Received: 19 July 2022 | Revised: 13 December 2022 | Accepted: 14 December 2022

DOI: 10.1111/ele.14177

ECOLOGY LETTERS WILEY

LETTER

The role of fire in terrestrial vertebrate richness patterns

Max A. Moritz[1,2] | **Enric Batllori**[3,4] | **Benjamin M. Bolker**[5]

[1]University of California Cooperative Extension, Oakland, California, USA

[2]Bren School of Environmental Science & Management, University of California, Santa Barbara, California, USA

[3]Departament de Biologia Evolutiva, Ecologia i Ciències Ambientals, Facultat de Biologia, Universitat de Barcelona (UB), Barcelona, Spain

[4]Institut de Recerca de la Biodiversitat (IRBio), Universitat de Barcelona (UB), Barcelona, Spain

[5]Departments of Mathematics & Statistics and Biology, McMaster University, Hamilton, Ontario, Canada

Correspondence
Max A. Moritz, Bren School of Environmental Science & Management, University of California, Santa Barbara, California 93106, USA.
Email: mmoritz@ucsb.edu

Funding information
National Center for Ecological Analysis and Synthesis, National Science Foundation, Grant/Award Number: EF-0553768; NSERC, Grant/Award Number: 05488-2016; Serra Hunter Program

Editor: Sally Archibald

Abstract

Productivity is strongly associated with terrestrial species richness patterns, although the mechanisms underpinning such patterns have long been debated. Despite considerable consumption of primary productivity by fire, its influence on global diversity has received relatively little study. Here we examine the sensitivity of terrestrial vertebrate biodiversity (amphibians, birds and mammals) to fire, while accounting for other drivers. We analyse global data on terrestrial vertebrate richness, net primary productivity, fire occurrence (fraction of productivity consumed) and additional influences unrelated to productivity (i.e., historical phylogenetic and area effects) on species richness. For birds, fire is associated with higher diversity, rivalling the effects of productivity on richness, and for mammals, fire's positive association with diversity is even stronger than productivity; for amphibians, in contrast, there are few clear associations. Our findings suggest an underappreciated role for fire in the generation of animal species richness and the conservation of global biodiversity.

KEYWORDS
biogeography, fire, global biodiversity, latitudinal species richness, net primary productivity

INTRODUCTION

Some of the most challenging questions in ecology and conservation concern biodiversity and its distribution across the planet (Brooks et al., 2006; Hoekstra et al., 2005; McGill et al., 2015; Myers et al., 2000). Latitudinal trends in species richness on land—generally high in equatorial biomes and decreasing poleward—have generated many hypotheses about the forces shaping these patterns. Proposed causal mechanisms include the size and historical stability of habitats, environmental heterogeneity, and the available energy to be partitioned among species (Gaston, 2000; Schluter & Pennell, 2017; Stein et al., 2014; Whittaker et al., 2001; Wiens & Donoghue, 2004; Willig et al., 2003). Although the relative importance of different mechanisms has long been debated, a common theme among terrestrial studies is that productivity is a dominant driver of speciation and macro-scale richness patterns (Cusens et al., 2012; Field et al., 2009; Gillman et al., 2015; Šímová & Storch, 2017) (Figure 1a). In most of these terrestrial ecosystems, however, fire has been a fundamental natural disturbance for at least the last 300 million years (Scott, 2000). By consuming primary productivity, fire has strong interactions with the vegetation of different ecosystems (Bond et al., 2005; Krawchuk & Moritz, 2011; McLauchlan

---

Enric Batllori and Benjamin M. Bolker have contributed equally to this work.

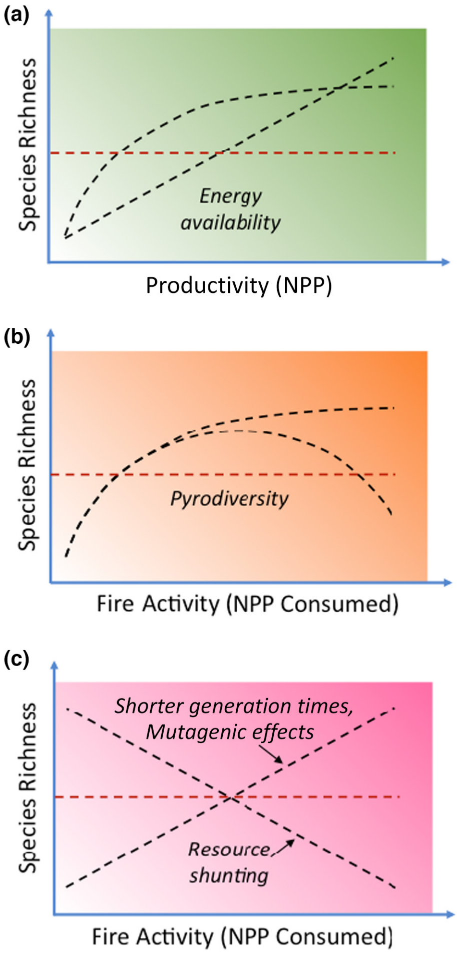

FIGURE 1 Macro-scale relationships of species richness to productivity and fire. Considering productivity as an influence on latitudinal species richness patterns (a), observed and hypothesised relationships are primarily positive, although the shape is debated (Gillman et al., 2015; Whittaker et al., 2001). Fire is also generally found to be positively related to species richness as an ecological driver (b), acting as an agent of 'pyrodiversity' that generates environmental heterogeneity (He et al., 2019). In an evolutionary context (c), fire could have multiple positive effects on species richness (He et al., 2019); however, via combustion fire also removes resources (Chen et al., 2010; Polis & Strong, 1996) that could otherwise fuel the maintenance and diversification of species richness. The 'null' response of no effect, already largely rejected for productivity (a), is also included as a horizontal line for each panel. Note that shapes here refer to untransformed data (i.e., original scale prior to log transformation). (Also see additional references in the text.)

et al., 2020), and the resulting 2–3 PG C emissions per year play a substantial role in the global carbon budget (Bowman et al., 2009; van der Werf et al., 2017). Given the important effects of fire on ecosystem characteristics and the lives of both plants and animals (Bond & Keeley, 2005; Carbone et al., 2019; He et al., 2019; Keeley et al., 2011; McLauchlan et al., 2020; Nimmo et al., 2019; Pausas & Parr, 2018), surprisingly little is known about how fire and productivity interact in affecting global species richness patterns.

Fire-prone ecosystems are often considered hotspots of biodiversity; much of that pattern is attributed to the effects of fire (Keeley et al., 2011; Kelly & Brotons, 2017; Pausas & Ribeiro, 2017). Over ecological timescales (Figure 1b), fire creates environmental heterogeneity and thus habitat diversity for different species (He et al., 2019; McLauchlan et al., 2020). Over evolutionary timescales (Figure 1c), mutagenic effects of heating or shorter generation times due to fire could both promote diversification (He et al., 2019). Longer exposure to more stable, fire-prone environments could also promote diversification, suggesting that fire regime predictability could be important (Mucina & Wardell-Johnson, 2011). Fire's consumption of standing biomass also opens up otherwise unavailable ecological niches, increasing near-term richness and simultaneously supporting higher diversification rates and total long-term richness under active fire regimes (Schluter & Pennell, 2017). In contrast, through combustion of primary productivity and long-distance transport of emissions (Chen et al., 2010), fire 'shunts' (sensu (Polis & Strong, 1996)) local energy and resources that could otherwise drive diversification and permit the maintenance of diversity. One might therefore suppose that fire's consumption of primary productivity would lead to slower speciation and lower species richness over evolutionary timescales, although such negative effects will depend on how metabolic rates of organisms scale up to influence patterns of diversity (Allen et al., 2002; Ernest et al., 2003). Clearly, a variety of complex effects mediate the net influence of productivity and an ecological disturbance like fire at the global scale (He et al., 2019; Huston, 2014; Krawchuk & Moritz, 2014; McLauchlan et al., 2020).

Here we ask the following basic question: What is the relationship between fire and global species richness patterns of amphibians, birds and mammals, after incorporating several other key environmental drivers. We focus on terrestrial vertebrates (although excluding reptiles; Jenkins et al., 2013) because there is a relative lack of information on global fire–diversity relationships in these taxa (He et al., 2019; Pausas & Parr, 2018). Our emphasis on fire and terrestrial vertebrate richness also complements many existing broad-scale studies and reviews that focus on fire, diversification and richness in plants (Bond & Scott, 2010; Cramer & Verboom, 2017; He et al., 2019; Keeley et al., 2011; Lamont & He, 2017; Pausas, 2015; Pausas & Ribeiro, 2017). To quantify the relative roles of fire and productivity on species richness, both average conditions and their variability through time are included in mixed effects models. We directly incorporate additional potential drivers that are deemed important to richness patterns, including area effects (via the size of each ecoregion) and historical phylogenetic effects (via biogeographic realms) (Chown & Gaston, 2000). We are thus able to test whether the net influence of productivity consumption by fire and its variability through time appear to increase or decrease richness overall, and we can isolate the functional form of global species richness responses to gradients in both productivity and fire (Figure 1).

MATERIALS AND METHODS

Data

We used annual net primary productivity (NPP) in our analyses, a reasonable approximation of available energy for trophic levels above plants (Šímová & Storch, 2017; Whittaker et al., 2001). Global productivity and fire observations data spanning roughly two decades (period 1997–2015) come from the Global Fire Emission Database at globalfiredata.org (Version 4.1, GFED4s), based on both the standard GFED4 burned area (Giglio et al., 2013) and on burned area derived from active fire information seen outside the burned area maps. The GFED4s provides cell area in m^{-2}, monthly burned area, as a fraction of grid cell area, NPP in $g\ C \cdot m^{-2}\ month^{-1}$, and fire carbon emissions (FEM) in $g\ C \cdot m^{-2}\ month^{-1}$ at a 0.25° resolution. Given that FEM represents the amount of plant biomass consumed by fire, we computed yearly NPP and FEM values for each grid cell and the fraction of NPP consumed by fire as FEM/NPP. For each cell, yearly data were averaged over the 1997–2015 period. The interannual coefficient of variation (CV) over the period was also calculated, as a measure of the variability in primary production and its consumption by fire. Average patterns of NPP and the fraction consumed by fire, as well as their variability through time over the period of analysis, are shown in Figure 2 (see also Figure S1).

Biodiversity data for amphibians, birds and mammals (Figure 2) at a 10-km resolution come from biodiversitymapping.org, version 2017 (Jenkins et al., 2013). These data use polygonal ranges of species distribution to assess the number of species present in a given grid cell; each species is considered present in a cell if the cell overlaps part of its polygonal range. Biodiversity data were aggregated at the extent and 0.25° resolution of the fire data set through bilinear interpolation.

Terrestrial ecoregions of the world (Olson et al., 2001) were obtained from WWF (www.worldwildlife.org). Ecoregions are defined as relatively large units of land or water containing a distinct assemblage of natural

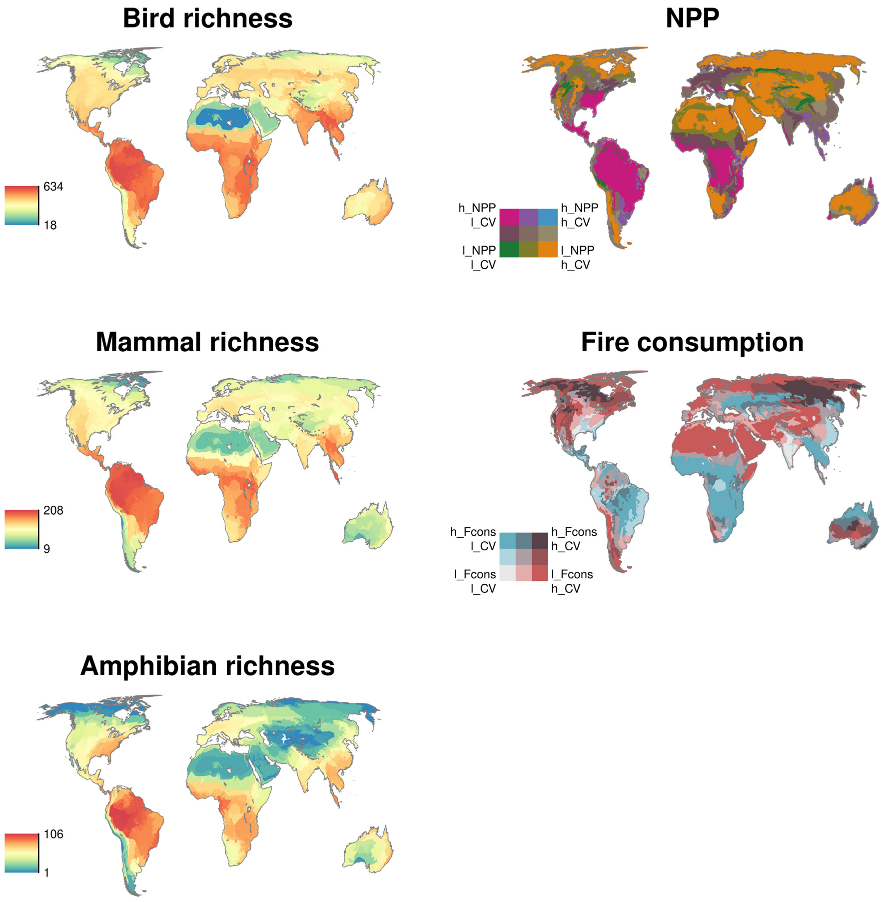

FIGURE 2 Spatial variation in terrestrial vertebrate richness patterns, productivity and fire's consumption of productivity. Species richness of different terrestrial vertebrate taxa (left panels) are examined with respect to average annual net primary productivity (NPP) and the fraction of NPP consumed by fire, as well as their variability through time represented by the coefficient of variation (CV) (right panels). (Please see Materials and Methods for data sources, other variables examined and modelling details.)

communities sharing a large majority of species, dynamics and environmental conditions. The original data set contains 867 terrestrial ecoregions, classified into 14 different biomes, excluding rock, ice and water, and six different biogeographic realms (Figure S2) (Olson et al., 2001). In all data sets, following Kreft et al. (2008), we retained data for those pixels within land masses equal to or larger than Australia (i.e., islands are excluded). Of the 867 ecoregions available, 620 were retained for birds and mammals, while 617 were retained for amphibians; some exclusions were due to missing data. For both fire and biodiversity data we computed ecoregion-level means. While running the analysis at the scale of 0.25° grid cells might have provided more information, it would have been much more computationally intensive (more than a 100-fold increase in observational units). Given that ecoregions are explicitly constructed to aggregate pixels that are ecologically similar, a finer-grained analysis also might not sharpen our inferences at the global scale very much. For biomes that cover less than 1% of the Earth's terrestrial surface (identified in Figure 3), we are less confident in results due to possible spatial resolution mismatches between data sources; a more detailed summary of biome-level characteristics is provided in Table S1.

Modelling

In our analysis, we log-transformed all response and predictor variables (we use natural logarithms throughout), except the interannual coefficients of variation. The data were hierarchically grouped at three levels: biome (e.g., tropical forest), realm (e.g., Neotropics) and their interaction (e.g., Neotropical forests).

We used mixed effects models (Bates et al., 2015) to quantify the net influence of all predictors. As fixed-effect (overall, global-scale) predictors, we incorporated ecoregion area (km^2) after excluding islands; mean NPP (g C·m^{-2} month^{-1}); average fraction of NPP consumed by fire annually (proportion 0–1); and the interannual CV (unitless) of NPP and fire consumption, as well as the pairwise interactions of all of these predictors except for area. Since all of these factors vary within all three of our grouping factors (biome, realm and biome × realm), the *maximal* random effects components of the model would include among-biome, among-realm and among-(biome × realm) variation in all of these effects, as well as the within-group correlations among them (Barr et al., 2013). For example, we would like to know if diversity was more sensitive than average to NPP, or to fire, in some biomes, and whether those biomes where richness had above-average sensitivity to NPP typically also had above-average sensitivity to fire (positive correlation), or below-average sensitivity (negative correlation). In order to simplify the model so that all the variances can be estimated (Bolker, 2015), we considered different versions of the random effects at each level: (1) the full variance–covariance matrix with all correlations estimated, (2) a diagonal covariance matrix that assumes independent variation of each effect across groups or (3) an intercept-only model assuming

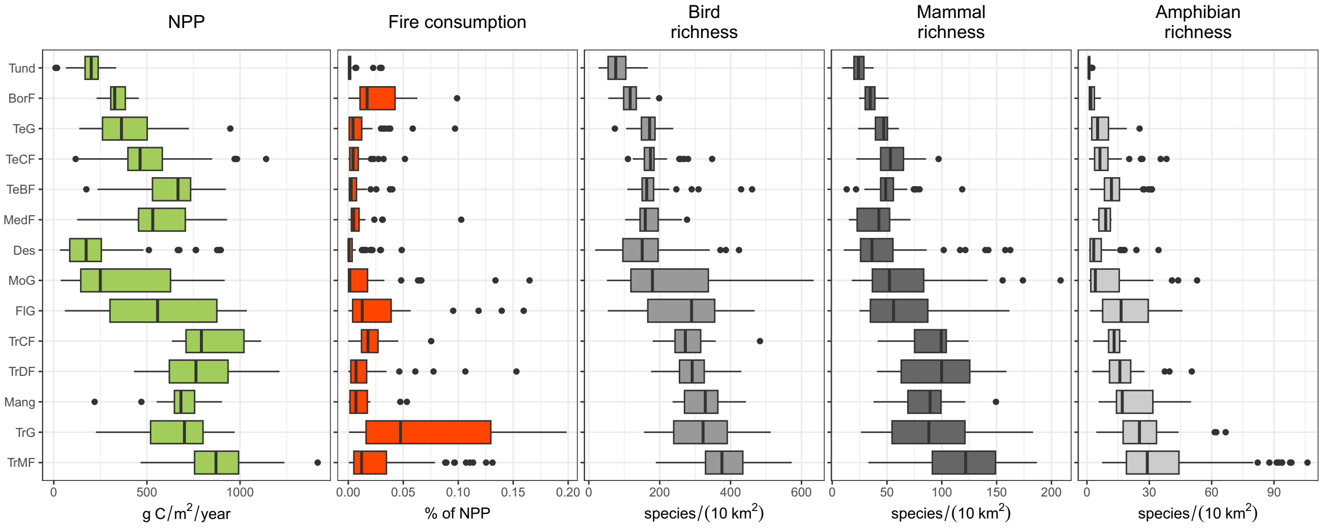

FIGURE 3 Biome-level summary of productivity, fire consumption and species richness for terrestrial vertebrate taxa. Average annual productivity rates are aggregated by biome and displayed here, along with annual average rates of NPP consumed by fire, and terrestrial vertebrate species richness in each biome. Biomes are shown in a roughly polar-to-equatorial ordering, based on mean ecoregion latitude. Abbreviations: Tund, tundra; BorF, boreal forests/taiga; TeG, temperate grasslands, savannas & shrublands; TeCF, temperate conifer forests; TeBF, temperate broadleaf & mixed forests; MedF, mediterranean forests, woodlands & scrub; Des, deserts & xeric shrublands; MoG, montane grasslands & shrublands; FIG*, flooded grasslands & savannas; TrCF*, tropical & subtropical coniferous forests; TrDF, tropical & subtropical dry broadleaf forests; Mang*, mangroves; TrG, tropical & subtropical grasslands, savannas & shrublands; TrMF, tropical & subtropical moist broadleaf forests (*These biomes cover less than 1% of the Earth's terrestrial area).

that only the overall richness varied across groups. We evaluated combinations of these three possible random-effects structures (full, independent, intercept-only) for each of three grouping levels (biome, realm and biome x realm) for a total of 27 model structures for each taxon. To account for residual spatial autocorrelation, the model also included a penalised spherical spline component (using the gamm4 package (Wood & Scheipl, 2014)). We discarded singular model fits (i.e., models where one or more component variances was estimated as zero) and selected the non-singular model with the best (lowest) AIC (Matuschek et al. (2017) have suggested a similar procedure, but based on stepwise regression using *p*-values).

For birds and amphibians, the selected model included independent effects of the predictors at the biome/realm interaction level and intercept-only (mean diversity) variation at the biome and realm levels; for mammals, the (independent) predictor effects were included at the realm level, with mean-diversity effects at the biome and biome/realm levels.

All parameters were centred and scaled for model fitting (Schielzeth, 2010); we convert the parameters back to their original scales when reporting or plotting them. Small-magnitude coefficients on the log scale are approximately equivalent to proportional changes (i.e., a coefficient of 0.05 corresponds to a proportional change of $\exp(0.05) = 1.051 \approx 5\%$ difference). Since both the predictor variables (e.g., NPP) and the response variable (species richness) are on the log scale, we can interpret the coefficients as *elasticities*: a coefficient of 0.05 would mean, for example, that a change of 1% in NPP would result in a change of $0.05 \times 1\% = 0.05\%$ in species richness. Alternatively, one can interpret log–log regression coefficients as *power law exponents*: if $\log y = a + b \log x$, then y is proportional to x^b. A similar argument applies for the variability effects (NPP CV, Fire consumption CV): these represent variability scaled to the mean, so a coefficient of 0.05 would mean that a change of 1 unit of variability *as a proportion of the mean* would lead to a change of 0.05 in the log of species richness, or a ≈5% difference.

We used *R^2 values* to assess the overall goodness of fit of selected models and *semi-partial R^2 values* (which represent the 'strength of association between a subset of predictors and the outcome, adjusted for other predictors in the full model') (Jaeger et al., 2017) to quantify the overall contributions of each term in the model. We used the standardised generalised variance approach (Jaeger et al., 2019) as implemented in the r2glmm package (Jaeger, 2017), with extensions to the package to adapt it for use with gamm4 models. In interpreting model fits, we typically replace 'significance' statements with those reflecting 'statistical clarity', which make the meaning of statistical tests easier to interpret and explain (Dushoff et al., 2019).

RESULTS

Species richness patterns in terrestrial vertebrates and NPP consumption by fire

Ranked by average annual productivity, the biomes of the world show a consistent pattern of increasing species richness with increasing NPP (Figure 3). The percentage of NPP consumed by fire, however, does not show the same trend. Instead, most biomes experience 1%–2% NPP losses each year, with some showing much higher annual rates (i.e., Boreal Forests at 4%; Tropical and Subtropical Grasslands, Savannas and Shrublands at 7%).

Model fits and variable importance

Based on a variety of mixed effects model specifications and sensitivity analyses, the environmental drivers we examined are able to explain the majority of the variation in global terrestrial vertebrate richness patterns (Figure 4a; Table S2). The strongest model is for bird richness ($R^2 = 0.71$), although models for both mammals and amphibians also performed well ($R^2 = 0.55$ and 0.58 respectively).

Across taxa, the most important variable related to richness patterns is NPP, whose partial R^2 values range from 0.13 to 0.25 (Figure 4a; Table S2) and also have statistically clear effects on richness for all taxa (Figure 4b). Fire's consumption of NPP has clear effects on richness for birds and mammals, although explaining only a moderate fraction of modelled variation in richness (partial $R^2 = 0.043$ and 0.093 respectively). Of the remaining NPP- and fire-related variables examined, the interaction between NPP and fire's consumption of NPP in bird richness models is the only one that is statistically clear (partial $R^2 = 0.015$). Area is moderately important in explaining variation in bird richness models (partial $R^2 = 0.055$) and less so in amphibian richness models (partial $R^2 = 0.0072$), the taxa for which this variable shows clear effects. The remaining variance explained is due to other variables in the model (e.g., random effects of biome and realm).

Productivity- and area-related influences on terrestrial vertebrate richness

As expected, increased NPP is consistently associated with increased richness at the macro-scale for all taxa examined. This relationship is evident in the plots of partial residuals (Figure 5; Table S3), which remove other effects and show only a single variable's relationship with richness. Amphibians (Figure 5g), whose richness is generally an order of magnitude lower than birds or mammals, are much more sensitive to differences in

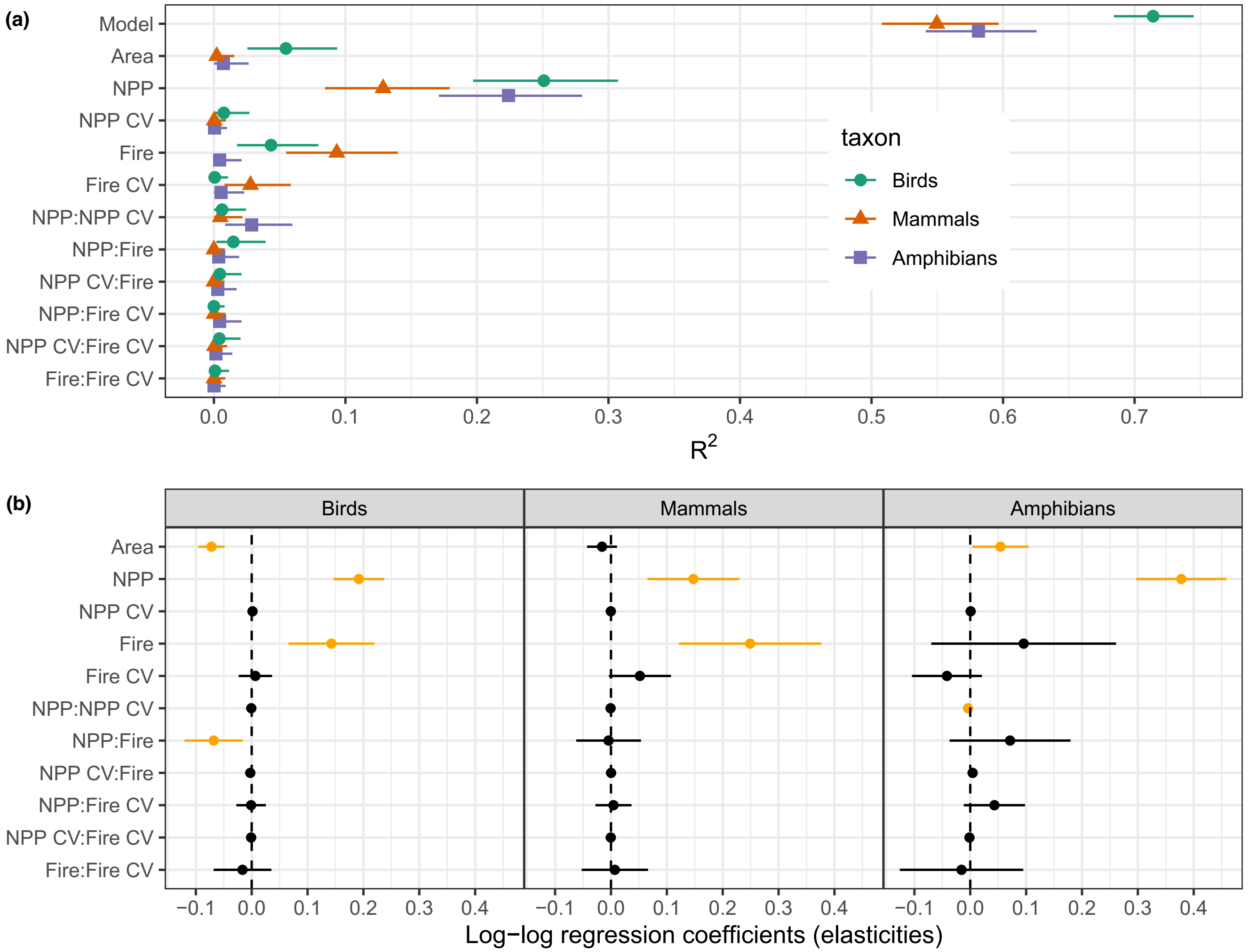

FIGURE 4 Variance explained and coefficients for global terrestrial vertebrate richness models. (a) R-square values for the full model and partial R-square of all model predictors for species richness of terrestrial vertebrate taxa. NPP is averaged annual net primary productivity; Fire is averaged annual fraction of NPP consumed by fire. In all variables, CV refers to the coefficient of variation, reflecting their inter-annual variability and thus predictability through time. (b) Model variable coefficients and their confidence intervals (statistically clear coefficients shown in orange).

average annual productivity (i.e., 3.8% increase in species richness for each 10% increase in NPP). Similar relationships were found for both bird and mammal richness (Figure 5a,d), but exhibiting roughly half the sensitivity of amphibians (i.e., 1.9% and 1.5% increases, respectively, for each 10% increase in NPP; Table S3). We did not find consistently clear effects of the temporal variability of NPP (i.e., its inter-annual coefficient of variation) on richness; however, our models suggest that bird species richness may be higher in ecoregions with more variable NPP from year to year (Figure 5b).

Although empirical studies and theoretical modelling suggest that richness might generally be expected to increase with ecoregion size, we found that the effects of ecoregion area vary across taxa after controlling for other variables. Amphibians show a small but clear positive trend (Figure 5i), reflecting an additional 0.54% richness for each 10% increase in ecoregion size. However, birds show a clear negative trend (Figure 5c), with 0.72% fewer species for the same 10% area increase. Mammal richness patterns also suggest a possible negative relationship (Figure 5f), although the area variable is statistically unclear.

Fire-related influences on terrestrial vertebrate richness

After accounting for the influence of other variables, increases in fire's consumption of productivity are consistently associated with increased terrestrial vertebrate richness, with relatively strong and statistically clear effects for birds and mammals (Figure 6a,c; Table S3). In fact, mammal richness is very sensitive to the fraction of NPP consumed by fire (i.e., 2.5% increase in richness for each 10% increase in fire), almost twice the influence of NPP itself. Fire has a weaker effect on bird richness (i.e., 1.4% increase in richness for each 10% increase in fire),

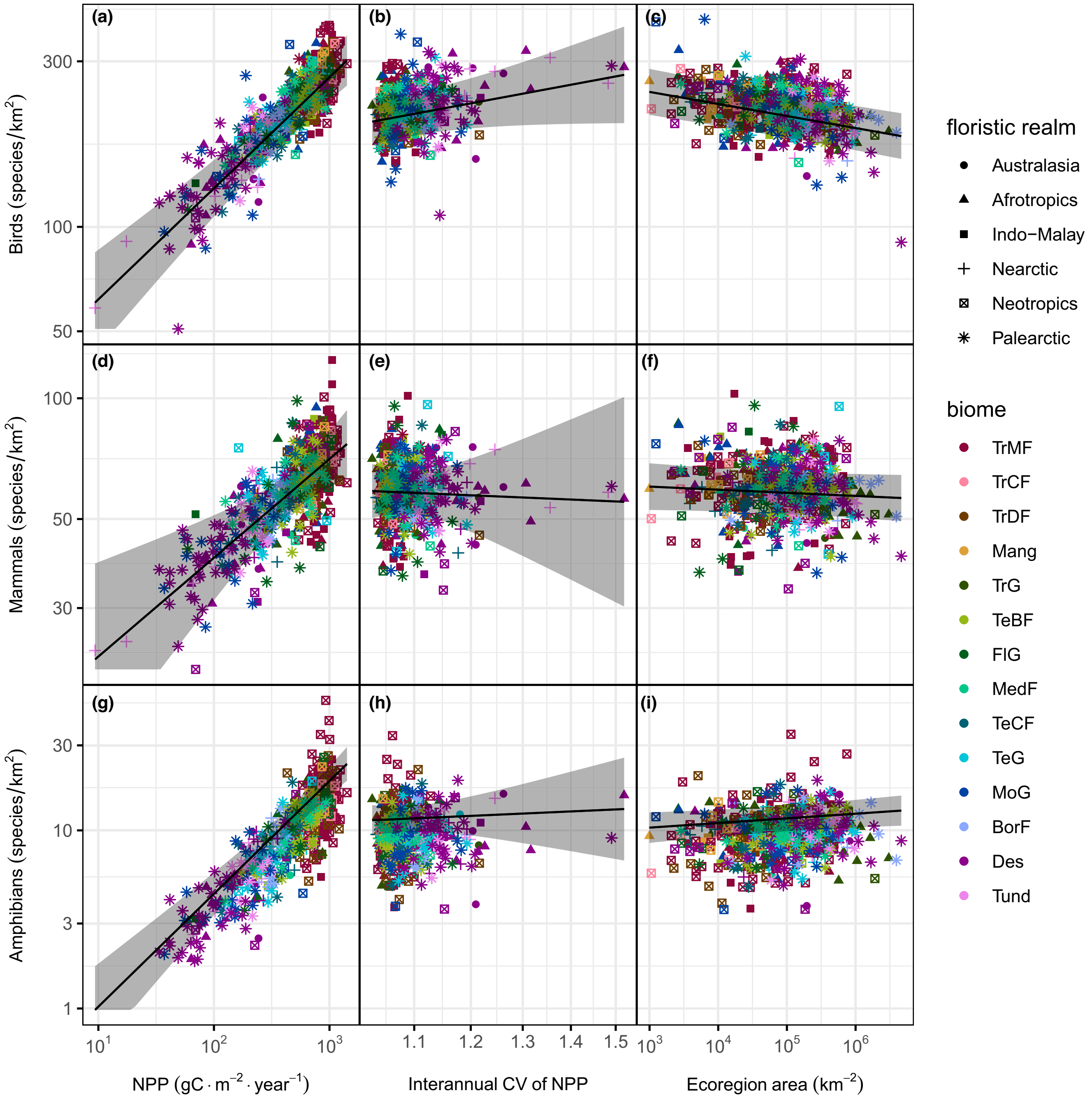

FIGURE 5 Productivity and area variables and their relationship to global terrestrial vertebrate richness. Partial residual plots show the unique contribution of productivity (a, d, g), variability of productivity through time (b, e, h) and area (c, f, i) to species richness of terrestrial vertebrate animals, after accounting for the influence of all other variables included in models. Points represent means for ecoregions, while colours reflect biomes and symbols reflect realms.

but it is still strong and approaches that of NPP. The statistically clear fire-related interaction between NPP and fire's consumption of NPP for birds is negative; in other words, increased fire consumption weakens productivity's positive effect on bird richness (Figure S5). Fire had smaller (and unclear) effects for amphibians (Figure 6e).

As with the variability of NPP, the variability of fire does not have statistically clear effects on species richness in our models. However, richness appears to increase in mammals as temporal variability of fire increases (Figure 6d). In amphibians, there is a tendency towards higher richness in areas with less variable fire activity through time (Figure 6f).

DISCUSSION

We identify a surprisingly strong influence of fire on global patterns of terrestrial vertebrate richness, and our models perform as well or better than most models

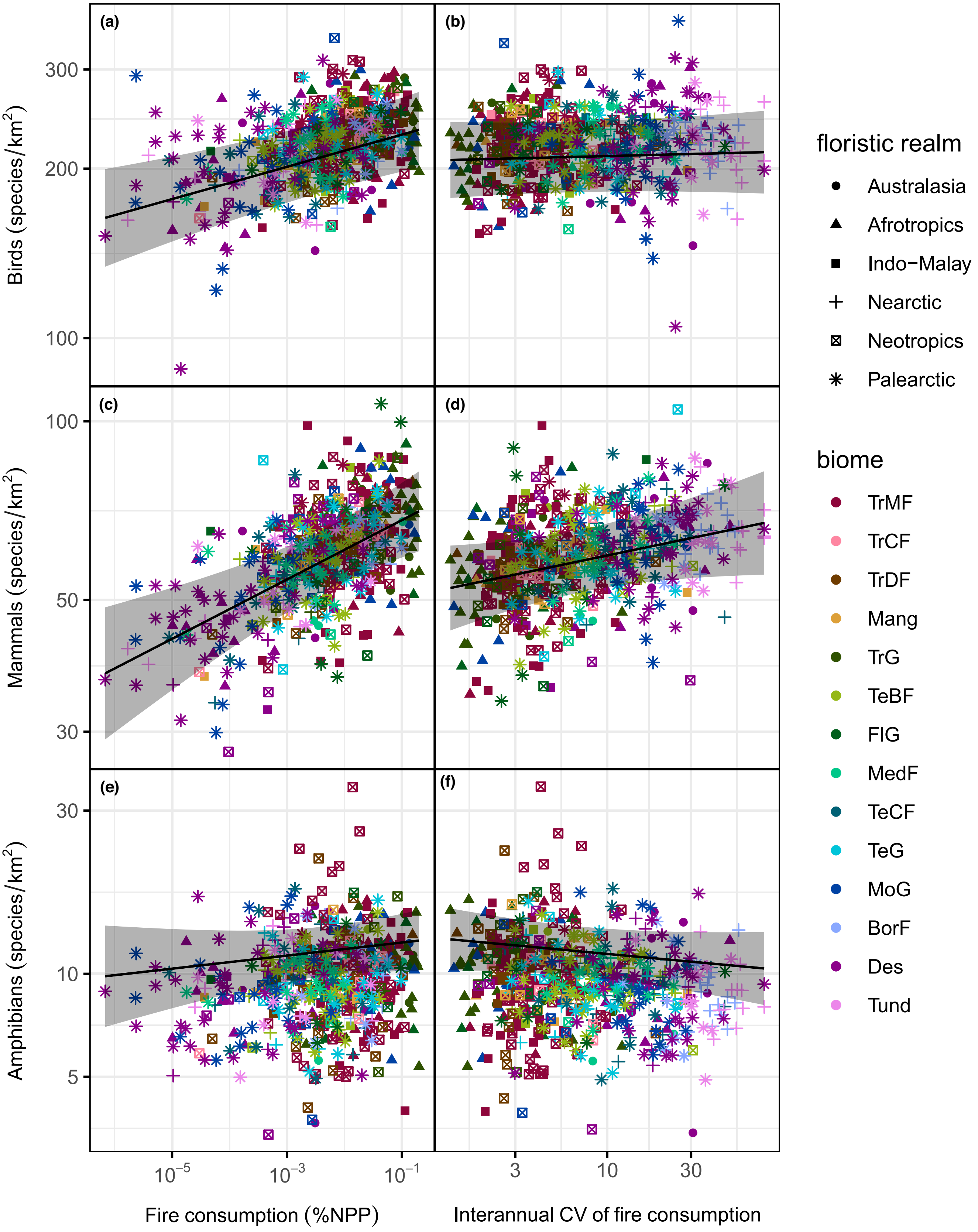

FIGURE 6 Fire variables and their relationship to global animal species richness. Partial residual plots show the unique contribution of fire's consumption of productivity (a, c, e) and the variability of that consumption through time (b, d, f) to species richness of terrestrial vertebrate animals, after accounting for the influence of all other variables included in models. Points represent means for ecoregions, while colours reflect biomes and symbols reflect realms.

created to explain global biodiversity patterns (Field et al., 2009). Consistent with many studies, we observe the important positive effect of productivity, represented here by NPP, which captures climatic influences in an internally consistent way (i.e., subsuming the effects of temperature-, moisture- and energy-related drivers). After controlling for productivity- and fire-related influences, area shows conflicting or unclear relationships to richness in different taxa (Table S3). This finding is consistent with some studies, such as recent work on mammal richness (Udy et al., 2021), but area effects may be hard to observe at the scale of the ecoregions used in our analysis. Alternatively, the influence of area may have been captured by the random-effects components of realm and/or biome, which could also incorporate other historical effects.

Fire appears to have both positive and negative effects on terrestrial vertebrate richness patterns. Despite a generally positive influence, our analysis shows a potentially detrimental impact of fire on bird richness: the clear negative interaction between productivity and the fraction consumed by fire illustrates that, for a given productivity level, increased burning weakens the positive effect of productivity on richness. Nevertheless, the net global effect of increasing fire is to increase bird richness, which is in agreement with some regional bird studies (e.g., Beale et al., 2018; Tingley et al., 2016) but not all (e.g., Taylor et al., 2012). The temporal variability of fire may also have a potentially detrimental impact on amphibian richness, although this variable (and average fire consumption itself) does not have clear effects in our models for amphibians. Such a result (i.e., the null hypothesis in Figure 1b,c) may not be surprising, however, given that fire probably plays a less consistent role in the relatively moist habitats that amphibians typically require. In contrast, mammal models suggest that more temporally variable fire regimes may increase richness, and fire's consumption of NPP has very strong positive effects on richness. This finding is consistent with important relationships between fire and mammal richness observed in African (Beale et al., 2018) and Australian (Lindenmayer et al., 2016) studies.

Whether the strong influence of fire on mammal and bird richness is primarily ecological or evolutionary in nature (i.e., rejecting the null hypothesis in Figure 1b,c respectively), our results only hint at their relative importance as mechanisms. As stated earlier, fire's consumption of NPP could alter rates of evolutionary processes of diversification and extinction, and this could extend to fire-related adaptations. Given the scarcity of clearly fire-adapted traits in animals (Pausas & Parr, 2018), however, the relatively strong positive influence of fire on bird and mammal richness would presumably be due to other mechanisms if evolutionary. Plants should experience the most direct evolutionary effects of fire, and there is strong evidence that fire activity has promoted diversification by shortening generation times (He et al., 2019). Similar evidence for animals may exist but has yet to be found. The same is true for fire as a mutagenic agent that would promote diversification. As an ecological mechanism, the environmental heterogeneity created by fire in space and time is widely thought to allow for coexistence of a variety of species at different seral stages and with different habitat needs. Despite widespread confidence in fire as an agent of pyrodiversity—that is, creation of environmental heterogeneity through variation in fire regimes—studies are not consistent in observing a positive effect (Jones & Tingley, 2022). A challenge here is in how one defines the diverse effects of fire and the spatio-temporal scale of analysis. Regardless, even if such terms were to be met, pyrodiversity could be both an ecological and evolutionary influence: Fire generates novel but transitory habitats by consuming plant biomass, yet this also facilitates higher speciation and long-term richness where fire is an ongoing force (Schluter & Pennell, 2017). For animals, adaptations could include traits that allow survival during fires (e.g., rapidly detecting and escaping impacts) and advantages in post-fire environments (e.g., locating and exploiting resources) (Pausas & Parr, 2018). How ecological and evolutionary drivers translate to effects on animal richness remains to be seen, but our findings show the cumulative effects to be strikingly positive, at least for bird and mammal richness.

Despite open questions about mechanisms, our results provide a new and exciting dimension in our understanding of global biodiversity patterns. Global fire regimes have admittedly shifted through time (i.e., tracking climatic shifts and human activity), yet the modern fire data used in our analyses appears to be reflective of past global fire activity that would have helped generate species richness patterns over prehistoric timescales (see paleo-fire comparison with Marlon et al., 2016 in SI). It should be noted, however, that our findings of fire as an apparent causal driver of species richness should not be taken to mean that ‘fire is good’ in any of these ecosystems. Species may be fire-sensitive if fire has prehistorically been relatively rare (e.g., hot and cold deserts, wet tropical forests, and mangroves) (He et al., 2019; McLauchlan et al., 2020). In these ecosystems fire is more of a modern threat than an important process to maintain, and recent fire activity in these systems is not a likely driver of richness. Even in ecosystems where fire has been a cyclical force over long periods, intentional deforestation fires and unusually severe events due to recent climate change may be quite different from natural fire regimes. Concern in these ecosystems is about maintaining desired frequencies, sizes, intensities and timing of fire events (Kelly & Brotons, 2017; Moritz et al., 2013). Higher resolution analyses of fire and productivity effects should eventually reveal how such relationships vary at the scale of individual biomes or ecoregions, in addition to where and how fire acts as a causal driver of biodiversity. Although species richness could certainly be affected by omitted variables that simply correlate with fire- or NPP-related patterns, it is not obvious what those variables would be. Productivity is widely seen as a dominant driver of broad-scale biodiversity, and we have accepted this causality as a given. Our goal has been to add insight by quantifying the under-appreciated effects that fire may have on terrestrial vertebrate richness patterns.

There has been substantial debate over the functional form of the relationships underpinning species richness patterns at different scales (Figure 1a) (Gillman et al., 2015; Whittaker et al., 2001), including those specifically for animals (Cusens et al., 2012). An advantage of our approach is the ability to remove the effects of other variables, in order to isolate a particular driver of interest. This feature is important because simple data plots may suggest a functional relationship that changes substantially after accounting for other influences. Although integrating additional predictor variables could alter future interpretations, our results (Figure 5) approximate a positive power-law relationship (i.e., linear scaling after log–log transformation); richness thus increases monotonically with higher productivity, but at a declining rate (i.e., the non-linear form in Figure 1a). This finding is consistent across taxa and appears to hold at the level of individual biomes (Figure S6). While positive relationships between productivity and richness agree with many biodiversity studies at broad scales (Cusens et al., 2012; Gillman et al., 2015; Whittaker et al., 2001), there are few accepted explanations for a power law form. However, an equation of state proposed recently as part of the Maximum Entropy Theory of Ecology (Harte et al., 2022), accurately predicts scaling relationships among productivity, biomass, species richness and abundance. Interestingly, a power law scaling also appears to hold for the positive relationship between terrestrial vertebrate richness and the fraction of productivity consumed by fire (Figure 6; Figure S7). Although this similarity does not necessarily indicate the same causal mechanism, it does suggest a role for fire as a facilitator of energy flows and cycling of resources, similar to temperature in the Metabolic Theory of Ecology (Allen et al., 2002; Ernest et al., 2003). Fire could thus be accelerating generation times and ecological filtering—and also resource cycling and availability, as captured by FCC—ultimately supporting greater potential for diversification and local species richness.

Anthropogenic climate change is a clear threat to Earth's biodiversity, and altered fire regimes are one of the ways that this threat will manifest itself (Bowman et al., 2009; Kelly et al., 2020; Moritz et al., 2012). Although this danger is real, our findings shed new light on the importance of maintaining fire's key role in terrestrial ecosystems, particularly for birds and mammals. Together, the interplay of plant productivity and the fire that consumes it are major drivers of global animal richness patterns, compelling us to more directly address the role of fire in frameworks explaining and protecting biodiversity. Given the surprisingly strong macro-scale relationships between fire and species richness, conservation of natural fire regimes may be as necessary as preserving habitat itself.

AUTHOR CONTRIBUTIONS

MAM, EB and BMB conceived the study. EB collected and processed the input data. BMB, EB and MAM designed the analyses, and BMB and EB performed the analyses. MAM, BMB and EB wrote and edited the manuscript.

ACKNOWLEDGEMENTS

We thank E. Newman for comments on an earlier draft. A portion of this work was conducted by M.A.M. as a Center Fellow at the National Center for Ecological Analysis and Synthesis, for which he is grateful (U.S. National Science Foundation EF-0553768). E.B.P. is a Serra Húnter Fellow, and he thanks the Serra Húnter program for its support. B.M.B. thanks the Canadian NSERC Discovery Grant Program (05488-2016) for its support.

FUNDING INFORMATION

National Center for Ecological Analysis and Synthesis, National Science Foundation, Grant/Award Number: EF-0553768; NSERC, Grant/Award Number: 05488-2016; Serra Hunter Program

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.14177.

DATA AVAILABILITY STATEMENT

All code and datasets used in analyses are available at https://doi.org/10.5281/zenodo.7453071.

ORCID

Max A. Moritz https://orcid.org/0000-0002-8995-8893
Enric Batllori https://orcid.org/0000-0002-2130-0489
Benjamin M. Bolker https://orcid.org/0000-0002-2127-0443

REFERENCES

Allen, A.P., Brown, J.H. & Gillooly, J.F. (2002) Global biodiversity, biochemical kinetics, and the energetic-equivalence rule. *Science*, 297, 1545–1548.

Barr, D.J., Levy, R., Scheepers, C. & Tily, H.J. (2013) Random effects structure for confirmatory hypothesis testing: keep it maximal. *Journal of Memory and Language*, 68, 255–278.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2015) Fitting linear mixed-effects models using lme4. *Journal of Statistical Software*, 67, 1–48.

Beale, C.M., Mustaphi, C.J.C., Morrison, T.A., Archibald, S., Anderson, T.M., Dobson, A.P. et al. (2018) Pyrodiversity interacts with rainfall to increase bird and mammal richness in African savannas. *Ecology Letters*, 21, 557–567.

Bolker, B.M. (2015) Linear and generalized linear mixed models. In: Fox, G.A., Negrete-Yankelevich, S. & Sosa, V.J. (Eds.) *Ecological* *statistics: contemporary theory and application*. New York, NY: Oxford University Press, pp. 309–334.

Bond, W.J. & Keeley, J.E. (2005) Fire as a global 'herbivore': the ecology and evolution of flammable ecosystems. *Trends in Ecology & Evolution*, 20, 387–394.

Bond, W.J. & Scott, A.C. (2010) Fire and the spread of flowering plants in the cretaceous. *New Phytologist*, 188, 1137–1150.

Bond, W.J., Woodward, F.I. & Midgley, G.F. (2005) The global distribution of ecosystems in a world without fire. *New Phytologist*, 165, 525–538.

Bowman, D.M.J.S., Balch, J.K., Artaxo, P., Bond, W.J., Carlson, J.M., Cochrane, M.A. et al. (2009) Fire in the earth system. *Science*, 324, 481–484.

Brooks, T.M., Mittermeier, R.A., Da Fonseca, G.A., Gerlach, J., Hoffmann, M., Lamoreux, J.F. et al. (2006) Global biodiversity conservation priorities. *Science*, 313, 58–61.

Carbone, L.M., Tavella, J., Pausas, J.G. & Aguilar, R. (2019) A global synthesis of fire effects on pollinators. *Global Ecology and Biogeography*, 28, 1487–1498.

Chen, Y., Randerson, J.T., Werf, G.R.V.D., Morton, D.C., Mu, M. & Kasibhatla, P.S. (2010) Nitrogen deposition in tropical forests from savanna and deforestation fires. *Global Change Biology*, 16, 2024–2038.

Chown, S.L. & Gaston, K.J. (2000) Areas, cradles and museums: the latitudinal gradient in species richness. *Trends in Ecology & Evolution*, 15, 311–315.

Cramer, M.D. & Verboom, G.A. (2017) Measures of biologically relevant environmental heterogeneity improve prediction of regional plant species richness. *Journal of Biogeography*, 44, 579–591.

Cusens, J., Wright, S.D., McBride, P.D. & Gillman, L.N. (2012) What is the form of the productivity–animal-species-richness relationship? A critical review and meta-analysis. *Ecology*, 93, 2241–2252.

Dushoff, J., Kain, M.P. & Bolker, B.M. (2019) I can see clearly now: reinterpreting statistical significance. *Methods in Ecology and Evolution*, 10, 756–759.

Ernest, S.K.M., Enquist, B.J., Brown, J.H., Charnov, E.L., Gillooly, J.F., Savage, V.M. et al. (2003) Thermodynamic and metabolic effects on the scaling of production and population energy use. *Ecology Letters*, 6, 990–995.

Field, R., Hawkins, B.A., Cornell, H.V., Currie, D.J., Diniz-Filho, J.A.F., Guégan, J.-F. et al. (2009) Spatial species-richness gradients across scales: a meta-analysis. *Journal of Biogeography*, 36, 132–147.

Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, 405, 220–227.

Giglio, L., Randerson, J.T. & van der Werf, G.R. (2013) Analysis of daily, monthly, and annual burned area using the fourth-generation global fire emissions database (GFED4). *Journal of Geophysical Research: Biogeosciences*, 118, 317–328.

Gillman, L.N., Wright, S.D., Cusens, J., McBride, P.D., Malhi, Y. & Whittaker, R.J. (2015) Latitude, productivity and species richness. *Global Ecology and Biogeography*, 24, 107–117.

Harte, J., Brush, M., Newman, E.A. & Umemura, K. (2022) An equation of state unifies diversity, productivity, abundance and biomass. *Communications Biology*, 5(1), 1–6.

He, T., Lamont, B.B. & Pausas, J.G. (2019) Fire as a key driver of Earth's biodiversity. *Biological Reviews*, 94, 1983–2010.

Hoekstra, J.M., Boucher, T.M., Ricketts, T.H. & Roberts, C. (2005) Confronting a biome crisis: global disparities of habitat loss and protection. *Ecology Letters*, 8, 23–29.

Huston, M.A. (2014) Disturbance, productivity, and species diversity: empiricism vs. logic in ecological theory. *Ecology*, 95, 2382–2396.

Jaeger, B. (2017) r2glmm: computes R squared for mixed (multilevel) models.

Jaeger, B.C., Edwards, L.J., Das, K. & Sen, P.K. (2017) An R2 statistic for fixed effects in the generalized linear mixed model. *Journal of Applied Statistics*, 44, 1086–1105.

Jaeger, B.C., Edwards, L.J. & Gurka, M.J. (2019) An R2 statistic for covariance model selection in the linear mixed model. *Journal of Applied Statistics*, 46, 164–184.

Jenkins, C.N., Pimm, S.L. & Joppa, L.N. (2013) Global patterns of terrestrial vertebrate diversity and conservation. *PNAS*, 110, E2602–E2610.

Jones, G.M. & Tingley, M.W. (2022) Pyrodiversity and biodiversity: a history, synthesis, and outlook. *Diversity and Distributions*, 28(3), 386–403.

Keeley, J.E., Pausas, J.G., Rundel, P.W., Bond, W.J. & Bradstock, R.A. (2011) Fire as an evolutionary pressure shaping plant traits. *Trends in Plant Science*, 16, 406–411.

Kelly, L.T. & Brotons, L. (2017) Using fire to promote biodiversity. *Science*, 355, 1264–1265.

Kelly, L.T., Giljohann, K.M., Duane, A., Aquilué, N., Archibald, S., Batllori, E. et al. (2020) Fire and biodiversity in the Anthropocene. *Science*, 370, eabb0355. Available from: https://doi.org/10.1126/science.abb0355

Krawchuk, M.A. & Moritz, M.A. (2011) Constraints on global fire activity vary across a resource gradient. *Ecology*, 92, 121–132.

Krawchuk, M.A. & Moritz, M.A. (2014) Burning issues: statistical analyses of global fire data to inform assessments of environmental change. *Environmetrics*, 25, 472–481.

Kreft, H., Jetz, W., Mutke, J., Kier, G. & Barthlott, W. (2008) Global diversity of Island floras from a macroecological perspective. *Ecology Letters*, 11, 116–127.

Lamont, B.B. & He, T. (2017) Fire-proneness as a prerequisite for the evolution of fire-adapted traits. *Trends in Plant Science*, 22, 278–288.

Lindenmayer, D.B., Blanchard, W., MacGregor, C., Barton, P., Banks, S.C., Crane, M. et al. (2016) Temporal trends in mammal responses to fire reveals the complex effects of fire regime attributes. *Ecological Applications*, 26, 557–573.

Marlon, J.R., Kelly, R., Daniau, A.-L., Vannière, B., Power, M.J., Bartlein, P. et al. (2016) Reconstructions of biomass burning from sediment-charcoal records to improve data–model comparisons. *Biogeosciences*, 13, 3225–3244. Available from: https://doi.org/10.5194/bg-13-3225-2016

Matuschek, H., Kliegl, R., Vasishth, S., Baayen, H. & Bates, D. (2017) Balancing type I error and power in linear mixed models. *Journal of Memory and Language*, 94, 305–315.

McGill, B.J., Dornelas, M., Gotelli, N.J. & Magurran, A.E. (2015) Fifteen forms of biodiversity trend in the Anthropocene. *Trends in Ecology & Evolution*, 30, 104–113.

McLauchlan, K.K., Higuera, P.E., Miesel, J., Rogers, B.M., Schweitzer, J., Shuman, J.K. et al. (2020) Fire as a fundamental ecological process: research advances and frontiers. *Journal of Ecology*, 108, 2047–2069.

Moritz, M.A., Hurteau, M.D., Suding, K.N. & D'Antonio, C.M. (2013) Bounded ranges of variation as a framework for future conservation and fire management. *Annals of the New York Academy of Sciences*, 1286(1), 92–107.

Moritz, M.A., Parisien, M.-A., Batllori, E., Krawchuk, M.A., Dorn, J.V., Ganz, D.J. et al. (2012) Climate change and disruptions to global fire activity. *Ecosphere*, 3, art49.

Mucina, L. & Wardell-Johnson, G.W. (2011) Landscape age and soil fertility, climatic stability, and fire regime predictability: beyond the OCBIL framework. *Plant and Soil*, 341(1), 1–23.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*, 403, 853–858.

Nimmo, D.G., Avitabile, S., Banks, S.C., Bird, R.B., Callister, K., Clarke, M.F. et al. (2019) Animal movements in fire-prone landscapes. *Biological Reviews*, 94, 981–998.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C. et al. (2001) Terrestrial ecoregions of the world: a new map of life on earth: a new global map of terrestrial ecoregions provides an innovative tool for conserving biodiversity. *Bioscience*, 51, 933–938.

Pausas, J.G. (2015) Bark thickness and fire regime. *Functional Ecology*, 29, 315–327.

Pausas, J.G. & Parr, C.L. (2018) Towards an understanding of the evolutionary role of fire in animals. *Evolutionary Ecology*, 32, 113–125.

Pausas, J.G. & Ribeiro, E. (2017) Fire and plant diversity at the global scale. *Global Ecology and Biogeography*, 26, 889–897.

Polis, G.A. & Strong, D.R. (1996) Food web complexity and community dynamics. *The American Naturalist*, 147, 813–846.

Schielzeth, H. (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*, 1, 103–113.

Schluter, D. & Pennell, M.W. (2017) Speciation gradients and the distribution of biodiversity. *Nature*, 546, 48–55.

Scott, A.C. (2000) The pre-quaternary history of fire. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 164, 281–329.

Šímová, I. & Storch, D. (2017) The enigma of terrestrial primary productivity: measurements, models, scales and the diversity–productivity relationship. *Ecography*, 40, 239–252.

Stein, A., Gerstner, K. & Kreft, H. (2014) Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology Letters*, 17, 866–880.

Taylor, R.S., Watson, S.J., Nimmo, D.G., Kelly, L.T., Bennett, A.F. & Clarke, M.F. (2012) Landscape-scale effects of fire on bird assemblages: does pyrodiversity beget biodiversity? *Diversity and Distributions*, 18(5), 519–529.

Tingley, M.W., Ruiz-Gutiérrez, V., Wilkerson, R.L., Howell, C.A. & Siegel, R.B. (2016) Pyrodiversity promotes avian diversity over the decade following forest fire. *Proceedings of the Royal Society B: Biological Sciences*, 283(1840), 20161703.

Udy, K., Fritsch, M., Meyer, K.M., Grass, I., Hanß, S., Hartig, F. et al. (2021) Environmental heterogeneity predicts global species richness patterns better than area. *Global Ecology and Biogeography*, 30, 842–851.

van der Werf, G.R., Randerson, J.T., Giglio, L., van Leeuwen, T.T., Chen, Y., Rogers, B.M. et al. (2017) Global fire emissions estimates during 1997–2016. *Earth System Science Data*, 9, 697–720.

Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general, hierarchical theory of species diversity. *Journal of Biogeography*, 28, 453–470.

Wiens, J.J. & Donoghue, M.J. (2004) Historical biogeography, ecology and species richness. *Trends in Ecology & Evolution*, 19, 639–644.

Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, 34, 273–309.

Wood, S. & Scheipl, F. (2014) gamm4: generalized additive mixed models using mgcv and lme4. R Package Version 0.2-3.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Moritz, M.A., Batllori, E. & Bolker, B.M. (2023) The role of fire in terrestrial vertebrate richness patterns. *Ecology Letters*, 26, 563–574. Available from: https://doi.org/10.1111/ele.14177