

LETTER

Niches versus neutrality: uncovering the drivers of diversity in a species-rich community

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Abstract

Ecological models suggest that high diversity can be generated by purely niche-based, purely neutral or by a mixture of niche-based and neutral ecological processes. Here, we compare the degree to which four contrasting hypotheses for coexistence, ranging from niche-based to neutral, explain species richness along a body mass niche axis. We derive predictions from these hypotheses and confront them with species body-mass patterns in a highly sampled marine phytoplankton community. We find that these patterns are consistent only with a mechanism that combines niche and neutral processes, such as the emergent neutrality mechanism. In this work, we provide the first empirical evidence that a niche-neutral model can explain niche space occupancy pattern in a natural species-rich community. We suggest this class of model may be a useful hypothesis for the generation and maintenance of species diversity in other size-structured communities.

Keywords

Biodiversity, body mass, coexistence, competition, migration, neutrality, niche space, niche-based processes, species similarity.

Ecology Letters (2009) 12: 1079–1090

INTRODUCTION

After half a century of research, it is still not understood how species-rich communities are maintained in the face of the theoretical prediction that single-species dominance is more likely than the stable coexistence of numerous species competing for small numbers of common resources (Hutchinson 1961). Generally, theoretical and empirical studies have explained the coexistence of competing species in terms of either niche-based or neutral processes (Gaston & Chown 2005). Niche-based models assume differences in resource use between species; species thereby avoid competition and are able to coexist (Gause 1934; Hardin 1960; Chesson 2000). In contrast, neutral models assume that all species are identical: consequently no single species is at a competitive advantage or disadvantage, and exclusion does not occur (Bell 2000; Hubbell 2001, 2005). The point has been made that considering niche and neutral perspectives separately may be incorrect (Leibold & McPeck 2006). For coexistence to occur, niche-based processes must be strong enough to cancel out the dissimilarities in average fitness among species. These niche-based processes need only be weak when average fitness differences between species are small, such as in communities close to neutrality. Processes that push communities toward neutrality are said to be equalizing.

In recent years, models combining equalizing and niche-based processes have been developed (Bonsall *et al.* 2004; Holt 2006; Scheffer & van Nes 2006; Cadotte 2007). However, empirical studies that could confirm this dual mechanism for species coexistence are lacking.

A suite of coexistence hypotheses exists that differ in the relative importance they give to neutral processes in maintaining diversity. These form a continuum ranging from ‘strong’ neutrality when equalizing processes are maximal, to complete niche differentiation when they are absent. Here, we highlight four hypotheses that span the neutrality-niche continuum and predict contrasting patterns of niche-space occupancy by competing species within communities. The aim of this study was to derive predictions of distributions of species in niche space from each hypothesis and to test their consistency with data. This will allow measuring the importance of different processes along this continuum.

As a model that is purely neutral, *Hubbell's neutrality hypothesis* (Hubbell 2001) posits that the entire community is composed of identical species, leading to the expectation of uniform, trait-independent distributions of species in niche space. A model that incorporates both niche and neutral mechanisms is the *emergent neutrality hypothesis* (Scheffer & van Nes 2006) which predicts aggregated species richness

distributions along a single synthetic niche axis. This reflects the simultaneous operation of processes of competitive exclusion and neutral coexistence of very similar species, resulting in species-rich aggregations where competition is weak and gaps where competition is strong. A purely niche-driven model of coexistence is *Holling's textural model* (Holling 1992) which also predicts aggregated species richness distributions although the underlying mechanism differs. Here, it is the distribution and fractionation of available resources, rather than species interactions that results in aggregations of the species using these resources. Finally, the *high dimensionality hypothesis* (Clark *et al.* 2007) proposes that coexistence of apparently similar species occurs because of 'hidden' additional niche dimensions along which differences exist. This is a purely niche-based explanation: within multi-dimensional niches overlap in time and/or space is never large enough to lead to competitive exclusion and equalizing processes are absent.

Equalizing processes can theoretically contribute to species coexistence; however, their true importance for generating diversity within actual communities is poorly understood. In this paper, we begin by taking the four models outlined above to make predictions about the distributions of species in niche space and their dynamics over time. We then test these predictions using data from a species-rich community of marine phytoplankton in which niche characteristics are summarized by a single synoptic axis (body mass) and for which we have a long time-series. We show that the models make overlapping but differentiable predictions, and that the data are consistent only with models that combine both niche and neutral processes.

MATERIAL AND METHODS

Data

Phytoplankton communities are particularly well-suited to test for a combined influence of niche-based and neutral processes because they consist of a set of apparently similar species that respond in a predictable way to the environment (Reynolds 1989). It has been widely shown that phytoplankton species of similar mass are functionally similar. Indeed, they co-occur in space and time in similar hydrodynamic regimes and conditions (Huisman *et al.* 1999; Rodriguez *et al.* 2001), share common predators (Armstrong 2003) and have similar critical concentration thresholds for nutrients (Chisholm 1992). Competition for nutrients is size-based in phytoplankton; with small-bodied individuals dominating under low nutrient conditions and large-bodied ones outcompeting smaller species and dominating under high nutrient conditions. The fundamental process of photosynthesis also scales with body mass (Marañón *et al.* 2007).

We used data collected in the Western English Channel (<http://www.westernchannelobservatory.org.uk/14/Phytoplankton>), 10 nautical miles off the coast of Plymouth (50°15' N, 4°13' W), at the L4 station. This is an extensive data set, consisting of 12 years of weekly sampling (1992–2003) of phytoplankton abundance and their corresponding biomasses and average cell size for 192 different taxa. For each observation, a 100 mL sample was taken at 10 m depth. Phytoplankton cells were immediately fixed then let to settle for a minimum of 48 h. Species were identified and individuals enumerated using inverted microscopy. For each taxa, the average cell volume was determined from a 50 individual sample at the beginning of the sampling period, following the equations proposed by Kovala & Larrance (1966). Average cell volumes were recalculated regularly throughout the sampling period to check for deviance from these initial values. When deviance was high additional size groups were created. Cell volume was converted into carbon mass (in pg) using Eppley's algorithm (Eppley *et al.* 1970) (R.P. Harris, D. Bonnet and C. Widdicombe, Plymouth Marine Laboratory, personal communication). More details on the sampling method are provided in Appendix S1.

Predictions to be tested

Prediction 1: species biomass and position on the body mass niche axis
Niche-based coexistence theories predict that the intensity of competition for common resources depends on niche similarity and will result in non-uniform distributions of dominant species. In contrast, the neutral theory predicts uniformly distributed species' biomasses along the body mass niche axis (Table 1).

Prediction 2: species richness aggregations along the body mass niche axis

The neutral theory suggests that species positions in niche space are independent from their traits, which would lead to a uniform distribution of species richness along the body mass niche axis. The high dimensionality hypothesis makes a similar prediction, albeit for different reasons: indeed if all species have narrow niches that hardly overlap, then species interactions are minimized and hence there should be no structure in the positioning of species in niche space. Both the emergent neutrality hypothesis and the textural hypothesis predict the presence of distinct aggregations, i.e. clusters of species separated by gaps, of competing species in niche space (Table 1).

Prediction 3: permanent and occasional species along the body mass niche axis

In communities, permanent and occasional species often show different patterns and are governed by different ecological processes (Magurran 2007). Permanent commu-

Table 1 Predictions for the four considered species coexistence hypotheses

Test	Neutral	Niche-neutral	Grainy niche (textural hypothesis)	Multi-dimensional niche
Body mass distribution of dominant species	Uniform	Non-uniform	Non-uniform	Non-uniform
Overall SBMD	Uniform	Multimodal	Multimodal	Uniform
Permanent/occasional SBMD	No difference	Distinct distributions	No difference	No difference
Synchrony	No relationship with body mass difference	Decrease with increasing body mass difference	Decrease with increasing body mass difference within aggregations only	No Prediction

SBMD, species richness body mass distributions.

nity members are abundant and representative of the mean local conditions (Magurran & Henderson 2003). They will therefore interact strongly and consistently and interactions will play an important role in determining the densities of these species. In contrast, species found occasionally in the community are migrants: rarer, weaker interactors that belong primarily to other communities (Magurran & Henderson 2003). Occasional phytoplankton species are passively transported by currents from a wider metacommunity (Leibold & Norberg 2004). Their densities will largely be a function of locally unusual environmental conditions and the composition of the metacommunity, which will differ from the local one in that it reflects the factors that drive abundances within other distant communities. Emergent neutrality predicts that competitive interactions create empty areas within niche space. If emergent neutrality prevails, we predict that the emergence of aggregations in niche space should only occur in permanent members of the community and not in migrant occasional species. In contrast, the other hypotheses predict no differences in the niche distributions of permanent and occasional species: specifically, for the same prevailing abiotic conditions, the textural hypothesis predicts that the aggregated species richness body mass distributions found in permanent and migrant species should be the same (Table 1).

Prediction 4: population synchrony and relative body mass

High population synchrony (i.e. when two time series are in phase or in opposite phase) is expected between functionally similar species, i.e. organisms that share the same resources and react in the same way to the same environmental conditions. The biomass fluctuations of coexisting populations in saturated neutral communities are necessarily synchronized to some extent (Loreau & de Mazancourt 2008). However, the neutral model predicts no relationship between the difference in species niches (i.e. distance between species on the body mass niche axis) and synchrony. The emergent neutrality hypothesis and the

textural hypothesis both predict aggregated species richness body mass distributions but yield different synchrony patterns. In the emergent neutrality model, competition occurs everywhere on the niche axis, with pairwise synchrony depending on species niche overlap (Scheffer & van Nes 2006). Synchrony should therefore decrease with increasing body mass difference, with a weaker relationship expected for pairs belonging to the same aggregations where species tend towards neutrality. The textural hypothesis posits that species distribution matches resource distribution along the body mass axis, which means that species only exploit the patch of resource that is available at their scale (Allen *et al.* 2006). In that case, competition occurs only among neighbours packed in the same species aggregations and does not occur across scales among distant species. The high dimensionality hypothesis makes no prediction about synchrony (Table 1).

Statistical methodology

Prediction 1

The influence of niche overlap on species biomass was estimated using the standardized effect size methodology (Mason *et al.* 2008). If the most abundant species (in terms of biomass) are not uniformly distributed along the niche axis, niche-based processes are at work. Abundant species can either be clustered on the part of the axis matching the prevailing environmental conditions or positioned far apart if negative interactions prevent neighbours from all reaching high biomass. In both cases, the most abundant species should show a non-uniform pattern of niche overlap. If the null hypothesis cannot be rejected, neutrality, or a mixture of niche-based processes cancelling out each other, is likely. Biomass-weighted niche overlap is quantified using the Standardized Effect Size (SES) index.

$$SES = \frac{I_{obs} - I_{exp}}{\sigma_{exp}}$$

I_{obs} is the observed biomass-weighted distance on the body mass axis and is calculated as follows:

$$I_{\text{obs}} = \sum_{i=1}^{S-1} \sum_{j=i+1}^S I_{ij} p_i p_j$$

with S the number of species in the community, I_{ij} the distance between the positions of species i and j on the body mass axis and p_i and p_j the biomass of species i and j respectively. I_{exp} and σ_{exp} are obtained by attributing at random (following a uniform distribution) observed biomasses over the set of observed body masses for 10 000 simulations and taking respectively the average biomass-weighted distance and its standard deviation across all randomizations (Mason *et al.* 2008). The statistical significance of the SES index is found by comparing I_{obs} with the distribution of I_{exp} under the null hypothesis.

Prediction 2

We tested for the presence of aggregations of high species richness separated by species-poor gaps along a body mass axis using bootstrapped Generalized Additive Models (GAM) (Fewster *et al.* 2000). This method is based on sampling the observed species richness–body mass distributions with replacement ($n = 400$), fitting a GAM to each replicate and calculating the corresponding second-order derivatives, which identify significant turning points (peaks and troughs) in the species richness–body mass distributions. The 95% confidence intervals are computed for both the GAMs and second derivatives. Peaks and troughs correspond respectively to a negative second derivative flanked by two higher values and a positive second derivative flanked by two lower ones. All GAM fitting was performed using the R *mgcv* package (Wood 2006).

Prediction 3

The presence of species richness aggregations along the body mass axis cannot on its own allow the distinction between large-scale abiotic (textural hypothesis) and local biotic (emergent neutrality) niche space partitioning mechanisms. To differentiate between these two possibilities, we examine the degree of aggregation of permanent and occasional community members. We defined permanent species as the ones reported at least once in one month during each of the sampled years. Species observed at a lower frequency are considered occasional. We checked and found that permanent species were more abundant than occasional ones, throughout the whole sampling period. This supports our assumption that competition by occasional species on the rest of the community is weaker (see Figure S1).

Occasional species are, by definition, less frequently detected than permanent ones. Consequently the mean

number of occasional species for each of the 12 months of the year can be lower than the mean number of permanent species. To compensate for this sampling artefact and make sure that any difference between permanent and occasional species is genuine, the GAM technique was applied to subsamples of the permanent distributions (see Appendix S2).

Prediction 4

We use mutual information at lag zero (MI) (Cazelles 2004) to quantify synchrony between the dynamics of permanent species as a function of the ratio of their body masses. We expect to find a large range of MI values for a group of strongly interacting species irrespective of whether species dynamics are the product of low dimensional nonlinear processes (species of similar body mass have similar overall niches) or high-dimensional linear noise (species of similar body mass differ largely over other niche axes). This is because, in a multispecies system, competition between species leads to a variance in the degree of synchrony: for example, an increase in the density of one species would impact negatively on some competitors (negative correlation); however, the indirect effects of this interaction could yield positive effects on some species via competitive release, or increases in the resource base could yield positive effects on the densities of all species using a similar resource (both leading to positive correlation).

If body mass differences influence synchrony, we expect at least maximum MI values at a given body mass ratio to show a significant decline along the body mass ratio axis. Quantile regression is an appropriate tool to describe the boundaries of such relationships. Obtaining MI involves converting time-series into a succession of symbols describing dynamic states (i.e. ‘decrease’, ‘increase’, ‘peak’, ‘trough’) and calculating mutual entropy from each possible pair of symbolic series.

$$MI_{SU} = H_S + H_U - H_{SU}$$

H_S and H_U are the entropy of the symbolic series S and U , respectively, and H_{SU} is the joint entropy. Entropy for the symbolic series S is given by the equation:

$$H_S = - \sum_{i=1}^k p(s_i) \log_2 [p(s_i)],$$

with $p(s_i)$ the frequency of the symbol (i) in the series.

For each pair of species, the mean value of a null distribution of mutual information is computed. To obtain null distributions, surrogate time series are generated under the hypothesis that the time order of the values of a time series A has no influence on its dynamic cohesion with a time series B. The technique we used differs from the one presented in Cazelles’ (2004) work in the sense that our null

model also accounts for seasonal effects: indeed all phytoplankton species are likely to see their biomass increase during the warmer period and decrease during winter, regardless of competition relationships between them. For each species, we therefore calculated the probabilities that any symbol (D, I, P or T for ‘decrease’, ‘increase’, ‘peak’ and ‘trough’) occurs for all months of the year, then used these probabilities to compute 500 surrogate symbolic series spanning the sampling period (observations made for 127 months from 1992 to 2003). The calculation of statistical significance ensures that no pair of species is attributed high synchrony by chance, for example if two species are absent in most observations. On average permanent species were present in 7 months per sampled year and the data set therefore contained relatively few zeros.

RESULTS

Species biomass and position on the body mass niche axis

The most abundant species, in terms of biomass, lie very far apart on the body mass axis (Fig. 1a). The observed biomass-weighted niche overlap is significantly smaller from that expected by chance. Consequently, we reject the null hypothesis that abundant species are uniformly distributed along the body mass niche axis (P -value < 5%; Fig. 1b). This suggests that the strong interspecific competition exerted by the best competitors on the body mass axis prevents other similarly-sized species from also reaching high abundances. Neutrality fails to explain this pattern, which instead is consistent with the predictions made under the other three hypotheses.

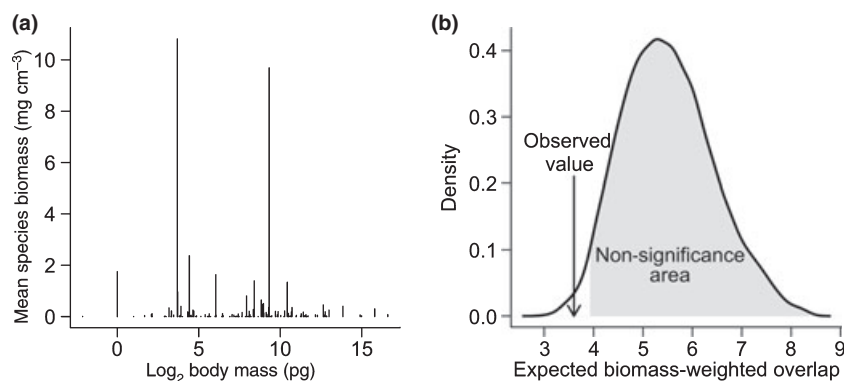


Figure 1 Influence of niche overlap on species biomasses. (a) Distribution of the species average monthly biomass over the body mass niche axis (in pgC) for the L4 station English Channel phytoplankton community. Biomass (in mgC m³) was averaged over the 12 years of sampling. The most abundant species lie far apart along the body mass axis and therefore have a smaller niche overlap. (b) Position of the observed biomass-weighted niche overlap (black arrow) relatively to the distribution expected under the null hypothesis, i.e. no effect of niche overlap on species biomasses. The observed overlap between the most abundant phytoplankton species along the body mass niche axis is significantly smaller than expected by chance (shaded area) at a five percent confidence level.

Permanent and occasional species richness–body mass distributions

Species richness distributions differ markedly between permanent and occasional species. There are two very distinct peaks in the time-averaged body mass spectra of permanent species that persist from month-to-month over the seasonal production cycle (Fig. 2). By contrast, occasional species exhibit flat unimodal distribution patterns, overlain by weak secondary peaks that vary with time (Fig. 3). These results are robust to a range of definitions of permanent and occasional species and to the use of biovolumes instead of body masses (see Figures S2 and S3, respectively). This strongly indicates that aggregation of species along the body mass axis is due to the influence of the most permanent species on the overall distribution. Diatoms were by far the most dominant group in the community (75% of the permanent species and 62% of the occasional ones) but taxonomy could not explain observed differences in body mass distributions as higher levels of aggregations for permanent species held within all systematic groups (see Figure S4).

Population synchrony and relative body mass

At the community level, maximum (99th quantile) and mean synchrony between pairs of species dynamics decrease significantly with increasing differences in body mass (slope = -0.024 and -0.0033 at $P < 5\%$), compared with a null model which predicts much weaker synchrony independent of body mass ratio (Fig. 4a). This result can be interpreted as a decrease in the strength of interaction as niche overlap decreases. The shaded area contains the

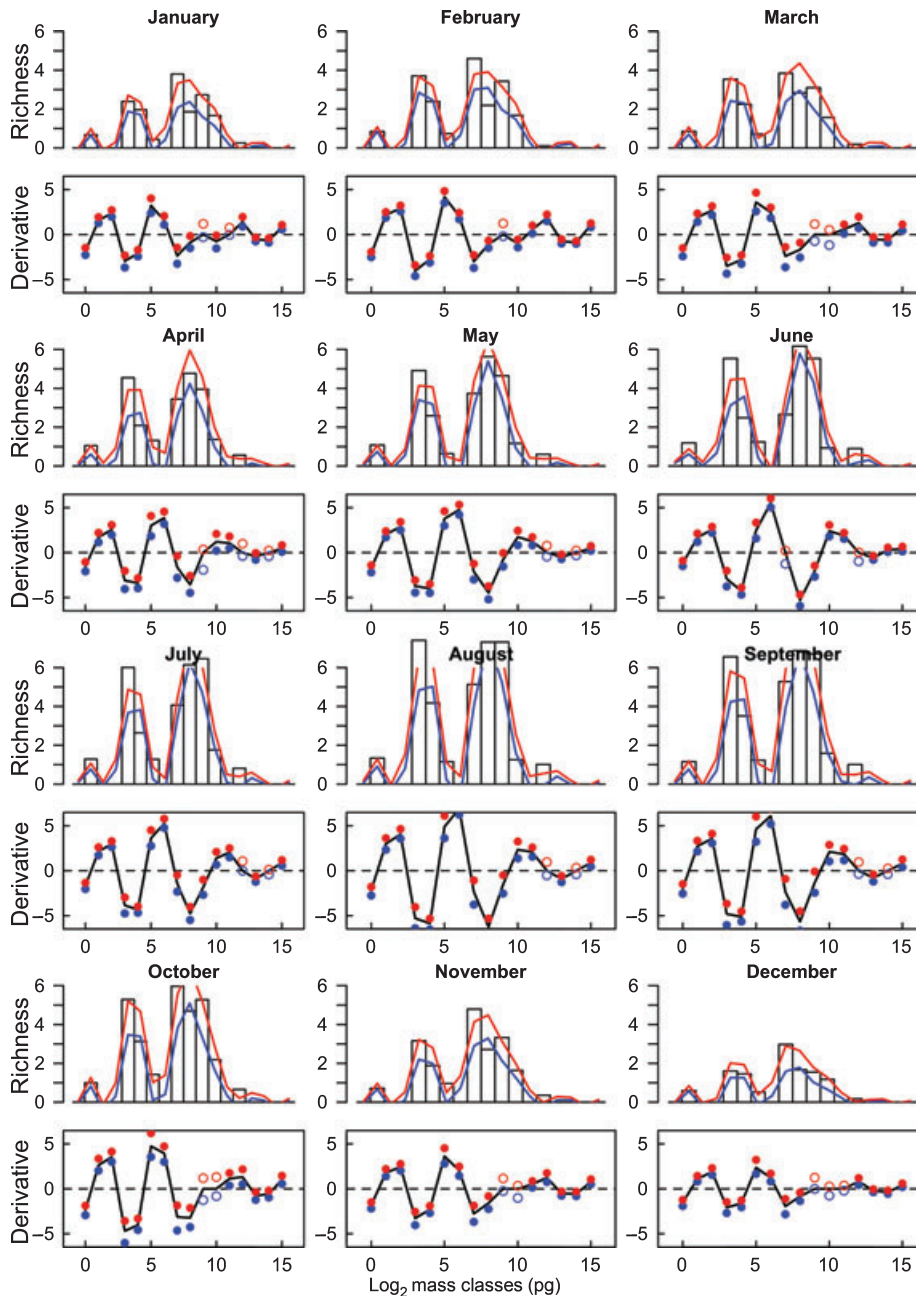


Figure 2 Distribution of species richness along the body mass axis for permanent species. Histograms of average monthly species richness body mass (in pgC) distributions for the permanent species show two strong aggregations that are remarkably stable throughout the year and across the production regime. The red and blue curves represent the upper and lower limit of the 95% GAM confidence envelopes, respectively. Significant peaks and troughs are indicated by significant turning points (filled points) in the second derivative analyses shown below each monthly barplot. The red and blue points are respectively the upper and lower limit of the 95% GAM confidence envelopes. Statistical significance is achieved if the upper and lower limits of the second derivative confidence interval are both negative (the curve turns downward) or both positive (the curve turns upward). The thick black lines link the medians of the GAM confidence envelopes.

species pairs belonging to the same aggregations – note that the negative relationship between synchrony and body mass ratio extends beyond the limits of this area (Fig. 4a).

Figure 4b,c confirms that the decrease of synchrony with increasing body mass ratio holds for pairs of species both within (maximum synchrony slope = -0.018 at $P < 5\%$,

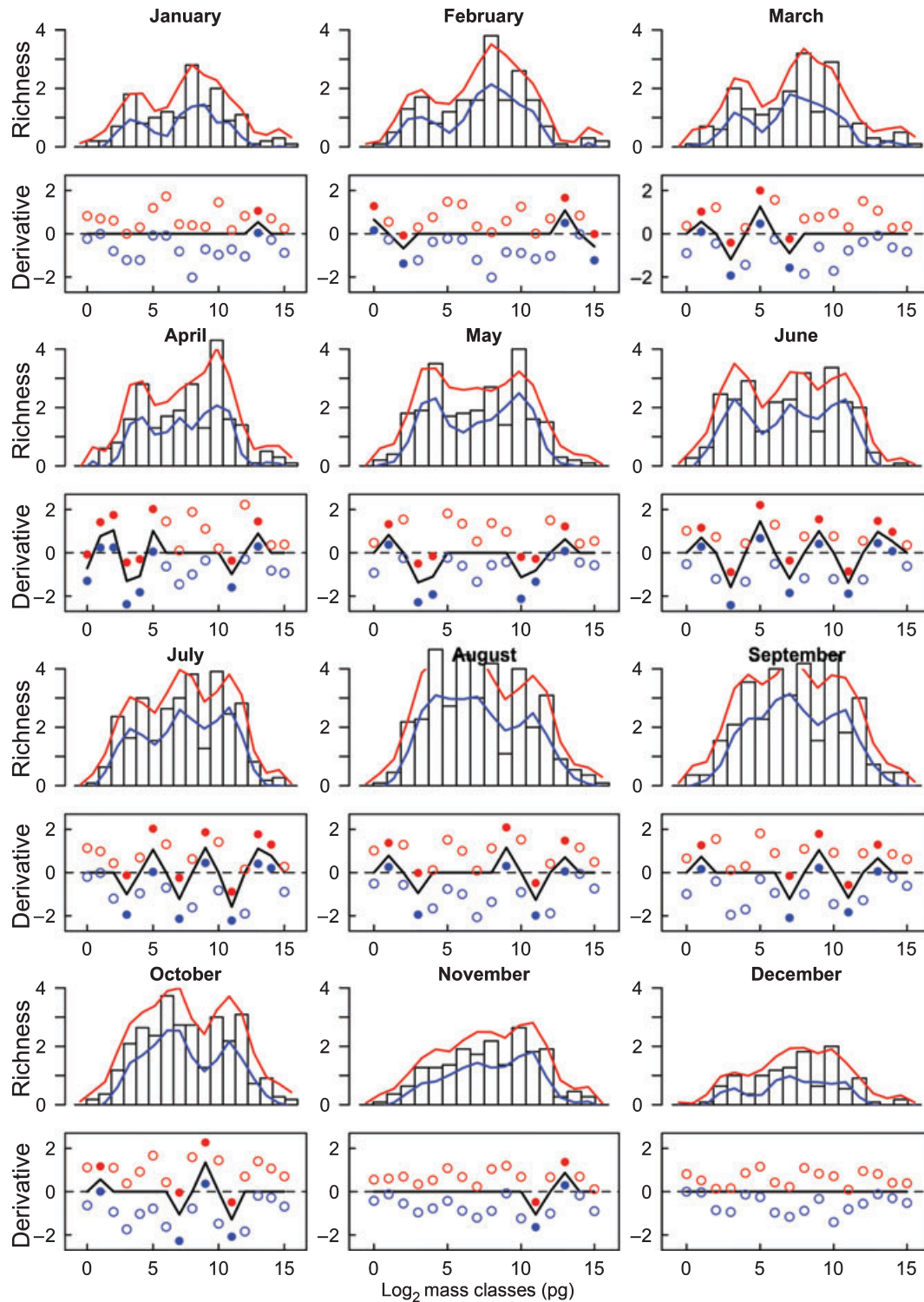


Figure 3 Distribution of species richness along the body mass axis for occasional species. Analysis of average monthly species richness body mass (in pgC) distributions for the occasional species shows weak and variable aggregations, a pattern that greatly differs from the permanent species distributions. Colours and symbols as in Fig. 2.

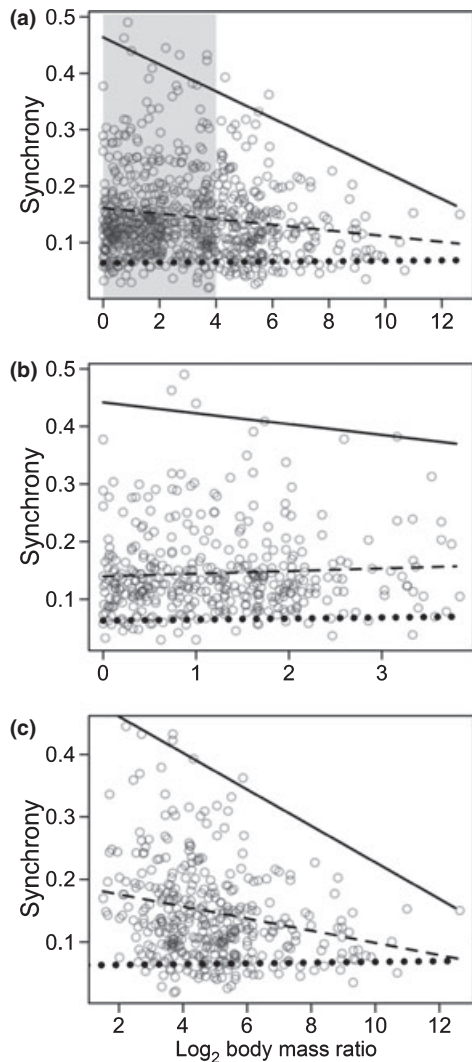


Figure 4 Relationship between synchrony and body mass ratio for all permanent species (a), for permanent species clustered in the same species richness body mass aggregations only (b) and for permanent species belonging to different aggregations only (c). Synchrony between permanent species dynamics was measured using mutual information (MI). Each fading black points represents MI for a pair of species. The black line represents the relationship between maximum MI and body mass ratio (99th quantile). The dashed black line is the linear regression for MI values averaged across binned body mass ratios. Mean values under the null hypothesis (i.e. independent species dynamics) are represented by a dotted black line. The shaded area represents the extent of the detected species richness–body mass aggregations.

mean synchrony slope non-significant) and among species richness aggregations (maximum synchrony slope = -0.029 , mean synchrony slope = -0.01 at $P < 5\%$). For species belonging to different aggregations, we checked that the

negative slopes were not an artefact due to the disproportionate influence of the rarer very large body mass ratios (see Figure S5). Species within aggregations are interacting with species outside – this is inconsistent with Holling’s textural hypothesis which predicts differing patterns of synchrony within and between aggregations. The neutral model predicts no relationship between synchrony and body mass ratio at the community level and can also be rejected here. The low slope of the relationship between synchrony and body mass ratio within aggregations suggests that similarly-sized species are nearly neutral; however, the significant interactions that exist between species inside aggregations and species outside is not in accordance with the idea of isolated, purely neutral substructures. Decreasing synchrony with increasing body mass ratios across all species pairs is consistent only with the niche-neutral model.

DISCUSSION

Here, we have taken a hypothesis-based approach to test the relative importance of niche-based and equalizing, neutral processes for maintaining coexistence in a species-rich natural community. We have described non-uniform patterns of biomass, species richness and species synchrony along a body mass axis in a long-term marine phytoplankton data set. We compared these observations with expectations derived from four hypotheses spanning a continuum of processes ranging from fully neutral to entirely niche-based. Although each of our tests taken individually was not sufficient to rule out all but one coexistence hypothesis, the group of four tests yielded compelling results. Our study strongly suggests that a combination of niche-based and equalizing processes best explains the patterns and species dynamics within the L4 station marine phytoplankton community (Table 2). To the best of our knowledge, this is the first empirical evidence for the combined role of niche and neutral processes in structuring species diversity in a natural community.

Many hypotheses have been formulated for species coexistence in marine phytoplankton (Roy & Chattopadhyay 2007), but they account only for a few different roles for equalizing processes whose range is well spanned in this study. For example, subtle physiological differences among seemingly identical species or high-frequency environmental changes are both high dimensionality hypotheses. This is because they assume no role for equalizing processes and coexistence is purely allowed by niche-based processes that limit niche overlap in space and time. Importantly, an aggregated species richness body mass distribution cannot be diagnostic of purely niche-based processes. Aggregations of similar species separated by empty niche areas would be a common output of any model integrating elements of neutrality and niche-based processes along a single niche

Table 2 Agreement of the results with the predictions made under the four considered hypotheses

Test	Grainy niche			
	Neutral	Niche-neutral	(textural hypothesis)	Multi-dimensional niche
Body mass distribution of dominant species	No	Yes	Yes	Yes
Overall SBMD	No	Yes	Yes	No
Permanent/occasional SBMD	No	Yes	No	No
Synchrony	No	Yes	No	NA

SBMD, species richness body mass distributions.

axis. Indeed, whether these models envisage negative or positive effects of species on their neighbours, the intensity of processes at any point of the niche axis depends on the relative position of all interacting individuals. As a consequence, and because the assumption of evenly distributed species is not realistic, the strength of positive or negative forces varies along the axis and creates niche space regions where coexistence is more likely than others. This alternation of favourable and less favourable niche spaces predicted by all niche-neutral models should result systematically in aggregated patterns of species richness. Note that in systems where processes are not size-based, or where another single niche axis cannot be used, the model would not be appropriate.

The existence of robust patterns and dynamics in natural systems such as the L4 station phytoplankton community is assumed to reflect underlying mechanisms. However, inferring causality without recourse or the ability to undertake large-scale experimentation is always problematic. The recent development of sophisticated inference has however proven a powerful approach for narrowing down the mechanisms most likely to underlie large-scale macroecological patterns. The basis of the approach is to confront large-scale real-world biological patterns with predictions generated by a range of plausible mechanisms and to draw inference on which mechanism is most likely (Brown 1995; Hilborn & Mangel 1997; Gaston & Blackburn 2000). At the L4 station phytoplankton community this pattern-to-mechanism protocol allows to identify one most likely hypothesis for coexistence mechanisms.

Deviation from a clear body size/ecological function relationship and the existence of sampling biases are two factors that can alter the strength of our conclusions. There is necessarily a degree of scatter around the relationship between body mass and species role in pelagic systems. For example, at similar size dinoflagellates are more mobile than diatoms and differ in their nutrient requirements (Broekhuizen 1999; Ragueneau *et al.* 2002). However, if they exist, the global signals that can be picked up over long periods of time or large spatial extents are not sensitive to such small-scale variance (Brown 1995). This is clearly the case at the L4 station where

patterns emerging from 12 years of weekly sampling in a species-rich community show statistically significant size-based features. In samples, the smallest organisms are harder to detect and the largest ones are rarer and more likely to be missed by an observer. At the L4 station, such biases cannot explain the presence of a species-empty area over intermediate size classes of the permanent species richness body mass distribution, where there is no particular difficulty in detecting organisms. Both permanent and occasional species richness body mass distributions are dominated by diatoms, which makes detection biases due to taxonomy unlikely.

Despite the early promise of the neutral theory, many detailed analyses have rejected the assumption of ecological equivalence in a wide range of communities, including phytoplankton, coral reefs, tropical trees, birds, marine invertebrates and mammals (Chave 2004; Dornelas *et al.* 2006; McGill *et al.* 2006; Ricklefs 2006; Kelly *et al.* 2008). Specifically for phytoplankton, Walker & Cyr (2007) tested for neutrality in a number of lake communities using the conventional Species Abundance Distribution fit and found that in most cases the observed community structure differed significantly from that predicted by the neutral model. Many tests of neutrality such as this are termed 'weak' macroecological tests (McGill 2003). Our analysis relied on a much stronger test than a simple goodness-of-fit and assessed the ecological relevance of neutrality through the analysis of body mass patterns and species dynamics, and similarly suggests that neutrality alone is insufficient to account for species richness – abundance patterns. Backed up by ecological observations showing that phytoplankton species are affected differently by environmental changes (Reynolds 1989), formal hypothesis testing therefore clearly indicates that phytoplankton communities are not in general neutral in the 'strong' sense (Bell 2000) of the word.

The textural hypothesis typically prevails at large scale and explains aggregations of species in niche space through the physical partitioning of their resources across spatial scales. At the L4 station, the existence of such partitioning is doubtful because some occasional species are systematically found within species-poor parts of the body mass axis, which are therefore not empty of resource. The relationship

between synchrony and species body mass ratios describes a continuous, body mass ratio-dependent competition between all permanent species. This is different from the interaction pattern predicted by the textural hypothesis where only species belonging to the same aggregations compete for common resources. The relationship between ecological processes and processes occurring at coarser temporal and spatial scales is rarely addressed in classic niche-based species diversity models (Tokeshi & Schmid 2002), yet they have a major influence on local distributions (Raffaelli *et al.* 2000; Warwick 2007). Size-based physiological constraints for example are likely to shape niche space occupation by species at the L4 station (Maurer 2003). Even though our tests suggested these mechanisms were not primarily responsible for the aggregated patterns observed at the L4 station, a good understanding of the theory of species coexistence within communities cannot ignore this possibility.

The high dimensionality hypothesis was first proposed as a way to tackle explicitly the observed complexity of the natural world and an alternative to other, low dimensionality models that may be misleading where lack of evidence for differences in species niches does not equate actual similarity (Clark *et al.* 2007). The complexity of Nature is obvious but within communities some species have more similar niches than others and share a number of ecological characteristics. Similarity could therefore influence the effect of competition on species relative abundances and ultimately could play a role in maintaining species diversity. The coexistence of similar species within aggregations separated by troughs along the body mass axis (Fig. 2) is not predicted by the high dimensionality hypothesis, but suggests that equalizing processes play a role in allowing coexistence at the L4 station phytoplankton community.

Overall, our tests suggest that a combination of niche processes and neutrality, the emergent neutrality hypothesis, is the most likely mechanism for species coexistence at the L4 station phytoplankton community. Crucially, and contrary to Hubbell's vision of neutrality, emergent neutrality does not require perfect equivalence to arise; in fact, niche differences are necessary for aggregations to emerge and neutrality is an outcome rather than an assumption. Hubbell (2005) has evoked the possibility that neutrality does not hold at the community level, but within functional substructures. His model however does not articulate in a mechanistic way neutrality with niche-based processes whose importance in allowing species coexistence has largely been proven. Niche-neutral models such as emergent neutrality do not rule out neutrality as a concept, on the contrary they give it considerably more credibility by explicitly making that link with niche-based processes. Like Hubbell's neutral model, the emergent neutrality model only describes an unstable coexistence at the scale of the local

community but a number of realistic mechanisms that very commonly occur within natural communities can turn transient neutral aggregations into permanent structures (Scheffer & van Nes 2006).

Multi-modal species size distributions are extremely frequent in nature (Allen *et al.* 2006). Our results provide the first empirical evidence for groups of similar species coexisting in an otherwise niche-driven community (Leibold & McPeck 2006). There is a major obstacle in the development of improved diversity models based purely on the principle of niche. Indeed, the theory stipulates that the division of resource among competing species depends on their particular traits: the amount of complexity that should be taken into account to build sufficiently generic niche-based models has so far been prohibitive. The use of body mass as a synopsis of species niches is common in marine ecology, and offers great potential to develop models that explicitly consider competition in relation to species traits. Further exploring of the relevance and consequences in terms of coexistence of size-based species similarity is needed and the many aggregated body mass distributions documented within pelagic systems would seem to constitute a particularly promising line of study.

ACKNOWLEDGEMENTS

We acknowledge the Western Channel Observatory, as part of the Sustained Observations Theme of NERC Oceans 2025, for the collection and analysis of the L4 data. We thank Roger Harris for providing the data as well as Delphine Bonnet and Claire Widdicombe for making available the details of the sampling methodology and ecology of the L4 station phytoplankton community. We thank Tom Webb and Yunne Shin for their constructive criticism of the manuscript. This work is a contribution to EUR-OCEANS Network of Excellence funded by the European Commission. RV was funded through a EUR-OCEANS scholarship. NKD is funded by the Canadian Natural Sciences and Engineering Research Council and the Canada Research Chairs Program. RPF is funded by the UK Royal Society University Research Fellowship.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

- Figure S1** Relative contributions to total biomass of occasional and permanent species over the sampling period.
- Figure S2** Sensitivity analysis of species richness–body mass distributions to the definition of permanence.
- Figure S3** Species richness–biovolume distributions for permanent and occasional species.
- Figure S4** Species richness–body mass distributions within taxonomic groups.

Figure S5 Sensitivity of the relationship between body mass ratio and synchrony for permanent community members belonging to different species richness body mass aggregations.

Appendix S1 Detailed sampling methodology.

Appendix S2 Detailed sub-sampling method for permanent species.

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Editor, Helmut Hillebrand

Manuscript received 1 April 2009

First decision made 7 May 2009

Second decision made 3 July 2009

Manuscript accepted 17 July 2009

Appendix S1: additional details on sampling methodology

During the 12 years covered by sampling, 192 taxa were identified by a single observer, among which 147 to the species level. A Leica DMIRB inverted microscope was used for species identification. Sampling was systematically done at the same time of the day, in the morning. Phytoplankton is sampled using water bottles and immediately fixed in Lugol's iodine and buffered formaldehyde. All plankton cells are counted in the Lugol's sub-sample and coccolithophores identified and enumerated in the formaldehyde sub-sample. The most abundant cells are counted in either fields of view or two transects (one vertical and one horizontal) and then extrapolated to concentration per mL. The rest are enumerated in the settled sample. Eppley's algorithm for conversion from cell volume (in μm^3) to body mass (in pg carbon) is as follows:

$$\text{Protozoa (exclu diatoms) pgC cell-1} = 0.6 \times \text{volume}^{0.94}$$

$$\text{Diatoms pgC cell-1} = 0.352 \times \text{volume}^{0.76}$$

On a log scale Eppley's algorithm yields results nearly identical to those given by the more recent Menden-Deuer & Lessard's equations (2000), which are now also used at the L4 station (exponents are 0.939 (non-diatoms) and 0.811 (diatoms)).

References:

Menden-Deuer S. & Lessard E.J. (2000). Carbon to Volume Relationships for Dinoflagellates, Diatoms, and Other Protist Plankton. *Limnology and Oceanography*, 45, 569-579.

Appendix S3

For all 127 months for which observations were available, permanent distributions are sub-sampled to match the number of species appearing in the corresponding occasional distributions. This is because the detection by GAM fitting of significant species richness aggregations along the body mass axis is sensitive to the number of species present in the distributions. For each month, this re-sampling process is performed 500 times following the observed probability distributions that a permanent species occurs in any given body mass class at a given month. Average sub-sampled distributions are then used for GAM fitting and second derivative analysis.

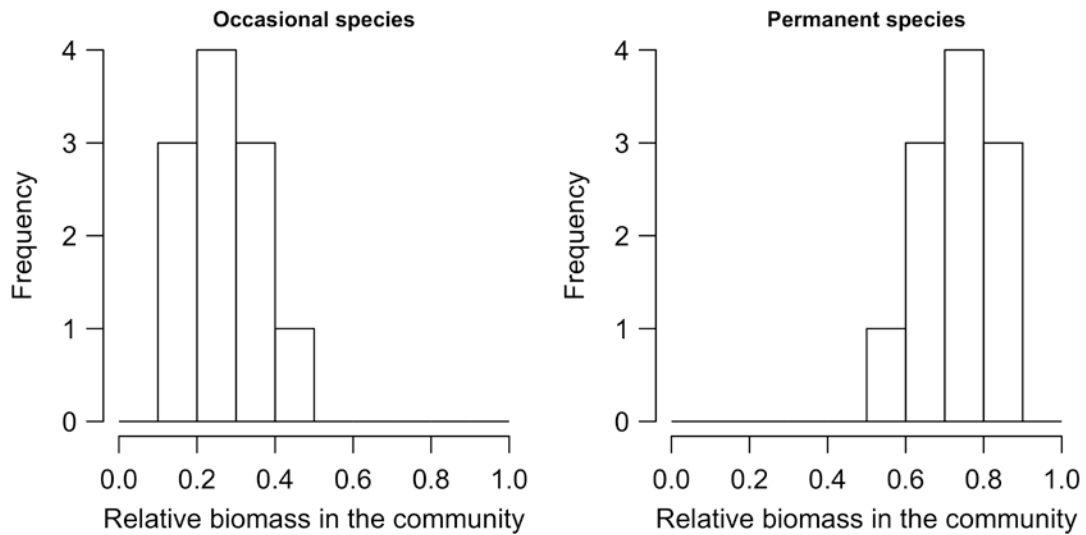


Figure S1: frequency distribution of relative contributions to total biomass of occasional and permanent species across all sampled years.

At the L4 station occasional species account for less than 30% in 70% of the cases. These species never represent more than 50% of the biomass. This result supports the idea that the negative impact of competition exerted by permanent members of the community is stronger.

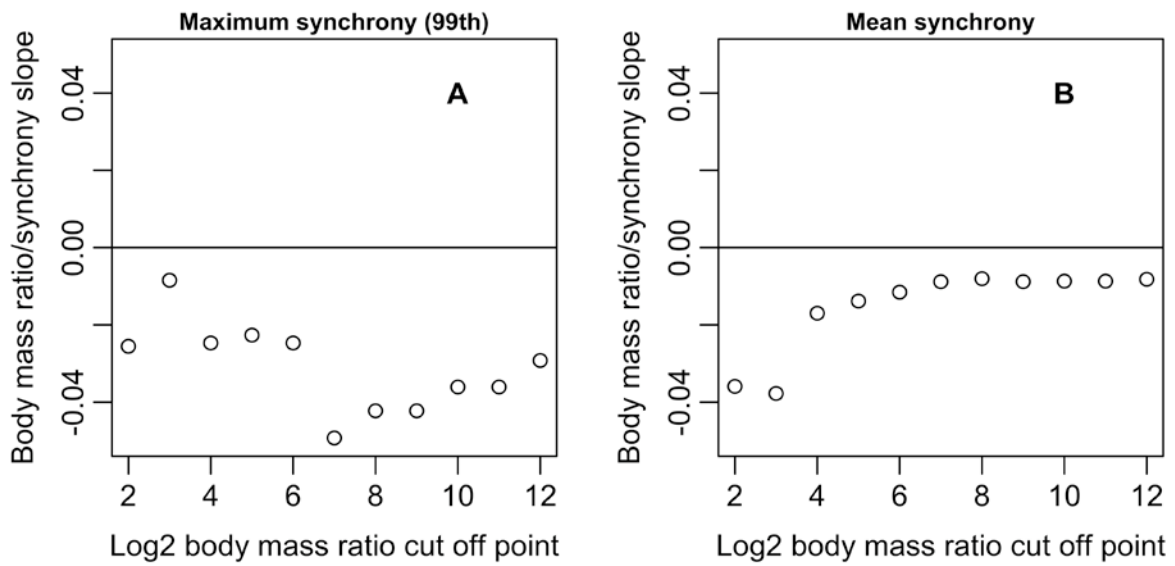


Figure S5. A: Sensitivity of the 99th slope of the body mass ratio/synchrony relationship to large body mass ratios, for permanent community members belonging to different species richness body mass aggregations. From right to left an increasing number of large body mass ratios are excluded from the linear regression. B: For the same species, similar analysis for the mean synchrony slope.

In both cases, the slopes remain negative for all data subsets, which rules out the possibility of an artefact due to the influence of rarer large body mass ratios.

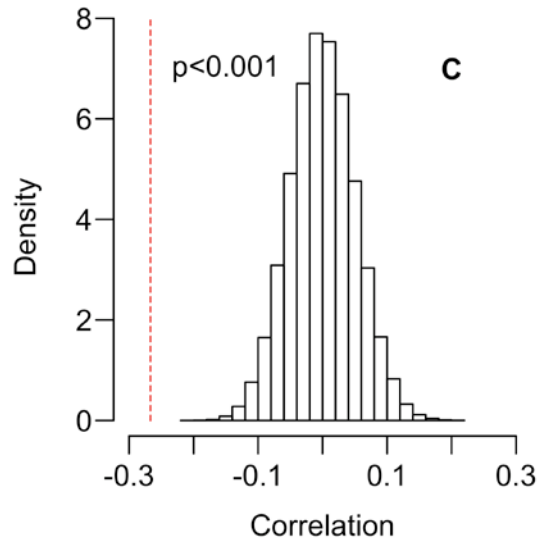


Figure S7 C: For permanent species belonging to different species richness body mass aggregations, statistical significance of the observed correlation (red dashed line) between body mass ratio and synchrony compare to a null distribution (histogram).

Significance is obtained by comparing the observed correlation with a null distribution computed by randomization (100000 reshuffles) under the hypothesis that there is no relationship between synchrony and body mass ratio. The observed value (-0.27) is significantly more negative than expected under the null hypothesis ($p < 0.001$). This means that there is a global significant negative correlation between synchrony and body mass ratios. This result again dismisses the possibility of an artifactual relationship.