

# Biodiversity–productivity relationship in ponds: Community and metacommunity patterns along time and environmental gradients

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**Abstract** Primary production correlates with diversity in various ways. These patterns may result from the interaction of various mechanisms related to the environmental context and the spatial and temporal scale of analysis. However, empirical evidence on diversity–productivity patterns typically considers single temporal and spatial scales, and does not include the effect of environmental variables. In a metacommunity of macrophytes in ephemeral ponds, we analysed the diversity–productivity relationship patterns in the field, the importance of the environmental variables of pond size and heterogeneity on such relationship, and the variation of these patterns at local (community level) and landscape scales (metacommunity level) across 52 ponds on twelve occasions, over five years (2005–2009). Combining all sampling dates, there were 377 ponds and 1954 sample-unit observations. Vegetation biomass was used as a proxy for productivity, and biodiversity was represented by species richness, evenness, and their interaction. Environmental variables comprised pond area, depth and internal heterogeneity. Productivity and species richness were not directly related at the metacommunity level, and were positively related at the community level. Taking environmental variables into account revealed positive species richness–productivity relationships at the metacommunity level and positive quadratic relationships at the community level. Productivity showed both positive and negative linear and nonlinear relationships with the size and heterogeneity of ponds. We found a weak relationship between productivity and evenness. The identity of variables associated with productivity changed between spatial scales and through time. The pattern of relationships between productivity and diversity depends on spatial scale and environmental context, and changes idiosyncratically through time within the same ecosystem. Thus, the diversity–productivity relationship is not only a property of the study system, but also a consequence of environmental variations and the temporal and spatial scale of analysis.

**Key words:** area, evenness, heterogeneity, macrophytes, species richness–biomass relationship.

## INTRODUCTION

The plant biodiversity–productivity relationship (BPR) is bidirectional in terms of causality: biodiversity affects productivity and the other way around (Loreau *et al.* 2001; Schmid 2002; Cardinale *et al.* 2009). Although experiments may isolate the two directions of causality, in the field we see patterns of correlation. These patterns are diverse, and our understanding of that diversity is limited. The spatial scale of analysis and the environmental context may be highly associated with this diversity of correlated patterns of productivity and diversity (Chase & Leibold 2002;

Chase & Ryberg 2004). Under the current scenario of biodiversity loss and accelerated environmental change, knowing the variation of plant diversity and primary productivity across large gradients of environmental variables is a major ecological challenge.

The most frequent patterns reported in experimental designs and in the field are linear and asymptotic increases of productivity as plant diversity increases, but several studies have shown U-shaped, humped, linear negative and non-significant relationships (Hector *et al.* 1999; Loreau *et al.* 2001; Hooper *et al.* 2005; Thompson *et al.* 2005; Mokany *et al.* 2008; Chalcraft 2013). The scale of analysis (from local to landscape) and the environmental context may account for these variations of the BPR (Cardinale *et al.* 2004). At the local scale (hereafter community

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level), most empirical studies show that richness-productivity relationships are either linear positive or non significant (Tilman *et al.* 2001; Chalcraft 2013), while theoretic works claim that productivity could peak at intermediate species richness (humped function, Bond & Chase 2002) a pattern less frequently seen in the field (Hector *et al.* 1999). At the landscape scale (hereafter metacommunity level, Leibold *et al.* 2004: scattered communities that are linked by dispersal of multiple potentially interacting species), positive relationships, both linear and U-shaped, were observed (Hector *et al.* 1999; Loreau *et al.* 2001; Chalcraft 2013).

Environmental variables may be directly associated with diversity and productivity or may alter the relationship between them (Loreau *et al.* 2001). In ecosystems with natural boundaries, such as lakes, size is an important variable that affects both diversity and productivity (Waide *et al.* 1999). In addition, environmental heterogeneity is associated with diversity because it increases the number of niches that can inhabit the ecosystem (Hérault & Thoen 2008). It may also affect productivity because of the increasing chance of including particularly productive habitats (Van de Bogert *et al.* 2012). The pervasive effect of area and heterogeneity on diversity (Rosenzweig 1995; Olf & Ritchie 2002; Ritchie 2010) and their potential effect on the BPR suggest that these environmental variables may account for the variety of patterns of the BPR (Loreau *et al.* 2001).

The variation of BPR patterns may be also accounted for by temporal variations of ecosystem conditions and the strength and nature of the mechanisms regulating the BPR. Seasonal and inter-annual variations of biotic and abiotic factors may change the shape and the strength of the BPR (Waide *et al.* 1999). However, most experimental and observational studies have considered short time periods, mostly one sampling date, and thus have not been able to detect the temporal variation of the BPR within a single system (Cardinale *et al.* 2004; Giller *et al.* 2004). A few long-term studies of the connection between diversity and ecosystem function have shown temporal variations of the relationships and highlighted the contingent role of some species on particular years (Isbell *et al.* 2011, 2013).

Most BPR studies have been carried out in grasslands (Balvanera *et al.* 2006). Ephemeral ponds have three properties that make them a good model for the specific analysis of the influence of scale, environmental conditions and time on the BPR. First, pond size, determined by area and depth, highly varies among ponds providing a relevant gradient for analysis. Second, the average and the internal variation of water depth is a main source of habitat heterogeneity (Laufer *et al.* 2009; Arim *et al.* 2010, 2011). These two factors may directly affect diversity and productivity, and thus

account for part of the variation of BPR patterns. Finally, ephemeral ponds present a large range of productivity, which increases the potential to detect significant BPRs.

In summary, three main sources of variation may be associated with the BPR. First, the spatial scale of analysis may reveal different relationships at the community and metacommunity levels. Second, environmental conditions (e.g. area and heterogeneity) could be associated with diversity, productivity or with their relationship. Third, the duration of experiments and observational studies constrain the range of patterns that can be detected (Díaz *et al.* 2003). These factors have been independently analysed in BPR studies, but their simultaneous natural variation has rarely been studied. In addition, some ecosystems such as ephemeral ponds have been underrepresented in empirical studies. Our main objective was to analyse the relationship between diversity and productivity of plant communities in ephemeral ponds at the community and metacommunity level and how this relationship changes with environmental variables across 12 dates, across a five-year period.

## METHODS

The study site was situated on the Northern border of the *Castillos* lagoon basin in the Eastern Wetlands region of Uruguay, declared Biosphere Reserve by the MAB program, UNESCO, and presently used for private cattle farming (34°15'24.38"S, 53°58'29.79"W; Laufer *et al.* 2009; Arim *et al.* 2010, 2011). The landscape is composed of a number of natural ephemeral, oval-shaped ponds scattered within a matrix of mesic grassland.

Each year, from autumn to early spring, these mesic grasslands receive several pulses of rainfall, which together with the low radiation and low temperatures of the season favour the filling of temporary ponds. Typically, ponds fill with the first autumn rains and remain in that condition until late spring. With the beginning of the flooding season, plant species composition shifts from mesic grasses to aquatic macrophytes.

We analysed the diversity-productivity relationship of plants and the influence of environmental variables at the metacommunity and community levels (according with Leibold *et al.* 2004) throughout 12 sampling dates across five years. The metacommunity level refers to the comparison among ponds, whose area varied by four orders of magnitude (2.5–17378 m<sup>2</sup>). The community level refers to the comparison among sample units (sample frames of 400 cm<sup>2</sup>) within ponds.

We surveyed 52 ponds on twelve dates: September 2005, May and June 2006; June, July and August 2007; June, August and October 2008; June, July and October 2009. On each date, the 52 ponds were visited, but only those containing water were sampled (minimum 10, maximum 52). Combining all sampling dates, there were 377 pond and 1954 sample-unit observations.

For each pond, we marked two diameters: a primary diameter (the longest possible line passing through the centre of

the pond) and a secondary diameter that ran perpendicular to the primary one. Pond shape and area were determined by water limit and varied across dates. Thus, diameters and the location of sampling units varied across sampling dates. Sample units for biomass and diversity were located along the primary diameter. For primary diameters  $\leq 10$  m, sample units were 2 m apart. For primary diameters between 10 and 50 m, we located 5 sample units at equidistant intervals. For primary diameters  $> 50$  m, we added sample units at 10 m intervals until the edge of the pond was reached. In each sample unit, we harvested all aerial biomass, submerged and over the water. Plant biomass was sorted into green and dead. Only green biomass was sorted by species and oven dried (60–80°C) for 72 h. Water depth was measured in the same sampling units as plant biomass and richness and in the intermediate position between two consecutive sample units. The number of dry lands above water surface, hereafter called 'islands', was counted along the two diameters of each pond. Island density was calculated as the ratio between island number and length (Sutherland 2006) and indicated both pond heterogeneity and the amount of terrestrial-aquatic boundaries that could affect productivity, diversity and their relationship.

At each level (community and metacommunity) and date, the direct relationship between biomass production and species richness was estimated by means of linear and quadratic relationships (Sokal & Rohlf 1995). Next, we evaluated the influence of environmental variables and evenness on these direct relationships. On the recognition that local communities are modulated by local and landscape process (Cornell 1992; Loreau 2000; Leibold *et al.* 2004; Barton *et al.* 2013), at the community level we took into account environmental variables of landscape scale (pond area and heterogeneity).

By considering the environmental variables we were not interested in explaining a larger proportion of productivity, but in evaluating their role as potential modifiers of the BPR. Ecosystem size and internal heterogeneity are potentially linked with biodiversity, and as a result may influence the BPR either by changing its shape or making it evident. In particular, our study did not aim at accounting for the variation of productivity among and within temporary ponds, but at finding variables that could modify the relationship between productivity and diversity. The environmental variables we selected are related to pond size and heterogeneity. These variables may affect the relationship between productivity and diversity by affecting both variables in an interactive form. For example, ponds with similar diversity may have different productivity if they have different heterogeneity. Small islands within ponds may act as a source of resources from terrestrial to aquatic systems. Similarly, variations of depth may represent differences in light availability that could in turn result in more or less productivity for similar diversity values. As a consequence of focusing on the variation of BPR rather than on accounting for the variation of productivity, variables directly related to site productivity were not included.

Biomass was used as a proxy for primary productivity in all analyses (as in Tilman *et al.* 1997; Tilman *et al.* 2001; Lambers *et al.* 2004; Adler *et al.* 2011). When the ponds fill with water, plant species composition shifts from terrestrial grasses to aquatic macrophytes, so the vegetation biomass

collected was produced during each ephemeral flooding season. As a result, standing, green macrophyte biomass is all produced within the growing season and relates to production. Biomass loss by domestic herbivores was insignificant and the losses by senescence were assumed homogeneous across sample units and ponds. Thus, we assumed that the variation in biomass across sample units or ponds largely reflected variation in productivity. Mean biomass varied from  $3 \text{ g m}^{-2}$  to  $596 \text{ g m}^{-2}$  at the metacommunity level, and from  $0 \text{ g m}^{-2}$  to  $1790 \text{ g m}^{-2}$  at the community level. Plant species richness varied from 2 to 22 species at the metacommunity level (entire pond), and 1 to 10 at the community level (sample unit). Although sample units may appear small ( $400 \text{ cm}^2$ ), they included a large proportion of pond species: mean species richness of sample units represented 42% of species richness at the metacommunity level. Moreover, ponds were dominated by small macrophyte species (i.e. *Eleocharis viridans*, *Luziola peruviana*, *Hydrocotyle ranunculoides*, *Leersia hexandra*, *Lilaea scilloides*).

Plant diversity was represented by species richness, evenness, and their interaction. Empirical and theoretical studies on the BPR focus almost exclusively on species richness as a representation of biodiversity. The few studies explicitly considering evenness revealed its role in ecosystem function both directly and through its effect on species richness (Hillebrand *et al.* 2008; Isbell *et al.* 2009). Thus, we did not merge richness and evenness into a combined index. Our independent consideration of evenness and richness is based on the potential independent and interactive effects of these two components of biodiversity, and on the proposition of different mechanisms connecting the two metrics with ecosystem functioning. Pond evenness was calculated as  $H'/\ln S$ , where  $S$  is richness and  $H'$  is the Shannon diversity index:  $H' = -\sum \ln(p_i)p_i$ , where  $p_i$  is the proportion of species  $i$ . The environmental variables were pond size (mean water depth and area of water surface), heterogeneity at the metacommunity level (coefficient of variation of depth and the density of islands) and sample unit depth at the community level.

## Statistical analyses

### *Species richness versus biomass*

At both metacommunity and community levels, we searched for direct species richness–biomass relationships. At the metacommunity level, we used ordinary least squares (OLS) regression. At the community level, we avoided dependence among sample units by using linear mixed effects models (lme) with ponds as hierarchical factor (Zuur *et al.* 2009). We selected the best random structure of each model among the random intercept model, the random intercept and slope model, and the random effects model by Akaike information criterion (AIC) and ANOVAs among models (Zuur *et al.* 2009). At both levels, quadratic relationships were tested.

### *Multiple models including biodiversity and environmental variables*

At the metacommunity level, sixteen explanatory variables were considered. Some described species diversity: pond

species richness and its quadratic term, evenness and its quadratic term, interaction between species richness and evenness with quadratic terms (evenness  $\times$  richness, evenness<sup>2</sup>  $\times$  richness, evenness  $\times$  richness<sup>2</sup>, evenness<sup>2</sup>  $\times$  richness<sup>2</sup>). Others described the environment: pond area ( $\log_{10}$  (area)), mean pond depth, density of islands, coefficient of variation of depth, and their quadratic forms. At the community level, ten explanatory variables were considered: sample unit species richness, sample unit depth and environmental variables describing the pond: pond area ( $\log_{10}$  (area)), density of islands, coefficient of variation of depth, and their quadratic forms, which could represent environmental filters or enhancers of sample-unit species richness and productivity.

At both the metacommunity and community levels, we used biomass as the response variable and diversity and environmental variables as explanatory variables. First, we performed a search for best subset models, ranking models conforming to Akaike information criterion corrected for small samples size (AICc, Burnham & Anderson 1998). In order to deal with multicollinearity we used an exhaustive method to find the best model instead of the usual stepwise methods. In addition, the selection by AIC avoided multicollinearity biases. Final models were selected according to three criteria. First, to avoid overfitting, the maximum number of variables included in the models was constrained to a minimum number of eight observations for each estimated parameter (Crawley 2007). Second, only models with less than two units of difference in comparison with the lowest AICc observed were considered (Burnham & Anderson 1998; Crawley 2007). Third, the whole model and all its parameters had to be significant ( $P < 0.05$ ).

Then, only at community level, after the selection procedure, the selected best models were fitted by linear and nonlinear mixed effects models (nlme) in order to deal with dependence among sample units. In linear and nonlinear mixed effect models, ponds were the hierarchical factor and the explanatory variables included in previously selected best model were the fixed structure. We selected the best random structure of each model among the random intercept model, the random intercept and slope model, and the random effects model by AIC and ANOVAs among models (Zuur *et al.* 2009).

We explored if the temporal variation of BPR slopes showed seasonal or interannual trends and if changes in species composition accounted for some of the variation of BPR over time. We plotted the slopes of the BPR of different sampling dates over time and contrasted the pattern with seasonal and interannual patterns. In order to explore the association between BPR slopes and species composition, we followed two approaches. First, we performed a correspondence analysis (CA) in order to explore whether particular combinations of dominant species were associated with particular sampling dates, seasons or years and affected BPR. We considered dominant species as the 32 species, out of 119, present in more than 1% of the sampling units.

Second, we performed a regression analysis between the dissimilarity of species composition and the dissimilarity of the BPR slopes between pairs of sampling dates. In detail, we built a matrix of dissimilarity indices by Euclidean distance of species composition between all pairs of the nine dates that presented significant BPR. Similarly, we built a matrix of

dissimilarity indices by Euclidean distance of the BPR slopes of the same nine dates. Each matrix consisted of  $9 \times 8 / 2 = 36$  comparisons. Euclidean distances were calculated as:  $d[jk] = \text{square root } \sum_{i=1}^N (x[ij] - x[ik])^2$ , for species composition  $x[ij]$  and  $x[ik]$  refer to the quantity on species (column)  $i$  and dates (rows)  $j$  and  $k$ , for dissimilarity of the BPR slopes  $x[ij]$  and  $x[ik]$  refer to the slopes  $i$  between the dates (rows)  $j$  and  $k$ .

All the analyses were performed with R using the *leaps*, *vegan* and *nlme* packages (Lumley 2009; Oksanen *et al.* 2013; Pinheiro *et al.* 2013; R Core Team 2013).

## RESULTS

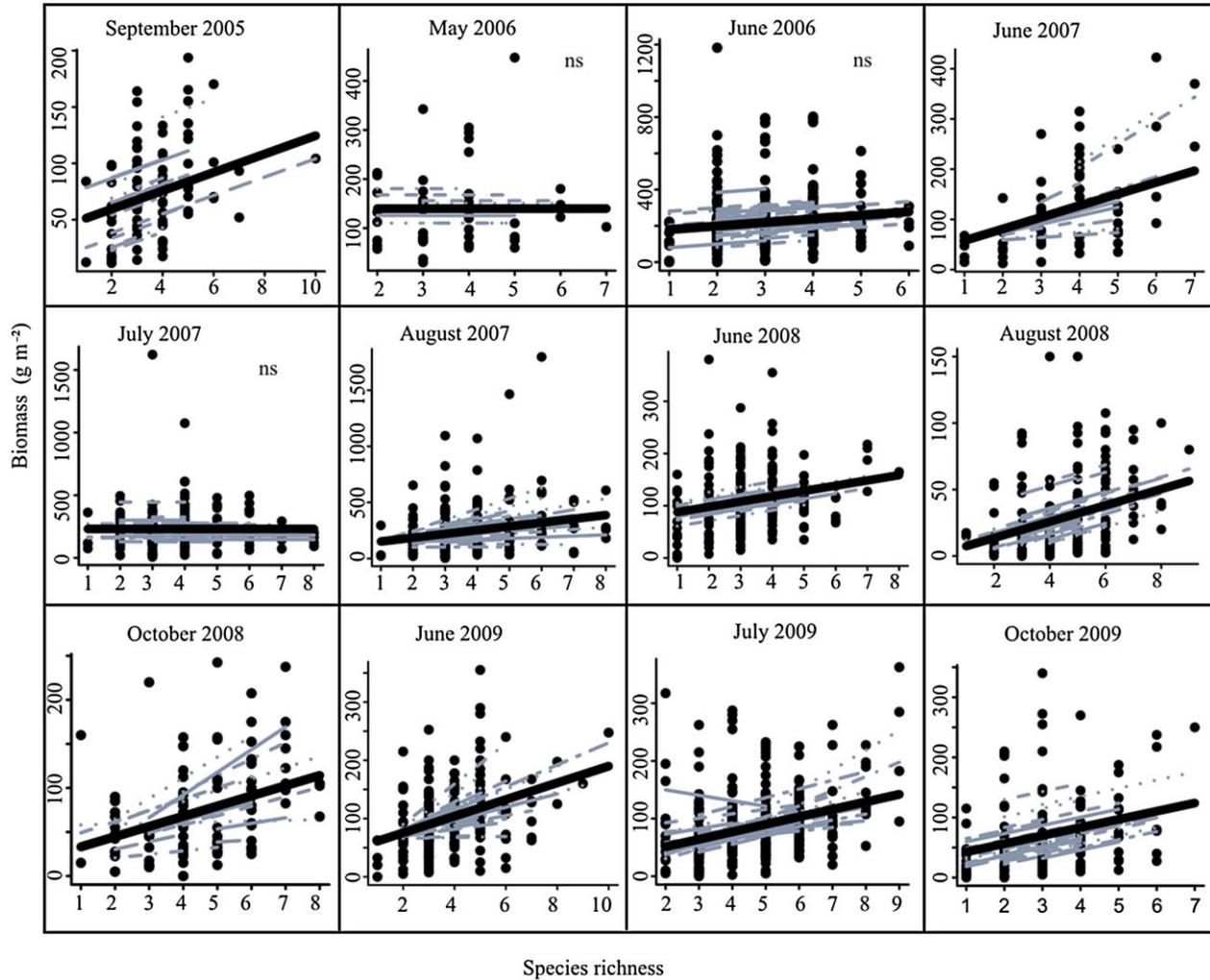
### Species richness versus biomass

At the metacommunity level, biomass was not significantly related to species richness on any sampling date. In contrast, at the community level, biomass significantly increased with richness at nine of the twelve sampling dates (Fig. 1, Table 1). The general positive pattern on community level was consistent among ponds, but there were some quantitative differences. On five of the nine dates (June and August 2007, October 2008, June and July 2009), both the slope and the intercept differed among ponds, whereas on the other four dates only the intercept did (gray lines Fig. 1 and standard deviation in Table 1).

### Multiple models including biodiversity and environmental variables

At the metacommunity level, biomass was significantly associated with environmental variables in seven of the twelve dates (Table 2, Fig. 2). On two dates, including environmental variables revealed a relationship between biomass and richness: biomass was positively associated with species richness, and negatively with either pond area (August 2008) or heterogeneity measured as the density of islands (October 2008, Table 2, Fig. 2). Combining environmental variables and species richness, the range of association with biomass variation was 13–59% (Table 2). Biomass was related to islands in contrasting ways over time, covering positive (September 2005) and negative (October 2008) linear and humped relationships (July 2007). The relationship between biomass and mean depth was positive on one date (May 2006) and negative on another (June 2008, Table 2). Finally, on October 2009, biomass variation among ponds was accounted for by the coefficient of variation of depth, its quadratic term, and the interaction between evenness and species richness (Table 2).

At the community level, adjusting for environmental variables changed the relationship between species



**Fig. 1.** Biomass – species richness relationships through 12 sampling dates at the community level (each data point corresponds to a sample unit). Models were fitted by linear mixed effects models. Gray lines represent each pond taken as random factor and the thick black line represents the fitted line obtained by the fixed component (richness) of the model. In May and June 2006 and July 2007 species richness was not related to biomass (ns, Table 1).

**Table 1.** Mixed effects models relating biomass ( $\text{g m}^{-2}$ ) to species richness (richness) at the community level

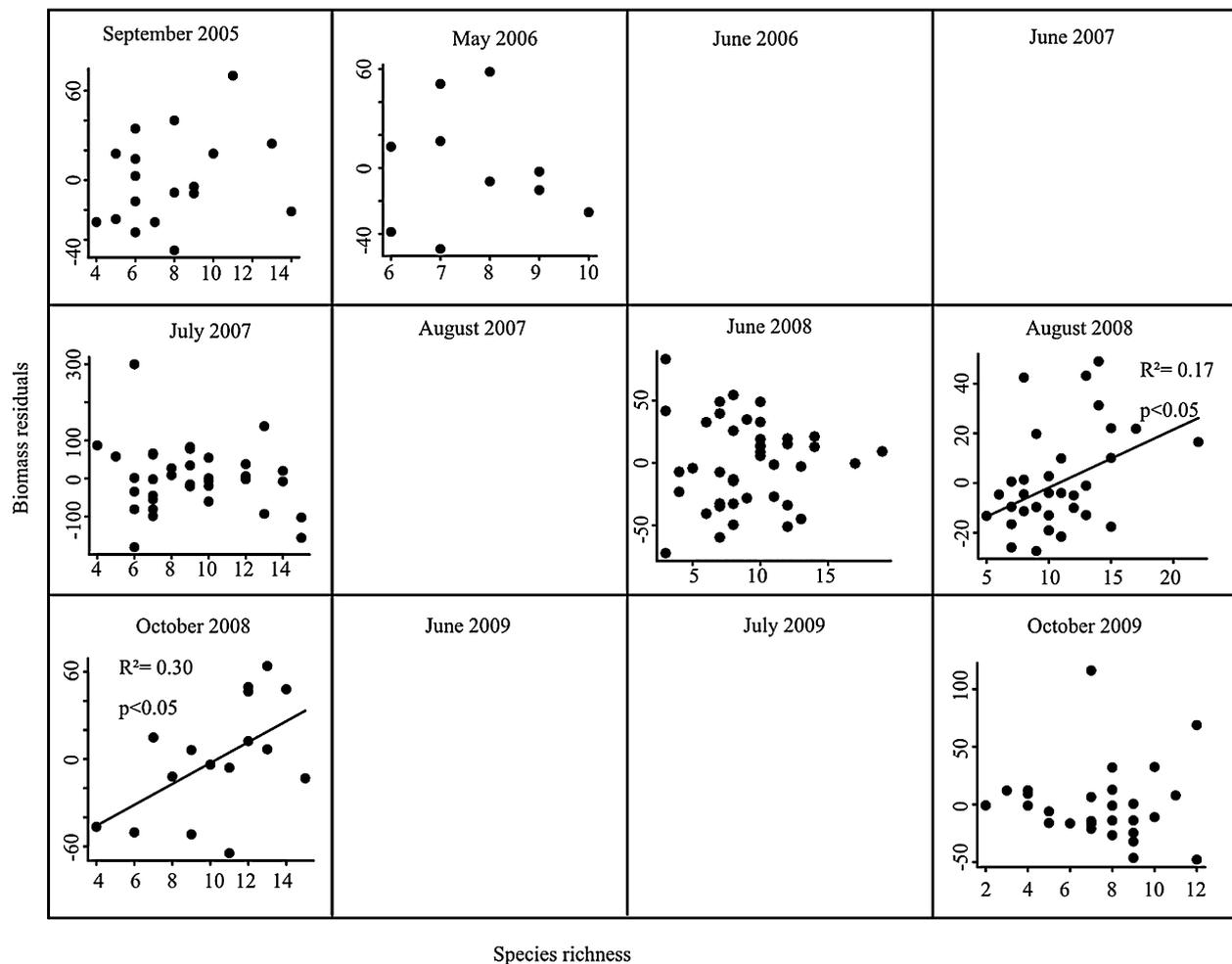
Date	Selected models	d.f.
September 2005	Biomass = 43.15 (28.3) + 8.14 richness	65
June 2007	Biomass = 34.6 (13.3) + 23.2 (16.5) richness	52
August 2007	Biomass = 117.8 (66.9) + 33.6 (30.3) richness	195
June 2008	Biomass = 77.7 (19.6) + 10.1 richness	167
August 2008	Biomass = 1.3 (14.3) + 6.14 richness	141
October 2008	Biomass = 21.6 (30.18) + 11.6 (9.52) richness	76
June 2009	Biomass = 46.9 (12.07) + 14.3 (9.36) richness	152
July 2009	Biomass = 25.1 (55.5) + 13 (10.9) richness	224
October 2009	Biomass = 29.2 (36.4) + 13.6 richness	125

Only the nine dates with a significant relationship are presented. When random effects were included into the final model the standard deviation of estimated parameters are shown. This deviation represents the variation in mean plant biomass and/or its dependence from species richness determined by pond identity. All models were significant at  $P < 0.01$ .

**Table 2.** Linear regression models relating biomass ( $\text{g m}^{-2}$ ) to environmental and diversity variables at the metacommunity level

Date	Selected models	P-value	$R^2$
September 2005	Biomass = $53.4 + 47.4$ islands	0.054	0.21
May 2006	Biomass = $71.9 + 730.0$ depth	<0.05	0.49
July 2007	Biomass = $154.6 + 370.7$ islands – $233.4$ islands <sup>2</sup>	<0.001	0.37
June 2008	Biomass = $143.9 - 367.4$ depth	<0.05	0.13
August 2008	Biomass = $39.14 + 3.54$ richness – $20.42$ area	<0.01	0.29
October 2008	Biomass = $62.77 + 7.69$ richness – $92.06$ islands	<0.05	0.38
October 2009	Biomass = $277.63 - 179.2$ cv_depth + $28.23$ cv_depth <sup>2</sup> + $12.33$ (evenness $\times$ richness)	<0.001	0.59

Only the seven dates with a significant relationship are presented. Determination coefficient ( $R^2$ ) and the statistical significance ( $P$ -value) of the relationships are indicated. Abbreviated variable names are: species richness (richness), community evenness (evenness), density of islands (islands), the coefficient of variation of depth of each pond (cv\_depth), the mean depth of each pond (depth) and the  $\log_{10}$  (area) of each pond (area).



**Fig. 2.** Biomass-species richness relationships at the metacommunity level (each data point corresponds to a pond). Biomass is expressed as the residuals of the relationship between biomass and environmental variables. Only the seven dates with statistically significant relationship were plotted. In June 2006, June 2007, August 2007, June 2009 and July 2009 there were not statistically significant relationship between biomass and explanatory variables. August and October 2008 incorporated species richness into the models, so the curve functions are shown. Partial determination coefficient ( $R^2$ ) and the statistical significance ( $P$ ) of the relationship are indicated within each plot. In September 2005, May 2006, July 2007 and June 2008, species richness was not related with biomass and the models selected included only environmental variables. In October 2009, biomass was related with the interaction between species richness and community evenness and with environmental variables (Table 2).

**Table 3.** Mixed effects models relating biomass ( $\text{g m}^{-2}$ ) to environmental and diversity variables at the community level

Date	Selected models	d.f.
September 2005	Biomass = 26.39 (24.8) + 7.77 richness + 42.97 islands	65/16
May 2006	Biomass = 367 (0.005) - 178 area + 31 area <sup>2</sup>	40/7
June 2007	Biomass = 92.2 (48.3) + 23.7 richness - 9.6 depth + 0.3 depth <sup>2</sup>	50
July 2007	Biomass = 250 (51.3) + 501 islands - 313 islands <sup>2</sup> - 52 area	149/30
August 2007	Biomass = -299.3 (80.8) + 35.9 richness + 304 area - 52.2 area <sup>2</sup>	195/41
June 2008	Biomass = -112 (8.33) + 11 richness + 774 cv_depth - 742 cv_depth <sup>2</sup> - 56 islands + 58 islands <sup>2</sup>	167/36
August 2008	Biomass = 48.8 (10.5) + 0.7 richness <sup>2</sup> + 127.1 cv_depth - 68.8 cv_depth <sup>2</sup> + 20.7 islands - 55.9 area + 8.5 area <sup>2</sup>	141/28
October 2008	Biomass = -196 (20) + 11 richness + 585 islands - 454 islands <sup>2</sup> + 20 area	76/12
June 2009	Biomass = 72.8 (19.8) + 13.6 richness - 7.2 depth + 0.2 depth <sup>2</sup> + 74.5 islands - 63.7 islands <sup>2</sup>	150/36
July 2009	Biomass = 114.3 (41.7) + 1.4 (0.95) richness <sup>2</sup> - 62 (32.73) area + 13.9 (5.7) area <sup>2</sup>	224/49
October 2009	Biomass = 260.2 (26.6) + 2.3 richness <sup>2</sup> - 146.1 cv_depth + 23.3 cv_depth <sup>2</sup>	125/25

Only the eleven dates with a significant relationship are presented. Abbreviated variable names and deviation from random effects are as in previous tables, except 'depth' which refers to water depth at sampling unit location. All models were significant at  $P < 0.01$ . When degrees of freedom (d.f.) differed between variables are presented as: d.f. of species richness and intercept/d.f. of environmental variables. In May 2006 and July 2007 only environmental variables were related with biomass.

richness and biomass (Table 3, Fig. 3). On eleven of the twelve dates we found significant relationships. On nine of these eleven dates, environmental variables were related to additional variation in biomass and on six of these nine dates environmental variables did not change the shape of the relationship between biomass and richness (Table 3). In contrast, in the remaining three of these nine dates (August 2008, and July and October 2009), including environmental variables changed the relationship between species richness and biomass to a positive quadratic function (Table 3, Fig. 3). On the two remaining dates of the eleven with significant relationships, May 2006 and July 2007, environmental variables related to size (area) and heterogeneity (density of islands and coefficient of variation of depth) significantly correlated with biomass. In June 2006, neither species richness nor environmental variables were related to biomass. On the remaining sampling dates, biomass was linearly related to species richness, with the additional effect of environmental variables as pond area (August 2007), heterogeneity (density of islands and coefficient of variation of depth on September 2005 and June 2008), a combination of pond heterogeneity and size (October 2008, June 2009), or the water depth at the sampling unit location (June 2007, see Table 3). All these relationships with environmental variables followed linear positive, linear negative, U-shaped or humped patterns (Table 3).

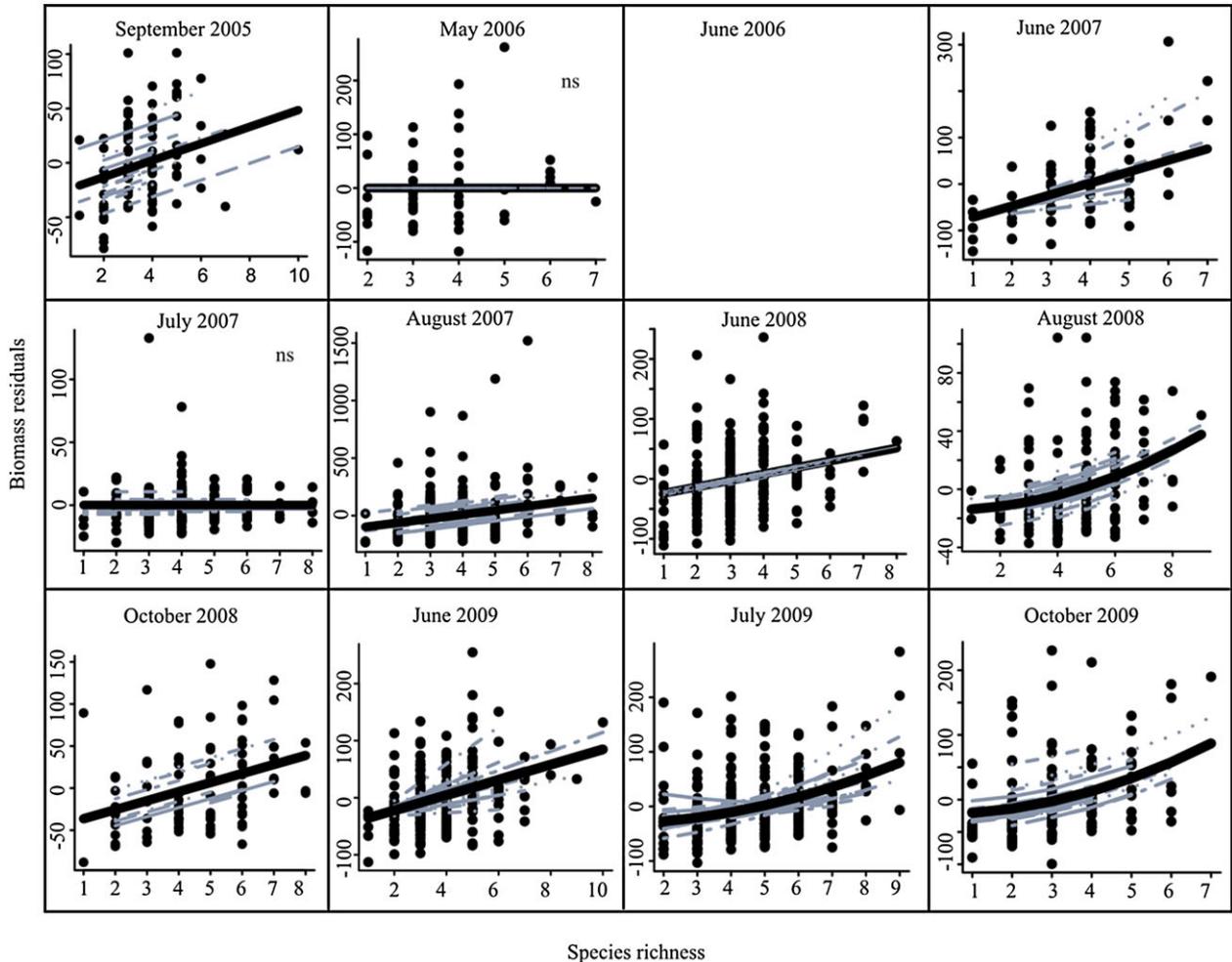
The CA did not show any clear association between dominant species composition and dates (Fig. 4a), with the first two principal components explaining 46 % of the variance. The slopes of the different BPR models of Fig. 1 and Table 1 did not show any trend over time that could be associated with particular seasons or years (Fig. 4b). The differences between the

BPR slopes of different sampling dates (Table 1) were not associated with the dissimilarity of species composition ( $F_{1,34} = 0.646$ ,  $P = 0.43$ ).

## DISCUSSION

As a whole, our results congruently point to a positive relationship between biodiversity and productivity. However, the large degree of contingency we observed indicates that productivity of a single metacommunity was tightly linked to species richness on some dates and not associated on others. Further, the relationship varied with environmental variables, whose identity and strength of association changed with time. Finally, the observed relationship changed with the scale of analysis.

At the metacommunity level, the BPR was evident only on two dates after accounting for the covariation of environmental variables, while at the community level it was a frequent pattern. At the metacommunity level, this relationship has been frequently reported as positive linear and U-shaped (Hector *et al.* 1999; Loreau *et al.* 2001; Chalcraft 2013). At the community level, a variety of functional relationships have been found, including linear positive, linear negative and non-significant relationships (Thompson *et al.* 2005; Mokany *et al.* 2008). Our results confirm that the temporal and spatial scale of analysis affect the BPR pattern (Hector *et al.* 1999; Waide *et al.* 1999; Loreau *et al.* 2001; Reich *et al.* 2012; Chalcraft 2013). In spite of the recognition of a main role of scale in the observed pattern, few studies have explicitly contrasted the BPR across scales with a coherent methodological approach (Chalcraft 2013).



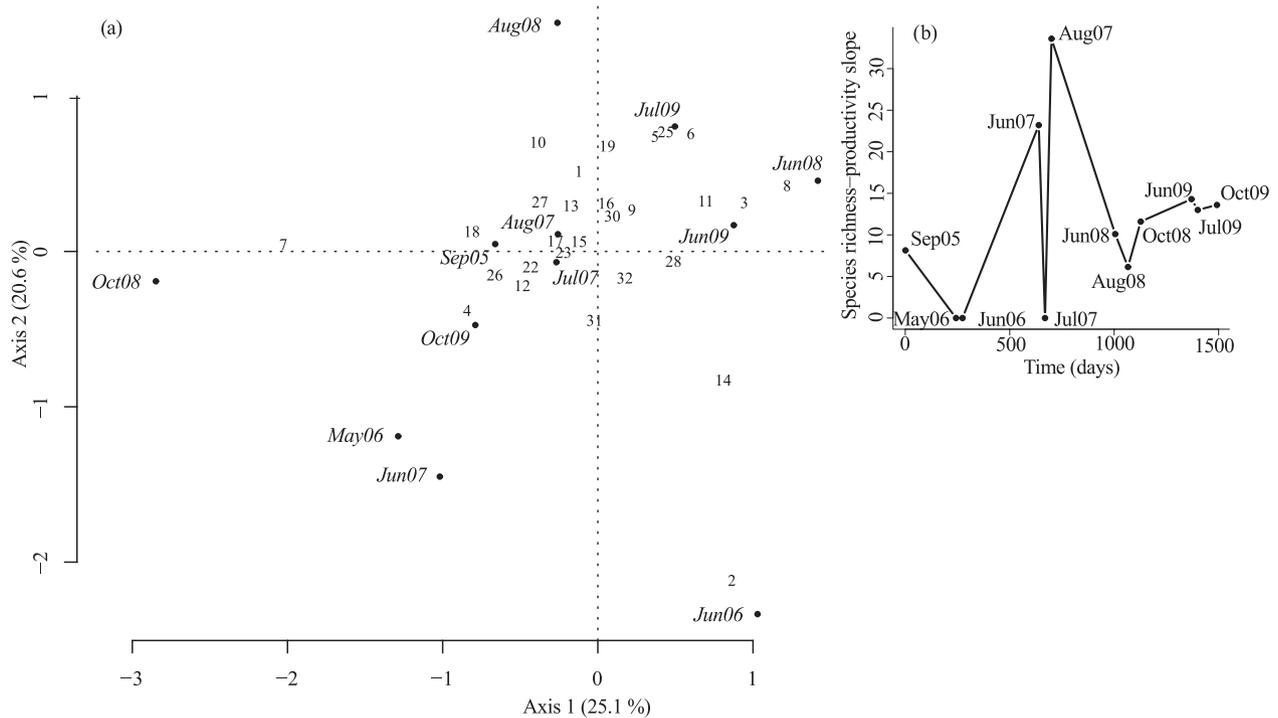
**Fig. 3.** Biomass-species richness relationship at the community level (each data point represents a sampling unit). Biomass is expressed as the residuals of the relationship between biomass and environmental variables. Models were fitted by linear mixed effects models. Gray lines represent each pond taken as random factor and the thick black line represents the fitted line obtained by the fixed component of the model (richness). Only the eleven dates with statistically significant relationship were plotted. In June 2006 there was not statistically significant relationship between biomass and explanatory variables. In May 2006 and July 2007 species richness was not related with biomass (ns) and the models selected included only environmental variables (Table 3).

The inclusion of environmental variables modulated the strength, significance and shape of the BPR, suggesting a variety of mechanisms linked to spatial scale and context. This relation between the BPR and the environmental context was suggested by previous studies (Waide *et al.* 1999; Hooper *et al.* 2005; Chalcraft 2013). Our results suggest that the BPR is best understood when taking into account the environmental context (Loreau *et al.* 2001; Cardinale *et al.* 2009; Marquard *et al.* 2009).

Evenness is a main component of diversity. However, we found a weak relationship between productivity and evenness at one date, October 2009. Most likely, this weak relationship was due to the low variability of evenness compared with richness and environmental variables in our data sets. As our species composition results showed, most variation was given

by a large group of rare species, which did not influence evenness. In addition, indirect effects of evenness on productivity, mediated by changes in richness were not relevant here as both evenness and richness were considered together in statistical models. Species evenness and richness are declining in all ecosystems worldwide, highlighting the importance of understanding their role in ecosystem functioning (Chapin *et al.* 2000; Isbell *et al.* 2009). In spite of the prevailing attention to species richness, theoretical predictions and empirical evidence suggest a strong influence of evenness on ecosystem functioning, with particularly strong implications under scenarios of environmental change (Yachi & Loreau 1999; Balvanera *et al.* 2006; Wittebolle *et al.* 2009).

Previous studies on the BPR and its potential mechanisms were usually based on single-date obser-



**Fig. 4.** (a) Correspondence analysis of dominant species composition among dates and species composition. Only 32 species with constancy larger than 1% were considered. Filled circles are sampling dates with their abbreviated names. Plotted numbers represent the 32 species listed at the end of this legend. (b) Represents the slopes of the BPR obtained from the regression models of Table 1 versus sampling time. Here, the time is plotted in days and the first day corresponds to the first sampling date (September 2005). Abbreviated names of sampling dates are closest to each data point. (1) *Eleocharis* sp3, (2) *Eleocharis* sp., (3) *Paspalum notatum*, (4) *Utricularia*, (5) *Mentha aquatica*, (6) *Eryngium echinatum*, (7) *Ranunculus bonariensis*, (8) *Axonopus affinis*, (9) *Ludwigia peploides* ssp. *montevidensis*, (10) *Nostoc*, (11) *Eclipta elliptica*, (12) *Echinodorus longiscapus*, (13) *Lilaeopsis attenuata*, (14) *Stenotaphrum secundatum*, (15) *Eryngium horridum*, (16) *Gratiola peruviana*, (17) *Marsilea anyclopoda*, (18) *Micranthemum umbrosum*, (19) *Ranunculus flagellifolius*, (20) *Pratia hederacea*, (21) *Alternanthera philoxeroides*, (22) *Ludwigia peploides* ssp. *peploides*, (23) *Eleocharis* sp1, (24) *Eleocharis* sp2 (overlapped with species 22), (25) *Setaria geniculata*, (26) *Myriophyllum aquaticum*, (27) *Lilaea scilloides*, (28) *Cynodon dactylon*, (29) *Leersia\_hexandra* (overlapped with species 15), (30) *Hydrocotyle ranunculoides*, (31) *Luziola peruviana*, (32) *Eleocharis viridans*.

vations or experiments that did not encompass the temporal dynamics of the same ecosystem (Waide *et al.* 1999; Loreau 2000; Loreau *et al.* 2001). However, in recent years long-term studies have become more common (Reich *et al.* 2012; Chalcraft 2013). Our 5-year study showed that the correlations varied idiosyncratically over time. Our results at both scales (Fig. 1–3) did not show any particular trend over time (month sequences, sampling dates order of each flooded season, or seasonality). This idiosyncratic temporal change of the BPR was not accounted for by changes in dominant species composition (Fig. 4). The BPR has been usually treated as an ecosystem-dependent relationship (Waide *et al.* 1999). However, we found in the same ecosystem a variety of BPRs. These changes through time make the BPR less predictable than previously thought.

A few important features of our results deserve special attention. First, the patterns revealed are just correlative evidence of natural patterns and do not

reflect causality between richness or environmental variables and productivity. Removal experiments in which species richness, diversity and productivity are manipulated may contribute to advance on the specific mechanisms involved in the BPR causality (Díaz *et al.* 2003; Cardinale *et al.* 2009; Hooper *et al.* 2012). Second, our determination coefficients were under 0.60, which is within the range found by previous studies, and in some cases situated at the upper limits of these relationships (Tilman *et al.* 2001; Mokany *et al.* 2008; Reich *et al.* 2012). This relatively low proportion of variation of productivity accounted for by richness or environmental variables indicates that, in nature, other variables represent stronger controls of productivity. Third, some degree of inaccuracy in the estimation of productivity through biomass may be responsible for the varying nature of our BPR results. Fourth, we restricted the analysis to above-ground productivity, while biomass allocation belowground could be associated with water depth

variation. Unfortunately, the large scale of the study did not allow us to include belowground biomass, a common deficiency in this type of study (Wardle *et al.* 2011). Finally, our results are limited to one aspect of ecosystem function, that is, primary productivity. Future studies should consider other ecosystem functions in order to address potential implications of global diversity loss.

In summary, we draw two main conclusions. First, environmental variables affected the BPR and therefore need to be accounted for when developing BPR. Second, the strength of the BPR changed over spatial and temporal scales. Additionally, this ephemeral pond system adds a less explored ecosystem type to the BPR literature, with interesting patterns at the metacommunity (among ponds) and the community (within ponds) levels. As a consequence, the construction of a more complete idea about the patterns of variation of the BPR depends on integral studies covering a large set of processes, including environmental variables across relevant temporal and spatial scales, and expanding the variety of ecosystem types being considered.

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