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ASSESSING AND COMPARING RELATIONSHIPS BETWEEN ECOSYSTEM FUNCTIONING AND SPECIES DIVERSITY ACROSS FOREST ECOSYSTEMS

Tesis que presenta

MARÍA DE LOURDES CADENA FERNÁNDEZ

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Director de tesis

Dr. Ernesto Iván Badano

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I

Constancia de aprobación de la tesis

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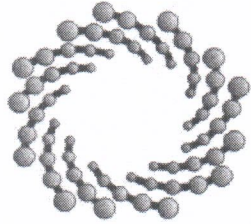
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que se desarrolló bajo la dirección de

Dr. Ernesto Iván Badano _

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Dedicatoria

A mi padre por ser siempre la historia más grande de vida que conozco, a mi madre por ser mi amiga infalible, y a mi hermano por ser el mejor compañero de travesuras.

Son el mejor ejemplo a seguir que alguien puede desear.

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A "papá Canelo", donde quiera que estés, espero te sientas orgulloso.

Contenidos

Contenidos

Abstract

Ecosystems are the fundamental unit in ecology, it is at this level that fundamental processes for the ecosystem functions are made; in recent years it has been proved that this processes are positively related to the species diversity, nevertheless, there are no global studies that could actually define this relation. The principal goal for this research is to implement a new methodology to evaluate the relationships between ecosystem function and species diversity at a global scale. In order to use this methodology it was necessary to use the databases of A.H. Gentry from the SALVIAS project which contain information from more than 200 forests worldwide. With this information, Monte Carlo simulations were carried out (re-sampling proportional to the sample size) for each database, and the shape of the curve was observed as a result of the mean of the accumulated biomass groups as the species richness increased. Afterwards, regressions were applied (with the formula $F = \alpha S^{\beta}$) in order to classify the curves according to the parameters of the curve α and β. These parameters were later compared with several biotic and abiotic factors (Holdridge life-zones, precipitation, elevation, latitude and species richness). We got 152 positive deceleration response curves, 39 positive quasilinear and 7 positive accelerative curves, a clear relationship was observed between α and β parameters and the Holdridge life-zones, in addition tendency curves were appreciated when comparing the parameters with elevation, latitude and species richness.

Keywords: Ecosystems, Ecosystem function, Species diversity, Monte Carlo Simulation.

Resumen

Los ecosistemas son la unidad fundamental de la ecología, y es a ese nivel que se realizan procesos fundamentales para el funcionamiento del mismo, en los últimos años se ha corroborado que dichos procesos se relacionan de manera positiva con la diversidad presente en dicho ecosistema, sin embargo, no existen estudios a escala global que puedan ayudar a determinar esta relación. El objetivo principal de este estudio radica en implementar una metodología para evaluar las relaciones entre funcionamiento ecosistémico y diversidad de especies a nivel global. Para poder implementar la metodología fue necesario utilizar las bases de datos de A.H. Gentry del proyecto SALVIAS las cuales contienen información de más de 200 bosques alrededor del mundo. Con esta información, se realizaron simulaciones Monte Carlo (re-muestreo proporcional al tamaño de la muestra) para cada base de datos y se observó la forma de la curva que resultaba del promedio de grupos de biomasa acumulada a medida que la riqueza de especies aumentaba. Posteriormente se realizaron regresiones (mediante la fórmula $F = \alpha S^{\beta}$) para poder clasificar las curvas en base a los parámetros α y β. Dichos parámetros fueron después comparados con diversos factores tanto bióticos como abióticos (zonas de vida de Holdridge, precipitación, elevación, latitud y riqueza de especies). Se obtuvieron un total de 152 curvas positivas desacelerativas, 39 curvas positivas cuasi lineales y 7 curvas positivas acelerativas, se pudo apreciar una clara relación entre los parámetros α y β y las zonas de vida de Holdridge, además de apreciar líneas de tendencia al correlacionar con la elevación, latitud y riqueza de especies.

Palabras clave: Ecosistemas, Funcionamiento ecosistémico, diversidad de especies, simulaciones Montecarlo.

Introduction

An overview of relationships between ecosystem functioning and species diversity

Ecosystems are a fundamental unit in ecology because most processes involving the flow, storage and recycling of materials and energy in the biosphere occur at this level of organization (Kimmins 2003). These ecosystem processes result from the interaction between the abiotic components of the ecosystem, such as climate and soil type, and the biotic communities inhabiting them, which can vary in composition and diversity across spatial and temporal scales (Giller & O'Donovan 2002). The outcomes of these processes are usually referred as *ecosystem functions*, and include climate regulation, maintenance of soil fertility, carbon sequestration and biomass accumulation, among others (Chapin et al. 1997, Hector et al. 2001, Naeem & Wright 2003). In the last three decades, theoretical and empirical studies have shown that ecosystem functioning is positively related to the diversity of biotic communities (e.g., Elrich & Elrich 1981, Tilman et al. 1996, Hector et al. 1999, Wilsey & Potvin 2000, Jonsson & Malmqvist 2003, Tiunov & Scheu 2005, Badano & Marquet 2008, 2009, Cadotte et al. 2011). Therefore, understanding the relationships between ecosystem functioning and species diversity (hereafter, F-D relationships) has become a scientific imperative because of the extent and intensity with which human activities are threating both local and global biodiversity (Ehrlich & Wilson 1991, Chapin et al. 1998, Ceballos & Ehrlich 2002, Sala et al. 2000, Díaz et al. 2005, Nelson 2005). Despite the relevance of the F-D relationships may have to explain the impacts of biodiversity loss on the outcome of natural processes, integrative studies comparing the behavior of these relationships across ecosystems are still being scarce (but see Hector et al. 1999).

Perhaps the most intuitive way to determine the impacts of biodiversity loss on ecosystem functioning is by analyzing the shape of the F-D relationships across ecosystem differing in their species diversity and composition. However, such an approach is difficult to address because a wide number of mechanisms have been proposed to explain the F-D relationships (Giller & O'Donovan 2002). Most studies on this issue have shown that ecosystem functioning usually rises as communities become more diverse until reaching a saturating point above which functioning does not largely increase, even when diversity is still increasing (Giller & O'Donovan 2002). This asymptotic behavior has been attributed to the existence of *functionally redundant* species in the communities, which are able to replace each other in terms of their contribution to functioning (Tilman et al. 1996, Tilman 1997, Naeem 1998, Hector et al. 1999, Schwartz et al. 2000, Dukes 2001, Fonseca & Ganade 2001, Mikola et al. 2002, Cox et al. 2006, Badano & Marquet 2009). On the other hand, some studies have proposed that ecosystem functioning could increase linearly with diversity if species composing the community are *functionally complementary* and all of them perform substantial contributions to ecosystem processes (Schwartz et al. 2000, Loreau & Hector 2001, Cardinale et al. 2002, 2007, Reiss et al. 2009, Reich 2012). It has been also proposed that minor increases in ecosystem functioning should be expected with rising diversity if most species in the community are subjected to strong physical stress but, in these ecosystems, abrupt increases in functioning could be observed if a particular, ecologically unique species is introduced into the community. This later relationship has been proposed to occur when *keystone species* or *facilitator species* are included in the community and improve the performance of the other species (Sala et al. 1996, Naeem et al. 2002, Ebenman & Jonsson 2005, Chapin et al. 2011). These three mechanisms are commonly invoked to explain the shape of F-D relationships in the nature, but several other

hypothetical mechanisms have also been proposed (see Ehrlich & Ehrlich 1981, Carpenter 1996, Naeem, 1995, Rosenzweig & Abramsky 1994).

Since the primary focus of most empirical studies assessing F-D relationships was to determine the influence of the functional identity of species on ecosystem functioning, it is also important to note that of the wide majority of response curves obtained for these relationships were constructed by using extremely reductionist approaches. Experimental studies on this issue, for instance, commonly use communities composed by forbs and grasses, which are artificially assembled to experimentally manipulate their diversity and composition (e.g., Tilman & Downing 1994, Tilman et al. 1996, Hooper & Vitousek 1997, Dukes 2001, Cardinale et al. 2002, Badano & Marquet 2009, Flynn et al. 2011). Although these studies provided important insights on the mechanisms regulating ecosystem functioning, these experimentally-created communities probably neither reflect the full complexity of natural communities nor the diversity levels they actually can reach (Ruiz-Jaen & Potvin 2011). On the other hand, the few observational studies addressing F-D relationships in naturally assembled communities have constructed the response curves by using small samples of varying diversity that were taken along larger ecosystems (e.g., Cox et al. 2006, Badano & Marquet 2009). Therefore, although are more realistic, these F-D relationships may show a small, biased fraction of the ecosystems, and would not account for the mechanisms shaping them.

Comparing the shape of F-D relationships across ecosystems would then require establishing a standardized protocol for constructing their response curves. This protocol must be as realistic as possible in order to account for the mechanisms that shape these curves, and it must be general enough to allow the inclusion of species larger than forbs and grasses. This study focuses on this issue and proposes a novel statistical protocol, based on

resampling procedures, for constructing F-D relationships within single communities that were intensively sampled. To illustrate the performance of this method, it was used to assess and compare relationships between aerial biomass (the most commonly used surrogate of ecosystem functioning) and species richness (the most commonly used measure of diversity) across different forest ecosystems. These comparisons were firstly performed among different *life-zones* proposed in the Holdridge's ecosystem classification system, which uses bioclimatic features for grouping ecosystems with similar climate and vegetation types (Holdridge 1947). Thus, it can be hypothesized that those forest ecosystems belonging to closely related life-zone should more similar among them, in terms of their functionality, than ecosystems belonging to different life-zones. Further, in an attempt to identify what other factors may influence the shape of F-D relationships, a series of correlative analyses between functioning properties of forest ecosystems and their physical and biotic features were performed.

A generalized methodology for constructing F-D relationships

The first step for constructing F-D relationships within single communities would rely on knowing the contribution that each species perform to a given ecosystem function. This information can be obtained by taking a representative sample of the community and measuring an attribute of species directly linked to the function under study −*i.e.*, species biomass is linked to carbon sequestration (Curtis 2008). These data can later be arranged in two vectors; the first vector containing the identity of species and the second vector containing the total contribution that each species perform to the ecosystem function under study (see Table A1 in Appendix A). After that, we could assess whether these two vectors are related by constructing a bidimensional graph in which the output of the ecosystem

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function is accumulated on the *y*-axis, or functioning axis, as species diversity sequentially increases by adding the species on the *x*-axis, or diversity axis. This graph would reflect the behavior of ecosystem functioning as community diversity increases, providing an extremely simple manner to assess the shape of F-D relationships across all possible diversity levels within the community sample (*i.e.*, from 1 species to *S* species, where *S* is the maximum number of species in the sample). Although simple and intuitive, this method has an important caveat: the shape of the F-D relationships will depend on the manner in which species are arranged across the diversity levels. For instance, if species that perform major contributions to ecosystem functioning are included into earlier diversity levels, then positive deceleration curves will be always observed as species diversity raises (Figure 1A). Conversely, if species that perform minor contributions to ecosystem functioning are located in earlier into the lower diversity levels, then positive accelerating relationships will be always generated (Figure 1B) –the Appendix A contains the details about how these different relationships can be generated.

By using the procedure described above, the F-D relationships obtained for different ecosystems will always show the same shape, and this would depend on the arbitrary criteria used for sorting the species across the diversity levels. As an alternative, it can be proposed that diversity levels must be generated by randomly selecting 1, 2, 3,…*S* species from the community sample. Thus, ecosystem functioning at each diversity level will be defined by the contributions performed by the species composing it. Moreover, to capture the variability in species composition at each diversity level, this procedure can be repeated a given number of times for each diversity level by using Monte Carlo resampling procedures. For each level of diversity, this will generate as many values of ecosystem functioning as resampling events are performed. These data can be used to construct F-D

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relationships as described above, but this method also has an important caveat: it considers that all species in the community sample are equivalent and perform equally important contributions to ecosystem functioning. Consequently, the overall shape of these F-D relationships is unpredictable (Figure 1C; details in the Appendix A). In the nature, however, species are not equally probable to occur in a sample because they usually display different abundances. Moreover, irrespectively of their abundances, species are likely to perform different contributions to ecosystem functioning. Thus, to improve the reliability of the proposed method, the random selection of species across diversity levels should take into account these issues.

For such a proposal, we can consider that species in natural communities display different abundances and, in a random selection of species, those species with higher abundances are likely to be recorded earlier than those less abundant species (Gotelli & Colwell 2001). Therefore, when generating all possible diversity levels within a community sample, highly abundant species must have higher probabilities of inclusion in lower diversity levels than less abundant species (Badano & Marquet 2008). The species composition within a given diversity level will then be a random function of the relative abundance of species in the community sample. This can also be performed by using Monte Carlo resampling procedures in which a weighting factor (abundance, in our case) determines the probability of randomly selecting a given species.

By using this later procedure, the F-D relationships can take one of three well defined shapes, which will depend on the relative abundances of species and their individual contributions to ecosystem functioning (details in Appendix B):

(1) If species with higher abundances are those that perform major contributions to ecosystem functioning, then positive deceleration trends between functioning and

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species diversity will be obtained (Figure 2A); this type of response curve suggests that strong declines in ecosystem functioning are expected if highly abundant species are subtracted from the community.

(2) If major contributions to ecosystem functioning are performed by those species with lower abundances in the community sample, then positive acceleration relationships between ecosystem functioning and species diversity will occur (Figure 2B); in this type of response curve, ecosystem functioning is expected to abruptly decrease if low abundant species that strongly contributes to functioning are subtracted from the community.

(3) Finally, positive linear relationships will occur if all species in the community sample display similar abundances and perform similar contributions to ecosystem functioning (Figure 2C); this type of curve then indicates that ecosystem functioning would decrease monotonically as diversity is reduced, irrespectively of the species that are subtracted from the community.

The shape of these three F-D relationships can be described by a single power function with the form: $F = \alpha S^\beta$; here, F is the outcome of ecosystem functioning, S is the number of species in a given diversity level, and α and β are parameters (constants) that shape the F-D relationship. In this model, α defines the starting point the curve, when $S = 1$. On the other hand, β defines the shape of the curve and, depending on its value, the response curves of F-D relationships can be: positive deceleration when $0 < \beta < 1$ (*e.g.*, Figure 2A), positive acceleration when $\beta > 1$ (*e.g.*, Figure 2B), and approximately linear when $\beta \approx 1$ (Figure 2C). Both parameters of this function can be estimated by using ordinary least

squares regression procedures and these values of α and β can be compared among ecosystems to determine whether they differ in functionality (see Materials and Methods).

Materials and Methods

Assessing the performance of the proposed method

To determine whether the method described above is widely applicable to assess the shape of F-D relationships across ecosystems, we use it to determine the relationships between the aerial biomass and species richness in different forest ecosystems. This was performed by using the Forest Transect Data Set, created by Alwing Howard Gentry (1945-1993) and provided by the Missouri Botanical garden trough the SALVIAS project (Synthesis and Analysis of Local Vegetation Inventories Across Scales http://www.salvias.net). These datasets include information on the identity and diameter at breast height (DBH) of all woody species recorded within plots of 0.04-0.10 ha, and they are available for 228 forests located at different countries and continents (Phillips & Miller 2002).

Among the 228 datasets, only those performed on surface areas of 0.1 ha were selected in order to consider larger tree samples. This resulted in 197 datasets (Table 1) on which we estimated the relative abundance of each species and the aerial biomass of each individual within the sample. The relative abundances of species (p_i) were estimated as $p_i = n_i/N$, where n_i is the number of individuals of the ith species and N is the total number of individuals in the sample. The aerial biomass of each individual (M) was estimated by using the allometric power function proposed by Brown (1997), $M = 0.124\, DBE^{2.53}$; we choose this allometric function because it was proven to perform well to estimate the aerial biomass of the woody species contained in these datasets (Enquist & Nicklas 2001). The species biomasses at each dataset were calculated by adding the aerial biomass of all the individuals belonging to each species.

For each dataset, the estimated values of abundance and aerial biomass were arranged in three vectors: the first vector contained the identity of species, the second vector contained the estimated aerial biomass of each species, and the third vector contained the relative abundance of each species (examples of these data vectors are provided in the Appendix B). After that, the different diversity levels of each dataset were generated by randomly selecting species from the sample, but the relative abundances weighted the probability of each species to be included within a given diversity level. All random selections of species were conducted by using the module *Sampling with Probability Proportional to Size* of the software PopTools v. 3.2 (Hood 2010). The accumulated aerial biomass at each diversity level was then obtained by adding the biomasses of the species selected at each opportunity. This procedure was repeated 100 times for each diversity level. After that, we constructed the F-D relationships for all the 197 datasets by considering the 100 resamples of each diversity level and their respective vales of accumulated biomass. Nonlinear regression analyses were used to determine whether they fit to the power function indicated above and to estimate the values of the α and β at each relationship.

Comparing the shape of F-D relationships among life-zones

Besides providing information on the abundance and DBH of woody species included in the samples, the Forest Transect Data Set of A.H. Gentry also indicates the life-zone to which each sampled forest belongs according to the classification system proposed by Holdridge (1947). Thus, in order to compare the shape of the F-D relationships among life-zones, the 197 forest samples included in this study were grouped according to this classification system and the values of α and β estimated from each forest sample were

separately compared by using one-way ANOVAs. The *post hoc* Tukey test was applied if significant differences among life-zones were indicated. In these analyses, the life-zones were considered as treatments, while the values of α and β estimated for each forest sample were considered as replicates for each life-zone. Nevertheless, because ANOVAs require a minimum of three replicates for each treatment (Zar 2010), those life-zones including less than three forest samples were excluded from this analysis.

Analyzing the shape of F-D relationships along environmental gradients

After performing these comparisons among life-zones, we focused in determining whether the shape of F-D relationships varied along environmental gradients. For this, we assessed whether the values of α and β were correlated to a series of physical and biotic variables of each forest ecosystem. Thus, in these analyses, the values of α and β were considered as dependent variables, while latitude (either North or South Hemisphere), annual average precipitation, elevation and species richness of each site were the predictive variables. We used these variables as predictors because they are provided in the Forest Transect Data Set of A.H. Gentry (Phillips & Miller 2002). In all cases, values of α and β were separately regressed against each predictive variable by using simple regression models. Multiple regression analyses were not applied because most predictive variables are autocorrelated. Furthermore, since we can not predict the overall shape of these relationships *a priori*, these regression analyses were conducted by using different univariate models, including linear, potential and exponential regression functions. If data fit to more than one model, and after testing that assumptions of regression analyses were

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met (homocedasticity and normality of errors), we have chosen the model to which data fit

better –*i.e.*, the model with the higher value of r^2.

Results

F-D relationships from forest samples

   Across the 197 forest samples included in the analyses, the relationships between aerial biomass and species diversity showed the three response curves that were expected after applying the resampling methodology proposed in this study for constructing these F-D relationships (positive deceleration, positive acceleration and positive linear). The shape of these relationships strongly depends on the value of the parameter β estimated through regression procedures. Positive deceleration response curves occurred in 152 forest samples that showed values of β that varied between 0.287 and 0.849 (see Table 1 for statistical results; see figures in Appendix C). On the other hand, 39 forest samples showed quasilinear positive response curves in which the values of β varied between 0.858 and 1.144 (see Table 1 for statistical results; figures are in Appendix C). Finally, seven forest samples showed positive accelerating response curves in which the values of β were above 1.168 (see Table 1 for statistical results; figures are in Appendix C).

Comparisons of F-D relationships among life-zones

   The highest value of α (702.144) was estimated for a cold forest from Canada (plot code KITLOPE1 in Table 1), while the lowest value of this regression parameter (0.910) was estimated for a tropical forest located in Malaysia (plot code PASOH30 in Table 1). Conversely, the highest value of β (1.579) was estimated for a tropical forest located in Costa Rica (plot code LASELVA in Table 1), while its lower value (0.287) was estimated for a cold forests From Germany (plot code SUDERHAC in Table 1). These differences between cold and warm forests became statistically evident when the values of α and β

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were compared among life-zones. Overall, forests belonging to boreal and cold life-zones showed significantly higher values of α ($F_{(20,155)}$ = 7.670, p < 0.001; Figure 3A), but lower values of β ($F_{(20,155)}$ = 2.147, p = 0.004; Figure 3B), than forests included within warm, subtropical and tropical life-zones.

Gradient analyses of F-D relationships

No relationships were indicated when the values of either α or β were regressed against latitude, elevation, precipitation or species richness (Figure 4). This lacking of fit to the different mathematical models proposed (see the Methods) was mainly due to the extremely high variability in the values of α or β across forest ecosystems, which made very difficult to meet the assumption of normality of errors in the regression analyses. To explore whether the shape of F-D relationships varied along environmental gradients, we thus performed a series of regression analyses in which averages values of variables were computed by using data spans of ten units. To compute these averages, we firstly sorted data in ascending order according to the values each predictive variable (latitude, elevation, precipitation and species richness); this was separately performed for each predictive variable. After that, data were grouped in spans (subsets) of ten units; for each span, we computed the average value of the predictive variable and the correspondingly values of α and β. Regressions were later performed by using the different univariate mathematical models indicated in the Methods (linear, potential and exponential regression functions). In statistic, this procedure is usually known as smoothed regression fitting.

By using this regression procedure, the values of α were observed to increase with latitude by following an exponential function ($F_{(2,18)}$ = 385.503, p < 0.000; Figure 5A),

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which explained a substantial amount of variance for this independent variable ($r^2 = 0.909$).

Conversely, the values of β decreased linearly from the Equator Line to the Poles ($F_{(2,18)} = 7.441$, $p < 0.000$; Figure 5B); although the explicative power of this mathematical function was higher than that obtained for the other regression models, its explicative power was low ($r^2 = 0.292$).

The smoothed (averaged) values of α and β were not related to elevation ($p > 0.05$ in all cases; Figure 5C and 5D), but both parameters were significantly related to precipitation by following potential functions. Here, the values of α were negatively related to increasing precipitation ($F_{(2,18)} = 18.803$, $p < 0.000$; Figure 5E), while the values of β showed the opposite trend ($F_{(2,18)} = 1430.124$, $p < 0.000$; Figure 5F). In both cases, however, the explicative power of the models was below 35% (r^2 for $\alpha = 0.255$; r^2 for $\beta = 0.320$).

The average smoothed values of α and β were also significantly related to the number of species recorded in the forest sample. In this case, the values of α were negatively related to species richness by following a potential function ($F_{(2,18)} = 159.994$, $p < 0.000$; Figure 5G). Conversely, the values of β were positively and linearly related to species richness ($F_{(2,18)} = 29.627$, $p < 0.000$; Figure 5H). Interestingly, these two regression models that involved species richness as predictive variable had greater explicative power on the variance of α ($r^2 = 0.962$) and β ($r^2 = 0.622$), as compared with regressions models that included latitude, elevation or precipitation as predictive variables.

Discussion

The manner in which species diversity impacts on ecosystem functioning, the methodological approaches that must be used to assess these relationships, as well as the shape that these relationships must take are matter of strong debate in ecology (see Huston 1997, Tilman 1997, Tilman et al. 1997, Naeem 1998, Huston et al. 2000, Schwartz et al. 2000, Aarssen 2001, Giller & O'Donovan 2002, Naeem & Wright 2003, Petchey 2004, Carroll et al. 2011, Reich et al. 2012). This is because the wide variety of results obtained from the experimental studies addressing these issues. While most authors affirm that the relationships between ecosystem functioning and species diversity are positive (Naeem et al. 1994, Tilman et al. 1996, Hector et al. 1999, Loreau and Hector 2001, Badano & Marquet 2008, 2009), others have obtained inconsistent relationships between these variables (Hooper 1998, Kenkel et al. 2000, Mulder et al. 2001, Jiang 2007), or even negative relationships (Rusch & Oesterheld 1997, Wardle et al. 1997, Creed et al. 2009). Therefore, determining how F-D relationships can be assessed is still being a major challenge for ecologist (Chapin et al. 1998, Costanza et al. 1997, Cardinale et al. 2012, Hooper et al. 2012, Reich et al. 2012).

Our results suggest that the resampling protocol proposed in this study produces highly consistent relationships between the aerial biomass and species diversity within single community samples. Moreover, because a unique mathematical function that only requires estimating two parameters (*i.e.*, α and β) describes the shape of these relationships, the results also suggest that generalized statistical methods, such as ANOVAs and regression analyses, can be used to compare them among ecosystems. Here we only used aerial biomass as response variable, but the elevated consistence observed in F-D curves across

different forest ecosystems, belonging to quite different climate types, suggests that the methodology proposed in this study can be employed for analyzing the impacts of species diversity on a number of ecosystem functions. It is also important to highlight, however, that the proposed methodology is merely based on statistical procedures. Therefore, it does not account for the potential species interactions that may take place within communities, which may also influence the output of ecosystem functions (Cardinale et al. 2002, Aarssen 2003, Badano & Marquet 2008, 2009).

Once F-D relationships were mathematically determined for all forest samples included in this study, the parameters describing their shape (α and β) were indicted to be similar among life-zones sharing bioclimatic features. The higher values of α estimated for boreal and temperate life-zones suggest that the potential amount of biomass contained in a single, average species is greater in these forests ecosystems than those from warmer life-zones. The values of β, on the other hand, indicated that a few highly dominant species are supporting most aerial biomass in cold forests ecosystems, while biomasses in warmer forests would be evenly distributed across species with similar relative abundances. Overall, this suggest that low diversity levels are required to reach high values of aerial biomass at colder life-zones where, beyond a saturating point, increases in diversity due to the addition of low abundant, subordinate species would redound in irrelevant contributions to this ecosystem function. On the other hand, in forest from warmer life-zones, species seem to be functionally complementary in terms of their contribution to ecosystem biomass and, therefore, any increase in diversity would lead to higher ecosystem functioning.

The parameters describing F-D relationships were also indicated to vary along physical environmental gradients. After smoothed regressions were performed, the values of α

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exponentially increased from lower latitudes to higher latitudes, while the values of β linearly decreased in that direction. This indicates that high diversity levels are required to reach high biomass values in forest ecosystems near to the Equator Line, while a few highly abundant species are required to maintain most aerial biomass in forest ecosystems near to the Poles. These results are similar to those obtained in the comparisons among life-zones, and this is because latitude is a very important variable determining life-zones in the classification system proposed by Holdridge (1947). On the other hand, it is important to note that the shape of these F-D relationships changed from positive accelerate and linear curves to positive decelerate curves as forest ecosystems get farther to the Equator Line and the values of β decreased. In these analyses, however, the regression model used to assess changes in β along the latitudinal gradient was indicated to account for a small fraction of the variance in the data ($r^2 = 0.292$). Therefore, it can be suggested that latitude would not be a good predictor for assessing changes in the shape of the curve.

Neither α nor β were indicated to be related with elevation, but both regression parameters were indicated to be related with precipitation. The values of α potentially decreased as precipitation increased, while the values of β followed the converse pattern. These results allow to suggests that the shape of F-D curves may be somewhat influenced by precipitation, showing positive decelerate F-D response curves in forests ecosystems that receive less than 2000 mm of precipitation per year and positive linear, or accelerate relationships, in forest ecosystems that receive more than 2000 mm of precipitation per year. Nevertheless, as occurred with latitude, the low explicative power obtained for these relationships ($r^2 < 0.350$) makes precipitation a weak variable to predict the shape of F-D curves across forest ecosystems.

Although these abiotic variables seems not be good predictors for the shape of F-D relationships, the number of species recorded in the forests samples was indicated to have greater explicative power. In this case, the values of α were showed to decrease by following a potential function as species richness increased, while the values of β increased in a linear manner with larger species richness. Therefore, it can be suggested that the shape of the relationships between biomass and species diversity would change from decelerate curves to linear and accelerate curves as species diversity becomes greater. When we compare this results to those reported in the literature, because of the shape of the curve, if we were to explain the mechanisms behind this response curves, it would mean that those ecosystems with less number of species follow the redundant species theory (Tilman et al. 1996, Tilman 1997, Naeem 1998, Hector et al. 1999, Schwartz et al. 2000, Dukes 2001, Fonseca & Ganade 2001, Mikola et al. 2002, Cox et al. 2006, Badano & Marquet 2009) while as the number of species increases we can observe a more complex behavior that may be due to complementary relationships between the species(Schwartz et al. 2000, Loreau & Hector 2001, Cardinale et al. 2002, 2007, Reiss et al. 2009), this statement has yet to be proved as we did not took in account the mechanisms involved in the response curves.

It would be adventurous to state that the relationships between ecosystem functioning and diversity could be worldwide explained by the methodology proposed in this study for constructing F-D curves. However, at least for forest ecosystems, this methodology could be proposed as an important tool that may help to explain how an ecosystem function respond to changes in species biodiversity. Even though more research is needed to fully understand whether the proposed methodology can be applied to other ecosystem functions, this study allow us to conclude that the relationships between biomass and species diversity

in forest ecosystems would be weakly influenced by physical abiotic factors, such as latitude and precipitation, while the number of species contained in the ecosystems may be a critical determinant of the shape of these curves.

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Table 1. Forest samples included in this study. The table indicates the major geographic area, country and plot code of each sample, and the statistical results of regression analyses (*p*-value and r^2; critical *p*-value = 0.05) performed to determine whether relationships between accumulated aerial biomass (*F*) and species diversity (*S*) fit to the function $F = \alpha S^\beta$. The estimated regression parameters (α and β) of each forest sample are indicated in the last two columns of the table. Figures with data and regression curves are in Appendix C.

Major geographic area	Country	Plot code	*p*-value	r^2	α-value	β-value
Africa	Cameroon	KORUP	0.000	0.927	31.310	0.897
Africa	Cameroon	MTCAM	0.000	0.913	35.282	0.870
Africa	Cameroon	BANYONG	0.000	0.890	1.830	1.257
Africa	Central African Republic	NDAKANI	0.000	0.918	84.665	0.550
Africa	Gabon	MAKOKOU1	0.000	0.882	8.182	0.789
Africa	Gabon	MAKOKOU2	0.000	0.904	24.927	0.591
Africa	Madagascar	BEZA2	0.000	0.966	5.738	0.683
Africa	Madagascar	ANKARIF	0.000	0.837	17.729	0.671
Africa	Madagascar	PERINET	0.000	0.895	20.206	0.614
Africa	Madagascar	BEZA1	0.000	0.815	102.183	0.371
Africa	Mauritius	BRISEFER	0.000	0.904	99.112	0.515
Africa	Nigeria	OMOFOR	0.000	0.912	22.289	0.694
Africa	Tanzania	PUGU	0.000	0.874	12.325	0.727
Caribbean	Cuba	SIERRARO	0.000	0.861	58.689	0.504
Caribbean	Jamaica	ROUNDSLO	0.000	0.933	33.533	0.382
Caribbean	Jamaica	ROUNDTOP	0.000	0.879	39.001	0.463
Caribbean	Puerto Rico	LUQUILLO	0.000	0.942	29.950	0.782
Caribbean	Puerto Rico	MOGOTE	0.000	0.797	86.436	0.350

Table 1 (continue)

Major geographic area	Country	Plot code	*p*-value	r^2	α-value	β-value
Central America	Costa Rica	OSASIREN	0.000	0.754	2.181	1.297
Central America	Costa Rica	LASELVA	0.000	0.880	2.454	1.579
Central America	Costa Rica	CARARA	0.000	0.873	2.564	1.168
Central America	Costa Rica	RANCHOQU	0.000	0.905	7.335	0.978
Central America	Costa Rica	MAGSASAY	0.000	0.886	18.879	0.624
Central America	Nicaragua	CERROOLU	0.000	0.884	6.504	0.996
Central America	Nicaragua	CERROELP	0.000	0.933	115.337	0.677
Central America	Panama	MADDEN	0.000	0.863	4.696	0.900
Central America	Panama	PIPELINE	0.000	0.931	5.527	0.751
Central America	Panama	CURUNDU	0.000	0.912	5.949	0.792
Europe	Finland	RUISSALO	0.000	0.843	124.957	0.622
Europe	Finland	LIESJVAR	0.000	0.801	283.310	0.466
Europe	Germany	ALLACHER	0.000	0.895	54.382	0.575
Europe	Germany	SUDERHAC	0.000	0.740	188.848	0.287
Europe	Sweden	UPPSALA	0.000	0.926	79.912	0.821
North America	Canada	MTSTHILA	0.000	0.858	169.684	0.541
North America	Canada	KITLOPE2	0.000	0.809	614.831	0.649
North America	Canada	KITLOPE1	0.000	0.906	702.144	0.680
North America	Mexico	CHAMELA3	0.000	0.906	7.724	0.926
North America	Mexico	CHAMELA1	0.000	0.883	9.939	0.664
North America	Mexico	TUXTLAS	0.000	0.884	12.401	0.769
North America	Mexico	CHAMELA2	0.000	0.943	17.453	0.444
North America	Mexico	BENITO	0.000	0.923	31.019	0.912
North America	Mexico	BOSQUEDE	0.000	0.846	61.396	0.743
North America	Mexico	LASJOYAS	0.000	0.885	84.758	0.800
North America	Mexico	MOTOZINT	0.000	0.845	169.192	0.406
North America	Mexico	QUINCEOC	0.000	0.898	321.492	0.303
North America	USA	INDIANCA	0.000	0.872	26.289	0.873

Table 1 (continue)

Major geographic area	Country	Plot code	*p*-value	r^2	α-value	β-value
North America	USA	BURLING	0.000	0.893	29.168	0.954
North America	USA	BABLERSP	0.000	0.735	29.690	0.519
North America	USA	NWBRANCH	0.000	0.816	35.108	1.028
North America	USA	CEDARBLU	0.000	0.924	36.666	0.688
North America	USA	VALLEYVI	0.000	0.838	41.267	0.569
North America	USA	CARY	0.000	0.951	41.342	0.697
North America	USA	SANFELAS	0.000	0.892	46.878	0.824
North America	USA	TYSONGLA	0.000	0.792	49.343	0.408
North America	USA	UFHORTIC	0.000	0.943	51.920	0.584
North America	USA	TYSONWOO	0.000	0.751	64.709	0.439
North America	USA	POTOMAC	0.000	0.843	65.769	0.780
North America	USA	HEUSTOBM	0.000	0.869	76.584	0.700
North America	USA	BANKAMP	0.000	0.890	79.629	0.589
North America	USA	CUIVRE	0.000	0.859	88.795	0.459
North America	USA	KANEALLE	0.000	0.786	96.884	0.629
North America	USA	MONTGOME	0.000	0.834	97.051	0.739
North America	USA	JONESMIL	0.000	0.921	103.609	0.590
North America	USA	HEUSTOMF	0.000	0.858	135.054	0.540
North America	USA	TIDROUTE	0.000	0.917	143.452	0.598
North America	USA	LAURELRI	0.000	0.781	196.591	0.502
South America	Argentina	PARQUEER	0.000	0.836	5.393	1.171
South America	Argentina	SALTA	0.000	0.911	18.244	0.788
South America	Argentina	RIACHUEL	0.000	0.829	61.981	0.672
South America	Bolivia	MADIDI	0.000	0.914	4.158	0.919
South America	Bolivia	NUEVOMUN	0.000	0.882	4.690	0.939
South America	Bolivia	YANAIGUA	0.000	0.946	5.564	1.270
South America	Bolivia	RIONEGRO	0.000	0.898	8.640	0.725
South America	Bolivia	PERSEVER	0.000	0.885	9.966	0.718

Table 1 (continue)

Major geographic area	Country	Plot code	*p*-value	r^2	α-value	β-value
South America	Bolivia	ENCANTO	0.000	0.898	12.055	0.755
South America	Bolivia	QUIAPACA	0.000	0.887	16.216	0.631
South America	Bolivia	INCAHUAR	0.000	0.893	16.606	0.559
South America	Bolivia	CURUYUQU	0.000	0.949	16.846	0.849
South America	Bolivia	MADIDIRI	0.000	0.940	19.893	0.584
South America	Bolivia	SANTACRU	0.000	0.817	25.337	0.696
South America	Bolivia	CURUYUQR	0.000	0.863	34.851	0.738
South America	Bolivia	CHAQUIMA	0.000	0.943	35.574	0.567
South America	Bolivia	SACRAM	0.000	0.830	40.360	0.390
South America	Brazil	MANAUS	0.000	0.923	3.172	0.619
South America	Brazil	DUCKE	0.000	0.930	6.712	0.797
South America	Brazil	LINHARES	0.000	0.906	7.619	0.824
South America	Brazil	CARAJAS	0.000	0.887	9.265	0.934
South America	Brazil	CARLOSBO	0.000	0.938	12.428	0.664
South America	Brazil	CAMORIN	0.000	0.895	12.650	0.750
South America	Brazil	BELEM	0.000	0.886	13.411	0.735
South America	Brazil	ALTERDOC	0.000	0.873	22.523	0.478
South America	Brazil	BORACEIA	0.000	0.939	29.529	0.627
South America	Chile	MIRADOR	0.000	0.906	143.197	0.668
South America	Chile	MARTIN	0.000	0.793	278.534	0.620
South America	Chile	PUYEHUE	0.000	0.800	512.341	0.776
South America	Colombia	COLORADO	0.000	0.826	1.918	1.078
South America	Colombia	LARAYA	0.000	0.888	3.972	0.957
South America	Colombia	MURRI	0.000	0.872	5.841	0.844
South America	Colombia	RIOMANSO	0.000	0.900	6.156	0.803
South America	Colombia	CALIMA	0.000	0.944	6.157	0.685
South America	Colombia	TAYRONA	0.000	0.937	7.397	0.891
South America	Colombia	ARARACUA	0.000	0.876	7.850	0.762

Table 1 (continue)

Major geographic area	Country	Plot code	p-value	r^2	α-value	β-value
South America	Colombia	TUTUNEND	0.000	0.860	8.885	0.648
South America	Colombia	COLOSOI	0.000	0.870	9.216	0.804
South America	Colombia	CAMPANO	0.000	0.895	11.229	0.948
South America	Colombia	ANTADO	0.000	0.844	12.063	0.761
South America	Colombia	GALERAZ	0.000	0.877	12.315	0.675
South America	Colombia	LAPLANAD	0.000	0.877	15.966	0.706
South America	Colombia	CUEVA	0.000	0.888	16.021	0.742
South America	Colombia	PROVIDEN	0.000	0.923	17.139	0.652
South America	Colombia	CUEVAS	0.000	0.865	18.064	0.705
South America	Colombia	CEDRAL	0.000	0.827	19.575	0.731
South America	Colombia	CERROESP	0.000	0.862	20.178	0.888
South America	Colombia	KENNEDY	0.000	0.946	21.783	0.736
South America	Colombia	UCUMARI	0.000	0.915	23.068	0.654
South America	Colombia	CARPANTA	0.000	0.909	24.234	0.777
South America	Colombia	SANTOTOM	0.000	0.860	28.146	0.552
South America	Colombia	ANCHICAY	0.000	0.852	30.174	0.583
South America	Colombia	SIETECUE	0.000	0.874	30.434	0.557
South America	Colombia	ALTODEMI	0.000	0.881	31.925	0.628
South America	Colombia	SABANARU	0.000	0.806	44.613	0.820
South America	Colombia	FINCAM	0.000	0.878	46.051	0.584
South America	Colombia	MARIQUIT	0.000	0.893	58.784	0.520
South America	Colombia	ALTOSAPA	0.000	0.866	108.732	0.444
South America	Colombia	FARALL	0.000	0.854	263.971	0.387
South America	Ecuador	ESMERALD	0.000	0.821	3.355	1.144
South America	Ecuador	JATUNSAC	0.000	0.908	4.716	0.845
South America	Ecuador	RIOPAL1	0.000	0.775	8.911	0.729
South America	Ecuador	PERROMUE	0.000	0.811	9.132	0.872
South America	Ecuador	CENTINEL	0.000	0.877	12.329	0.756

Table 1 (continue)

Major geographic area	Country	Plot code	p-value	r^2	α-value	β-value
South America	Ecuador	MAQUIPUC	0.000	0.900	13.900	0.792
South America	Ecuador	BILSA	0.000	0.892	15.887	0.689
South America	Ecuador	MIAZI	0.000	0.932	16.120	0.662
South America	Ecuador	JAUNECHE	0.000	0.812	17.164	0.603
South America	Ecuador	SANSEBAS	0.000	0.892	19.885	0.683
South America	Ecuador	CUANGOS	0.000	0.918	20.312	0.642
South America	Ecuador	RIOPAL2	0.000	0.893	22.912	0.666
South America	Ecuador	HUAMANI	0.000	0.888	24.672	0.621
South America	Ecuador	CAPEIRA	0.000	0.912	28.804	0.826
South America	Ecuador	ELCORAZO	0.000	0.881	124.205	0.539
South America	French Guiana	SAUL	0.000	0.831	4.367	1.062
South America	Guyana	BERBICER	0.000	0.839	152.874	0.386
South America	Paraguay	JEJUIMI	0.000	0.923	8.079	0.977
South America	Peru	COCHACAS	0.000	0.825	2.412	1.032
South America	Peru	TAMBUPL	0.000	0.762	2.511	1.123
South America	Peru	RIOHEATH	0.000	0.837	3.191	0.960
South America	Peru	JENAROHE	0.000	0.896	3.205	0.885
South America	Peru	CONSTANC	0.000	0.904	3.421	0.923
South America	Peru	ALLPAHUA	0.000	0.896	3.628	0.947
South America	Peru	YANAMTAH	0.000	0.910	3.825	1.203
South America	Peru	MISHWS	0.000	0.935	4.208	0.774
South America	Peru	RIOTAVAR	0.000	0.886	4.524	0.905
South America	Peru	YANAM2	0.000	0.878	4.775	0.858
South America	Peru	CABEZADE	0.000	0.906	5.238	0.739
South America	Peru	TAMBO	0.000	0.907	5.394	0.940
South America	Peru	TAMBOALL	0.000	0.857	5.812	0.992
South America	Peru	SHIRINGA	0.000	0.879	6.295	0.726
South America	Peru	MISHNFL	0.000	0.930	6.533	0.675

Table 1 (continue)

Major geographic area	Country	Plot code	*p*-value	r^2	*α*-value	*β*-value
South America	Peru	CANDAMO	0.000	0.951	6.892	0.806
South America	Peru	INDIANA	0.000	0.909	6.903	0.838
South America	Peru	TAHUAMPA	0.000	0.863	7.183	0.802
South America	Peru	TARAPOTO	0.000	0.934	8.240	0.666
South America	Peru	TAMBLAT2	0.000	0.877	10.380	0.779
South America	Peru	AMOTAPE	0.000	0.904	10.777	0.927
South America	Peru	CUZCOAMA	0.000	0.819	14.299	0.735
South America	Peru	LAGENOA	0.000	0.931	14.363	0.661
South America	Peru	YANAM1	0.000	0.810	15.637	0.665
South America	Peru	VENCER	0.000	0.810	34.024	0.576
South America	Peru	HUMBOLDT	0.000	0.966	39.835	0.341
South America	Peru	CHIRINOS	0.000	0.905	45.199	0.703
South America	Peru	CERROAYP	0.000	0.899	50.062	0.609
South America	Peru	CUTERVO	0.000	0.925	54.031	0.579
South America	Peru	CUYAS	0.000	0.883	85.515	0.628
South America	Venezuela	UCHIRE	0.000	0.931	2.054	0.937
South America	Venezuela	BLOHMR	0.000	0.951	19.287	0.629
South America	Venezuela	CERONEB1	0.000	0.873	36.528	0.408
South America	Venezuela	CERONEB2	0.000	0.778	43.010	0.540
Tropical Asia and Oceania	Australia	DAVIES	0.000	0.901	13.361	0.821
Tropical Asia and Oceania	India	NADUGANI	0.000	0.970	15.115	0.725
Tropical Asia and Oceania	India	MUDUMAL2	0.000	0.828	44.590	0.813
Tropical Asia and Oceania	India	MUDUMAL1	0.000	0.848	65.528	0.687
Tropical Asia and Oceania	India	AVALANCH	0.000	0.909	85.509	0.574
Tropical Asia and Oceania	Japan	CHIBA	0.000	0.892	105.869	0.577
Tropical Asia and Oceania	Malaysia	PASOH30	0.000	0.853	0.910	1.078
Tropical Asia and Oceania	Malaysia	SEMENGOH	0.000	0.880	3.373	0.914
Tropical Asia and Oceania	Malaysia	PASOH40	0.000	0.804	7.513	0.786

Table 1 (continue)

Major geographic area	Country	Plot code	*p*-value	r^2	α-value	β-value
Tropical Asia and Oceania	Malaysia	GENTING	0.000	0.914	8.221	0.825
Tropical Asia and Oceania	Malaysia	BAKOSAR	0.000	0.875	18.090	0.638
Tropical Asia and Oceania	New Caledonia	NEWCALDO	0.000	0.921	28.682	0.522
Tropical Asia and Oceania	Papua New Guinea	BAITETE	0.000	0.748	2.924	1.056
Tropical Asia and Oceania	Papua New Guinea	VARIRATA	0.000	0.940	10.742	0.726
Tropical Asia and Oceania	Philippines	PALANAN	0.000	0.860	82.703	0.547
Tropical Asia and Oceania	Taiwan	NANJENSH	0.000	0.944	38.999	0.464
Tropical Asia and Oceania	Taiwan	KENTING	0.000	0.948	96.924	0.312
Tropical Asia and Oceania	Thailand	KHAOYAI	0.000	0.867	11.394	0.813
Tropical Asia and Oceania	Thailand	SAKAERAT	0.000	0.867	29.490	0.612
Tropical Asia and Oceania	Thailand	SAKAERA2	0.000	0.847	80.682	0.385

Figure captions

Figure 1. Response curves for F-D relationships resulting from accumulating ecosystem functioning across all possible levels of diversity within a single community sample when: (A) species that perform the major contributions to ecosystem functioning are included into earlier diversity levels, (B) species that perform minor contributions to ecosystem functioning are included into earlier diversity levels, and (C) specie are randomly selected without replacement within each diversity level (C). Details about how these curves were constructed are given in the Appendix A.

Figure 2. Theoretical F-D relationships resulting from the resampling procedures described in the text to generate the diversity levels. In all cases, the species composition of diversity levels is generated by using a random function of the relative abundance of each species, where species at each diversity level are randomly selected from the community sample without replacement. The panels of the figure show the results of three resampling events for each diversity level when: (A) species with higher abundances are those that perform the major contributions to ecosystem functioning, (B) species with lower abundances are those that perform the major contributions to ecosystem functioning, and (C) all species have similar abundances and perform similar contributions to ecosystem functioning. Details about how these curves were constructed are given in the Appendix B.

Figure 3. Average values ($\pm$ 2 S.E.) of the parameter α (A) and the parameter β (B), both estimated through regression procedures to assess the fit of F-D relationships to the

function $F = \alpha S^\beta$, when their values were classified according to the Holdridge life zones to which each forest ecosystem belongs. Life zones with less than three values of either α or β (B) were excluded. Different letters indicate significant differences between averages (critical provability value of the *post hoc* Tukey test = 0.05).

Figure 4. Values of the parameters α (left column) and β (right column) estimated for each forest ecosystem when plotted against their respective values of latitude (A, B), elevation (C, D), precipitation (E, F) and species richness (G, H). No significant relationships were detected in any case.
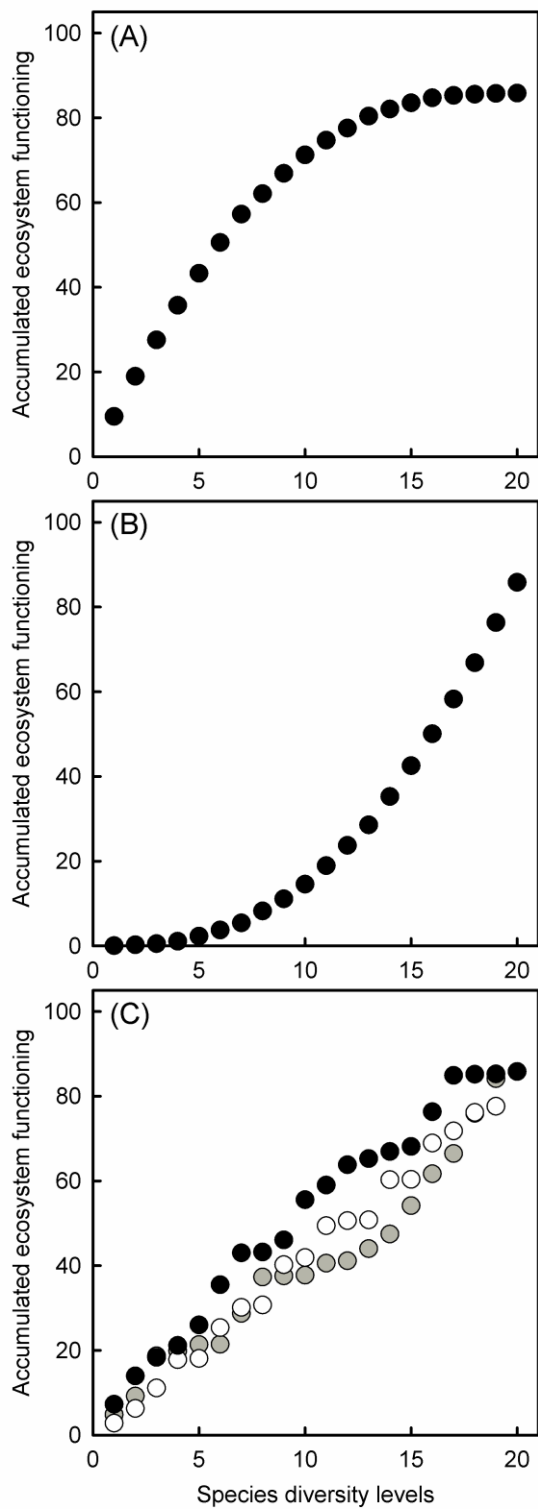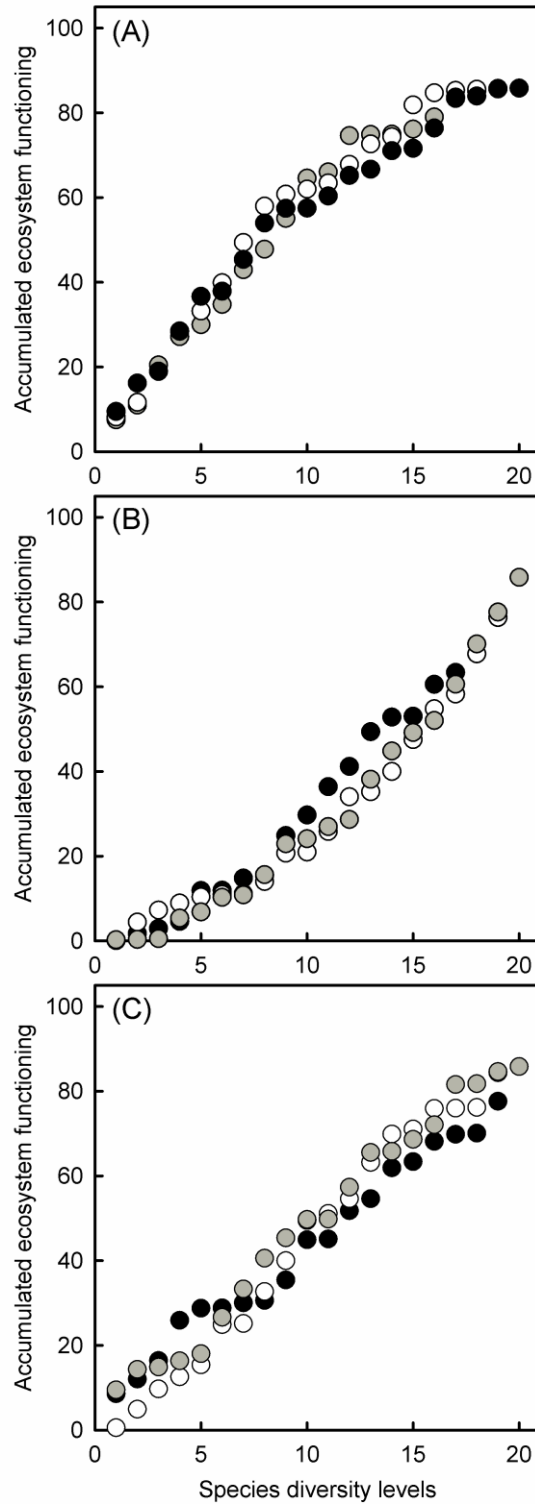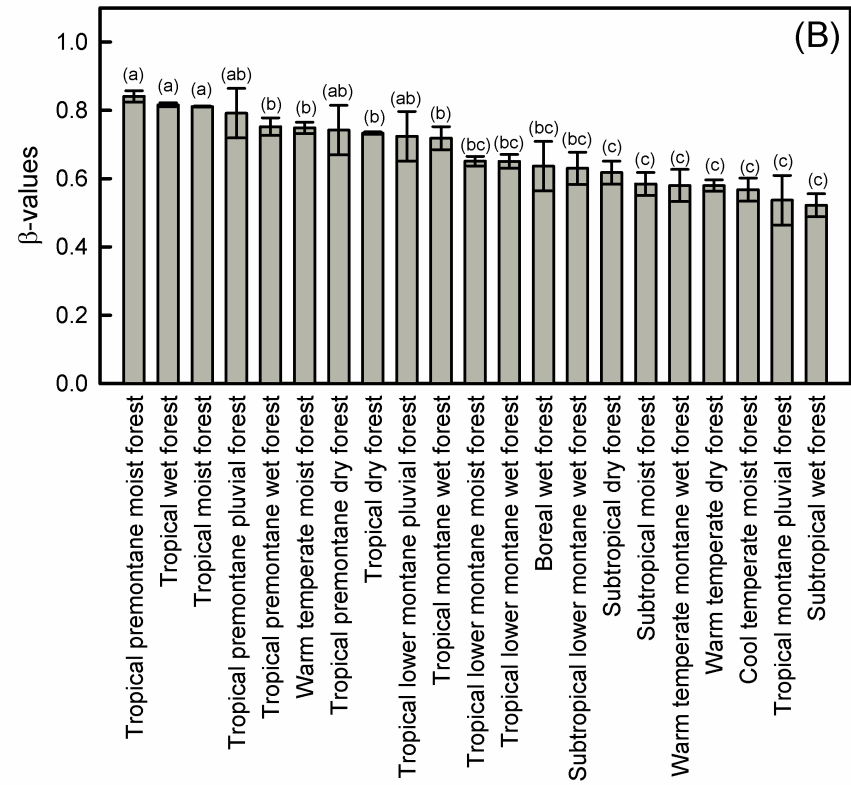
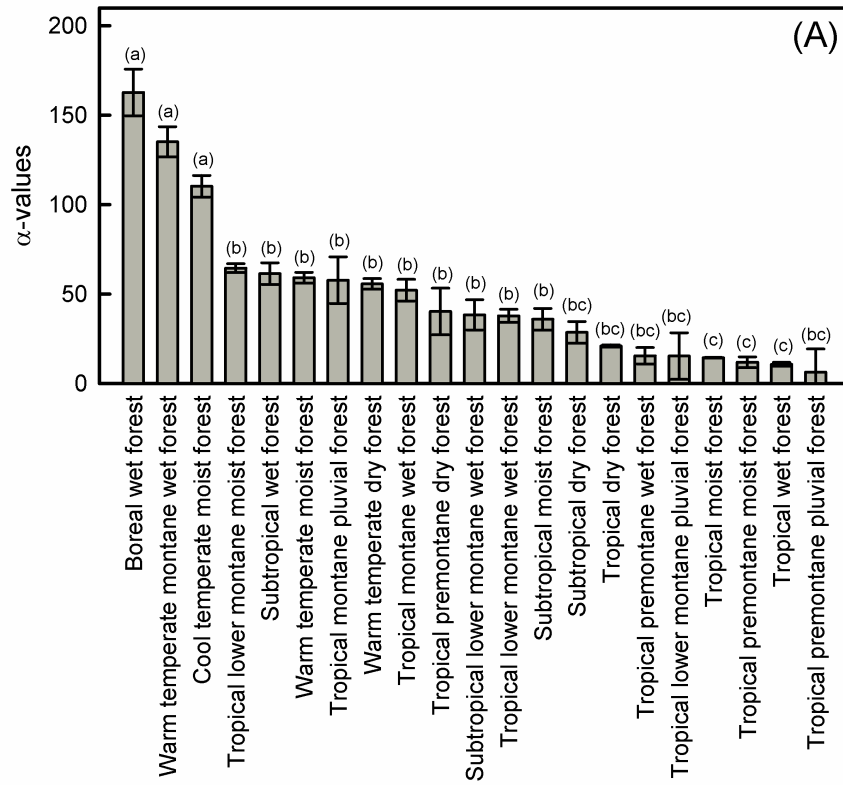**Figure 1.**
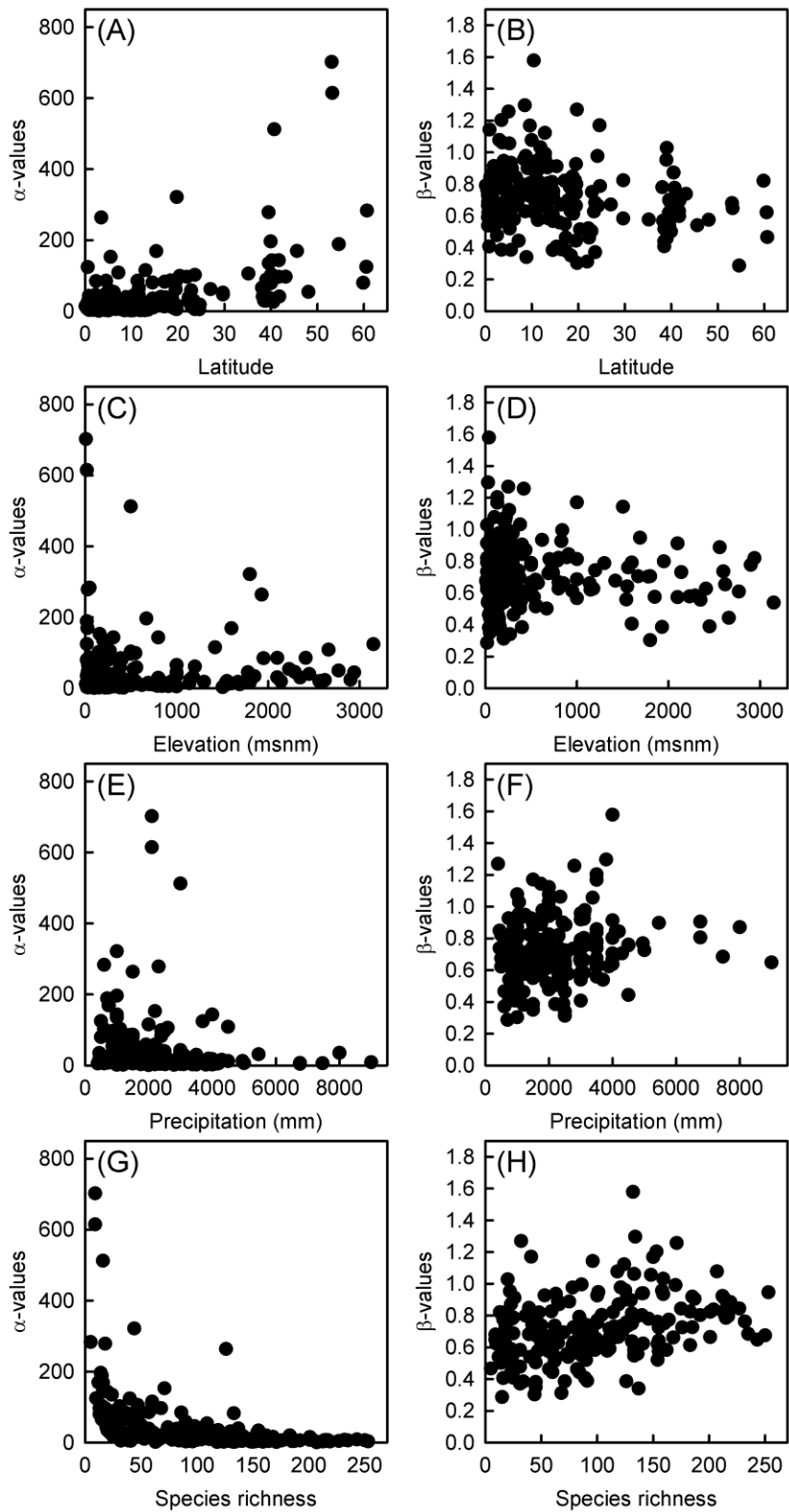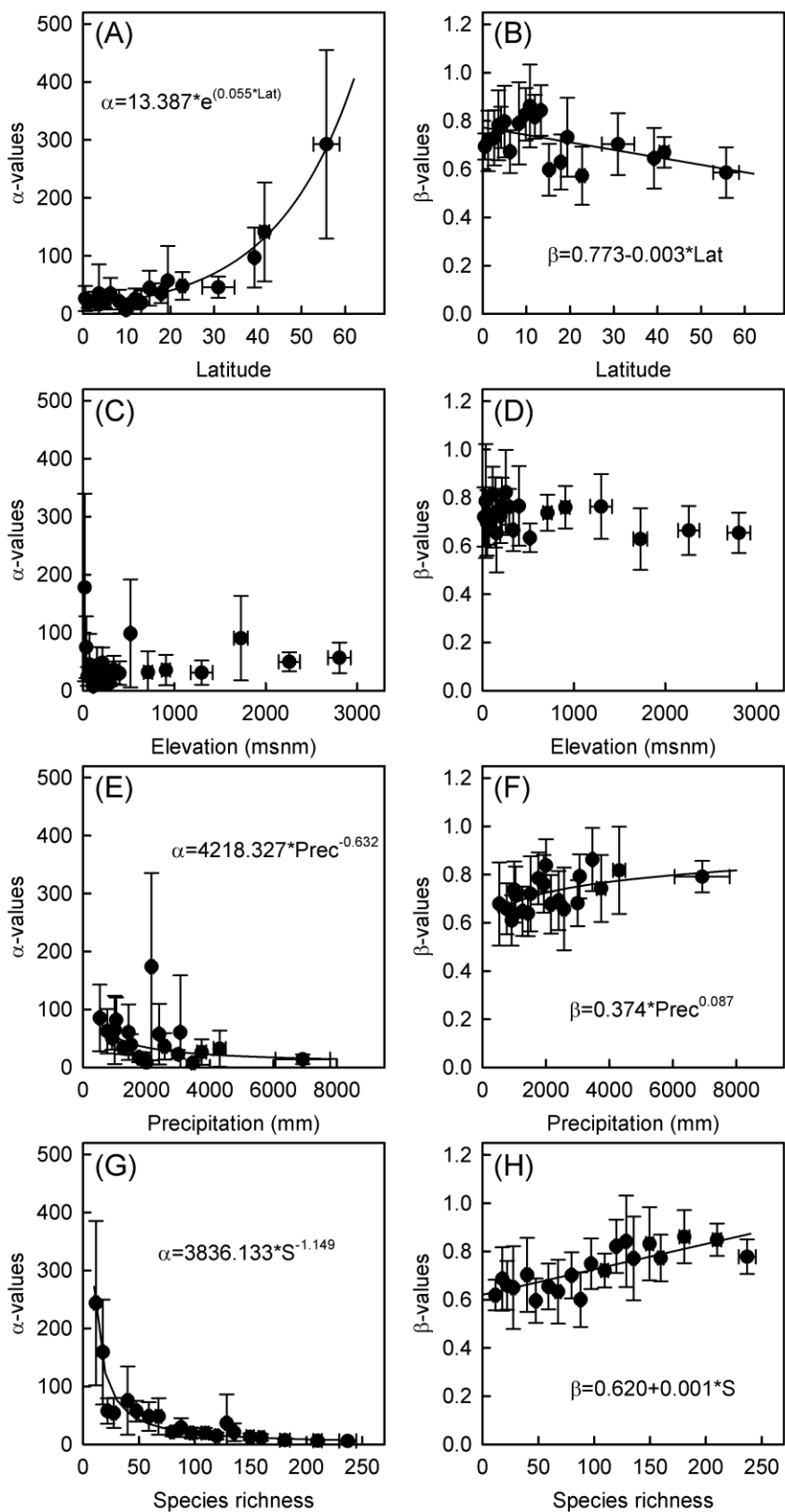
Figure 2.

Figure 3.

Figure 4.

Figure 5.

Appendices

APPENDIX A

This appendix contains the data of a hypothetical community used to illustrate how the shape of the relationships between ecosystem functioning and species diversity can vary depending on the manner in which species are sorted across diversity levels. In Table A1, the first data vector indicates the species name and the second vector indicates the total contribution of each species to ecosystem functioning. Data in the functioning vector (vector 2) were obtained by randomly assigning values between 1 and 100 units to each species. The last column of the table defines all possible diversity levels within the community, which range from 1 species to S species (S = the maximum number of species in the community = 20, in this case).

Table A1

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning	Diversity levels
Sp. A	7.284	1
Sp. B	8.582	2
Sp. C	3.459	3
Sp. D	1.681	4
Sp. E	0.187	5
Sp. F	7.532	6
Sp. G	0.568	7
Sp. H	4.847	8
Sp. I	2.820	9
Sp. J	2.860	10
Sp. K	8.192	11
Sp. L	0.069	12
Sp. M	4.371	13
Sp. N	0.270	14
Sp. O	9.496	15
Sp. P	4.784	16
Sp. Q	6.687	17
Sp. R	1.194	18
Sp. S	9.481	19
Sp. T	1.459	20

Species can be firstly sorted as the magnitude of their contribution to ecosystem functioning decrease and, later, these values can be sequentially accumulated across the diversity levels (see Table A2). Therefore, the curve shown in the Figure 1A is obtained by plotting the accumulated functioning on the y-axis and the respective diversity levels on x-axis. Conversely, the curve shown in Figure 1B is obtained when species are sorted according to their increasing contributions to ecosystem functioning (see Table A3).

Table A2

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning (arranged in decreasing order)	Diversity levels	Accumulated functioning with increasing diversity
Sp. O	9.496	1	9.496
Sp. S	9.481	2	18.977
Sp. B	8.582	3	27.559
Sp. K	8.192	4	35.751
Sp. F	7.532	5	43.282
Sp. A	7.284	6	50.567
Sp. Q	6.687	7	57.253
Sp. H	4.847	8	62.100
Sp. P	4.784	9	66.884
Sp. M	4.371	10	71.256
Sp. C	3.459	11	74.715
Sp. J	2.860	12	77.575
Sp. I	2.820	13	80.395
Sp. D	1.681	14	82.076
Sp. T	1.459	15	83.534
Sp. R	1.194	16	84.729
Sp. G	0.568	17	85.297
Sp. N	0.270	18	85.567
Sp. E	0.187	19	85.754
Sp. L	0.069	20	85.824

Table A3

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning (arranged in increasing order)	Diversity levels	Accumulated functioning with increasing diversity
Sp. L	0.069	1	0.069
Sp. E	0.187	2	0.256
Sp. N	0.270	3	0.527
Sp. G	0.568	4	1.095
Sp. R	1.194	5	2.289
Sp. T	1.459	6	3.748
Sp. D	1.681	7	5.429
Sp. I	2.820	8	8.249
Sp. J	2.860	9	11.109
Sp. C	3.459	10	14.568
Sp. M	4.371	11	18.939
Sp. P	4.784	12	23.723
Sp. H	4.847	13	28.570
Sp. Q	6.687	14	35.257
Sp. A	7.284	15	42.541
Sp. F	7.532	16	50.073
Sp. K	8.192	17	58.265
Sp. B	8.582	18	66.847
Sp. S	9.481	19	76.327
Sp. O	9.496	20	85.824

Finally, curves in Figure 1C are obtained by randomly sorting the species across the diversity levels by using Monte Carlo resampling procedures (see Table A4-A6). In this case, each Monte Carlo run assumes that all species are equally probable to occur in all diversity levels. The random arrangements of data contained in the three tables below contains the results of three independent Monte Carlo runs; all Monte Carlo runs were conducted by using the module Simple Random Sample of the software PopTools v. 3.2 for Microsoft Excel (Hood 2010).

Table A4

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning (randomly sorted; first Monte Carlo run)	Diversity levels	Accumulated functioning with increasing diversity
Sp. H	4.847	1	4.847
Sp. M	4.371	2	9.218
Sp. O	9.496	3	18.715
Sp. R	1.194	4	19.909
Sp. T	1.459	5	21.367
Sp. L	0.069	6	21.436
Sp. A	7.284	7	28.721
Sp. B	8.582	8	37.302
Sp. N	0.270	9	37.573
Sp. E	0.187	10	37.760
Sp. I	2.820	11	40.580
Sp. G	0.568	12	41.149
Sp. J	2.860	13	44.009
Sp. C	3.459	14	47.467
Sp. Q	6.687	15	54.154
Sp. F	7.532	16	61.686
Sp. P	4.784	17	66.470
Sp. S	9.481	18	75.950
Sp. K	8.192	19	84.143
Sp. D	1.681	20	85.824

Table A5

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning (randomly sorted; second Monte Carlo run)	Diversity levels	Accumulated functioning with increasing diversity
Sp. I	2.820	1	2.820
Sp. C	3.459	2	6.279
Sp. H	4.847	3	11.126
Sp. Q	6.687	4	17.813
Sp. N	0.270	5	18.083
Sp. A	7.284	6	25.367
Sp. P	4.784	7	30.151
Sp. G	0.568	8	30.720
Sp. O	9.496	9	40.216
Sp. D	1.681	10	41.897
Sp. F	7.532	11	49.429
Sp. R	1.194	12	50.623
Sp. E	0.187	13	50.810
Sp. S	9.481	14	60.290
Sp. L	0.069	15	60.360
Sp. B	8.582	16	68.942
Sp. J	2.860	17	71.802
Sp. M	4.371	18	76.173
Sp. T	1.459	19	77.631
Sp. K	8.192	20	85.824

Table A6

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning (randomly sorted; third Monte Carlo run)	Diversity levels	Accumulated functioning with increasing diversity
Sp. A	7.284	1	7.284
Sp. Q	6.687	2	13.971
Sp. M	4.371	3	18.342
Sp. I	2.820	4	21.162
Sp. H	4.847	5	26.009
Sp. S	9.481	6	35.490
Sp. F	7.532	7	43.022
Sp. E	0.187	8	43.209
Sp. J	2.860	9	46.069
Sp. O	9.496	10	55.565
Sp. C	3.459	11	59.024
Sp. P	4.784	12	63.808
Sp. T	1.459	13	65.266
Sp. D	1.681	14	66.948
Sp. R	1.194	15	68.142
Sp. K	8.192	16	76.334
Sp. B	8.582	17	84.916
Sp. N	0.270	18	85.186
Sp. L	0.069	19	85.255
Sp. G	0.568	20	85.824

APPENDIX B

This appendix contains the data we used to illustrate how the relationships between ecosystem functioning and species diversity can be constructed by analyzing the outcome of Monte Carlo resampling procedures in which the species composition within each diversity level is a random function of the relative abundance of the species occurring in the sample. In all cases, we used the same basic data for a hypothetical community; the first data vector indicates the species name (Vector 1 in Table B1), the second vector indicates the total contribution of each species to ecosystem functioning (Vector 2 in in Table B1), and the third vector indicates the number of individuals of each species in the community sample (Vector 3 in Table B1). The fourth vector contains the relative abundance of each species (Vector 4 in Table B1), which were calculated as the ratio between the number of individuals of each species and the total number of individuals in the sample. Both data in vector 2 (functioning vector) and vector 3 (number of individuals) were obtained by randomly assigning a value between 1 and 100 units to each species. The last column to the table defines all possible diversity levels within the community, which range from 1 species to S species, being S = the maximum number of species in the community.

Table B1

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning	Vector 3: number of individuals of each species in the sample	Vector 4: relative abundance of each species in the community sample	Diversity levels
Sp. A	7.284	54	0.064	1
Sp. B	8.582	79	0.094	2
Sp. C	3.459	40	0.048	3
Sp. D	1.681	33	0.039	4
Sp. E	0.187	6	0.007	5
Sp. F	7.532	66	0.079	6
Sp. G	0.568	12	0.014	7
Sp. H	4.847	48	0.057	8
Sp. I	2.820	35	0.042	9
Sp. J	2.860	38	0.045	10
Sp. K	8.192	74	0.088	11
Sp. L	0.069	5	0.006	12
Sp. M	4.371	42	0.050	13
Sp. N	0.270	8	0.010	14
Sp. O	9.496	95	0.113	15
Sp. P	4.784	42	0.050	16
Sp. Q	6.687	51	0.061	17
Sp. R	1.194	22	0.026	18
Sp. S	9.481	94	0.112	19
Sp. T	1.459	29	0.035	20
Total number of individuals in the sample	**873**			

For illustrative proposals, data in the previous table were firstly arranged in such a way that species with higher abundances are those that perform the major contributions to ecosystem functioning. The Monte Carlo resampling procedure mentioned above was applied on this data by using the module Sampling with Probability Proportional to Size, which is available in the software PopTools v. 3.2 for Microsoft Excel (Hood 2010). The results of three resampling runs that were conducted with these data are shown in the tables below (see Tables B2-B4). These resampling runs were conducted without replacement of species. These resampling runs were used to construct the Figure 2A of the manuscript.

Table B2

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning (randomly sorted; first Monte Carlo run)	Vector 3: abundance of each species in the community sample	Vector 4: relative abundance of each species in the community sample	Diversity levels	Accumulated functioning with increasing diversity
Sp. F	7.532	66	0.079	1	7.532
Sp. C	3.459	40	0.048	2	10.991
Sp. S	9.481	94	0.112	3	20.471
Sp. Q	6.687	51	0.061	4	27.158
Sp. I	2.820	35	0.042	5	29.978
Sp. P	4.784	42	0.050	6	34.762
Sp. K	8.192	74	0.088	7	42.954
Sp. H	4.847	48	0.057	8	47.801
Sp. A	7.284	54	0.064	9	55.086
Sp. O	9.496	95	0.113	10	64.582
Sp. T	1.459	29	0.035	11	66.040
Sp. B	8.582	94	0.094	12	74.622
Sp. N	0.270	8	0.010	13	74.892
Sp. L	0.069	5	0.006	14	74.962
Sp. R	1.194	22	0.026	15	76.156
Sp. J	2.860	38	0.045	16	79.016
Sp. M	4.371	42	0.050	17	83.387
Sp. D	1.681	33	0.039	18	85.068
Sp. E	0.568	6	0.007	19	85.637
Sp. G	0.187	12	0.014	20	85.824

Table B3

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning (randomly sorted; second Monte Carlo run)	Vector 3: abundance of each species in the community sample	Vector 4: relative abundance of each species in the community sample	Diversity levels	Accumulated functioning with increasing diversity
Sp. K	8.192	74	0.088	1	8.192
Sp. C	3.459	40	0.048	2	11.651
Sp. A	7.284	54	0.064	3	18.935
Sp. S	9.481	94	0.112	4	28.416
Sp. P	4.784	42	0.050	5	33.200
Sp. Q	6.687	51	0.061	6	39.886
Sp. O	9.496	95	0.113	7	49.383
Sp. B	8.582	79	0.094	8	57.965
Sp. I	2.820	35	0.042	9	60.785
Sp. R	1.194	22	0.026	10	61.979
Sp. T	1.459	29	0.035	11	63.437
Sp. M	4.371	42	0.050	12	67.809
Sp. H	4.847	48	0.057	13	72.656
Sp. D	1.681	33	0.039	14	74.337
Sp. F	7.532	66	0.079	15	81.868
Sp. J	2.860	38	0.045	16	84.729
Sp. G	0.568	12	0.014	17	85.297
Sp. N	0.270	8	0.010	18	85.567
Sp. E	0.187	6	0.007	19	85.754
Sp. L	0.069	5	0.006	20	85.824

Table B4

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning (randomly sorted; third Monte Carlo run)	Vector 3: abundance of each species in the community sample	Vector 4: relative abundance of each species in the community sample	Diversity levels	Accumulated functioning with increasing diversity
Sp. O	9.496	95	0.113	1	9.496
Sp. Q	6.687	51	0.061	2	16.183
Sp. I	2.820	35	0.042	3	19.003
Sp. S	9.481	94	0.112	4	28.484
Sp. K	8.192	74	0.088	5	36.676
Sp. R	1.194	22	0.026	6	37.870
Sp. F	7.532	66	0.079	7	45.402
Sp. B	8.582	79	0.094	8	53.984
Sp. C	3.459	40	0.048	9	57.442
Sp. L	0.069	5	0.006	10	57.512
Sp. J	2.860	38	0.045	11	60.372
Sp. H	4.847	48	0.057	12	65.219
Sp. T	1.459	29	0.035	13	66.678
Sp. M	4.371	42	0.050	14	71.049
Sp. G	0.568	12	0.014	15	71.617
Sp. P	4.784	42	0.050	16	76.401
Sp. A	7.284	54	0.064	17	83.685
Sp. N	0.270	8	0.010	18	83.956
Sp. D	1.681	33	0.039	19	85.637
Sp. E	0.187	6	0.007	20	85.824

Data in Table B1 were later arranged in such a way that species with lower abundances are those that perform the major contributions to ecosystem functioning (See Table B5). Later, the Monte Carlo resampling was applied three times on this data by following the same procedure described above (results in Tables B6-B8). These resampling runs were used to construct the Figure 2B of the manuscript.

Table B5

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning	Vector 3: number of individuals of each species in the sample	Vector 4: relative abundance of each species in the community sample	Diversity levels
Sp. A	7.284	29	0.033	1
Sp. B	8.582	8	0.009	2
Sp. C	3.459	42	0.048	3
Sp. D	1.681	51	0.058	4
Sp. E	0.187	94	0.108	5
Sp. F	7.532	22	0.025	6
Sp. G	0.568	74	0.085	7
Sp. H	4.847	35	0.040	8
Sp. I	2.820	48	0.055	9
Sp. J	2.860	42	0.048	10
Sp. K	8.192	12	0.014	11
Sp. L	0.069	95	0.109	12
Sp. M	4.371	40	0.046	13
Sp. N	0.270	79	0.090	14
Sp. O	9.496	5	0.006	15
Sp. P	4.784	38	0.044	16
Sp. Q	6.687	33	0.038	17
Sp. R	1.194	66	0.076	18
Sp. S	9.481	6	0.007	19
Sp. T	1.459	54	0.062	20
Total number of individuals in the sample		**873**		

Table B6

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning (randomly sorted; first Monte Carlo run)	Vector 3: abundance of each species in the community sample	Vector 4: relative abundance of each species in the community sample	Diversity levels	Accumulated functioning with increasing diversity
Sp. N	0.270	79	0.090	1	0.270
Sp. T	1.459	54	0.062	2	1.729
Sp. R	1.194	66	0.076	3	2.923
Sp. D	1.681	51	0.058	4	4.604
Sp. A	7.284	29	0.033	5	11.888
Sp. L	0.069	95	0.109	6	11.957
Sp. J	2.860	42	0.048	7	14.817
Sp. G	0.568	74	0.085	8	15.386
Sp. S	9.481	6	0.007	9	24.866
Sp. H	4.847	35	0.040	10	29.713
Sp. Q	6.687	33	0.038	11	36.400
Sp. P	4.784	38	0.044	12	41.184
Sp. K	8.192	12	0.014	13	49.376
Sp. C	3.459	42	0.048	14	52.835
Sp. E	0.187	94	0.108	15	53.022
Sp. F	7.532	22	0.025	16	60.554
Sp. I	2.820	48	0.055	17	63.374
Sp. M	4.371	40	0.046	18	67.746
Sp. B	8.582	8	0.009	19	76.327
Sp. O	9.496	5	0.006	20	85.824

Table B7

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning (randomly sorted; second Monte Carlo run)	Vector 3: abundance of each species in the community sample	Vector 4: relative abundance of each species in the community sample	Diversity levels	Accumulated functioning with increasing diversity
Sp. L	0.069	95	0.109	1	0.069
Sp. M	4.371	40	0.046	2	4.441
Sp. I	2.820	48	0.055	3	7.261
Sp. D	1.681	51	0.058	4	8.942
Sp. T	1.459	54	0.062	5	10.400
Sp. G	0.568	74	0.085	6	10.969
Sp. E	0.187	94	0.108	7	11.156
Sp. J	2.860	42	0.048	8	14.016
Sp. Q	6.687	33	0.038	9	20.703
Sp. N	0.270	79	0.090	10	20.973
Sp. H	4.847	35	0.040	11	25.820
Sp. K	8.192	12	0.014	12	34.012
Sp. R	1.194	66	0.076	13	35.206
Sp. P	4.784	38	0.044	14	39.990
Sp. F	7.532	22	0.025	15	47.522
Sp. A	7.284	29	0.033	16	54.806
Sp. C	3.459	42	0.048	17	58.265
Sp. S	9.481	6	0.007	18	67.761
Sp. B	8.582	8	0.009	19	76.343
Sp. O	9.496	5	0.006	20	85.824

Table B8

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning (randomly sorted; third Monte Carlo run)	Vector 3: abundance of each species in the community sample	Vector 4: relative abundance of each species in the community sample	Diversity levels	Accumulated functioning with increasing diversity
Sp. N	0.270	79	0.090	1	0.270
Sp. L	0.069	95	0.109	2	0.340
Sp. E	0.187	94	0.108	3	0.527
Sp. H	4.847	35	0.040	4	5.374
Sp. T	1.459	54	0.062	5	6.832
Sp. C	3.459	42	0.048	6	10.291
Sp. G	0.568	74	0.085	7	10.860
Sp. P	4.784	38	0.044	8	15.644
Sp. A	7.284	29	0.033	9	22.928
Sp. R	1.194	66	0.076	10	24.122
Sp. J	2.860	42	0.048	11	26.982
Sp. D	1.681	51	0.058	12	28.663
Sp. S	9.481	6	0.007	13	38.143
Sp. Q	6.687	33	0.038	14	44.830
Sp. M	4.371	40	0.046	15	49.201
Sp. I	2.820	48	0.055	16	52.022
Sp. B	8.582	8	0.009	17	60.604
Sp. O	9.496	5	0.006	18	70.100
Sp. F	7.532	22	0.025	19	77.631
Sp. K	8.192	12	0.014	20	85.824

Finally, to obtain the Figure 2C, we assumed that all species are equally abundant in the community sample (see Table B9) and, on this data, the Monte Carlo resamplings were performed three times on by following the same procedure described above (Results in Table B10-B12).

Table B9

| Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning	Vector 3: number of individuals of each species in the sample	Vector 4: relative abundance of each species in the community sample	Diversity levels
Sp. A	7.284	44	0.050	1
Sp. B	8.582	44	0.050	2
Sp. C	3.459	44	0.050	3
Sp. D	1.681	44	0.050	4
Sp. E	0.187	44	0.050	5
Sp. F	7.532	44	0.050	6
Sp. G	0.568	44	0.050	7
Sp. H	4.847	44	0.050	8
Sp. I	2.820	44	0.050	9
Sp. J	2.860	44	0.050	10
Sp. K	8.192	44	0.050	11
Sp. L	0.069	44	0.050	12
Sp. M	4.371	44	0.050	13
Sp. N	0.270	44	0.050	14
Sp. O	9.496	44	0.050	15
Sp. P	4.784	44	0.050	16
Sp. Q	6.687	44	0.050	17
Sp. R	1.194	44	0.050	18
Sp. S	9.481	44	0.050	19
Sp. T	1.459	44	0.050	20
Total number of individuals in the sample	873			

Table B10

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning (randomly sorted; first Monte Carlo run)	Vector 3: abundance of each species in the community sample	Vector 4: relative abundance of each species in the community sample	Diversity levels	Accumulated functioning with increasing diversity
Sp. S	9.481	44	0.050	1	9.481
Sp. H	4.847	44	0.050	2	14.328
Sp. G	0.568	44	0.050	3	14.896
Sp. T	1.459	44	0.050	4	16.355
Sp. D	1.681	44	0.050	5	18.036
Sp. B	8.582	44	0.050	6	26.617
Sp. Q	6.687	44	0.050	7	33.304
Sp. A	7.284	44	0.050	8	40.588
Sp. P	4.784	44	0.050	9	45.372
Sp. M	4.371	44	0.050	10	49.744
Sp. L	0.069	44	0.050	11	49.813
Sp. F	7.532	44	0.050	12	57.345
Sp. K	8.192	44	0.050	13	65.537
Sp. N	0.270	44	0.050	14	65.807
Sp. I	2.820	44	0.050	15	68.627
Sp. C	3.459	44	0.050	16	72.086
Sp. O	9.496	44	0.050	17	81.582
Sp. E	0.187	44	0.050	18	81.770
Sp. J	2.860	44	0.050	19	84.630
Sp. R	1.194	44	0.050	20	85.824

Table B11

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning (randomly sorted; second Monte Carlo run)	Vector 3: abundance of each species in the community sample	Vector 4: relative abundance of each species in the community sample	Diversity levels	Accumulated functioning with increasing diversity
Sp. G	0.568	44	0.050	1	0.568
Sp. M	4.371	44	0.050	2	4.940
Sp. P	4.784	44	0.050	3	9.724
Sp. J	2.860	44	0.050	4	12.584
Sp. I	2.820	44	0.050	5	15.404
Sp. O	9.496	44	0.050	6	24.900
Sp. N	0.270	44	0.050	7	25.170
Sp. F	7.532	44	0.050	8	32.702
Sp. A	7.284	44	0.050	9	39.986
Sp. S	9.481	44	0.050	10	49.467
Sp. D	1.681	44	0.050	11	51.148
Sp. C	3.459	44	0.050	12	54.607
Sp. B	8.582	44	0.050	13	63.189
Sp. Q	6.687	44	0.050	14	69.875
Sp. R	1.194	44	0.050	15	71.069
Sp. H	4.847	44	0.050	16	75.916
Sp. L	0.069	44	0.050	17	75.986
Sp. E	0.187	44	0.050	18	76.173
Sp. K	8.192	44	0.050	19	84.365
Sp. T	1.459	44	0.050	20	85.824

Table B12

Vector 1: Species	Vector 2: Total contribution of each species to ecosystem functioning (randomly sorted; third Monte Carlo run)	Vector 3: abundance of each species in the community sample	Vector 4: relative abundance of each species in the community sample	Diversity levels	Accumulated functioning with increasing diversity
Sp. B	8.582	44	0.050	1	8.582
Sp. C	3.459	44	0.050	2	12.041
Sp. M	4.371	44	0.050	3	16.412
Sp. O	9.496	44	0.050	4	25.908
Sp. J	2.860	44	0.050	5	28.768
Sp. L	0.069	44	0.050	6	28.838
Sp. R	1.194	44	0.050	7	30.032
Sp. G	0.568	44	0.050	8	30.600
Sp. H	4.847	44	0.050	9	35.447
Sp. S	9.481	44	0.050	10	44.928
Sp. E	0.187	44	0.050	11	45.115
Sp. Q	6.687	44	0.050	12	51.801
Sp. I	2.820	44	0.050	13	54.622
Sp. A	7.284	44	0.050	14	61.906
Sp. T	1.459	44	0.050	15	63.364
Sp. P	4.784	44	0.050	16	68.148
Sp. D	1.681	44	0.050	17	69.830
Sp. N	0.270	44	0.050	18	70.100
Sp. F	7.532	44	0.050	19	77.631
Sp. K	8.192	44	0.050	20	85.824

Relationships between tree aerial biomass and species diversity for the 197 datasets selected from the Forest Transect Data Set of Alwing Howard Gentry for this study. Scatterplots below (black symbols) are the different values of biomass estimated at each diversity level by using the resampling procedure described in the article. Figures also show the response curve (grey line) obtained after fitting data to the power function $F = \alpha S^{\beta}$ (F = accumulated biomass; S = number of species in the diversity level). Statistical results of the regression analysis performed for each dataset (see the plot code) are given in Table 1 of the article.
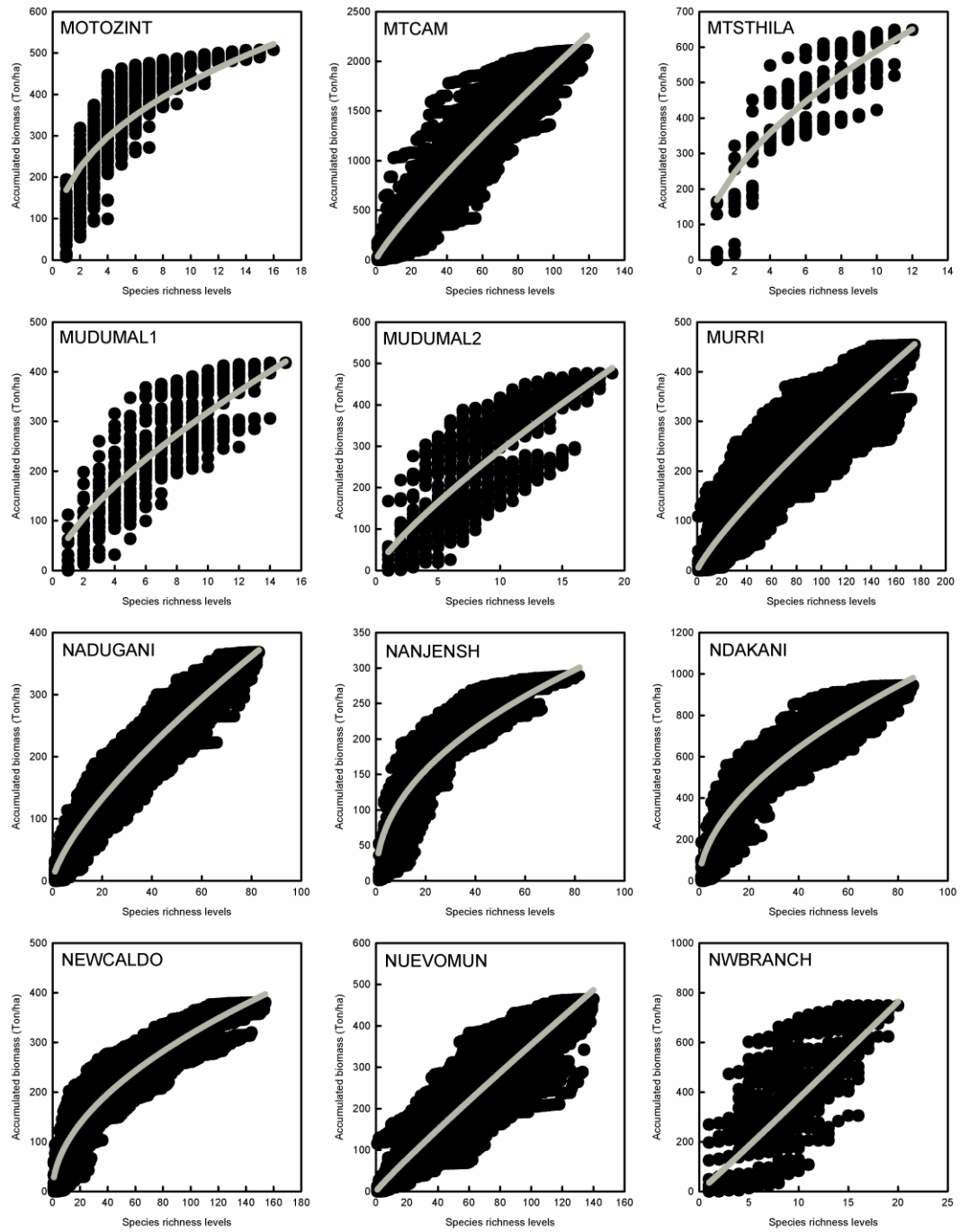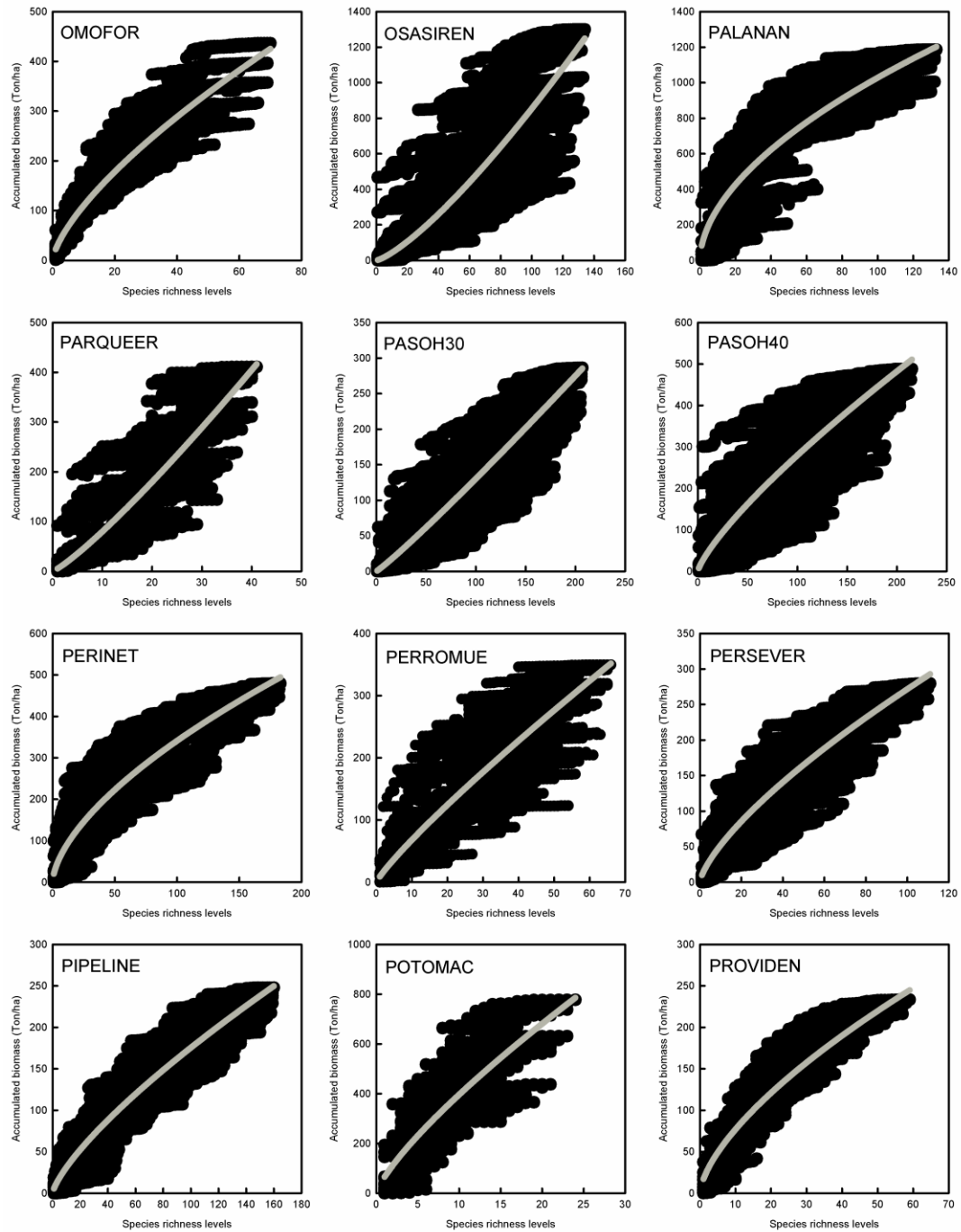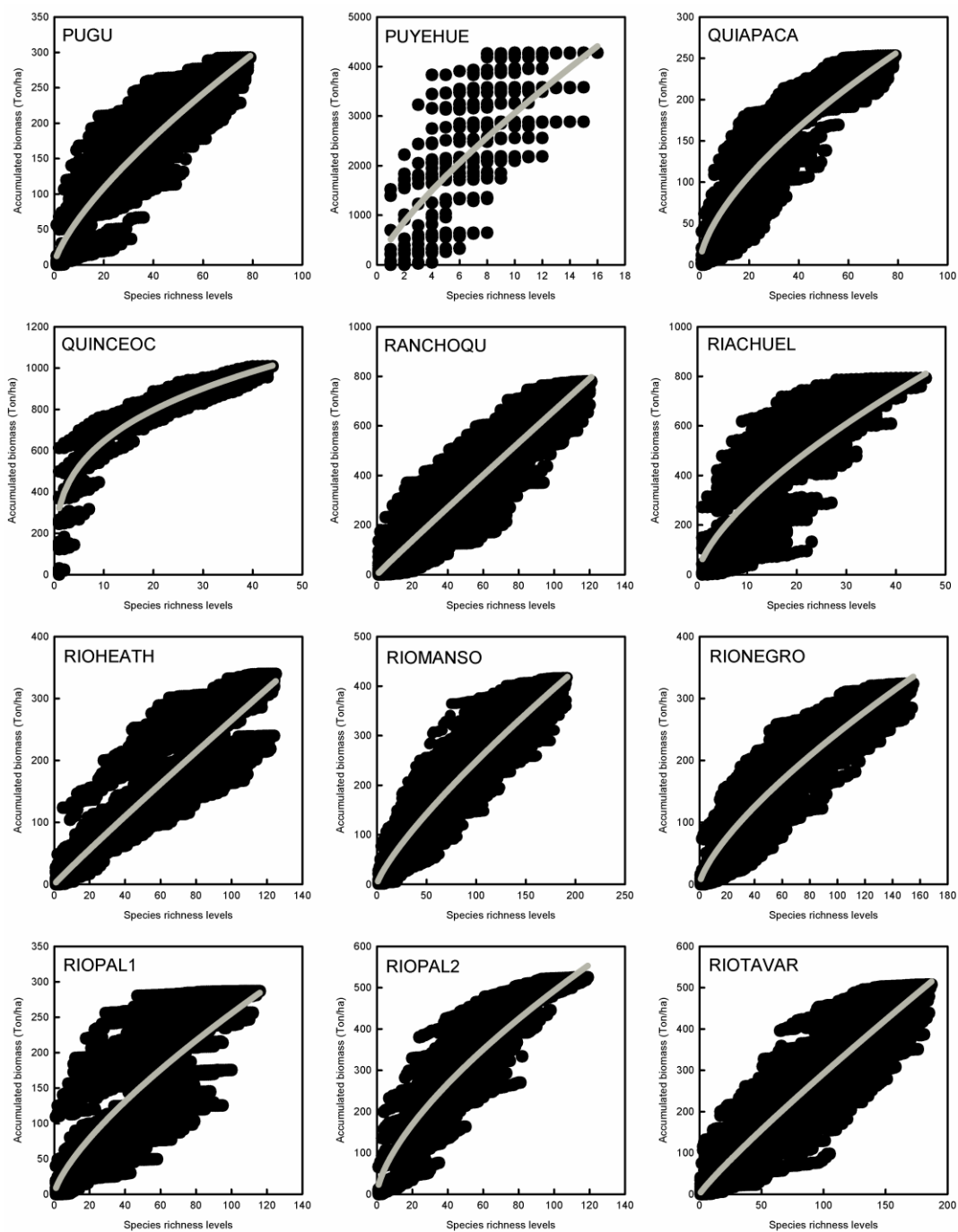
Relationships between aerial biomass and species richness (panel 1)
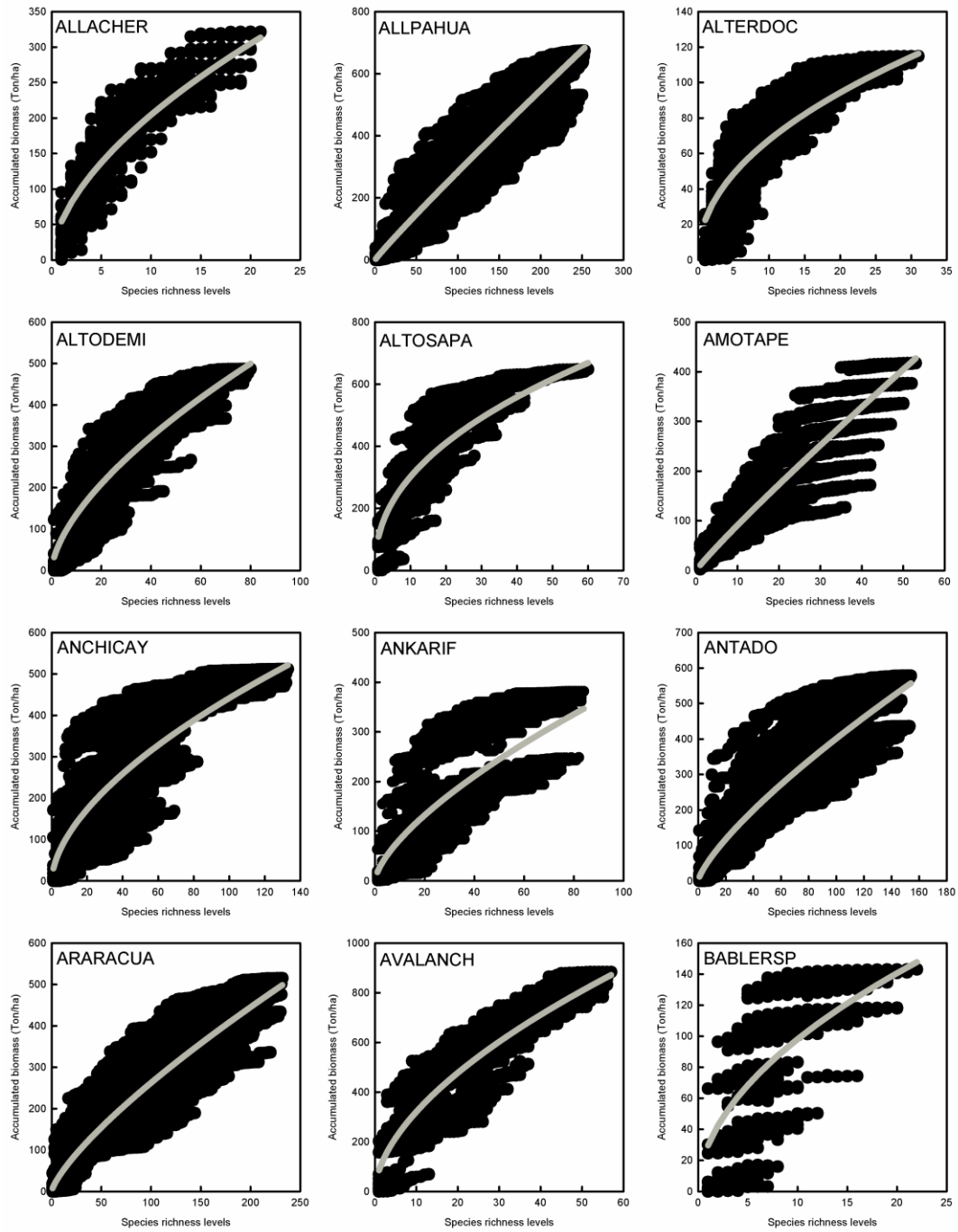
Relationships between aerial biomass and species richness (panel 2)
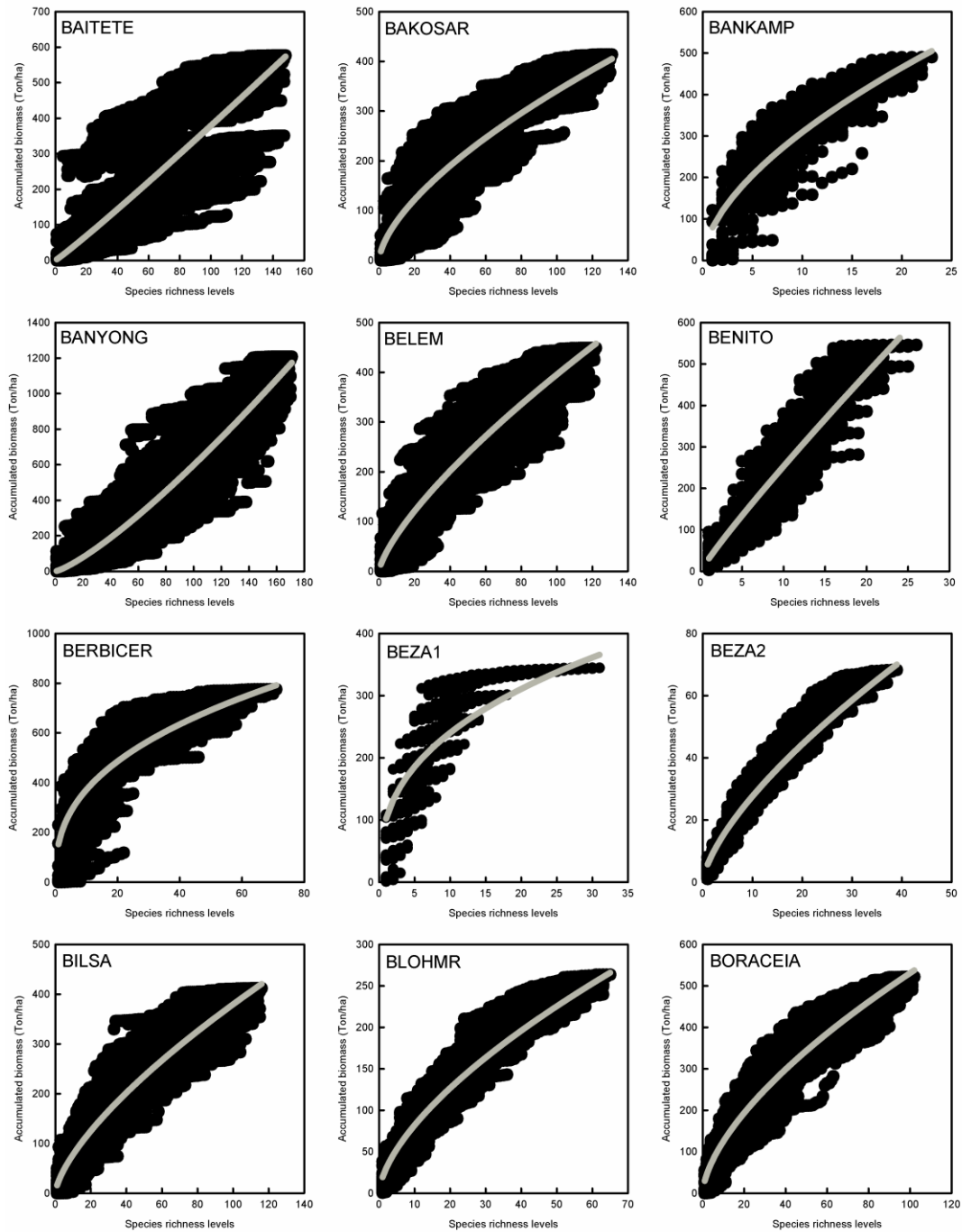
Relationships between aerial biomass and species richness (panel 3)
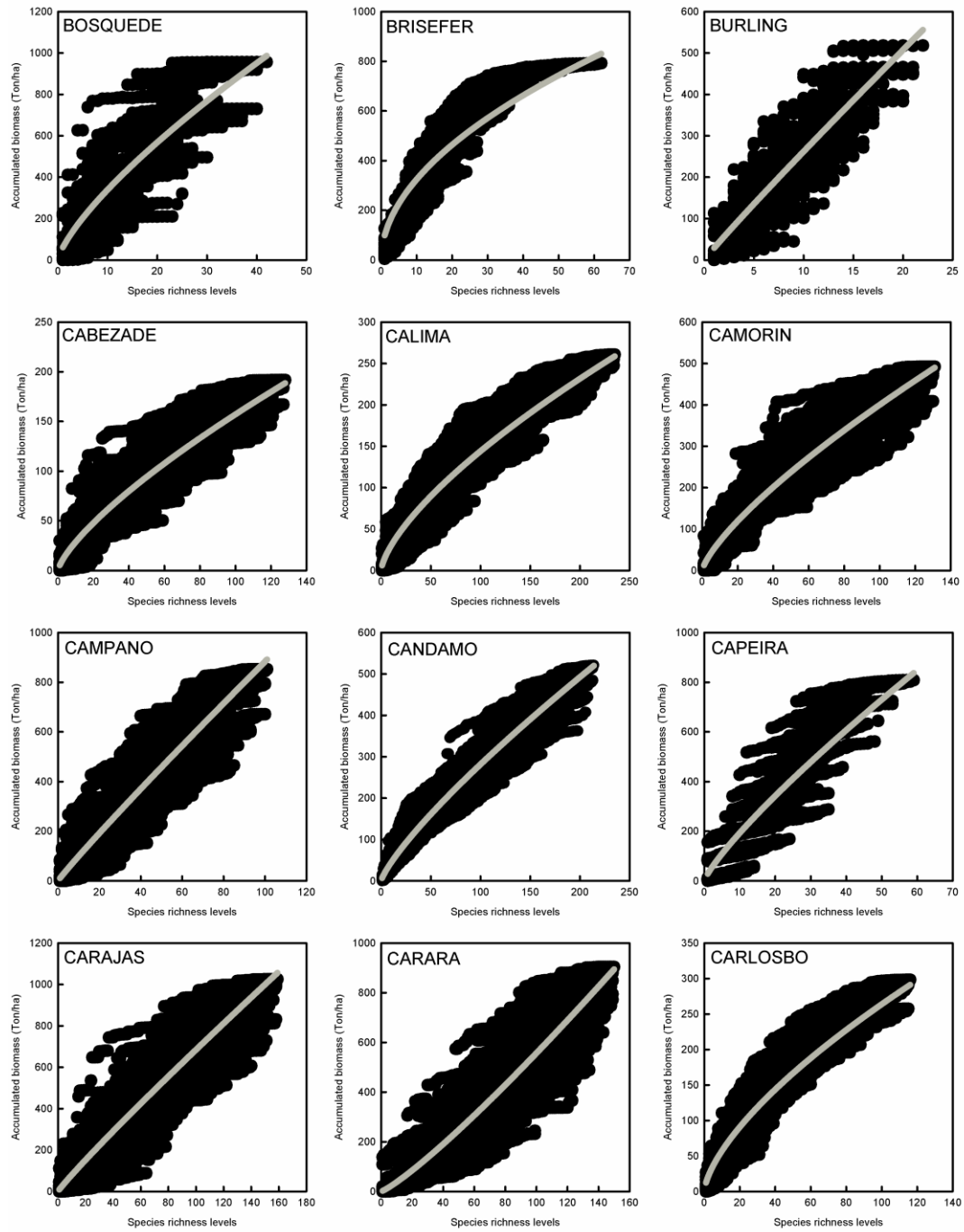
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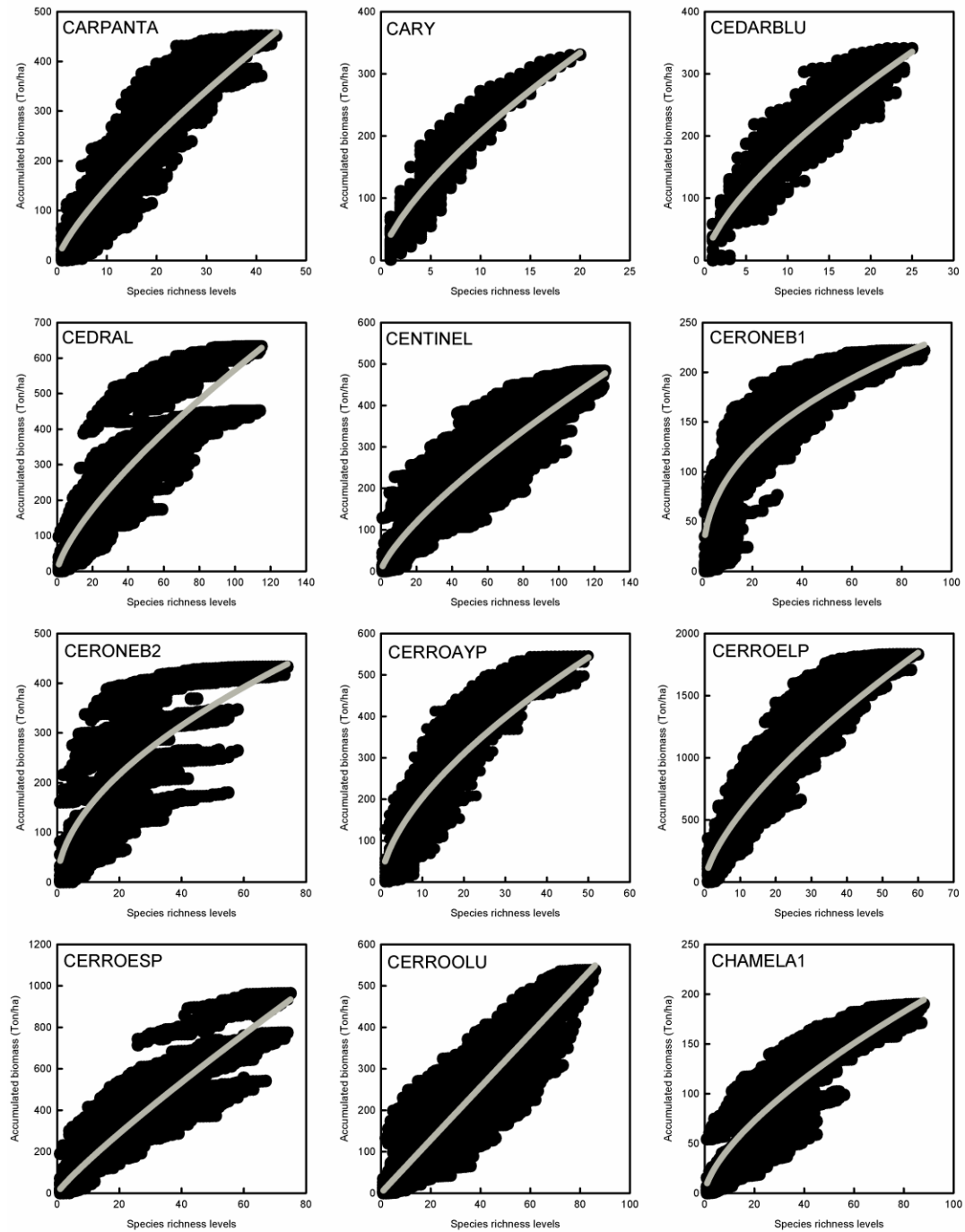
Relationships between aerial biomass and species richness (panel 5)
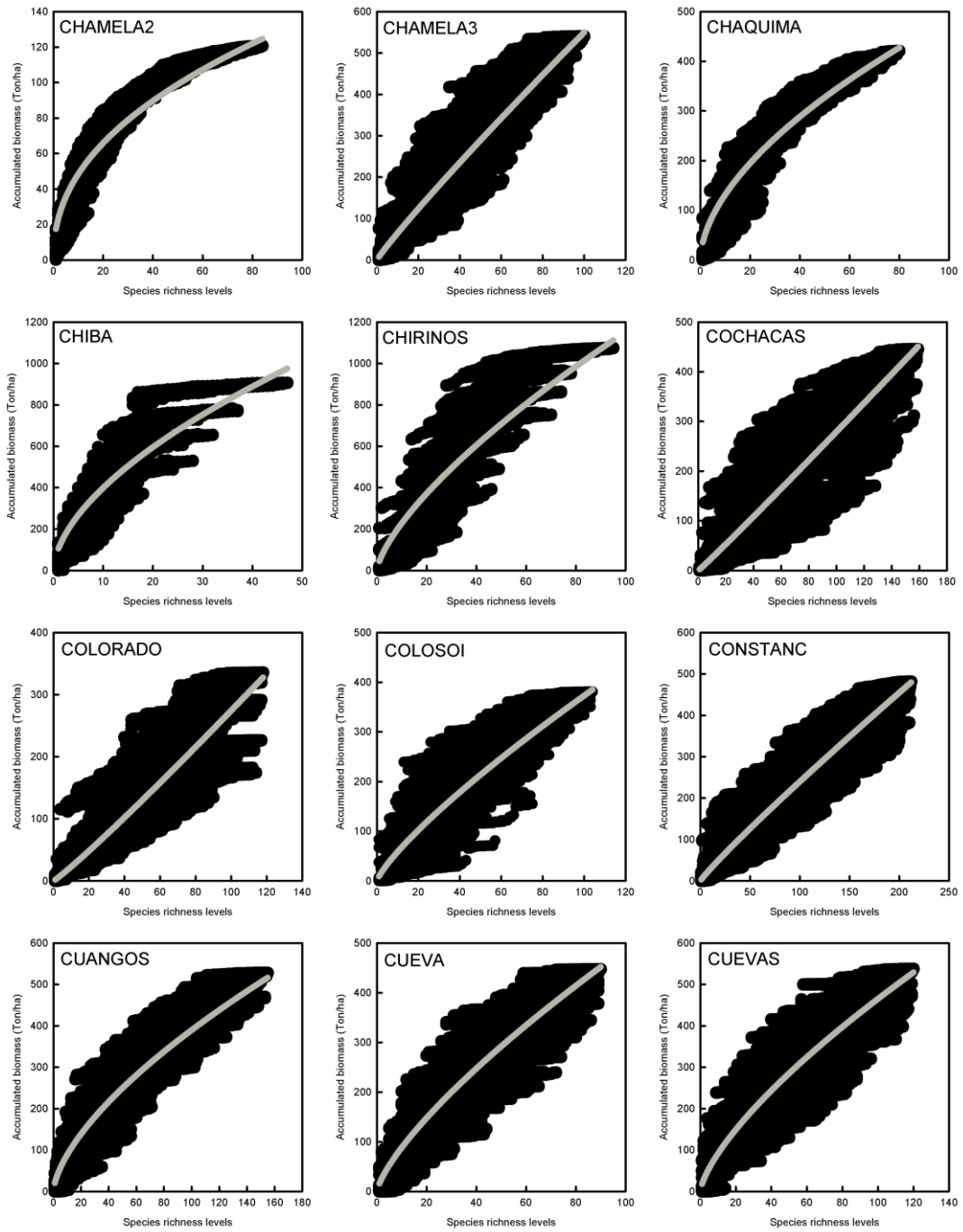
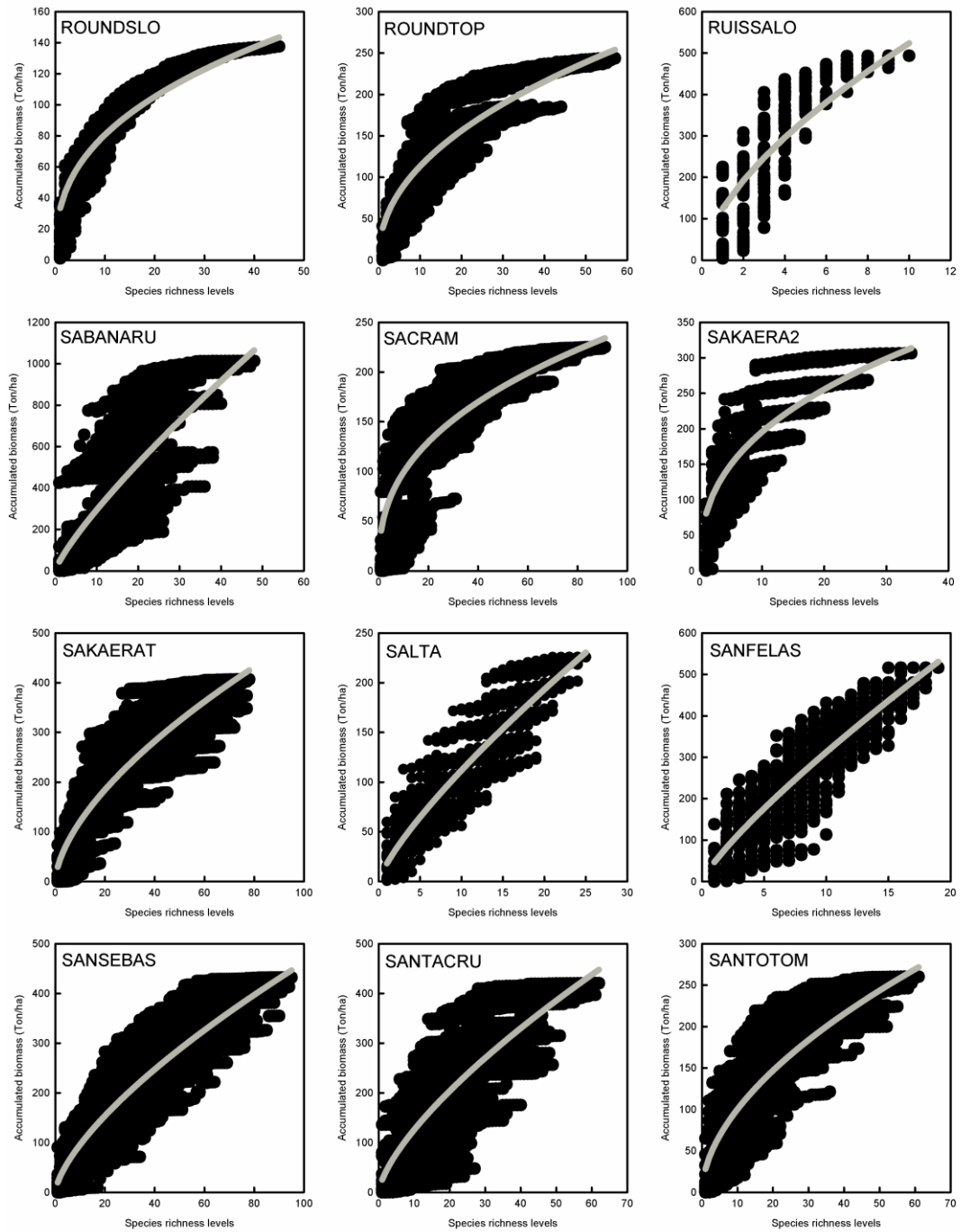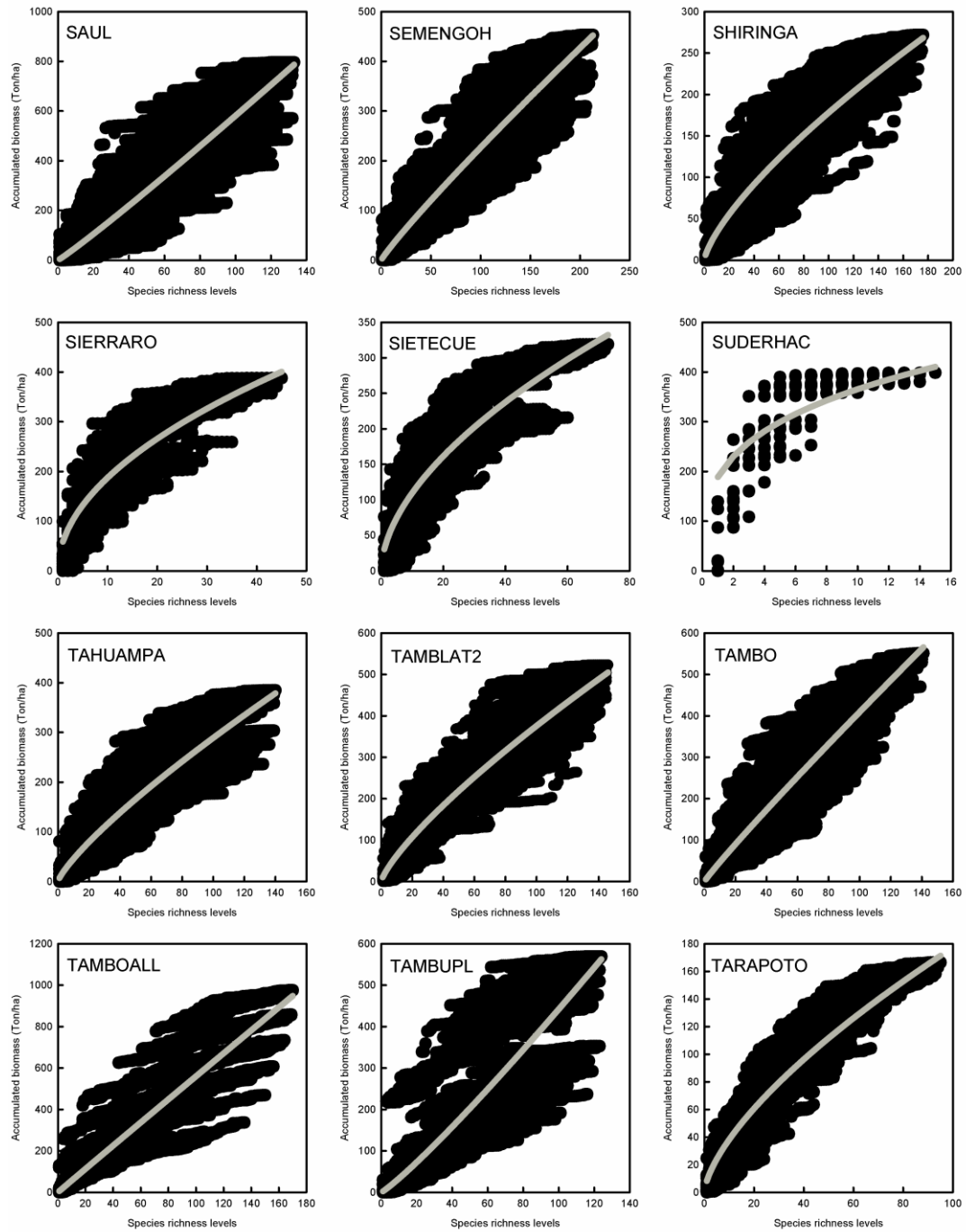**Relationships between aerial biomass and species richness (panel 6)**
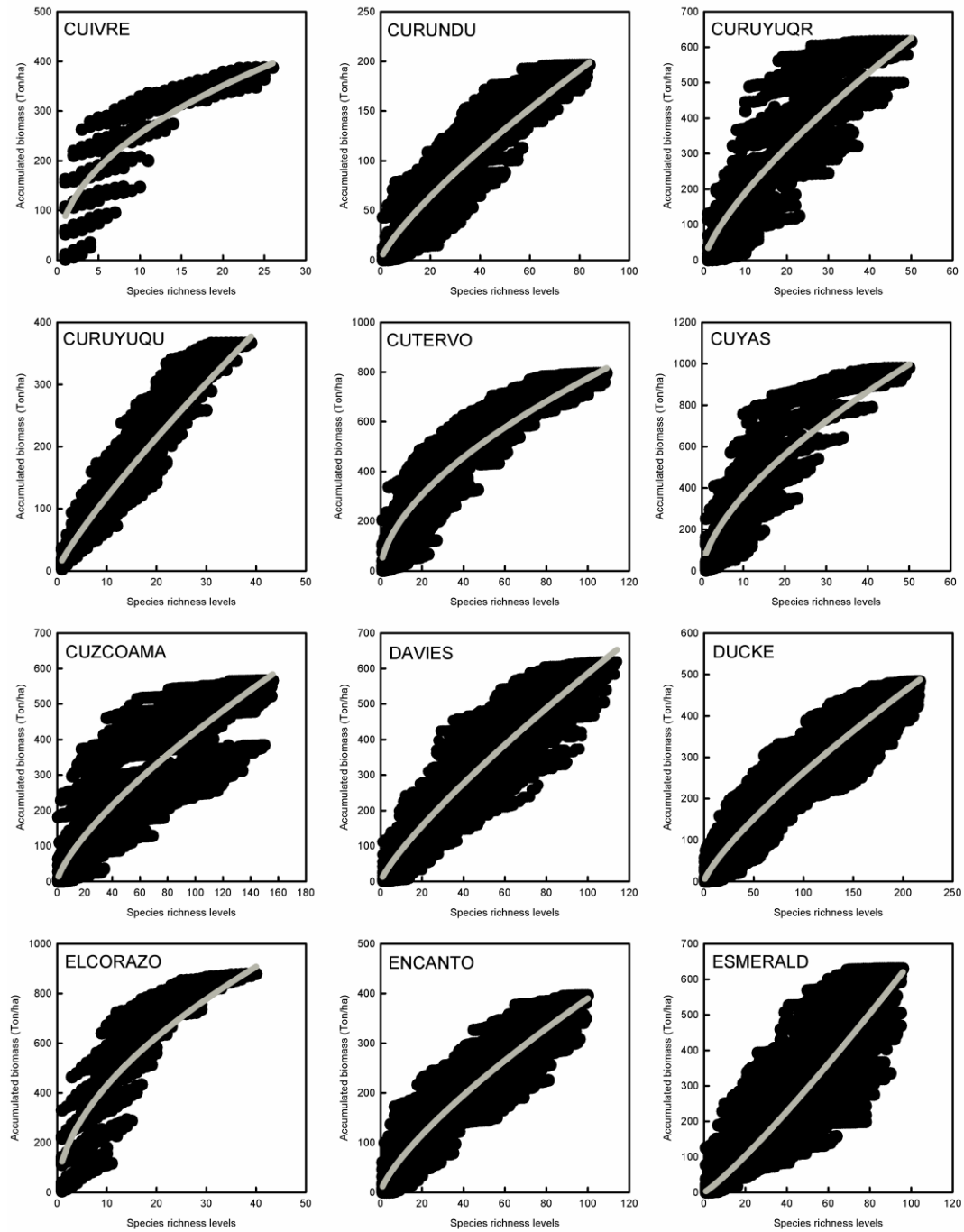
Relationships between aerial biomass and species richness (panel 7)
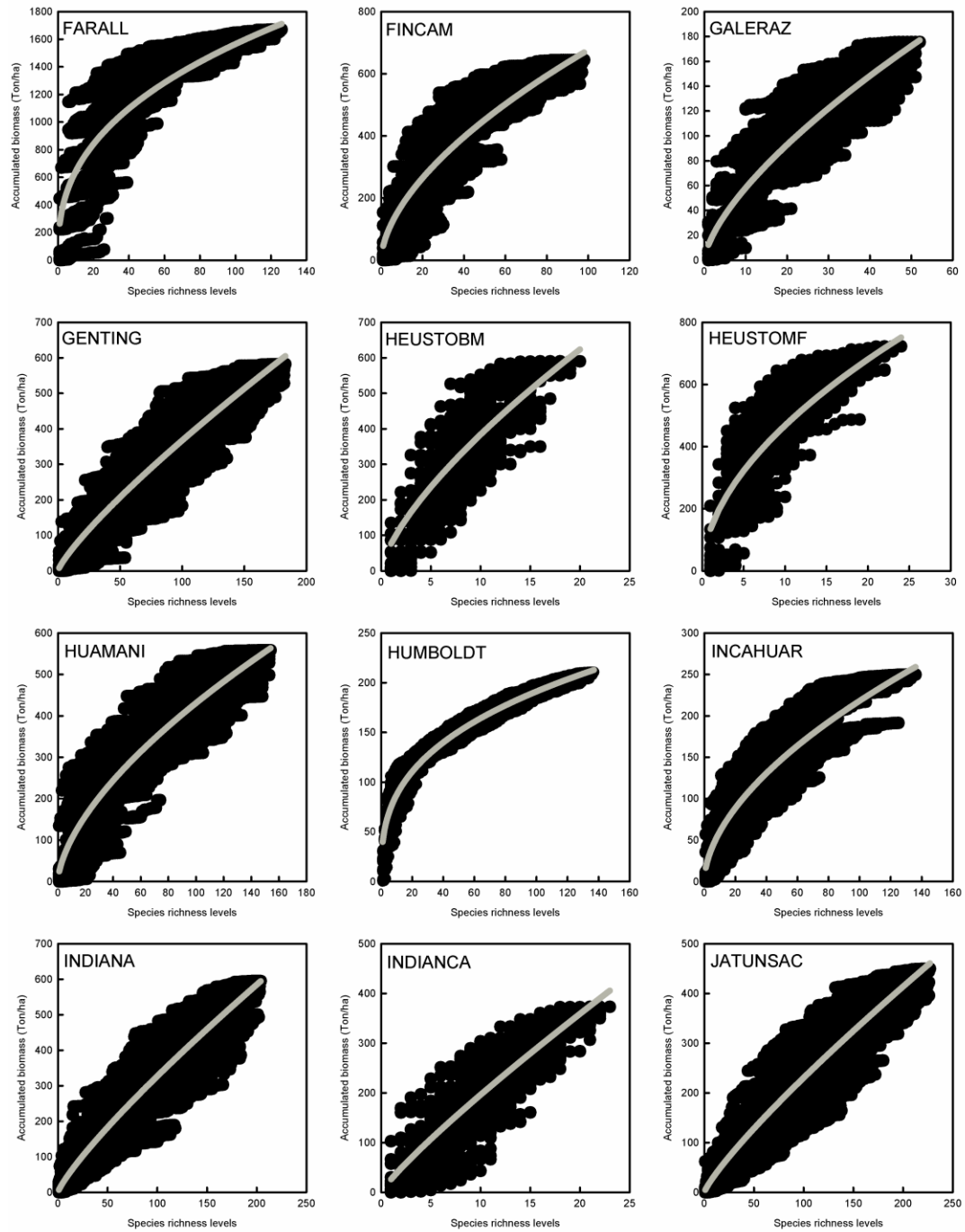
Relationships between aerial biomass and species richness (panel 8)
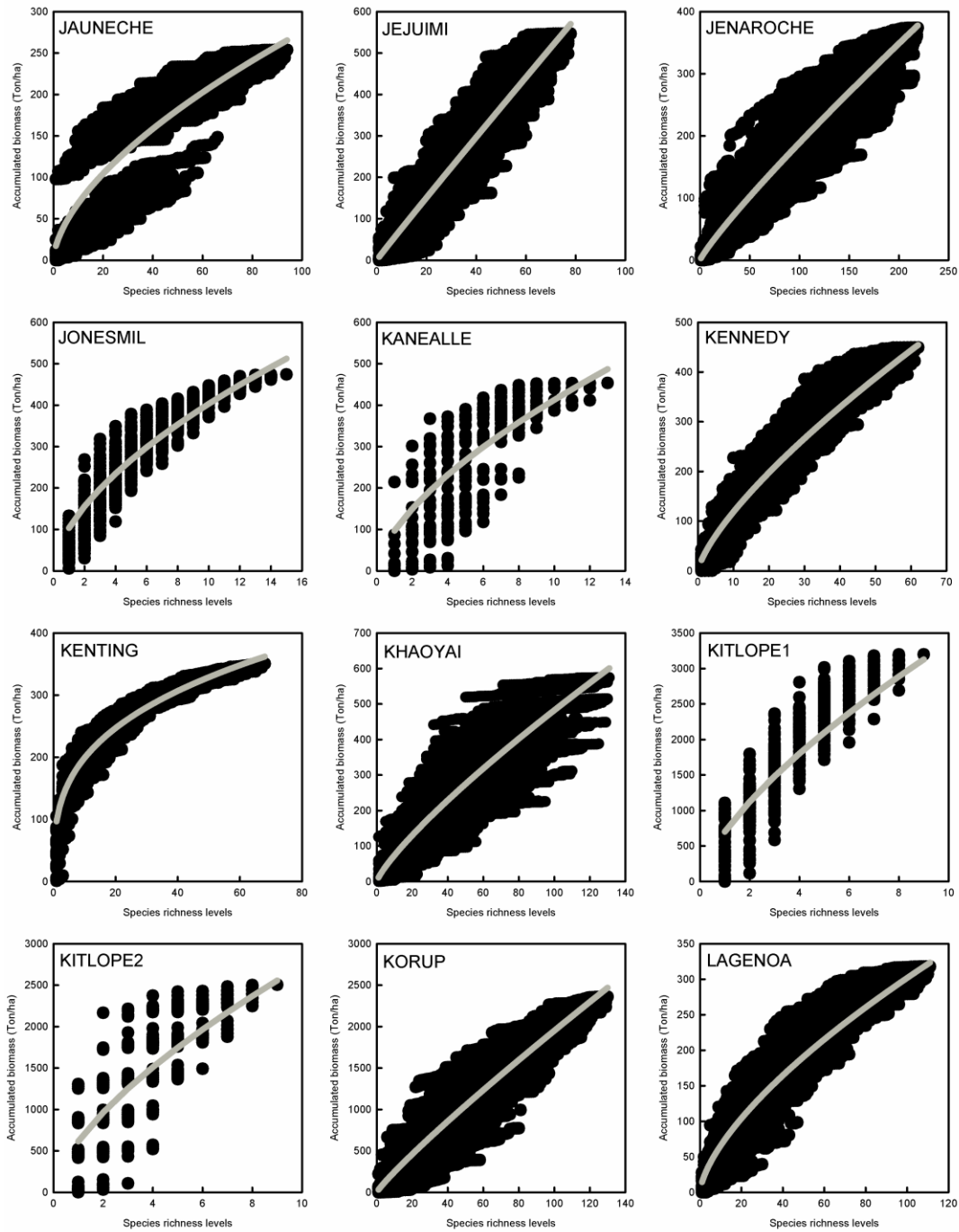
Relationships between aerial biomass and species richness (panel 9)
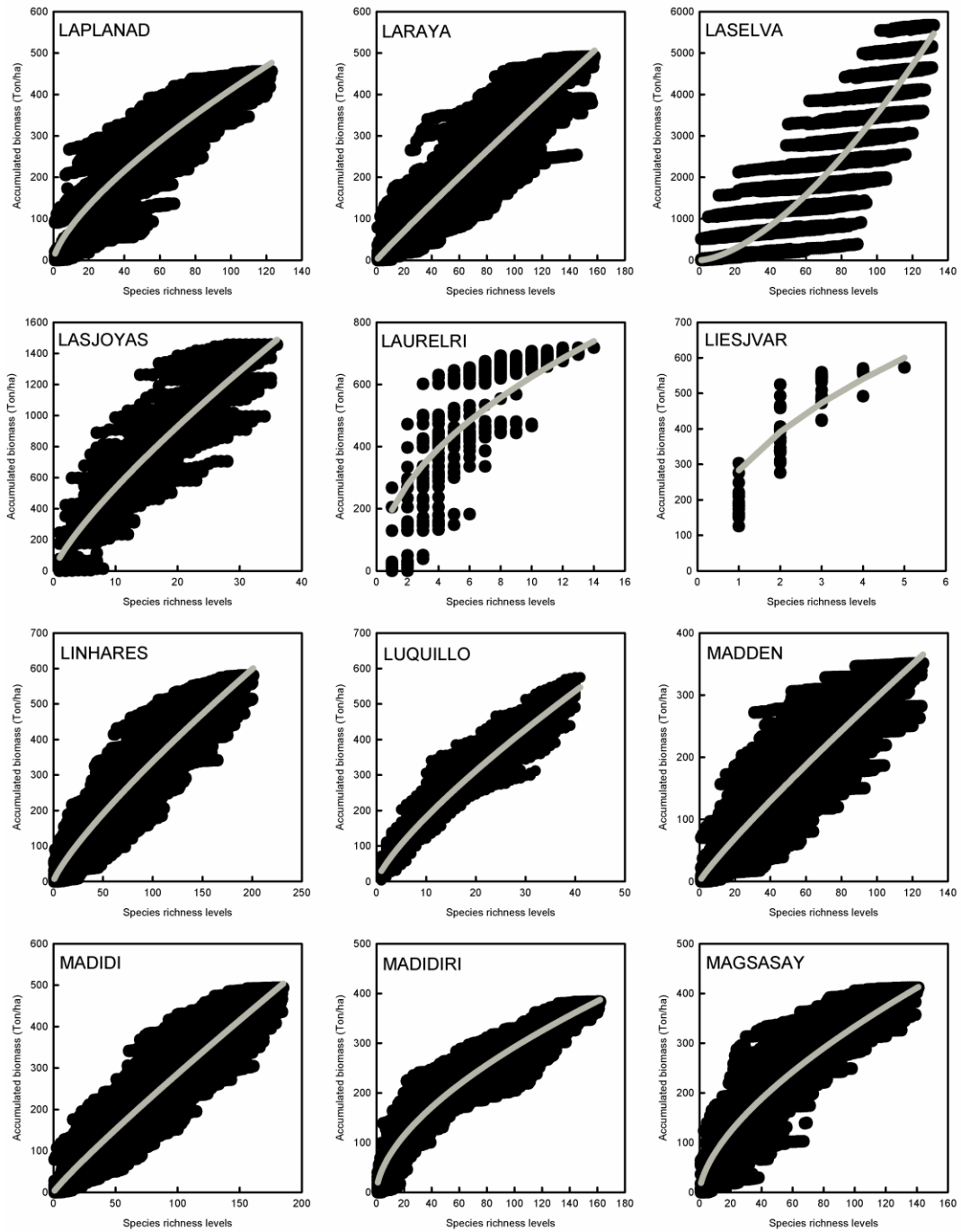
Relationships between aerial biomass and species richness (panel 10)
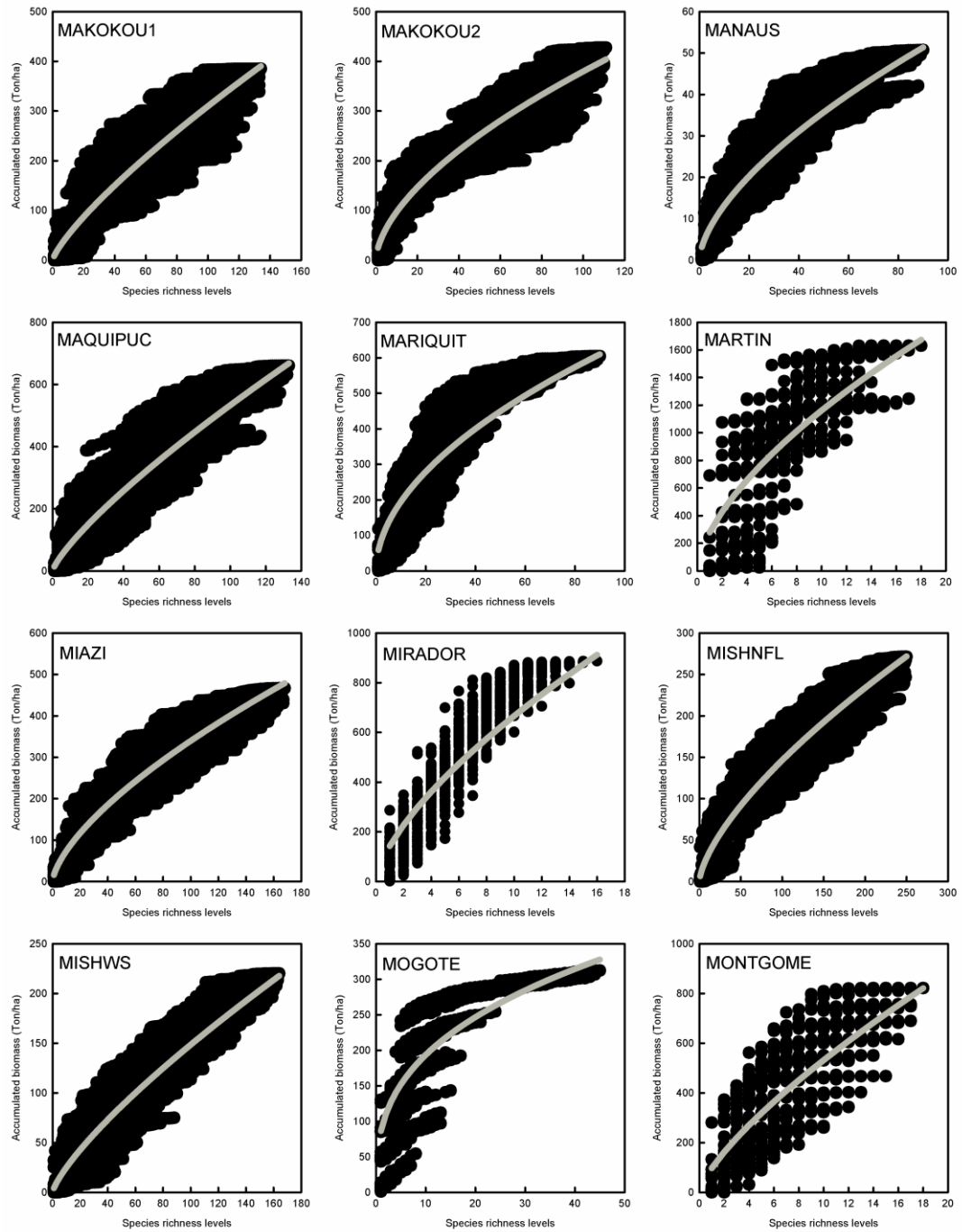
Relationships between aerial biomass and species richness (panel 11)

Relationships between aerial biomass and species richness (panel 12)

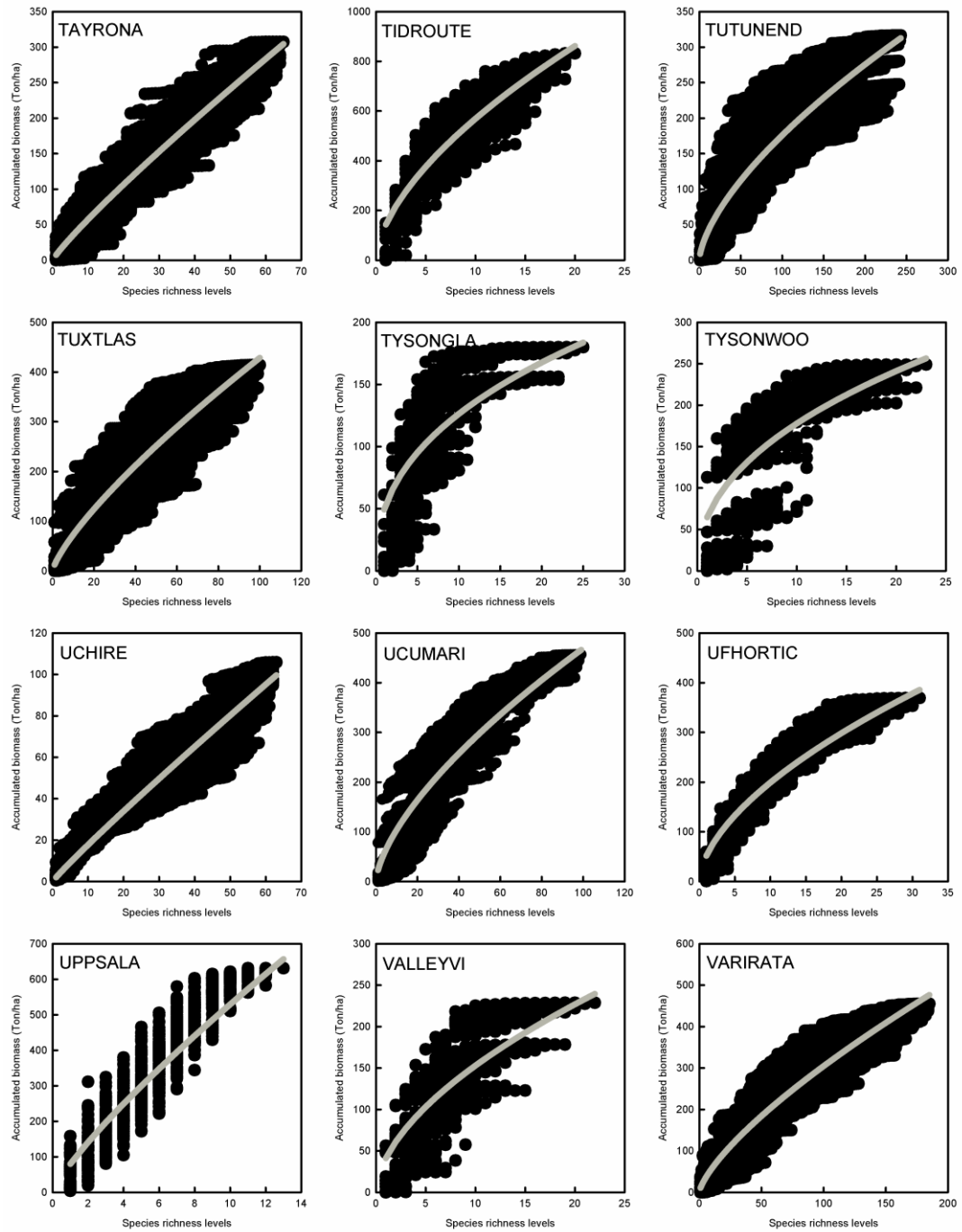**Relationships between aerial biomass and species richness (panel 13)**

Relationships between aerial biomass and species richness (panel 14)

Relationships between aerial biomass and species richness (panel 15)

Relationships between aerial biomass and species richness (panel 16)

Relationships between aerial biomass and species richness (panel 17)