# Productivity begets less phylogenetic diversity but higher uniqueness than expected

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# ABSTRACT

Aim: The positive effect of primary productivity on animal species richness is one of the most conspicuous ecological features on Earth. However, less is known on the relationship between ecosystems primary productivity and the evolutionary history of biota. Documentation of this relationship will contribute novel information to understand why biodiversity often scales with productivity. Here, we analyse how global primary productivity relates to the phylogenetic structure of vertebrate assemblages, and to the distribution of the most distinct lineages and recently diversified clades.

# Location: Global

# Taxon: Amphibians, birds and mammals

**Methods:** For each 200km pixel around the world, for each of the three taxa and across a range of phylogenetic trees, we calculated relative phylogenetic diversity (i.e. phylogenetic diversity corrected for species richness), standardized effect size of the richness of top 25% evolutionary distinct species and of top 25% species-level lineage diversification rates. We related these three metrics to mean net primary productivity at the global scale, and for each zoogeographic region. We also tested the influence of the spatial scaling of species pool on the overall analyses (global, hemispheric and zoogeographic regions-based species pools).

**Results:** Phylogenetic diversity (corrected for species richness) of the three taxa decreases with NPP (in contrast to species richness) and varies considerably in space. High productivity sites harbour more closely related species than low productivity sites consistently across zoogeographical zones. However, the most phylogenetically distinct species are also found in high productivity sites, while the top fast diversifying lineages are found in the least productive sites. Modifying the spatial extent of the species pool did not drastically change results.

**Conclusions:** Benign conditions in high productivity sites i) result in closer niche packing and thus allow for the coexistence of many related species and ii) prolong the persistence of evolutionary distinct species. Low productivity sites may harbour fewer, more distinct and temporarily more variable niches and thus require that species adapt to these conditions. Primary productivity links to evolutionary and biogeographic history at a global scale and tends to secure evolutionary distinct species.

#### **1 INTRODUCTION**

The increase in species richness with increasing primary productivity is one of the most ubiquitous patterns in ecology, and one of few ecological patterns that holds across scales (Evans et al., 2005), and through geologic time (Fritz et al., 2016). The processes behind this richnessproductivity pattern have been long debated with several ecological and evolutionary hypotheses on why there are more species in productive areas. From an ecological perspective, productivity could directly impact the number of species through supporting higher densities, more ecological opportunities, higher specialisation and larger niche space (Wright et al., 1993; Currie et al., 2004; Evans et al., 2005; Wright & Rohde, 2013; Brown, 2014; Storch et al., 2018). However, from an evolutionary perspective, productivity could also influence diversification by either decreasing species' extinction rates or by enabling higher in situ speciation rates due to higher population densities and thus more total mutations per unit of time (Rosenzweig, 1995), stronger biotic interactions or higher ecological opportunities (Allen & Gillooly, 2006; Schemske et al., 2009; Schluter & Pennell, 2017; Rabosky et al., 2018). In both cases, evolutionary trajectories were also substantially altered by historical environmental stability and glaciation cycles in some regions, which is also relevant to understanding the productivity-diversity relationship. For instance, the latitudinal gradient hypothesis posits that climatic variation (e.g. glaciation cycles) in temperate regions may have led to large-scale extinction events and potentially enhanced speciation (Weir & Schluter, 2007). That would imply that low productivity regions that experienced major glaciations could represent post-glaciation assembly in many cases, with speciation happening during these events. These ecological and evolutionary explanations are impossible to differentiate with existing studies focused on species (or genus) richness, because their common expectation is more species in highly productive areas. Only combining species diversity with additional biodiversity patterns can forward our understanding of the driving processes. Here, we re-examine the productivity-diversity relationship in light of the evolutionary history of species and resulting phylogenetic diversity patterns to provide a novel understanding of why primary productivity leads to more diversity in certain regions but not in others.

The above mentioned ecological and evolutionary processes are expected to result in a broad range of geographic and phylogenetic biodiversity patterns that we can observe today, including the diversity of assemblages in local areas (e.g. are the species in an assemblage phylogenetically closely or rather distantly related?) and characteristics of individual species (e.g. does a species belong to a fast diversifying group or does it belong to a phylogenetically distinct lineage?). For example, if net primary productivity (NPP) promotes diversification through increased in situ speciation, then we would expect to see in local species assemblages increasing density of species that belong to rapidly radiating clades and species that are closely related. However, if NPP promotes diversification through reduced extinction rates, we would also expect to observe a few species that are phylogenetically distinct, as "old" lineages could have survived. In contrast and from the ecological perspective, if high NPP regions increase niche space and allow for finer niche partitioning and species' niches are phylogenetically conserved (Lavergne *et al.*, 2010), we would expect significant higher phylogenetic diversity (when correcting for species richness) and higher numbers of phylogenetically distinct species with different adaptations in high NPP regions (see Table 1 for a summary of the expectations).

Studying the multiple imprints that ecological and evolutionary processes leave in species' assemblages should contribute novel information to understand why species richness often scales with productivity. Here, we propose to complement the positive species richness-productivity relationship with information on how productivity correlates with phylogenetic diversity, the richness of top evolutionary distinct species and the richness of top species-level lineage diversification rates. As the three complementary measures are inherently influenced by species richness, they need to be corrected by species richness to be useful for further interpretation. Thus, in this paper, we analyse how the worldwide spatial distribution of richness corrected phylogenetic diversity (i.e. relative phylogenetic diversity, rPD hereafter), the relative richness of top 25% most evolutionary distinct (ED) species and species with the fastest species-level lineage diversification rate (DR) in terrestrial amphibians, birds and mammals relates to the distribution of net primary productivity (NPP). We considered NPP since it is a suitable measurement of primary energy production metric for investigating consumer species-energy relationships and consistency in productivity-richness studies (Evans et al., 2002). We tested also whether patterns observed at global scales hold within zoogeographical regions [regions harbouring relatively homogenous species assemblages from a taxonomic and phylogenetic point of view (Holt et al., 2013)]. We thus conducted this analysis at both the global scale and within the different zoogeographical regions of the world (Holt et al., 2013) but also by varying the spatial extent of the species pool considered when calculating relative phylogenetic diversity (Kissling et al., 2012). Finally, we tested whether those trends are driven by the response of specific lineages within the three main vertebrate taxa considered.

We addressed these objectives by using the geographic range maps of amphibians, birds and mammals of the world from the IUCN Red List Assessment and from BirdLife (at 200km resolution), combined with comprehensive sets of species-level phylogenies for the three groups.

#### 2 METHODS

*Distribution data* - We used the distribution maps provided by the Amphibian and Mammal Red List Assessment (<u>http://www.iucnredlist.org/</u>) for 5547 and 4616 species, respectively. For birds,

breeding ranges distribution maps were extracted from BirdLife (<u>http://www.birdlife.org/</u>) for 9993 species. Since the best resolution to use these maps is still under discussion in the literature, we used a 200x200km resolution (equal-area projection), which is the most commonly used at the global scale {Ficetola, 2014 #6878;Hurlbert, 2007 #6877;Pollock, 2017 #6944}. The total number of grid cells was 3646. Domestic and fully aquatic species were excluded from the analysis.

*Net primary productivity* – NPP was extracted from the <u>Socioeconomic Data and Applications</u> <u>Center</u> - A Data Center in NASA's Earth Observing System Data and Information System. NPP is measured in units of elemental carbon (grams of carbon per year per pixel) and represents the primary energy source for secondary productivity. This data set is distributed by the Columbia University Center for International Earth Science Information Network {CIESIN, \Imhoff, 2006 #6879;Imhoff, 2004 #6880}).

*Zoogeographic regions* – Holt *et al.* {, 2013 #6875} defined zoogeographic regions as regions of evolutionarily unique assemblages, with distinct regionalization for the three classes. The classification of vertebrate assemblages into zoogeographic units was done to get between 6 (amphibians and birds) and 8 regions (mammals) to be consistent between the three groups (see Fig. S2 for the distribution and naming of the zoogeographic regions). Regions were then converted to a raster grid at a 200 km resolution (200\*200km at the equator).

*Phylogenetic trees* – We used a random set of 100 time-calibrated, ultrametric phylogenetic trees from {Bininda-Emonds, 2007 #5147;Fritz, 2009 #5144} and from {Jetz, 2012 #5899}, respectively for both mammals and birds. We updated the mammal phylogenetic trees by replacing the Carnivora clade with a highly resolved supertree published more recently {Nyakatura, 2012 #6338}. For amphibians, we used the single supertree available for all amphibians of the world {Isaac, 2012 #6881}.

*Phylogenetic metrics* – Phylogenetic diversity (PD) was calculated for each single pixel as "the branch length sum of all branches that are members of the corresponding minimum spanning path", in which 'branch' is a segment of a tree, and the minimum spanning path is the minimum patristic distance between nodes including the roots {Faith, 1992 #5130;Faith, 2002 #2553}. PD was estimated using each of the 100 trees available (for all groups excepted for amphibians where a single tree was used). To calculate the richness-controlled version of PD (called relative PD hereafter, rPD), we used the PhyloMeasures package in R {Tsirogiannis, 2016 #6882}. For each single assemblage (pixel in this study), the observed PD value is compared to an expected

distribution of possible PD values derived from a particular null model. In our case, we used a null model where the species richness of the assemblage, the species pool phylogenetic tree topology and branch lengths are held constant but tip labels are shuffled (see below for various definition of the species pool). The rPD value is obtained by subtracting the mean expected PD and then dividing by the expected PD standard deviation. Note that these rPD values are also sometimes approximated using a randomization procedure (e.g. randomly shuffling the tree tip labels 1000 time to compute the expected PD distribution). However, the exact rPD values provided by the PhyloMeasures R package is preferred here because of reduced computational time.

We measured species evolutionary distinctiveness (ED) as the sum of the branch length from the species tip to the root of the tree divided by the number of species subtended to each branch (function evol.distinct in R package picante, measure 'equal-split' {Redding, 2014 #6595}. We measured species-level lineage diversification rate (DR) as the inverse of the species' distinctiveness measure {see \Jetz, 2012 #6316} for a complete description of the measure and its relationships with traditional clade level diversification rate).

Richness of top 25% evolutionary distinctiveness (top ED) and of top 25% species-level lineage diversification rates (top DR) was taken as the number of species that belong to the top 25% of each of the two classes. Since these measures correlate positively with total species richness by pure sampling effects, we ran a null model in which the distinctiveness and diversification measures were randomised among species. The richness of top 25% species was then recalculated. The null model was repeated 999 times and the standardised effect size richness of top 25% evolutionary distinctiveness (SES of top ED) and top 25% species-level lineage diversification rates (SES of top DR) was calculated by subtracting the mean richness and dividing by the standard deviation of this measure. Note that while ED and DR are mathematically linked by calculation, this is not the case when focusing on the richness of the standardised effect size of the top 25% species from each different group and there are no a priori expectations on their relationships.

## Spatial extents for the sampling pools

The three metrics (rPD, SES of top ED and SES of top DR) were initially calculated using a global species pool. In other words, the analytical solution for rPD and the null models for SES of top ED and top DR considered that under random expectation, every species could be everywhere, independently of dispersal constraints and historical contingencies. Since a global species pool might seems too liberal, we also calculated the three metrics for two other species pools (Kissling

*et al.*, 2012). In one case, we considered a hemispheric species pool ('New World' and 'Old World') and, in the other case, we considered the zoogeographic regions themselves. Practically, rPD, SES of top ED and top DR were thus also calculated against random expectation coming from the appropriate species pool. For instance, for pixels occurring in Europe, the species pool for the hemispheric case was 'Old World', and North Hemisphere for the zoogeographic species pool. Varying the extent of the species pool allows to test whether, within a continent or a zoogeographic region, the relationship between our three metrics and NPP widely differ or not, which consequences on the interpretation of the observed patterns (Kissling *et al.*, 2012)

## Statistical analyses

Standard ordinary least square regressions were run between rPD, SES of top ED, SES of top DR, and NPP at the global scale, and for each of the zoogeographic regions. We then extracted the adjusted  $R^2$  values of the regressions. For mammals and birds, regression analyses were carried out for the 100 available trees. We thus reported mean  $R^2$  and the associated standard errors. In the main text, we represented the relationship between NPP and our three metrics per zoogeographical regions with a global species pool for Fig. 1, 3 and 4, and while varying the spatial extent of the species pool in Fig. 2.

#### **3 RESULTS**

rPD strongly varied in space and between the different groups (Fig. 1). A striking common result among the three taxa was that rPD was generally negative across the globe (i.e. lower than the expected PD given the species richness of the assemblage). For both birds and mammals, less than 1% of the cells were actually positive, against  $\sim 20\%$  for amphibians. This is expected given the spatial structuring of phylogenetic groups at global scales {Holt, 2013 #6875}, which implies that local assemblages harbour less PD than randomly expected {e.g. \Mazel, 2015 #6581}. Some regions consistently host much lower PD than expected, like Indonesia and South America (notably around the Andes). Those regions either harbour relatively closely related species that belong to a single group in the phylogeny or several distinct groups distributed across the phylogeny. Group specific results show that rPD of mammals and amphibians was negatively related to NPP (Fig. 1, Fig. S3 for the general trends with  $R^2 = 0.54$  and 0.29 for amphibians and mammals, respectively, Table S1A, B), with the lowest peaks in Madagascar, south-east Brazil and Indonesia for amphibians and in western US, western South-America and Indonesia for mammals. Thus, the most phylogenetically diverse assemblages (with respect to species richness) were consistently found in areas with low NPP. This result was consistent across the 100 phylogenetic trees analysed for mammals (data limitations prevented this test for amphibians). In contrast, rPD of birds was the lowest in the Andes, Himalaya and northern America, and was weakly negatively related to NPP ( $R^2=0.03$ ), irrespective of the phylogenetic uncertainty (Fig. 1, Fig. S3, Table S1B).

Focusing on each zoogeographical region reveals diverging distribution of birds with respect to the other groups. While for birds there was relatively negative relationship between rPD and NPP for five regions ( $R^2$ =0.41 for Africa, Table S1B), a single large region ('North America') displayed a weak but positive relationship between rPD and NPP (Fig. 1, Table S1B). This relatively large outlier region explains the global weak relationship between rPD and NPP for birds. Interestingly, a similar observation occurred for mammals for the 'US' region. However, as this region is relatively small, it did not change the entire relationship much. In summary, the relationship between rPD and NPP was consistently negative both at the global and at the zoogeographic region scales, except for a zoogeographic region around North America for both birds and mammals (Table S1).

The observed relationship between NPP and evolutionary history was not constant across major lineages (Fig. S4 A-C). For amphibians, the three orders (Anura, Gymnophiona and Caudata) showed a coherent distribution of evolutionary history across the different zoogeographical regions (Fig. S4 A). However, for both birds and mammals, our analyses show that some particular orders diverge from the average relationship (Fig S4 B – C). For birds, the rPD of Passeriformes and Psittaciformes was strongly negatively correlated with NPP (Fig. S4 B), while for mammals the relationship between rPD and NPP was even positive for one group (Cetartiodactyla). Striking differences appeared between orders within zoogeographic regions. The positive relationship between rPD and NPP in 'US' and 'North Hemisphere' was indeed driven by the Apodiformes, Charadriiformes, and Galliformes for birds, which are non-passeriformes (Fig. S4 B), and by the Rodentia and Soricomorpha for mammals (Fig. S4 C).

Interestingly, varying the spatial extent of the species pool to estimate relative phylogenetic diversity did not drastically change the overall patterns (Fig. 2). There were strong consistencies between the results obtained with the global and hemispheric species pools. Despite few notable exceptions (South America for both birds and mammals), the relationships between rPD and NPP was similarly negative or positive (i.e. US for mammals and North America for birds). For South America, there was a drastic shift from a strong negative to a strong positive relationship between rPD and NPP for both birds and mammals. For amphibians, the results did not differ much across the three spatial extent of the species pool. Only for the zoogeographic species pool, the overall estimated relationships between rPD and NPP were rather weak in most cases, while still generally consistent with the overall pattern calculated with the global species pool.

The analysis of the relationship between NPP and the standardized effect sizes of top 25% evolutionary distinctiveness (SES of top ED) and of top 25% species-level lineage diversification rates (SES of top DR) (both measured on the global phylogenies of the three clades) allows to evaluate whether regions of high NPP also hold more evolutionary distinct species and more species with high diversification rates than expected (cf. table 1). Both measures reveal strong relationships with NPP for birds and mammals but none for amphibians (Fig. 3 & 4, Fig. S5 & S6 for the general trends). For the former two groups, and consistently across zoogeographical regions, areas of high NPP harbour fewer than expected species from the top DR (Fig. 3, Fig. S5). Interestingly, for the three groups, areas with more than expected species from the top DR are only found in the Northern Hemisphere (with few exceptions in extreme western South Americas) (Fig. 3). Reciprocally, more species than expected from the top ED are found with increasing NPP (Fig. 4, Fig. S6). In general, striking differences exist in the distribution of SES of top ED and SES of top DR for both birds and mammals (Fig. 3 & 4, Fig. S5 & S6), while this is not as striking when considering the absolute richness of top ED and DR (Fig. S7). For instance, for birds, central

Africa and Madagascar, Indonesia and Australia were hotspots of evolutionary distinctiveness (with respect to species richness) but also coldspots of species-level lineage diversification rate (see Fig. S7 for the absolute richness). A similar pattern emerged for mammals, where South America (i.e. the Amazonian forest), Australia and Southern Africa (and Madagascar) were hotspots of evolutionary distinctiveness (with respect to species richness) but coldspots of species-level lineage diversification rates (see Fig. S7 for the absolute richness). However, despite slight differences in the relative numbers, the distribution of the two metrics was relatively similar between the two groups. For amphibians, the relationships were more homogenous except for the North Hemisphere, where North America hosts a high proportion of top DR but a low proportion of top ED. The opposite pattern emerges for Northern Europe and Russia (Fig. 3 & 4).

#### **4 DISCUSSION**

In this paper, we proposed to test if the commonly-observed positive species richnessproductivity relationship also hold for phylogenetic diversity, the richness of top evolutionary distinct species and the richness of top species-level lineage diversification rates. After controlling for species richness, we found that regions with higher productivity harbour relatively lower phylogenetic diversity, have an unexpectedly high number of evolutionary distinct species and an unexpectedly low number of species belonging to fast diversifying clades.

These seemingly contradictory results actually provide new insights into the processes that drive the relationship between vertebrate diversity distribution and primary productivity. The observation that highly productive sites harbour much lower than expected rPD suggests that elevated NPP (i) promotes radiations in certain parts of the tree of life, and/or (ii) promotes the coexistence of closely related species (Evans *et al.*, 2005). However, the relatively low number of species belonging to fast diversifying clades in sites of high NPP suggests that rapid diversification might not necessarily be a mechanism that drive the relationship between rPD and NPP (see also (Schluter, 2016). Rather, more local ecological processes that we cannot capture at our coarse resolution (filtering or niche partitioning) could be key in structuring assemblages, at least in high NPP regions. Interestingly, those regions also harbour a higher than expected richness in evolutionary most distinct species, suggesting that extinction might be reduced under these conditions. This finding is consistent with the hypothesis that the greater combined age and expansion of highly productive regions (usually tropical forest) have facilitated greater species accumulations without necessarily facilitating greater rates of speciation, yet by simply packing more species and by a reduced extinction rate (Jetz *et al.*, 2012; Belmaker & Jetz, 2015).

Low NPP regions harbour relatively high rPD, while having an unexpectedly low number of evolutionary distinct species and a high number of species belonging to clades with high diversification rates. This means that these areas harbour phylogenetically relatively distant species (e.g. sister species are unlikely to occur in the same pixel), but that these species belong to different disproportionately rapidly diversifying clades. Areas of high diversification rates are found throughout the northern hemisphere and the southwest of the South America zoogeographical regions (Fig. 3, see also Jetz *et al.*, 2012). Those areas are known to host several of the rapidly diversifying clades (e.g. warblers, gulls, some rodents), have all been characterized by strong climatic fluctuations from the Pliocene to the present, have generally lower NPP than tropical areas, and were mostly glaciated and experienced the fastest climate change during the last 40,000 years. In other words, the composition of these regions is the result of a recent assembly, rather than in-situ evolution. Interestingly, most species in these low NPP regions have

very broad ranges. We could hypothesize that low NPP regions were recolonized by certain distantly related but rapidly diversifying clades from more productive areas that have evolved broad niches and are better adapted to cold / less productive environments (Wiens *et al.*, 2006). None of these mechanisms are mutually exclusive and their strength likely varies with temporal and spatial scales.

In the Big Data era, it becomes clear that long standing hypotheses and descriptive analyses need to be revisited in light of the increasing availability of distribution and phylogenomic data. Here, we build on the most up-to-date distribution data for three vertebrate groups and analysed the relationships between evolutionary history and net primary productivity. Here, we wanted to revisit the NPP-diversity relationship, as studied before, but with large-scale data. Our analysis should eventually be complemented with a more detailed model of diversification rates (Schluter & Pennell, 2017; Rabosky et al., 2018). Of course, part of the non-explained variance in the regression analyses is likely due to other the effects if other environmental variables (e.g. temperature) and could open for more in-depth analyses to tease-apart their effects (but see Belmaker & Jetz, 2015). We acknowledge that our analyses suffer from the resolution of both distribution and phylogenetic data. In order to be more robust, the same type of analyses should be repeated at much higher resolution (perhaps using a combination of IUCN and GBIF data) to more rigorously test for niche packing which is rather difficult at 200km resolution and with more reliable phylogenetic trees. The amphibian phylogeny is for instance based on a few specimen and lack strong support in several places. In any case, we are confident that our analyses could pave the way for more in-depth analyses in the coming years given the rise of available data, to test more formally the effects of scale (Chase, 2010), community assembly processes and energy constraints (Barnes et al., 2014).

#### **5- BIOSKETCH**

Wilfried Thuiller is broadly interested in merging concepts and theories from biogeography, community ecology and spatial network ecology through the use of state-of-the-art statistical and mathematical approaches.

Author contributions: WT and DG conceived the ideas with the help of FM, TM and LJP. WT compiled all data and ran the analyses, prepared the figures, wrote the initial draft and lead the revisions of the paper. All authors contributed to interpreting the results and to writing the manuscript.

## **5- REFERENCES**

- Allen, A.P. & Gillooly, J.F. (2006) Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. *Ecology Letters*, **9**, 947-654.
- Barnes, A.D., Jochum, M., Mumme, S., Haneda, N.F., Farajallah, A., Widarto, T.H. & Brose, U. (2014) Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning. *Nature Communications*, 5
- Belmaker, J. & Jetz, W. (2015) Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients. *Ecology Letters*, 18, 563-571.
- Benjamini, Y. & Hochberg, Y. (1995) Controlling the False Discovery Rate a Practical and Powerful Approach to Multiple Testing. *Journal of the Royal Statistical Society Series B-Methodological*, 57, 289-300.
- Benjamini, Y. & Yekutieli, D. (2001) The control of the false discovery rate in multiple testing under dependency. *Annals of Statistics*, **29**, 1165-1188.
- Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R., Price, S.A., Vos, R.A., Gittleman, J.L. & Purvis, A. (2007) The delayed rise of present-day mammals. *Nature*, 446, 507-512.
- Brown, J.H. (2014) Why are there so many species in the tropics? *Journal of Biogeography*, **41**, 8-22.
- Chase, J.M. (2010) Stochastic Community Assembly Causes Higher Biodiversity in More Productive Environments. *Science*, **328**, 1388-1391.
- Currie, D.J., Mittelbach, G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7, 1121-1134.
- Evans, K.L., Warren, P.H. & Gaston, K.J. (2005) Species–energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, **80**, 1-25.
- Faith, D.P. (1992) Conservation evaluation and phylogenetic diversity. *Biological Conservation*, **61**, 1-10.
- Faith, D.P. (2002) Quantifying biodiversity: a phylogenetic perspective. *Conservation Biology*, **16**, 248-252.
- Fauth, J.E., Bernardo, J., Camara, M., Resetarits Jr, W.J., Van Busrirk, J. & McCollum, S.A. (1996) Simplifying the jargon of community ecology: a conceptual approach. *The American Naturalist*, 147, 281-286.
- Ficetola, G.F., Rondinini, C., Bonardi, A., Katariya, V., Padoa-Schioppa, E. & Angulo, A. (2014) An evaluation of the robustness of global amphibian range maps. *Journal of Biogeography*, 41, 211-221.
- Fritz, S.A., Bininda-Emonds, O.R.P. & Purvis, A. (2009) Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. *Ecology Letters*, **12**, 538-549.
- Holt, B.G., Lessard, J.-P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.-H., Graham, C.H., Graves, G.R., Jønsson, K.A., Nogués-Bravo, D., Wang, Z., Whittaker, R.J., Fjeldså, J. & Rahbek, C. (2013) An Update of Wallace's Zoogeographic Regions of the World. *Science*, **339**, 74-78.
- Hurlbert, A.H. & Jetz, W. (2007) Species richness, hotspots, and the scale dependence of range maps in ecology and conservation. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 13384-13389.
- Imhoff, M.L. & Bounoua, L. (2006) Exploring global patterns of net primary production carbon supply and demand using satellite observations and statistical data. *Journal of Geophysical Research-Atmospheres*, 111

- Imhoff, M.L., Bounoua, L., Ricketts, T., Loucks, C., Harriss, R. & Lawrence, W.T. (2004) Global patterns in human consumption of net primary production. *Nature*, **429**, 870-873.
- Isaac, N.J.B., Redding, D.W., Meredith, H.M. & Safi, K. (2012) Phylogenetically-Informed Priorities for Amphibian Conservation. *Plos One*, **7**
- Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012) The global diversity of birds in space and time. *Nature*, **491**, 444-448.
- Mazel, F., Renaud, J., Guilhaumon, F., Mouillot, D., Gravel, D. & Thuiller, W. (2015) Mammalian phylogenetic diversity area relationships at a continental scale. *Ecology*, 96, 2814-2822.
- Mazel, F., Davies, T.J., Gallien, L., Renaud, J., Groussin, M., Munkemuller, T. & Thuiller, W. (2016) Influence of tree shape and evolutionary time-scale on phylogenetic diversity metrics. *Ecography*, **39**, 913-920.
- Mishler, B.D., Knerr, N., Gonzalez-Orozco, C.E., Thornhill, A.H., Laffan, S.W. & Miller, J.T. (2014) Phylogenetic measures of biodiversity and neo- and paleo-endemism in Australian Acacia. *Nature Communications*, 5
- Nyakatura, K. & Bininda-Emonds, O.R.P. (2012) Updating the evolutionary history of Carnivora (Mammalia): a new species-level supertree complete with divergence time estimates. *Bmc Biology*, **10**
- Pollock, L.J., Thuiller, W. & Jetz, W. (2017) Large conservation gains possible for global biodiversity facets. *Nature*, **546**, 141-144.
- Rabosky, D.L., Chang, J., Title, P., Cowman, P.F., Sallan, L., Friedman, M., Kaschner, K., Garilao, C., Near, T.J., Coll, M. & Alfaro, M.E. (2018) An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, **559**, 392-395.
- Redding, D.W., Mazel, F. & Mooers, A.Ø. (2014) Measuring Evolutionary Isolation for Conservation. *PLoS ONE*, 9, e113490.
- Schluter, D. (2016) Speciation, Ecological Opportunity, and Latitude. *American Naturalist*, **187**, 1-18.
- Schluter, D. & Pennell, M.W. (2017) Speciation gradients and the distribution of biodiversity. *Nature*, **546**, 48-55.
- Storch, D., Bohdalková, E. & Okie, J. (2018) The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivity-diversity relationship. *Ecology Letters*, 21, 920-937.
- Tsirogiannis, C. & Sandel, B. (2016) PhyloMeasures: a package for computing phylogenetic biodiversity measures and their statistical moments. *Ecography*, **39**, 709-714.
- Tsirogiannis, C., Sandel, B. & Kalvisa, A. (2014) New Algorithms for Computing Phylogenetic Biodiversity. *Algorithms in Bioinformatics*, pp. 187-203.
- Weir, J.T. & Schluter, D. (2007) The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science*, **315**, 1574–1576.
- Wiens, J.J., Graham, C.H., Moen, D.S., Smith, S.A. & Reeder, T.W. (2006) Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: Treefrog trees unearth the roots of high tropical diversity. *American Naturalist*, 168, 579-596.
- Wright, D.H., Currie, D.J. & Maurer, B.A. (1993) Energy supply and patterns of species richness on local and regional scales. *Species diversity in ecological communities: Historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 66-74. Chicago University Press, Chicago.
- Wright, S.D. & Rohde, K. (2013) Energy and spatial order in niche and community. *Biological Journal of the Linnean Society*, **110**, 696-714.
- Zupan, L., Cabeza, M., Maiorano, L., Roquet, C., Devictor, V., Lavergne, S., Mouillot, D., Mouquet, N., Renaud, J. & Thuiller, W. (2014) Spatial mismatch of phylogenetic diversity across three vertebrate groups and protected areas in Europe. *Diversity and Distributions*, 20, 674–685.

	Metrics Meaning		Metric Correlation with NPP	
	<u>Low</u> (negative) values	<u>High</u> (positive) <u>values</u>	<u>Negative</u>	<u>Positive</u>
Relative PD	Closely related species co- occur	Distantly related species co- occur	High NPP enables tight niche packing or promotes diversification	High NPP enables loose niche packing or slowdowns diversification
SES of top ED	Evolutionary distinct species are <b>rare</b> in the assemblage	Evolutionary distinct species are <b>frequent</b> in the assemblage	High NPP decreases the survival of distinct species	High NPP promotes the survival of distinct species
SES of top DR	Species belonging to clades with high diversification rates are <b>rare</b> in the assemblage	Species belonging to clades with high diversification rates are <b>frequent</b> in the assemblage	High NPP decreases diversification in-situ or decrease the survival of species belonging to fast diversifying clades	High NPP promotes diversification in situ or promotes the survival of species belonging to fast diversifying clades

**Table 1 – Phylogenetic diversity metrics and associated interpretations of the correlation with NPP.** Relative PD relates to relative phylogenetic diversity, SES of top ED to standardized effect size of richness of top 25% evolutionary distinctiveness, and SES of top DR to standardized effect size of richness of top 25% species-level lineage diversification rate.

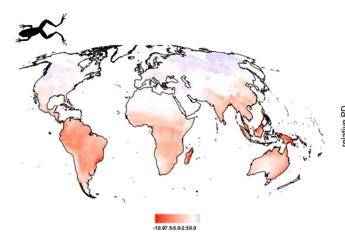
# **Figure Captions**

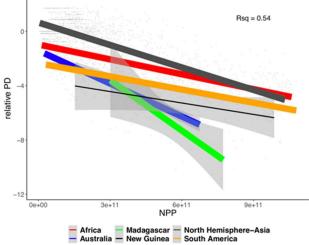
Figure 1. Maps of relative PD and the relationships with net primary productivity. Plots represent the global relationship estimated for the available trees (100 for mammals and birds, 1 for amphibians) represented as grey dots, while different colours represent the relationships for the different zoogeographic regions. The R<sup>2</sup> displayed on the play represent the explained variance of the global relationship between rPD and NPP (see Fig. S3). The width of the lines is proportional to the (mean) R square of the relationship between rPD and NPP calculated for each zoogeographic region (narrow: R<sup>2</sup>≤0.1, medium:  $0.1 < R^2 < 0.3$ , large: R<sup>2</sup>≥0.3). The distributions of the zoogeographic regions are presented in Fig. S2.

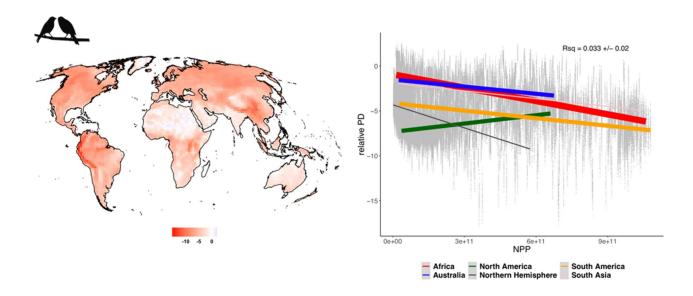
**Figure 2. Effect of sampling pool extent on the global relationship between relative PD and net primary productivity.** Plots represent the global relationship estimated for the available trees (100 for mammals and birds, 1 for amphibians) represented as grey dots, while different colours represent the relationships for the different zoogeographic regions. The distributions of the zoogeographic regions are presented in Fig. S2.

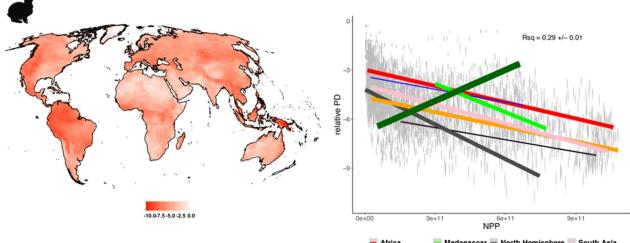
Figure 3. Maps of standardized effect size of richness of top 25% species-level lineage diversification rate (SES of top DR) and the relationships with net primary productivity (NPP). Plots represent the global relationship estimated for the available trees (100 for mammals and birds, 1 for amphibians) represented as grey dots, while different colours represent the relationships for the different zoogeographic regions. The width of the lines is proportional to the (mean) R square of the relationship (narrow:  $R^2 \le 0.1$ , medium:  $0.1 < R^2 < 0.3$ , large:  $R^2 \ge 0.3$ ). The distributions of the zoogeographic regions are presented in Fig. S2.

Figure 4. Maps of standardized effect size of richness of top 25% evolutionary distinctiveness (SES of top ED) and the relationships with net primary productivity (NPP). Plots represent the global relationship estimated for the available trees (100 for mammals and birds, 1 for amphibians) represented as grey dots, while different colours represent the relationships for the different zoogeographic regions. The width of the lines is proportional to the (mean) R square of the relationship (narrow:  $R^2 \le 0.1$ , medium:  $0.1 < R^2 < 0.3$ , large:  $R^2 \ge 0.3$ ). The distributions of the zoogeographic regions are presented in Fig. S2.



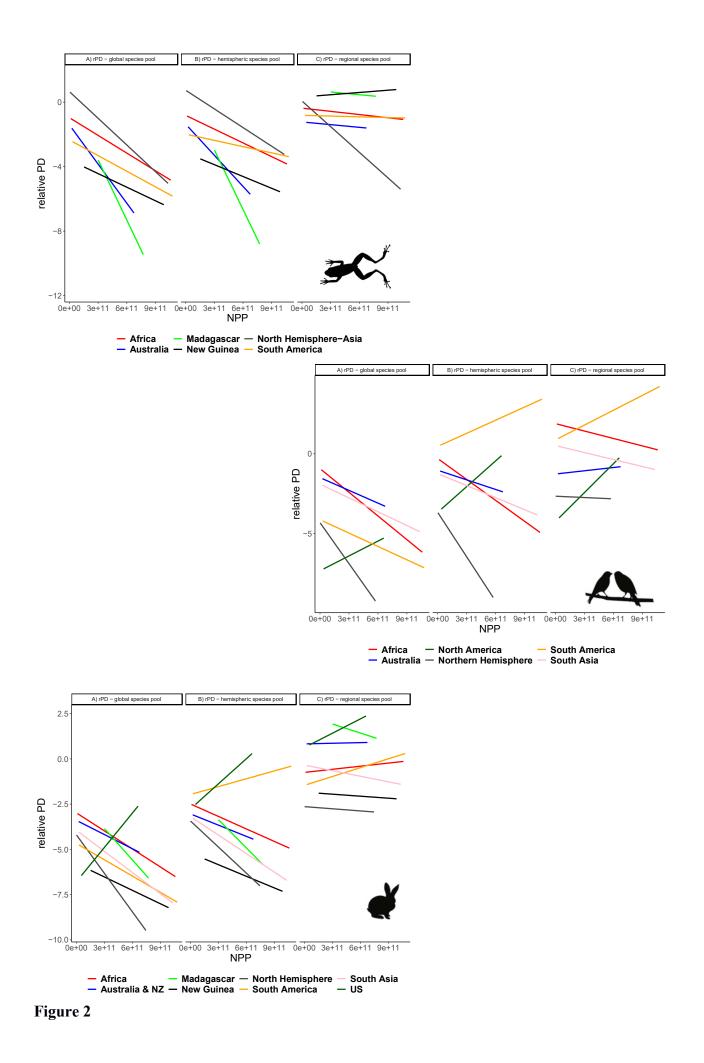


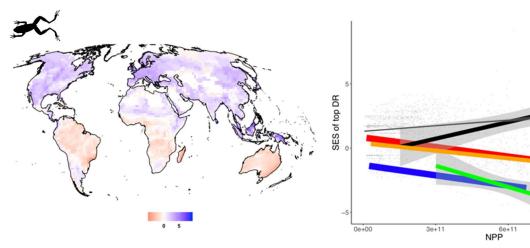




Africa Madagascar North Hemisphere South Asia Australia & NZ New Guinea South America US

Figure 1

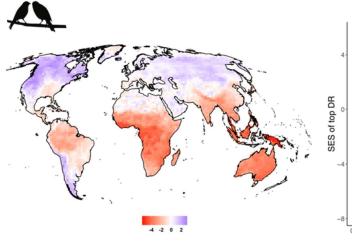


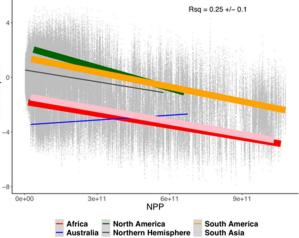


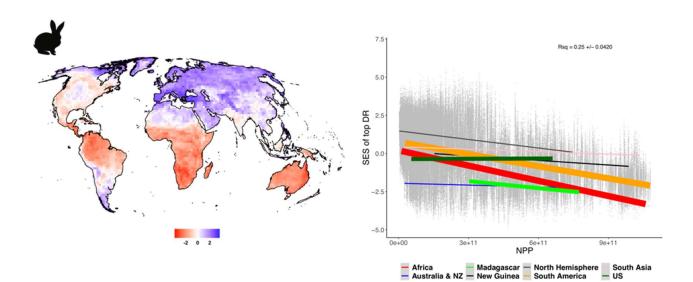
Africa Madagascar North Hemisphere-Asia Australia New Guinea South America

Rsq = 0.13

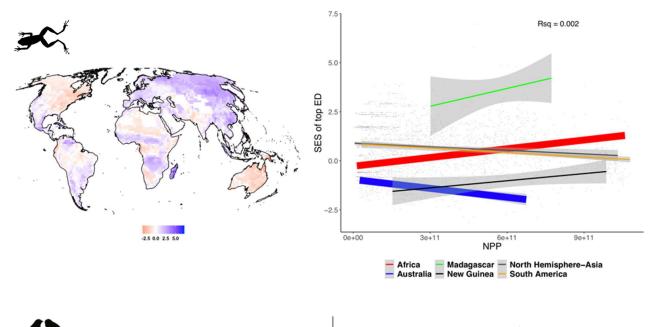
9e+11

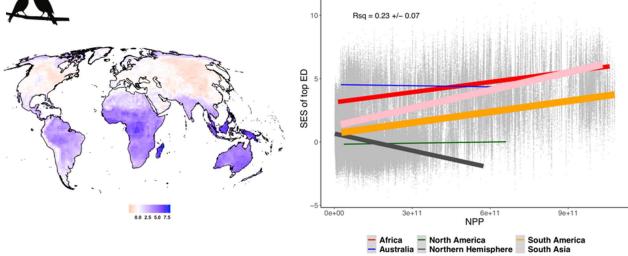












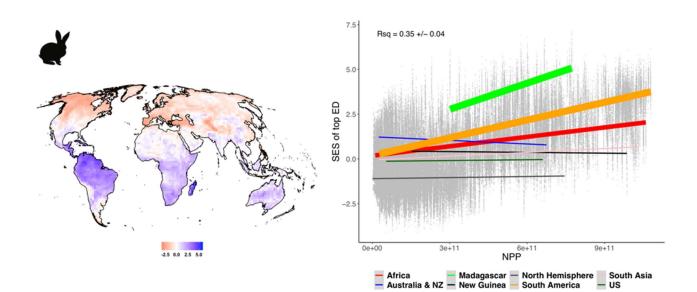


Figure 4

- Allen, A.P. & Gillooly, J.F. (2006) Assessing latitudinal gradients in speciation rates and biodiversity at the global scale. *Ecology Letters*, **9**, 947-654.
- Barnes, A.D., Jochum, M., Mumme, S., Haneda, N.F., Farajallah, A., Widarto, T.H. & Brose, U. (2014) Consequences of tropical land use for multitrophic biodiversity and ecosystem functioning. *Nature Communications*, 5
- Belmaker, J. & Jetz, W. (2015) Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients. *Ecology Letters*, **18**, 563-571.
- Brown, J.H. (2014) Why are there so many species in the tropics? *Journal of Biogeography*, **41**, 8-22.
- Chase, J.M. (2010) Stochastic Community Assembly Causes Higher Biodiversity in More Productive Environments. *Science*, **328**, 1388-1391.
- Currie, D.J., Mittelbach, G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A., Kaufman, D.M., Kerr, J.T., Oberdorff, T., O'Brien, E. & Turner, J.R.G. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7, 1121-1134.
- Evans, H., Straw, N. & Watt, A. (2002) Climate change: implications for insect pests. *Climate change: impacts on UK forests* (ed. by M. Broadmeadow), pp. 99-118. Forestry Commission.
- Evans, K.L., Warren, P.H. & Gaston, K.J. (2005) Species–energy relationships at the macroecological scale: a review of the mechanisms. *Biological Reviews*, **80**, 1-25.
- Fritz, S.A., Eronen, J.T., Schnitzler, J., Hof, C., Janis, C.M., Mulch, A., Bohning-Gaese, K. & Graham, C.H. (2016) Twenty-million-year relationship between mammalian diversity and primary productivity. *Proceedings of the National Academy of Sciences of the United States of America*, **113**, 10908-10913.
- Holt, B.G., Lessard, J.-P., Borregaard, M.K., Fritz, S.A., Araújo, M.B., Dimitrov, D., Fabre, P.-H., Graham, C.H., Graves, G.R., Jønsson, K.A., Nogués-Bravo, D., Wang, Z., Whittaker, R.J., Fjeldså, J. & Rahbek, C. (2013) An Update of Wallace's Zoogeographic Regions of the World. *Science*, **339**, 74-78.
- Jetz, W., Thomas, G.H., Joy, J.B., Hartmann, K. & Mooers, A.O. (2012) The global diversity of birds in space and time. *Nature*, **491**, 444-448.
- Kissling, W.D., Baker, W.J., Balslev, H., Barfod, A.S., Borchsenius, F., Dransfield, J., Govaerts, R. & Svenning, J.-C. (2012) Quaternary and pre-Quaternary historical legacies in the global distribution of a major tropical plant lineage. *Global Ecology and Biogeography*, 21, 909-921.
- Lavergne, S., Mouquet, N., Thuiller, W. & Ronce, O. (2010) Biodiversity and climate change: Integrating evolutionary and ecological responses of species and communities. *Annual Review of Ecology, Evolution and Systematics*, **41**, 321-350.
- Rabosky, D.L., Chang, J., Title, P., Cowman, P.F., Sallan, L., Friedman, M., Kaschner, K., Garilao, C., Near, T.J., Coll, M. & Alfaro, M.E. (2018) An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, 559, 392-395.
- Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge, UK.
- Schemske, D.W., Mittelbach, G.G., Cornell, H.V., Sobel, J.M. & Roy, K. (2009) Is There a Latitudinal Gradient in the Importance of Biotic Interactions? *Annual Review of Ecology Evolution and Systematics*, **40**, 245-269.
- Schluter, D. (2016) Speciation, Ecological Opportunity, and Latitude. *American Naturalist*, **187**, 1-18.
- Schluter, D. & Pennell, M.W. (2017) Speciation gradients and the distribution of biodiversity. *Nature*, **546**, 48-55.

- Storch, D., Bohdalková, E. & Okie, J. (2018) The more-individuals hypothesis revisited: the role of community abundance in species richness regulation and the productivitydiversity relationship. *Ecology Letters*, **21**, 920-937.
- Weir, J.T. & Schluter, D. (2007) The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science*, **315**, 1574–1576.
- Wiens, J.J., Graham, C.H., Moen, D.S., Smith, S.A. & Reeder, T.W. (2006) Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: Treefrog trees unearth the roots of high tropical diversity. *American Naturalist*, **168**, 579-596.
- Wright, D.H., Currie, D.J. & Maurer, B.A. (1993) Energy supply and patterns of species richness on local and regional scales. *Species diversity in ecological communities: Historical and geographical perspectives* (ed. by R.E. Ricklefs and D. Schluter), pp. 66-74. Chicago University Press, Chicago.
- Wright, S.D. & Rohde, K. (2013) Energy and spatial order in niche and community. *Biological Journal of the Linnean Society*, **110**, 696-714.