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Global diversity patterns are modulated by temporal fluctuations in primary productivity

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Abstract

Aim: To evaluate the role of seasonal and non-seasonal productivity fluctuations in global patterns of species richness.

Location: Worldwide.

Time period: 2000–2017.

Major taxa studied: Amphibians, birds, mammals.

Methods: We analysed time series of monthly variation of the Normalized Difference Vegetation Index (NDVI), a surrogate of primary productivity, within *c.* 100 km × 100 km cells across all continents, estimating the mean, periodic seasonal variation and aperiodic unpredictable fluctuations of the NDVI in these cells. We then explored the relationships between mean NDVI and the components of its temporal variation and evaluated the independent effects of the above-mentioned variables on species richness in the three vertebrate groups by means of variation partitioning.

Results: There is a hump-shaped relationship between mean productivity and variation in productivity, so that temporal variation in productivity is lowest in regions with minimum and maximum values of mean productivity. Although mean productivity is a strong determinant of species richness, both seasonal and non-seasonal productivity variation significantly affect the species richness of all studied taxa when accounting for mean productivity. However, the direction of these effects differs between regions differing in the mean productivity level. High variation in productivity has a negative effect on species richness in regions with moderate to high productivity levels, whereas species richness is higher in arid regions with high variation in productivity.

Main conclusions: Species richness is affected by temporal variation in productivity, but these effects differ regionally. In productive areas, high environmental stochasticity may increase population extinction rates, whereas arid regions probably benefit from resource fluctuations that promote species coexistence. Our results indicate that contemporary changes in patterns of temporal resource fluctuations may affect future global patterns of biological diversity on Earth.

KEYWORDS
diversity–productivity relationship, environmental unpredictability, latitudinal diversity gradient, productivity fluctuations, species richness patterns, storage effect

1 | INTRODUCTION

Species richness patterns are ultimately driven by the processes of speciation, colonization and extinction. These processes are modulated by the environment, leading to relatively predictable spatial diversity patterns (Hawkins et al., 2012). The most pronounced large-scale diversity pattern is the positive correlation between the number of species and climatic variables related to energy availability, namely precipitation, temperature and environmental productivity (e.g., Currie, 1991; Field et al., 2009; Hawkins, Field, et al., 2003; Jetz & Fine, 2012). Although there are several hypotheses explaining this climate–richness or species–energy relationship (Currie et al., 2004; Storch, 2012), three major mechanisms are especially important: High temperature can promote higher speciation rates (Allen, Gillooly, & Brown, 2007; Allen, Gillooly, Savage, & Brown, 2006); long-term climatic stability may lead to lower extinction rates and/or more time to adaptation, resulting in a higher number of coexisting species (Jablonski, Roy, & Valentine, 2006; Kozak & Wiens, 2012; Ricklefs, 2006; Wiens & Donoghue, 2004); and high environmental productivity may allow the persistence of higher total number of individuals and, consequently, a higher number of species with viable populations (Brown, 1981; Evans, Warren, & Gaston, 2005; Gaston, 2000; Srivastava & Lawton, 1998; Storch, Bohdalková, & Okie, 2018; Wright, 1983; Wright, Currie, & Maurer, 1993).

Recently, evidence has accumulated that high speciation rates are not systematically higher in areas with high species richness (Rabosky, Title, & Huang, 2015; Rabosky et al., 2018; Schluter, 2016) and although hot and humid tropical areas often host ancient lineages, species richness patterns seem to be largely decoupled from diversification history; although some regions are species-rich as a result of a long time for species accumulation, other regions have been colonized in relatively recent times and have reached high diversity due to high diversification rates (Belmaker & Jetz, 2015; Oliveira et al., 2016). This can be interpreted so that each region has a particular limit for species richness and this “carrying capacity for species richness” (Storch & Okie, 2019) can be reached either by slow species accumulation or by rapid diversification (Rabosky & Hurlbert, 2015). These limits probably emerge via the effect of environmental productivity on the number of viable populations that can persist in given environment (Gaston, 2000): For given amount of resources (or energy inflow), an increase of the number of species beyond particular levels necessarily leads to decreasing population sizes and, consequently, increasing extinction rates above the rate of species origination (Storch et al., 2018). Macroecological diversity patterns thus seem to be largely driven by population size-dependent extinction dynamics modulated by resource abundance (Rabosky & Hurlbert, 2015; Storch et al., 2018).

This has important implications. If the extinction dynamic is crucial for producing large-scale diversity patterns, it is reasonable to expect that all the factors that affect extinction rates beyond the effects of population sizes should also affect large-scale diversity patterns. Therefore, species richness is expected to be lower in environments characterized by greater short-term resource fluctuations, because these increase population fluctuations and thus extinction rates beyond the sole effect of population size (Ovaskainen & Meerson, 2010). Intuitively, any environment exhibiting higher environmental stochasticity and, consequently, higher extinction probability should, everything else being equal, host a lower number of species than an environment that is more stable or predictable. Environmental productivity is therefore predicted to affect species richness both by affecting the potential number of species with viable populations (Gaston, 2000) and via its temporal variation, by affecting the viability of populations through the extent of their fluctuations (Adler & Drake, 2008; Boyce, 1992; Lande, 1993).

Some studies have addressed the role of environmental fluctuations and their predictability on patterns of species distribution and diversity (Chesson & Huntly, 1997; Letten, Ashcroft, Keith, Gollan, & Ramp, 2013; Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017). However, most of these studies focused on running-water ecosystems and considered local scales only (Tonkin et al., 2017), or they did not test the effect of environmental fluctuations on species richness patterns (Jiang, Felzer, Nielsen, & Medlyn, 2017; Poff & Ward, 1989; Steel & Lange, 2007). Moreover, most studies on the role of environmental variation in determining species richness have explored only the effect of seasonality (Dalby, McGill, Fox, & Svenning, 2014; Gouveia, Hortal, Cassemiro, Rangel, & Diniz-Filho, 2013; Hurlbert & Haskell, 2003) and not the unpredictable component of environmental variation (but see Letten et al., 2013). In this respect, some studies have explored variation in temperature and precipitation (Jiang et al., 2017; Letten et al., 2013; Tonkin et al., 2017). However, although the observed patterns are illuminating (see Jiang et al., 2017), and temperature and precipitation surely affect species distribution and richness, these variables represent only the ultimate drivers of diversity patterns, acting through their effects on biological rates (Brown, Gillooly, Allen, Savage, & West, 2004) or resource levels (Storch, 2012). For this reason, we focus on a more proximate driver of species richness, namely environmental productivity (understood as the amount of available resources for all terrestrial animal groups), whose mean level as well as year-to-year fluctuations are predicted to drive extinction rates and, consequently, species richness.

Here, we test this prediction using data on global species richness patterns in three major vertebrate classes for which we have good global distributional data (amphibians, birds and mammals) and long-term data on resource fluctuations across the terrestrial surface of the Earth. We assume that resource availability for these vertebrate groups can be estimated based on a surrogate of net primary productivity, namely the Normalized Difference Vegetation Index (NDVI), which represents an estimate of the vegetation cover and its temporal changes. Thanks to the relatively long time series of NDVI, it is possible to analyse temporal variation in this surrogate of primary productivity and to decompose it into its periodic (seasonal) aspect and aperiodic component, which is essentially unpredictable. This is crucial because the periodic component of resource variation can have potentially very different consequences for species population dynamics compared with unpredictable environmental variation. Most importantly, although seasonality may act as an environmental filter (Gouveia, Hortal, Cassemiro, Rangel, & Diniz-Filho, 2013), species are able to adapt to seasonal oscillations by adjusting their life cycles; for example, by breeding during the favourable productive season or through dormancy, hibernation, energy storage or seasonal migrations during the harsh, unproductive season (Varpe, 2017; Williams et al., 2017). Consequently, periodic seasonal resource variation may not promote population fluctuations, although it may still affect the probability of population extinction by affecting overall population abundance; long-term mean population size is often determined by minimum resource availability over the course of the year (Hořák, Tószögyová, & Storch, 2015).

In contrast, aperiodic unpredictable resource fluctuations very probably have a direct effect on population dynamics and increase the chance that such dynamics will eventually lead to extinctions (Adler & Drake, 2008; Boyce, 1992; Ovaskainen & Meerson, 2010). Besides this effect, unpredictable environments impose additional filters on species occurrence (Tonkin et al., 2017), selecting for generalism and fast life strategies, which may impede coexistence. On the other hand, environmental fluctuation may, in some situations, promote species coexistence, e.g., via the storage effect (Chesson, 2000b). This occurs if abundant species compete fiercely during periods of resource peaks, whereas rare species can survive periods of resource scarcity by storing resources amassed during more favourable periods. The effect of resource fluctuation thus may not be only detrimental in terms of resulting species richness. Our aim was to test the effects of both periodic (seasonal) and aperiodic resource fluctuations on global species richness patterns of three classes of vertebrates to evaluate and compare the roles of mean productivity and its temporal fluctuations in macroecological diversity patterns.

2 | METHODS

Our time series of environmental productivity were composed of values of the MODIS-derived NDVI obtained from the NASA Land Processes Distributed Active Archive Center (LP DAAC) (https://lpdaac.usgs.gov/products/mod13c2v006/). The NDVI quantifies remotely sensed vegetation greenness, which is an appropriate proxy for the amount of available resources for all terrestrial animal groups (Gordo, 2007; Lafage, Secondi, Georges, Bouzillé, & Pétillon, 2014; Lassau & Hochuli, 2008). We could have used some other measures of environmental productivity, including the MODIS-based Net Primary Productivity, but such data typically do not provide sufficiently long and well-resolved time series. Moreover, because they are a result of complex models with many hidden assumptions, there is no evidence that they reflect real ecosystem productivity better than remotely sensed data obtained by more direct means (Šímová & Storch, 2017).

The global NDVI dataset consists of time series of 205 monthly averages over the period between February 2000 and February 2017, with a spatial resolution of 0.05°. We converted these data into a 1° equal-area map to make them compatible with species distributional data. We are aware of the fact that the 17 years-long time series is too short and too recent to represent the environmental variation that affected species richness patterns in our data, namely given that the species distribution data that we used integrate knowledge on species distributions collected over a much longer period. However, we assume that our relatively recent time series is representative in terms of capturing general properties of environmental variation in different places, at least during the last few centuries. It is probable that the overall global pattern of temporal environmental variation is relatively stable, so that the areas which reveal high seasonality and/or unpredictability during a recent 17 years-long time window were characterized by these properties also in previous decades or centuries, although it is possible that temporal variation

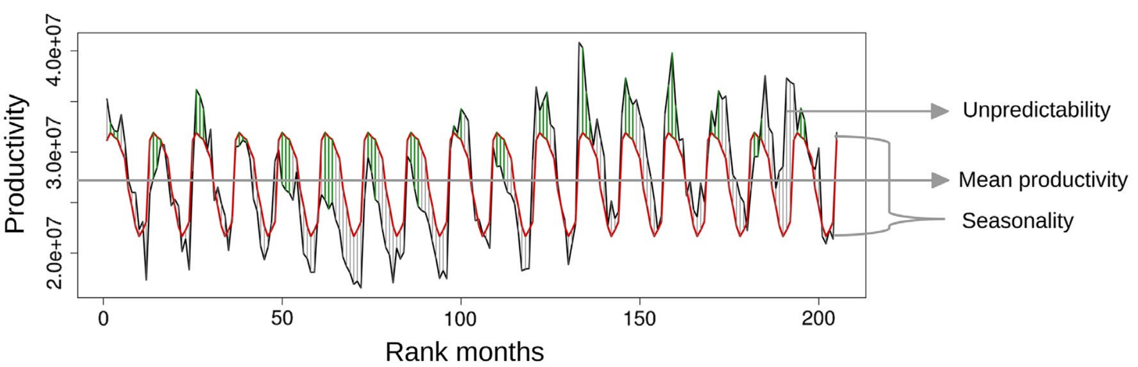

FIGURE 1 Time series of monthly values of environmental productivity [Normalized Difference Vegetation Index (NDVI)] over a period of 205 months (17 years) for one grid cell (black line). The red line represents the periodic seasonal trend constructed using mean values of the NDVI for each month over the 17 year period. Mean productivity is calculated as the mean value of the seasonal cycle. Seasonality is represented by the range of the seasonal cycle (i.e., the difference between the average minimum and average maximum productivity level). The vertical grey lines represent the residuals from the seasonal cycle. Unpredictability was calculated as the standard deviation of the residuals from the seasonal trend. The vertical green lines represent unpredictability in the productive season (i.e., the standard deviation of residuals from the three on average most productive months) [Colour figure can be viewed at wileyonlinelibrary.com]

in productivity was slightly more or less pronounced in particular regions during the more distant past.

The data on the distributions of mammalian and amphibian species were provided by the IUCN Global Species Programme (http://www.iucnredlist.org), and data on the distributions of avian species were obtained from BirdLife International (http://www.birdlife.org). These two databases contained distributional information on species ranges in geo-referenced polygons on 5,298 terrestrial mammal, 10,961 bird and 6,493 amphibian species (extinct species were excluded, and the species were included regardless of their seasonal presence), which we transformed into a 1° (~100.2 km) spatial grid using the Mollweide coordinate system (equal-area projection). The datasets of NDVI and all three taxa consisted of 12,606, 12,608 and 11,315 grid cells for mammals, birds and amphibians, respectively.

We decomposed the NDVI time series for each grid cell into three components: (a) mean; (b) seasonality; and (c) non-periodic fluctuations (unpredictability). First, we filtered out the overall linear or quadratic trend (depending on which one better captured the overall temporal pattern) over the whole 17 year period. The seasonal cycle was then constructed using the mean value of the NDVI for each month across the entire 17 year period, and this oscillation (17 times over the whole time period) was taken as the basis for calculating unpredictability using the residuals from this curve. Three variables were then calculated for each grid cell. *Mean productivity* was the mean NDVI value of the seasonal cycle (the same value as the mean NDVI value across all years) (Figure 1). *Seasonality* was the difference between the average maximum and average minimum productivity level (the range of the seasonal cycle) (Figure 1). *Unpredictability* was quantified based on the standard deviation of residuals from the periodic seasonal trend (Figure 1). Originally, we calculated several variables characterizing random non-periodic fluctuations using these residuals (Supporting Information Appendix S1), later selecting the best variable that explained most of the variance in species richness. It turned out that, besides unpredictability as defined above, unpredictability in the productive season (residuals from the three on average most productive months) was, in some cases, an especially strong predictor of species richness. We thus also explored the effect of this additional variable on species richness. For the purposes of the analyses, it was appropriate to use logarithmic transformation (base 10) of seasonality and unpredictability and of the species richness of birds and amphibians and square-root transformation of species richness of mammals, to ensure an approximately normal distribution of residuals of respective models. Mean productivity was not transformed.

We used a variation partitioning analysis to distinguish the separate independent explanatory effects of the three aforesaid variables on species richness. The variation partitioning was based on partial linear regression models. Following Peres-Neto, Legendre, Dray, and Borcard (2006), we applied the function of the variation partitioning analysis that provides adjusted R^2 to assess the variance explained by the explanatory variables and their combinations, because it is the only unbiased method. To estimate the significance of individual effects, we constructed generalized least squares regression models, with a spatial correlation structure to control for spatial autocorrelation. All analyses were performed in the R statistical computing environment (R Development Core Team, 2017).

3 | RESULTS

The species richness of all three groups was positively related to mean productivity (Figure 2a; Supporting Information Figure S1a). In contrast, the relationship between species richness and both seasonality and unpredictability was universally triangular, so that low seasonality and unpredictability allowed for both low and high richness values, whereas high values of these variables were uniformly associated with low richness (Figure 2b,c; Supporting Information Figure S1b,c). This pattern, however, was strongly affected by covariance between both the variables and mean NDVI; both seasonality and unpredictability reached their highest values in the temperate zone of the Northern Hemisphere and in less productive regions

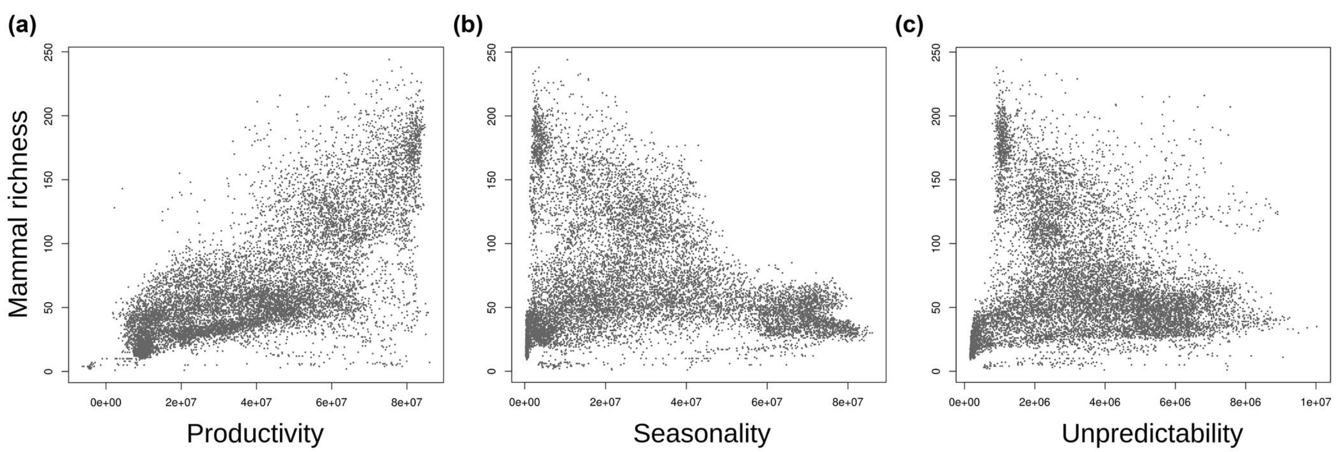

FIGURE 2 Relationships between the species richness of mammals and mean productivity (a), seasonality (b) and unpredictability (c). All these relationships are very similar in birds and amphibians (see Supporting Information Figure S1)

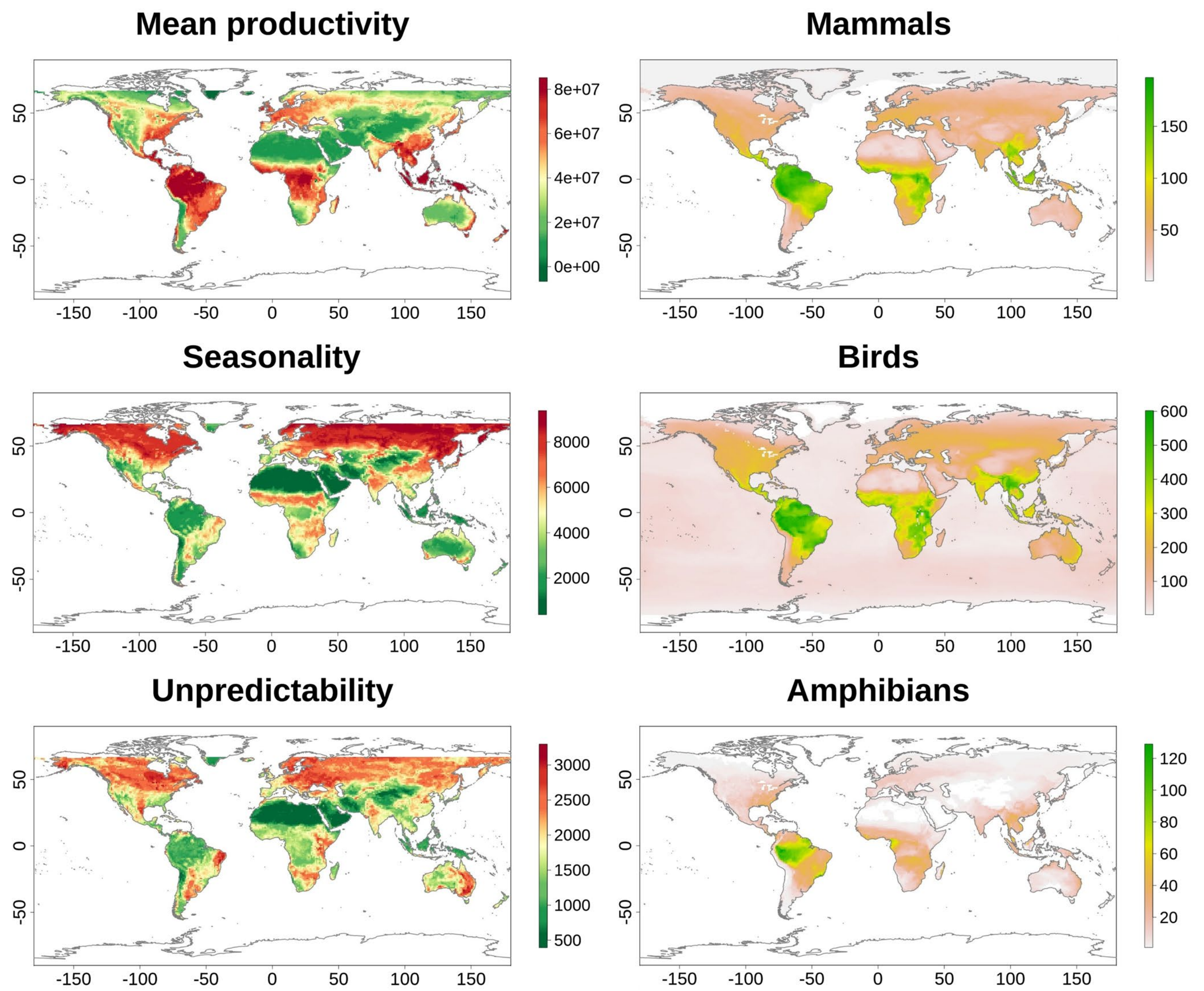

FIGURE 3 Left panels show geographical patterns of mean productivity, seasonality (square-root transformed) and unpredictability (square-root transformed). The highest values (red) of mean productivity occur in the tropics, whereas the highest values of seasonality and unpredictability are found in temperate regions. The lowest (green) variations in productivity, both seasonal and unpredictable, are distributed both in the wet tropics and in arid areas. Right panels show patterns of global species richness of the three taxonomic groups under study [Colour figure can be viewed at wileyonlinelibrary.com]

of the tropics of the Southern Hemisphere (Figure 3). In contrast, low values of both these variables (seasonality and unpredictability) characterizing temporal variation in productivity occurred not only in the productive tropics, but also in deserts. The overall relationship between mean productivity and temporal variation in productivity is therefore hump shaped (Figure 4), which implies that the effect of mean productivity on species richness could not be simply controlled for by using the residuals from the linear regression of productivity variation on mean productivity.

Although quadratic regression fitted on the hump-shaped relationship between mean productivity and variation in productivity could potentially have solved this problem, its fit was rather poor, and using residuals from this function would lump together regions with similar relative productivity fluctuations but extremely different mean productivity. For these reasons, we decided to explore the effects of productivity-controlled seasonality and unpredictability on species richness by dividing the dataset into three contrasting segments (regions) differing in their bivariate relationships between mean productivity and variation in productivity. Within each of these regions, the relationship between mean productivity and variation in productivity was linear (Figure 4), which enabled the testing of the independent effects by variation partitioning. These three segments roughly correspond to arid regions, temperate regions and the wet tropics, and the effects of mean productivity-controlled seasonality and unpredictability were tested separately for each region. Given that the division of the globe based on the

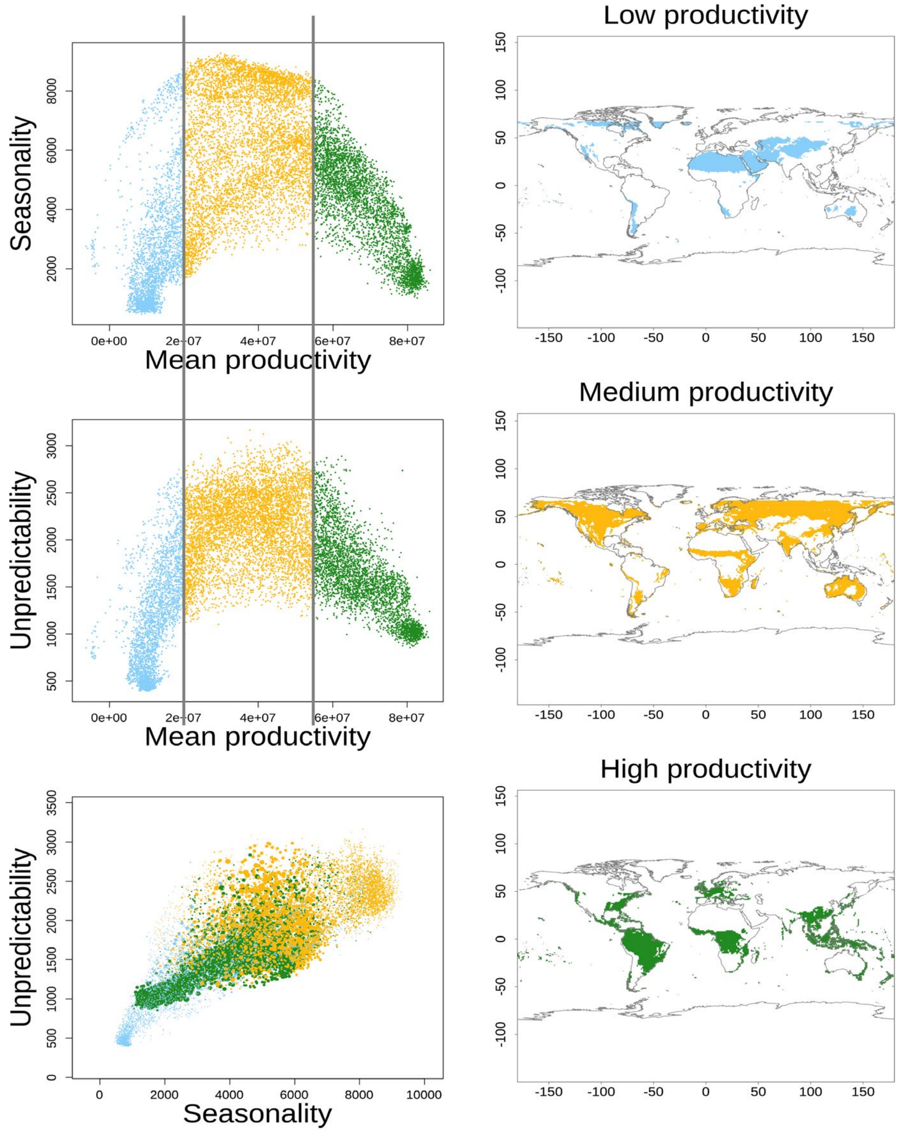

FIGURE 4 Left panels show relationships between mean productivity and seasonality (top) and unpredictability (middle), respectively. Based on these hump-shaped relationships, we distinguished three groups of regions: Regions with low productivity and a positive mean–variation relationship (blue); regions with medium productivity and no mean–variation relationship (yellow); and regions with high productivity and a negative mean–variation relationship (green). The bottom panel shows the correlation between seasonality and unpredictability; the size of the dots corresponds to the species richness of mammals, as an example. Right panels show maps of the corresponding three regions. With the exception of mean productivity, all the variables were square-root transformed [Colour figure can be viewed at wileyonlinelibrary.com]

hump-shaped relationship is partly arbitrary, we checked the results for robustness by shifting the dividing lines in both directions, confirming that alternative divisions did not affect the results (Supporting Information Figure S2).

Variation partitioning revealed that all the three components of our productivity time series independently affected the species richness of all three groups of vertebrates, albeit differently in the three different regions (Figures 5 and 6; Supporting Information Table S1). In low-productivity (arid) regions, the sole effect of unpredictability had the strongest positive effect on species richness in birds and mammals, whereas in amphibians the effect of seasonality was slightly greater, although this was not significant after accounting for spatial autocorrelation (see below). In low-productivity areas, all the effects of mean productivity, seasonality and unpredictability were positive. Unpredictability in the productive season was an even stronger predictor of species richness in arid regions, explaining (independently of mean productivity and seasonality) 15%, 23% and 13% of species richness variation in mammals, birds and amphibians, respectively (Figures 5b and 6b; Supporting Information Table S1). In regions with medium productivity (temperate), which

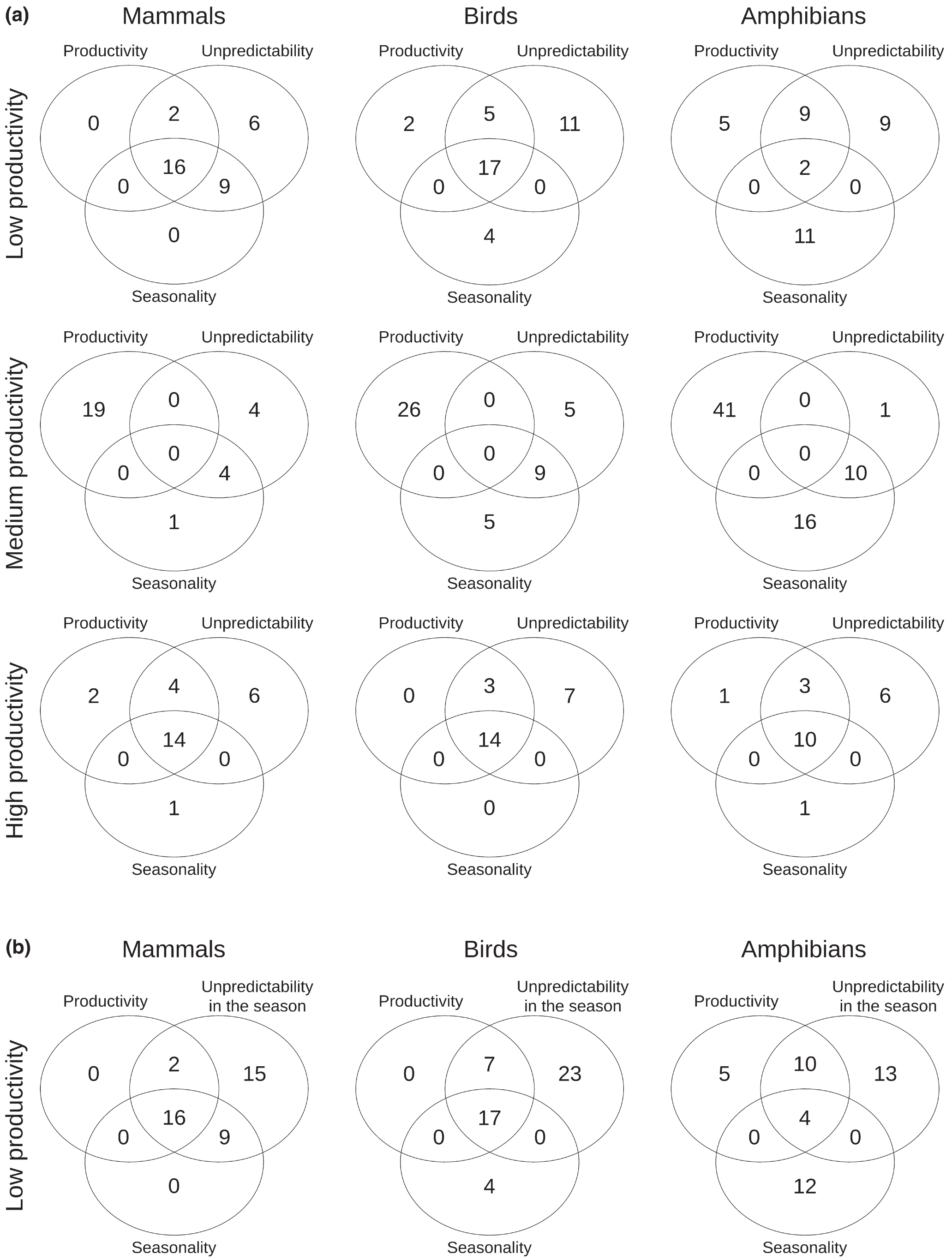

FIGURE 5 (a) Venn diagrams describing variation partitioning for the species richness of mammals, birds and amphibians by mean productivity and productivity seasonality and unpredictability in the three distinct regions (see Figure 4). (b) Variation partitioning for the species richness of mammals, birds and amphibians by mean productivity and its seasonality and unpredictability in the productive season in low-productivity regions. The diagrams show adjusted R^2 values (rounded) associated with each partition or for overlapping partitions. The separate independent effects of all explanatory variables were significant (after accounting for spatial autocorrelation) in their contributions to species richness (see Supporting Information Table S2). Unpredictability, especially during the productive season, was the strongest predictor of species richness in arid areas

exhibited no relationship between mean productivity and variation in productivity, unpredictability and seasonality did not show a strong effect on species richness (except in amphibians, where the effect of seasonality was strong and negative), whereas mean productivity affected species richness positively. Similar effects were observed in highly productive regions (wet tropics), in which unpredictability turned out to have a negative effect on species richness, whereas the sole independent effect of seasonality was

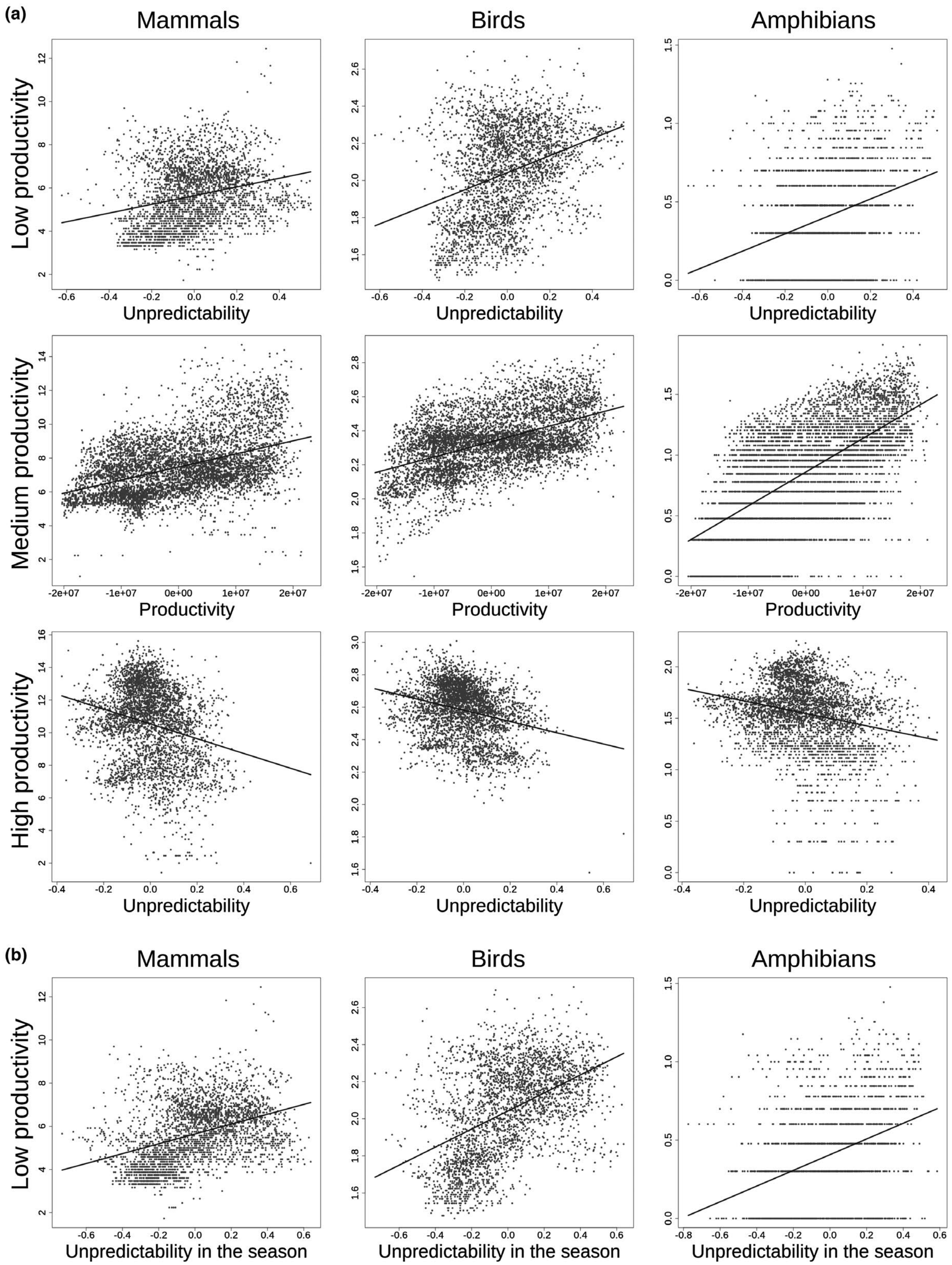

FIGURE 6 (a) Relationships between the species richness of mammals, birds and amphibians, and the sole effect (controlling for all the other effects) of the strongest environmental predictors (out of mean productivity, seasonality and unpredictability for the given vertebrate classes and regions). In the case of amphibians in the low-productivity region, we used the second strongest predictor, because the strongest predictor (seasonality) was not significant after accounting for spatial autocorrelation (see Supporting Information Table S2). (b) Relationship between species richness and mean productivity- and seasonality-controlled unpredictability during the productive season in the region with the lowest productivity. With the exception of mean productivity, all the variables were $\log_{10}$-transformed, and mammalian species richness was square-root transformed

very weak or non-existent. Similarly as in arid areas, unpredictability had the strongest independent effect on species richness, but in the opposite direction: Productive but relatively unpredictable areas had lower species richness than areas with stable and predictable productivity. In these two types of regions (moderately and highly productive ones), unpredictability in the productive season had an equal or slightly weaker effect than total unpredictability measured over the course of the whole year (not shown). Spatial generalized least squares models revealed that the relationship between species richness and all environmental variables (after accounting for the effects of the other variables) was statistically significant even after removing spatial autocorrelation, with the exception of the effect of seasonality on amphibian species richness in the arid areas (Supporting Information Table S2).

4 | DISCUSSION

Temporal resource variation should, in theory, affect species richness (e.g., Storch et al., 2018). However, the testing of this idea at a macroecological scale has been impeded by the lack of appropriate data and the complex covariation of the measures of environmental variation with other environmental predictors, namely mean productivity (which is known to be a good determinant of vertebrate species richness globally; Belmaker & Jetz, 2011; Davies et al., 2007; Hawkins, Field, et al., 2003; Hawkins, Porter, & Diniz-Filho, 2003; Wright et al., 1993). We found a nonlinear (hump-shaped) covariation between mean productivity and temporal productivity variation, expressed as seasonality and unpredictability (representing residuals from regular seasonal variation), respectively. Such non-linearity is expected, as regions with both the highest and the lowest productivity must necessarily exhibit relatively low productivity variation (otherwise, they could not reach extreme values of mean productivity). Such a relationship between mean productivity and its variation, however, implies the existence of three distinct types of environment differing in the regime of covariation between mean productivity and its variation. Arid areas are characterized by positive covariation of mean productivity and its temporal variation, whereas temperate areas with intermediate productivity are characterized by the absence of a relationship between these variables, and wet tropical areas reveal a negative relationship between mean productivity and its temporal variation, with the most productive areas simultaneously being very stable. Because of these basic differences, we treated the three types of environments or regions independently. We suggest that future analyses of the role of variation in productivity should account for these substantial differences between the major types of environment. The complex relationship between the mean value of productivity and its variation probably lies behind the scarcity of studies addressing these effects across large geographical extents.

In most productive areas, and partly also in areas with moderate productivity, the number of species decreases with both the seasonality and the unpredictability of productivity, when accounting for the overwhelming effect of mean productivity. This is in accord with the general notion that temporal resource fluctuations lead to more dramatic population dynamics, increasing extinction rates (Lande, 1993; Ovaskainen & Meerson, 2010), and with the formalization of this notion in the theory of Storch et al. (2018). The effects of seasonality and unpredictability are difficult to distinguish because of their covariation, but it is probable that both these effects may increase the probability that a local population will go extinct, albeit via a slightly different mechanism. Seasonality may decrease effective population size (Hořák et al., 2015), whereas unpredictability probably increases the extent of stochastic population fluctuations, which increase the chance that a population of given size goes extinct (Adler & Drake, 2008; Boyce, 1992; Lande, 1993).

The most surprising result is the positive effect of productivity unpredictability on species richness in unproductive areas. Although unpredictability can affect population fluctuations and thus increase the probability of stochastic extinction, it is possible that arid areas with unpredictable resource pulses are, for many species, more favourable than arid regions with stable (i.e., constantly low) resource levels. Unpredictable resource fluctuations may also increase the chances of species coexistence via the storage effect (Adler & Drake, 2008; Cáceres, 1997; Chesson, 2000a, 2000b; Chesson & Warner, 1981). Species may benefit from resource surplus in favourable periods and survive in adverse periods by storing energy resources, migrating (many desert birds are very mobile) or entering diapause (many desert frogs). At the same time, no species competitively prevails in such an environment, because high population growth in favourable periods leads to overcrowding of competitively superior species (Chesson, 2000b). In addition, some resources, such as seeds, are produced by plants during peaks of vegetation production, but they may persist as a food source also in subsequent periods. All these effects are in line with our observation that unpredictability in the productive season, corresponding mostly to an unpredictable excess of resources, was the best predictor of species richness in arid regions. In contrast, arid areas with constantly low production may host species with relatively stable (albeit small) population sizes, which utilize the majority of available production, thus limiting access to resources for other species.

Assuming that the relatively short time window during which we analysed temporal variation in NDVI provides a proper representation of the large-scale patterns of temporal productivity fluctuations, it appears that both predictable (seasonal) and unpredictable temporal variation in productivity affect species richness patterns. This can have serious implications for our ability to predict future changes in biodiversity linked to global climate change. Both increases and decreases in both the periodic and aperiodic components of variation in productivity can be expected in the future, and they will probably lead to further redistribution of biological diversity (Bonada, Dolédec, & Statzner, 2007; Tonkin et al., 2017). There is no doubt that mean values of climatic variables, including temperature and primary productivity, are important; changes in mean values have already been shown to be altering the current biota. However, temporal variation of these variables may turn out to be even more important and, probably, less predictable (Letten et al., 2013).

In sum, our results show that temporal variation in primary productivity affects global patterns of vertebrate species richness. Although mean productivity is a strong determinant of species richness, probably through its effect on the number of viable populations that can persist in a given environment (Gaston, 2000; Storch et al., 2018; Wright et al., 1993), productivity fluctuations can affect the viability of populations through its effect on the extent of population fluctuations (Lande, 1993; Ovaskainen & Meerson, 2010). Although the effect of regular annual oscillations of productivity (seasonality) may differ from that of productivity unpredictability, these two components of the variation in productivity are so highly correlated that they cannot be distinguished easily. Nevertheless, productivity unpredictability seems slightly more important in its effect on species richness patterns. In line with our original expectation, variation in productivity decreases species richness in areas with moderate to high productivity. However, in contrast to our expectation, its effect is the opposite in arid areas, where elevated variation in productivity leads to higher species richness, probably because resource fluctuations have a positive influence on species coexistence in such resource-poor environments. These findings imply that future diversity patterns may be strongly affected not only by gradual changes of the means of various environmental variables, such as temperature and precipitation, but also by changing regimes of environmental fluctuations and temporal variation of resource levels.

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DATA AVAILABILITY

The data that support the findings of this study are openly available at http://www.iucnredlist.org/, version no. 2017-1, downloaded on 23 May 2017, and available on request at http://datazone.birdlife.org/species/requestdis/, version 6.0 and at https://e4ftl01.cr.usgs.gov/MODV6_Cmp_C/MOLT/MOD13C2.006/, version MOD13C2 V006, https://doi.org/10.5067/MODIS/MOD13C2.006.

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BIOSKETCHES

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SUPPORTING INFORMATION

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