., Klausmeier, C.A., Thomas, M.K. & Yoshiyama, K. (2010). Linking traits to species diversity and community structure in phytoplankton. *Hydrobiologia*, 653, 15–28.

Macarthur, R. & Levins, R. (1967). The Limiting Similarity, Convergence, and Divergence of Coexisting Species. *Am. Nat.*, 101, 377–385.

Marañón, E. (2008). Inter-specific scaling of phytoplankton production and cell size in the field. *J. Plankton Res.*

Margalef, R. (1978). Life-forms of phytoplankton as survival alternatives in an unstable environment. *oceanologica*.

McGill, B.J., Enquist, B.J., Weiher, E. & Westoby, M. (2006). Rebuilding community ecology from functional traits. *Trends Ecol. Evol.*, 21, 178–185.

Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., Mouillot, *et al.* (2013). A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.*, 28, 167–177.

Oksanen, J. (2017). Vegan: ecological diversity. *R Packag. Version 2.4-4*.

Pavoine, S., Bonsall, M.B., Dupaix, A., Jacob, U. & Ricotta, C. (2017). From phylogenetic to functional originality: Guide through indices and new developments. *Ecol. Indic.*, 82, 196–205.

R Development Core Team, ., R Core Team, R Developement Core Team & R Development Core Team, . (2016). R: A language and environment for statistical computing. *R Found. Stat. Comput.*, 1, 409.

Reynolds, C. & Descy, J. (1996). The production biomass and structure of phytoplankton in large rivers. *Arch. Hydrobiol.*, 113, 161–187.

Reynolds, C.S. (2006). *The Ecology of Phytoplankton*. *Ecol. Phytoplankt.* Cambridge University Press, Cambridge.

Reynolds, C.S., Alex Elliott, J. & Frassl, M.A. (2014). Predictive utility of trait-separated phytoplankton groups: A robust approach to modeling population dynamics. *J. Great Lakes Res.*, 40, 143–150.

Reynolds, C.S., Descy, J.P. & Padisák, J. (1994). Are phytoplankton dynamics in rivers so different from those in shallow lakes? *Hydrobiologia*, 289, 1–7.

Roy, S. & Chattopadhyay, J. (2007). Toxin-allelopathy among phytoplankton species prevents competitive exclusion. *J. Biol. Syst.*, 15, 73–93.

Sakavara, A., Tsirtsis, G., Roelke, D.L., Mancy, R. & Spatharis, S. (2018). Lumpy species coexistence arises robustly in fluctuating resource environments. *Proc. Natl. Acad. Sci.*, 115, 738–743.

Sauterey, B., Ward, B., Rault, J., Bowler, C. & Claessen, D. (2017). The implications of eco-evolutionary processes for the emergence of marine plankton community biogeography. *Am. Nat.*, 190, 116–130.

Scheffer, M. & van Nes, E.H. (2006). Self-organized similarity, the evolutionary emergence of groups of similar species. *Proc. Natl. Acad. Sci.*

Scheffer, M., van Nes, E.H. & Vergnon, R. (2018). Toward a unifying theory of biodiversity. *Proc. Natl. Acad. Sci.*, 115, 201721114.

Scheffer, M., Vergnon, R., Van Nes, E.H., Cuppen, J.G.M., Peeters, E.T.H.M., Leijs, R., *et al.* (2015). The evolution of functionally redundant species; Evidence from beetles. *PLoS One*, 10, 1–10.

Segura, A.M., Calliari, D., Kruk, C., Conde, D., Bonilla, S. & Fort, H. (2011). Emergent neutrality drives phytoplankton species coexistence. *Proc. R. Soc. B Biol. Sci.*, 278, 2355–2361.

Segura, A.M., Kruk, C., Calliari, D., García-Rodriguez, F., Conde, D., Widdicombe, C.E., *et al.* (2013). Competition drives clumpy species coexistence in estuarine phytoplankton. *Sci. Rep.*, 3, 1–6.

Soares, M.C.S., Huszar, V.L.M. & Roland, F. (2007). Phytoplankton dynamics in two tropical rivers with different degrees of human impact (southeast Brazil). *River Res. Appl.*, 23, 698–714.

Thibault, K.M., White, E.P., Hurlbert, A.H. & Ernest, S.K.M. (2011). Multimodality in the individual size distributions of bird communities. *Glob. Ecol. Biogeogr.*

Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E. (1980). The River Continuum Concept. *Can. J. Fish. Aquat. Sci.*, 37, 130–137.

Vergnon, R., Dulvy, N.K. & Freckleton, R.P. (2009). Niches versus neutrality: Uncovering the drivers of diversity in a species-rich community. *Ecol. Lett.*, 12, 1079–1090.

Vergnon, R., van Nes, E.H. & Scheffer, M. (2012). Emergent neutrality leads to multimodal species abundance distributions. *Nat. Commun.*, 3, 663.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., *et al.* (2007). Let the concept of trait be functional! *Oikos*, 116, 882–892.

Violle, C., Thuiller, W., Mouquet, N., Munoz, F., Kraft, N.J.B., Cadotte, M.W., *et al.* (2017). Functional rarity: the ecology of outliers. *Trends Ecol. Evol.*, 32, 356–367.

Wang, C., Li, X., Lai, Z., Li, Y., Dauta, A. & Lek, S. (2014). Patterning and predicting phytoplankton assemblages in a large subtropical river. *Fundam. Appl. Limnol. / Arch. für Hydrobiol.*, 185, 263–279.

Wetzel, R.G. (2001). *Limnology: Lake and River Ecosystems*. *J. Phycol.*