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LETTER

Projected climatic changes lead to biome changes in areas of previously constant biome

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Abstract

Aim: Recent studies in southern Africa identified past biome stability as an important predictor of biodiversity. We aimed to assess the extent to which past biome stability predicts present global biodiversity patterns, and the extent to which projected climatic changes may lead to eventual biome changes in areas with constant past biome.

Location: Global.

Taxon: Spermatophyta; terrestrial vertebrates.

Methods: Biome constancy was assessed and mapped using results from 89 dynamic global vegetation model simulations, driven by outputs of palaeoclimate experiments spanning the past 140 ka. We tested the hypothesis that terrestrial vertebrate diversity is predicted by biome constancy. We also simulated potential future vegetation, and hence potential future biome patterns, and quantified and mapped the extent of projected eventual future biome change in areas of past constant biome.

Results: Approximately 11% of global ice-free land had a constant biome since 140 ka. Apart from areas of constant Desert, many areas with constant biome support high species diversity. All terrestrial vertebrate groups show a strong positive relationship between biome constancy and vertebrate diversity in areas of greater diversity, but no relationship in less diverse areas. Climatic change projected by 2100 commits 46%–66% of global ice-free land, and 34%–52% of areas of past constant biome (excluding areas of constant Desert) to eventual biome change.

Main conclusions: Past biome stability strongly predicts vertebrate diversity in areas of higher diversity. Future climatic changes will lead to biome changes in many areas of past constant biome, with profound implications for biodiversity conservation. Some projected biome changes will result in substantial reductions in biospheric carbon sequestration and other ecosystem services.

KEYWORDS
amphibians, biodiversity, biome stability, birds, ecosystem services, endemic bird areas, HadCM3, LPJ-GUESS, mammals, reptiles

1 | INTRODUCTION

Global biodiversity patterns have long fascinated biogeographers, leading to the proposal of a range of hypotheses as to the factors underlying their origins (Gaston, 2000). Of particular interest are those regions that are centres of biodiversity for one or more taxonomic groups, so-called biodiversity hotspots (Myers et al., 2000), especially those that are characterised by the co-occurrence of range-restricted or endemic species (Stattersfield et al., 1998). Hypotheses advanced to account for these patterns fall into two broad categories, the first focused on the present environment, and especially its ability to support biological productivity, and the second on historical factors, especially past environmental changes. A recent study focusing upon global patterns in centennial climatic stability since the last glacial maximum (LGM), and contrasting this with projected future climatic changes, showed a strong association between contemporary global species-richness patterns and measures of climatic stability during centuries of rapid global climatic change since the LGM (Brown et al., 2020). This study also concluded that projected 21st century climatic changes will likely disproportionately affect areas of the greatest species richness.

Disentangling the influences of present and historical factors, however, is difficult because factors in both categories, including measures of past climatic stability (Brown et al., 2020; Huntley et al., 2016), as well as diversity patterns, tend to be correlated with latitude. A recent study of plant diversity in the Cape Floristic Region, however, examined a longitudinal diversity gradient, enabling influences of present and historical factors to be distinguished (Colville et al., 2020). The historical factors examined were the degrees of climatic and of biome stability over the past 140,000 years, that is, the period since the penultimate glacial maximum, spanning the last glacial–interglacial cycle, and including last glacial millennial climatic fluctuations. These factors were contrasted with aspects of the present environment, including topographic diversity, as well as those associated with ecological opportunity, namely rainfall seasonality and productivity. Of the factors examined, biome stability was the strongest predictor of present regional diversity patterns, whereas ecological productivity had only a marginal influence. These results parallel those of a study of endemic birds of southern Africa that concluded the degree of biome persistence over the past 140,000 years more strongly predicted present patterns of endemic species-richness than did the degree of climatic stability (Huntley et al., 2016).

The strong relationship of present diversity to past biome stability demonstrated by these studies of southern Africa should not be surprising. Different biomes, being defined principally by the growth form, phenology and climatic tolerances of their dominant plants, offer distinctive suites of niches both for the other organisms that they support and for the regeneration of the dominants. Biome stability thus results in a stable suite of niches that, in turn, is likely to promote increasing specialisation, and hence speciation, of the organisms found in that biome. Biome stability is also likely to reduce the extinction rates of species associated with the biome. Furthermore, while biome boundaries are often diffuse when viewed at the landscape or regional scales, as are most ecological boundaries, at whatever scale biome boundaries are viewed they typically are associated with a strong turnover of available niche characteristics because biomes are defined by vegetation structure rather than by the taxonomic criteria generally used to define other ecological units.

SIGNIFICANCE STATEMENT

Using global biome patterns inferred from simulations made using the LPJ-GUESS dynamic global vegetation model, we show that a substantial fraction of areas that are simulated to have supported the same biome throughout the last glacial-interglacial cycle are projected to experience biome change as a consequence of 21st century climatic changes. We further show that, with the exception of some desert areas, areas of the highest past biome constancy correspond to areas of the highest terrestrial vertebrate diversity. As a result, the projected biome changes are likely to have disproportionately large negative impacts upon global biodiversity.

The stronger relationship of present diversity to past biome, as opposed to climatic, stability seen in the studies of southern Africa also should be no surprise. Both in southern Africa and globally the range of climatic conditions spanned by different biomes varies considerably. Thus, a given magnitude of climatic change may exceed the range of conditions spanned by one biome but be much less than the range spanned by another. While such a climatic change would be expected to lead to shifts in geographical location of both biomes, the area occupied by the more climatically restricted biome after the shift would not overlap its previous area, whereas a large part of the area initially occupied by the less climatically restricted biome would continue to support that biome, and hence exhibit biome stability (see Figure S1). Thus, a given degree of climatic instability is likely to have non-uniform impacts on species richness in different biomes, whereas a given degree of biome instability is likely to have a more uniform impact. Furthermore, as Huntley et al. (2016) illustrated, the differing climatic amplitudes of biomes result in a lack of concurrence between climatic and biome stability patterns.

Given these considerations, and evidence of the regional importance of biome stability for the development of high species diversity, we sought to test the hypothesis that such a relationship between biome stability and species diversity applies globally. In order to make this test, we assessed the degree of biome constancy globally using simulated biome maps for the past 140,000 years (Allen et al., 2020). We then analysed the relationship between biome constancy and species diversity for the four major terrestrial vertebrate groups, and examined biome constancy of those areas forming the global network of Endemic Bird Areas (EBAs, Stattersfield et al., 1998). We also simulated potential future global biome patterns, and assessed the extent to which future climatic changes will result in eventual biome change in areas of past biome stability. Such potential future biome changes in areas of past biome stability, many of which also are areas of high biodiversity, have profound implications for our ability to conserve global biodiversity in the face of projected climatic changes.

2 | MATERIALS AND METHODS

An internally consistent set of 93 climate experiments was made to simulate past, present and potential future climatic conditions. These experiments used HadCM3B-M2.1aD (Valdes et al., 2017), a version of the HadCM3 fully coupled atmosphere–ocean general circulation model coupled to the TRIFFID (Cox, 2001) dynamic vegetation model. The design of the palaeoclimate (the last 140 ka) and present (pre-industrial) experiments has been described elsewhere (Allen et al., 2020; Davies-Barnard et al., 2017; Singarayer & Valdes, 2010). Potential future simulations were driven using changing atmospheric greenhouse gas concentrations projected according to the RCP 4.5 and RCP 8.5 representative concentration pathways (van Vuuren et al., 2011), with land use, ice sheets and land–ocean configuration unchanged from the pre-industrial simulation, and excluding changes in aerosols as these are not included in the model version used. Mean climatic conditions for the 31-year periods 2035–2065 and 2085–2115, that is centred on 2050 and 2100, were simulated and used to drive vegetation simulations. Anomalies relative to the pre-industrial experiment were computed and interpolated to a half-degree grid as in our previous work (Allen et al., 2020) and input to the LPJ-GUESS dynamic vegetation model (Smith et al., 2001, 2014) used to simulate the potential vegetation in equilibrium with the climate simulated for each time slice.

LPJ-GUESS simulations used a consistent set of plant functional types (PFTs), comprising 11 tree, 7 shrub and 2 grass PFTs, details of which have been given previously (Allen et al., 2020). Biomes were inferred using a previously developed rule-based approach (Allen et al., 2020) applied to the carbon mass and leaf area index of each PFT simulated by LPJ-GUESS. Palaeovegetation and pre-industrial simulations used palaeoclimatic conditions, atmospheric carbon dioxide concentration ($[CO_2]_{atm}$), and orbital obliquity appropriate to the time slice (Allen et al., 2020). Potential future vegetation simulations used the future climatic conditions and mean mid-year $[CO_2]_{atm}$ projected for 2035–2065 and 2085–2115 for the RCP 4.5 (485 ppmv and 538 ppmv respectively) and RCP 8.5 (545 and 937 ppmv respectively) concentration pathways. Biome constancy was computed for each half-degree grid cell as the percentage of the 89 time slices, 140 ka to present, for which the grid cell was inferred to belong to the potential present biome. The number of distinct biomes inferred for each grid cell across the 89 time slices was also counted.

The magnitude of committed eventual biome changes projected for the future time slices and concentration pathways was assessed using an approach that takes into account both changes in overall vegetation structure (e.g. grassland to forest) and in the major climatic zone (e.g. boreal to temperate; Allen et al., 2020; see Appendix S1). Note that this approach gives a score of zero where the biome is changed but the climatic zone and vegetation structure are unchanged, for example where Tropical Raingreen Forest replaces Tropical Evergreen Forest. Thus, even where the change score is zero, the implications for diversity and ecosystem services may be substantial; on the change maps that we present such areas hence are distinguished from those where the biome is unchanged.

Ice-free land areas of grid cells, used to compute biome extents, extents of their constant areas and the fraction of those constant areas projected potentially to change biome in future, were estimated using a previously described approach (Allen et al., 2020). Eustatic sea level (ESL) was estimated as a function of global ice volume, as reflected by the marine $\delta^{18}O$ record (Martinson et al., 1987), and of a long-term relative sea level record from the Red Sea (Grant et al., 2012), using a model fitted to ESL data for 22 ka to present (Lambeck et al., 2014). The extent of ice cover was inferred using results from the ICE-6G model (Peltier et al., 2015).

The relationship between species richness and past constancy of the current biome was quantified for the four taxonomic groups of terrestrial vertebrates (mammals, birds, reptiles and amphibians) using quantile linear regressions and quantile generalised additive models. Global gridded species richness values for an equal-area grid (Howard et al., 2020) were interpolated to the half-degree grid used for our biome simulations. For all grid cells that are currently ice-free land, quantile models were fitted for quantiles from $\tau = 0.1$ to 0.9, quantile linear regressions being fitted using the 'rq' function, with the Barrodale and Roberts algorithm, in the R package 'quantreg' (Koenker, 2020) and quantile generalised additive models being fitted using the R package 'qgam' (Fasiolo, 2020) with adaptive regression splines and a smoothing parameter of $k = 20$.

3 | RESULTS

Biome stability since 140 ka was low over most of the present global land surface (Figure 1a), only 11.31% of the current ice-free land area having the same biome inferred for all 89 time slices (Table 1). Furthermore, for about half of the land area with a constant biome (5.79%) that biome was Desert. Over large areas not only was the biome not constant, but it was simulated to have changed multiple times, the median number of different biomes inferred for each individual grid cell being 4 (Figure 1b). Although 11 of the 21 biomes had constantly occupied some fraction of their present area, that fraction exceeded 1% in only seven cases (Desert, Tropical Grassland, Tropical Raingreen Forest, Tropical Evergreen Forest, Temperate Shrubland, Temperate Broad-leaved Evergreen Forest and Steppe), and in only three cases did the constant fraction exceed 10% of the present area (Desert, Tropical Evergreen Forest and Temperate Broad-leaved Evergreen Forest; Table 1).

The distribution and extents of the inferred potential present biomes (Figure 1c) match well with previously published biome

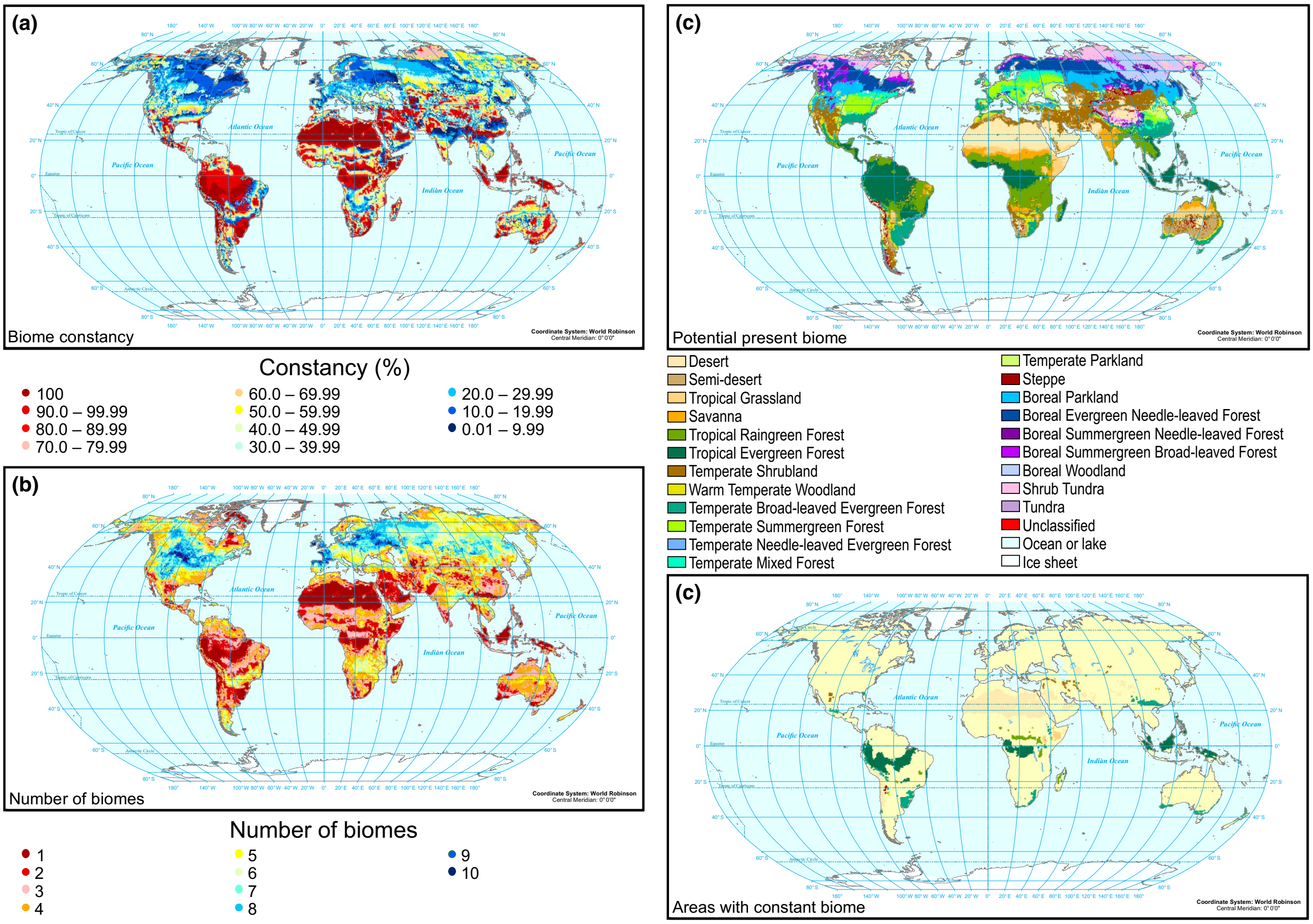


FIGURE 1 Biomes, biome constancy and number of biomes. (a) Percentage of the 89 time slices for which biomes were simulated, 140 ka to present, for which the inferred biome was the same as that inferred for the present, that is constancy of the present biome. (b) Number of distinct biomes inferred for each individual grid cell across the 89 time slices. (c) Potential present biome distributions and extents, as inferred from LPJ-GUESS simulation. (d) Areas where the present biome is also simulated for all 88 past time slices, 1–140 ka

maps, whether based upon global vegetation simulations (Prentice et al., 2011) or inferred from remaining stands of natural and semi-natural vegetation (Olson et al., 2001). There are also broad patterns of concurrence, with the exception of areas that have constantly been Desert, between areas of high biome constancy, principally in tropical latitudes (Figure 1a,d), and areas of high diversity of one or more of the terrestrial vertebrate groups (Figure 2). Many areas of biome constancy, especially in the tropics and southern hemisphere, correspond to areas identified as overall biodiversity 'hotspots' (Myers et al., 2000). For example the proportion of half-degree grid cells, at least part of which lies within an area identified as an EBA (Stattersfield et al., 1998), characterised by the co-occurrence of range-restricted and/or endemic bird species (Figure S2), and that have had a constant biome (16.84%), is almost double the global proportion of grid cells with a constant biome (8.70%). Similarly, the mean percentage constancy of grid cells coinciding with EBAs (64.24%) is about a third higher than the overall mean percentage constancy of grid cells (48.36%). Quantile models of the relationship between species richness of each of the four terrestrial vertebrate groups and percentage biome constancy show similar results for all four groups. Both quantile linear regressions and quantile generalised additive models showed species richness is not related to past constancy of the current biome for grid cells of low species richness, whereas for grid cells of high species richness there is a strong positive relationship (Figure 3; Figure S3; Table S1). The generalised additive models also showed this relationship to be nonlinear, species richness at $\tau = 0.9$ increasing more rapidly at higher biome constancies, whereas at $\tau = 0.5$ and 0.2 there is little or no relationship at low biome constancies, although often with a peak at around 90% constancy followed by a downturn at the highest constancies that likely reflects the generally low species richness but high biome constancy of the subtropical deserts.

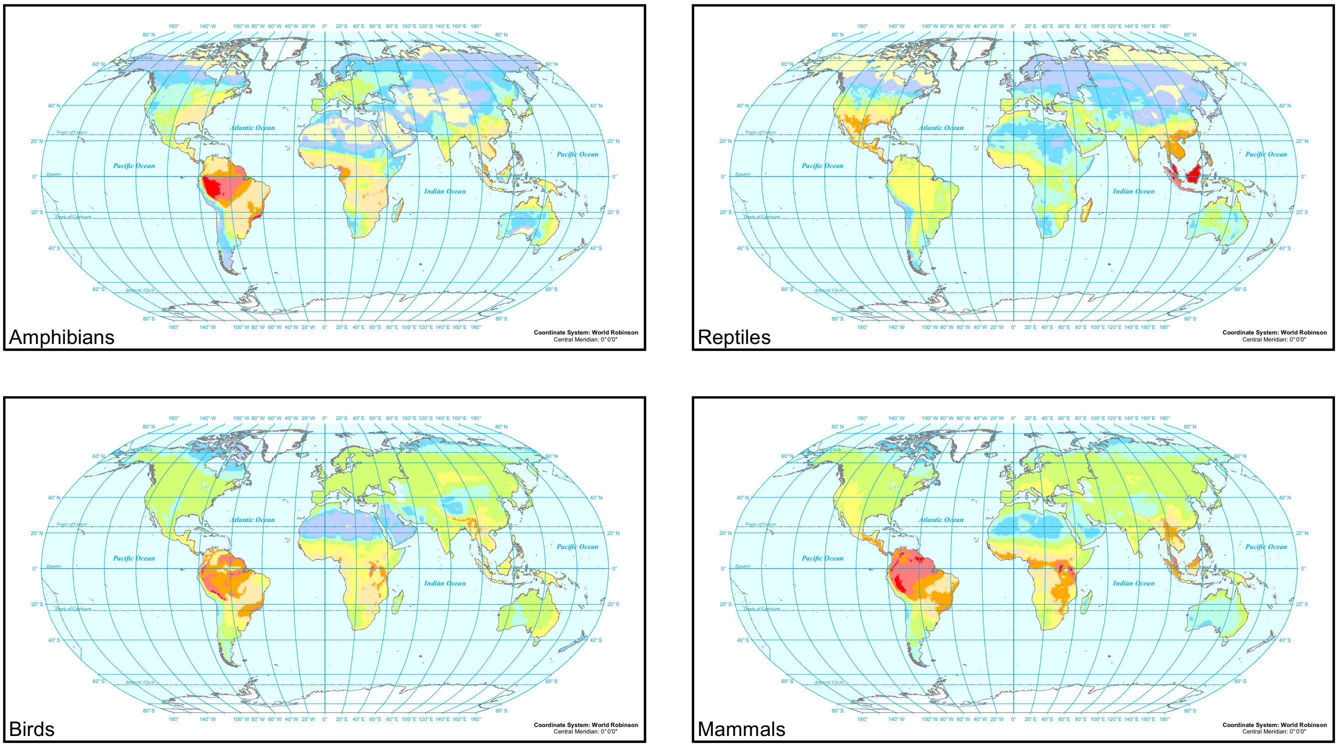
The potential future biome is committed to an eventual change in 20.17% of previously constant areas under the climate projected for 2100 for the RCP 4.5 representative concentration pathway (van Vuuren et al., 2011; Table 2; Figure 4a), and in 33.14% of those areas for RCP 8.5 (Figure 4b; see Figure S4 for committed biome changes for 2050 climates in areas of past biome constancy; Figure

TABLE 1 Biome extents and areas of constant biome occurrence 0–140 ka

Biome	Present biome area (Mm^2)	Area of constant occurrence (Mm^2)	Constant area as fraction of global ice-free land area (%)	Constant area as fraction of present biome area (%)
Desert	15.540	7.533	5.79	48.5
Semi-desert	4.910	0.0196	0.0151	0.400
Tropical Grassland	4.586	0.271	0.208	5.91
Savanna	5.701	0.0474	0.0364	0.832
Tropical Raingreen Forest	14.009	0.451	0.347	3.22
Tropical Evergreen Forest	15.715	4.611	3.54	29.3
Temperate Shrubland	13.432	0.250	0.192	1.86
Warm Temperate Woodland	2.595	0.0135	0.0103	0.518
Temperate Broad-leaved Evergreen Forest	7.946	1.495	1.15	18.8
Temperate Summergreen Forest	5.438	0.00522	0.00401	0.0960
Temperate Needle-leaved Evergreen Forest	0.448	0.0	0.0	0.0
Temperate Mixed Forest	3.851	0.0	0.0	0.0
Temperate Parkland	3.608	0.0	0.0	0.0
Steppe	1.897	0.0197	0.0152	1.04
Boreal Parkland	6.626	0.0	0.0	0.0
Boreal Evergreen Needle-leaved Forest	9.052	0.0	0.0	0.0
Boreal Summergreen Needle-leaved Forest	0.461	0.0	0.0	0.0
Boreal Summergreen Broad-leaved Forest	3.262	0.0	0.0	0.0
Boreal Woodland	4.023	0.0	0.0	0.0
Shrub Tundra	6.155	0.0	0.0	0.0
Tundra	0.869	0.0	0.0	0.0
Unclassified	0.0	0.0	0.0	–
Global total	130.122	14.716	11.31	–

S5 summarises the extent of commitments to eventual change under each of the four future climate scenarios examined). When previously constant areas of the Desert biome are excluded, the global proportions of previously constant areas committed to eventual biome change increase to 33.62% (RCP 4.5) and 52.38% (RCP 8.5) for the climates projected for 2100. Even more strikingly, when previously constant areas that today have terrestrial vertebrate species richness values in the top 10% for one of the four groups considered, the proportions committed to eventual change are substantially greater, ranging from 46.80% (reptiles) to 60.05% (birds) under the climate projected for 2100 for RCP 8.5 (Table S2). Although the entirety of the previously constant areas of Savanna, Temperate Summergreen Forest and Steppe are committed to eventual change already by 2050 under both RCP scenarios (Table 2), these are biomes with only small fractions of the constant area and generally do not coincide with areas of present high biodiversity. Of much greater impact in terms of potential biodiversity losses are the substantial fractions of the previously constant areas of Tropical Evergreen Forest (29.76%—RCP 4.5; 43.83%—RCP 8.5) and Temperate Broad-leaved Evergreen Forest (44.17%—RCP 4.5; 79.20%—RCP 8.5) committed to an eventual biome change under the climates projected for 2100 (Table 2). These biomes both have relatively large fractions of their present area that have been constant since 140 ka (Table 1), and that also have high present vertebrate diversity (Figure 2). Projected future climatic changes resulting in conditions within these previously constant areas that no longer support the persistence of these biomes are thus both unprecedented over the past 140 ka and likely to result in substantial biodiversity losses.

Projected future climatic conditions will lead to eventual biome replacement over an even greater proportion of the entire present global ice-free land area, ranging from 45.58% by 2050 under RCP 4.5 to 66.08% by 2100 under RCP 8.5, the other two scenarios both giving eventual biome replacement over more than half the global ice-free land area (51.73% for RCP 4.5 by 2100 and 52.34% for RCP 8.5 by 2050). Areas of high present biodiversity are not quite so badly impacted, but nonetheless between 38.18% (RPC 4.5) and



Legend

	●	●	●	●	●	●	●	●	●	●
Amphibians	0	1–2	3–5	6–10	11–15	16–25	26–50	51–75	76–100	101–135
Reptiles	0	1–2	3–5	6–10	11–15	16–30	31–40	41–60	61–80	81–101
Birds	0	1–25	26–50	51–100	101–200	201–300	301–400	401–500	501–600	601–796
Mammals	0	1–5	6–15	16–30	31–60	61–90	91–120	121–150	151–180	181–220

FIGURE 2 Terrestrial vertebrate diversity. Spatial patterns in the number of species recorded for each of the four terrestrial vertebrate groups on land areas, excluding Antarctica. (Maps drawn using half-degree grid-cell values interpolated from values for an equal area grid as presented by Howard et al., 2020)

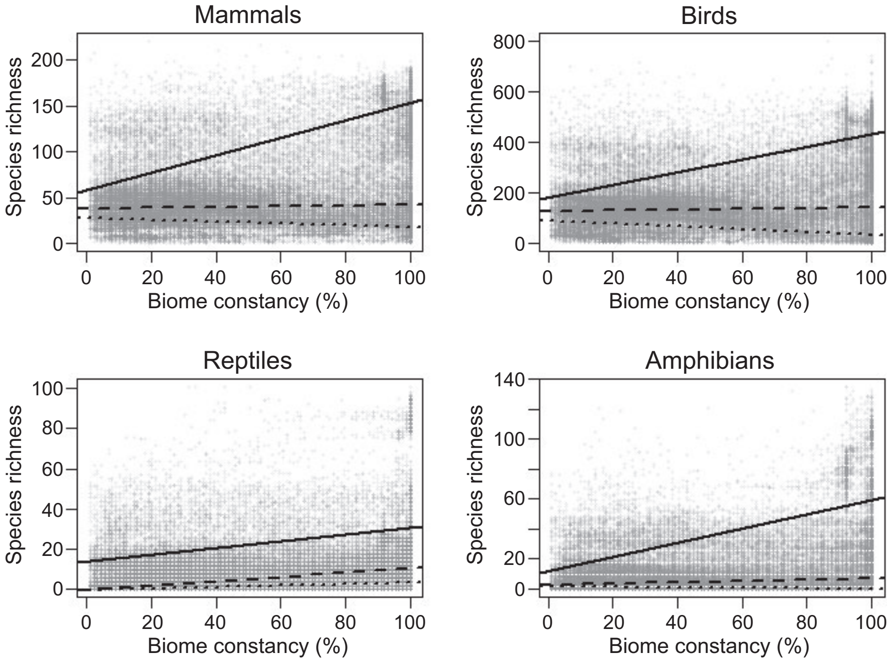
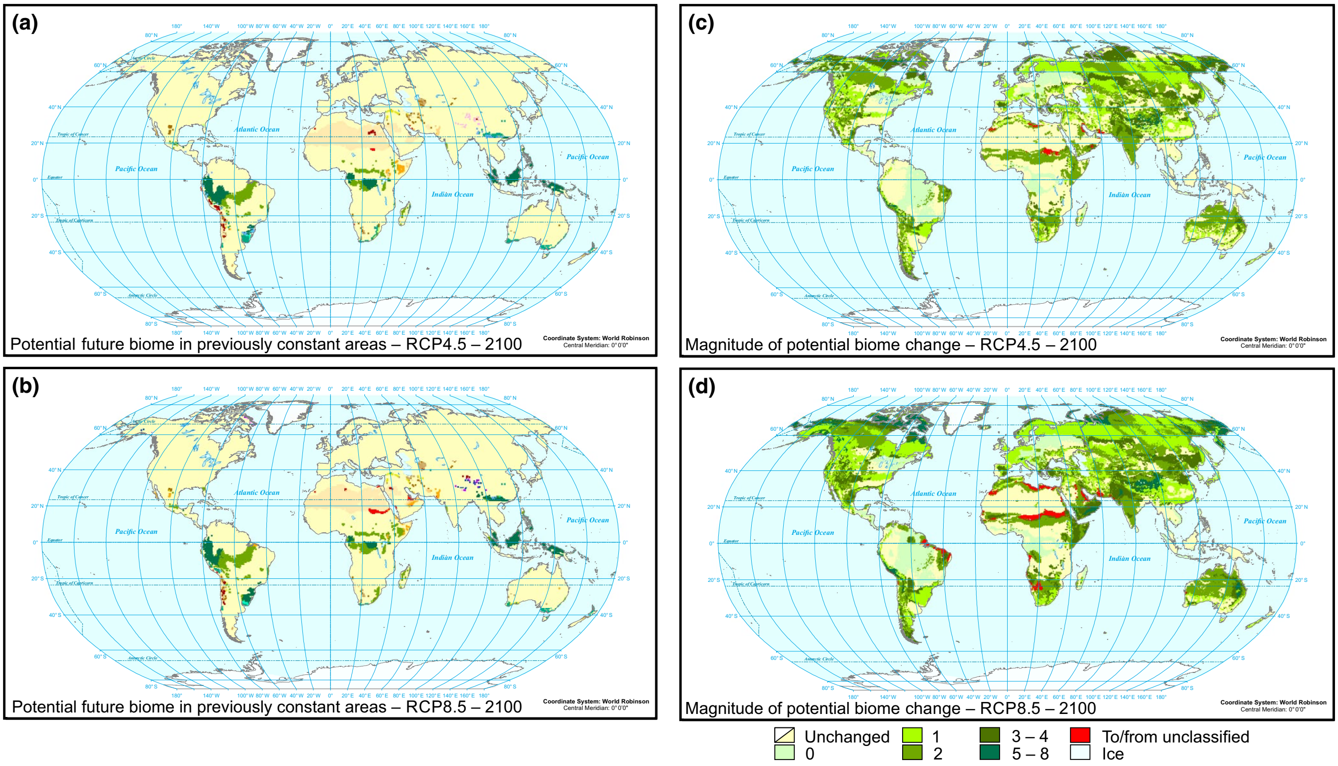


FIGURE 3 Quantile regressions of species richness on biome constancy. The relationship between total species richness and constancy of the present-day biome since 140 ka for four taxonomic groups of terrestrial vertebrates. Each symbol represents a 0.5° × 0.5° grid cell. Lines show fitted linear quantile regressions for τ = 0.2 (i.e. the 20th percentile, dotted), 0.5 (i.e. the median, dashed) and 0.9 (i.e. the 90th percentile, solid) quantiles. (see Table S1 for slopes of these relationships, as well as for those fitted for τ = 0.1, 0.3, 0.4, 0.6, 0.7 and 0.8)

TABLE 2 Projected future climatic change impacts on areas of past constant biome occurrence

	A				B			
	RCP 4.5		RCP 8.5		RCP 4.5		RCP 8.5	
Biome	**2050**	**2100**	**2050**	**2100**	**2050**	**2100**	**2050**	**2100**
Desert	7.13	7.35	10.07	14.80	26.01	18.65	23.68	22.86
Semi-desert	0.0	41.14	27.90	54.52	0.0	0.27	0.17	0.22
Tropical Grassland	49.81	68.68	84.12	99.999	6.54	6.27	7.12	5.56
Savanna	100.0	100.0	100.0	100.0	2.30	1.60	1.48	0.97
Tropical Raingreen Forest	5.03E-4	5.03E-4	5.03E-4	5.03E-4	1.10E-4	7.65E-5	7.08E-5	4.65E-5
Tropical Evergreen Forest	18.24	29.76	29.38	43.83	40.72	46.23	42.28	41.44
Temperate Shrubland	36.85	45.40	44.65	76.02	4.46	3.82	3.48	3.89
Warm Temperate Woodland	79.59	100.0	100.0	100.0	0.52	0.45	0.42	0.28
Temperate Broad-leaved Evergreen Forest	25.24	43.43	44.17	79.20	18.26	21.87	20.60	24.27
Temperate Summergreen Forest	100.0	100.0	100.0	100.0	0.25	0.18	0.16	0.11
Steppe	100.0	100.0	100.0	100.0	0.96	0.66	0.62	0.40
Global total	14.04	20.17	21.78	33.14	—	—	—	—

Note: A—Fraction of constant area committed to eventual change to a different biome (%). B—Fractional contribution to the global total of formerly constant areas committed to eventual change to a different biome (%).



Potential future biome in previously constant areas – RCP4.5 – 2100

Potential future biome in previously constant areas – RCP8.5 – 2100

Magnitude of potential biome change – RCP4.5 – 2100

Magnitude of potential biome change – RCP8.5 – 2100

FIGURE 4 Committed eventual future biome changes. Committed eventual future biomes in areas of biome constancy 140 ka to present, under the climate simulated for 2100: (a) for RCP 4.5; and (b) for RCP 8.5. (see Figure 1 for legend). Global extents and magnitudes of committed eventual biome changes for the climates simulated for 2100: (c) for RCP 4.5; and (d) for RCP 8.5. (see Supporting Information for details of how magnitudes of biome change were calculated)

54.03% (RPC 8.5) of the overall area of grid cells coinciding with EBAs is projected by 2100 to experience climatic conditions that will lead to eventual biome replacement.

The magnitude of projected biome change, assessed in terms of change in vegetation structure and/or in the major climatic zone (Allen et al., 2020; see Appendix S1), varies spatially, with higher magnitudes generally either at higher latitudes or associated with present ecotonal zones, for example the southern margin of the Sahara (Figure 4c,d, see also Figure S6). When potential future biome patterns (Figures S7 and S8) are compared with the present potential biome pattern (Figure 1c) then a number of overall features are apparent. On the northern hemisphere continents, there is a general northward shift of biomes, with an associated contraction of the treeless biomes that today characterise Arctic regions. There is a substantial expansion of the area of Tropical Raingreen Forest, in sub-Saharan Africa and South America largely at the expense of Tropical Evergreen Forest, but elsewhere, notably in the Indian subcontinent, at the expense of Savanna. Increasing numbers of grid cells have vegetation that does not correspond to any of the 21 biomes inferred for the present. Even for RCP4.5 at 2050, the extent of Unclassified areas (0.272% of global ice-free land area), although still very small, is an order of magnitude greater than the maximum for the period since 140 ka (0.026% at 126 ka, Allen et al., 2020); for RCP8.5 at 2100, this has increased to 1.83%. Furthermore, in contrast to the past 140 ka, during which time no systematic pattern of distribution of Unclassified grid cells was observed (Allen et al., 2020), although some future Unclassified grid cells are associated with other biomes, most are associated with the present margins of the Sahara and of other Desert areas, implying the potential future development in such areas of a no-analogue biome. Strikingly, there is no general correspondence between these areas of potential no-analogue biome and (the more extensive) areas projected in future to have 'novel climates' (Williams et al., 2007), a result that parallels that reported by Reu et al. (2014), albeit that their areas of no-analogue vegetation do not correspond to the areas of the potential future no-analogue biome. There is, however, some concurrence between areas with a higher magnitude of projected eventual biome change (Figure 4c,d; Figure S6) and areas of 'disappearing climates' (Williams et al., 2007).

4 | DISCUSSION AND CONCLUSIONS

The concentration of a substantial proportion of global species diversity in limited areas, the so-called 'hotspots' (Myers et al., 2000), represents both a virtue and a problem from the point of view of those striving to conserve global biodiversity. On the positive side, conservation efforts focused upon these relatively limited parts of the global land area can, at least in principle, be extremely cost-effective in terms of the diversity of species conserved. On the other hand, being of a relatively small extent renders these areas more vulnerable to a range of human activities, including those that are leading to changes in the wider global environment, notably climatic changes.

Although the origins of these areas of high species diversity remain a subject of debate, and it is unlikely that any one factor fully accounts for the overall global pattern of such areas of diversity concentration, an increasing body of recent evidence supports the role of historical factors (Brown et al., 2020; Colville et al., 2020; Huntley et al., 2016). In particular, a high degree of climatic and/or biome stability on glacial–interglacial time scales (Colville et al., 2020; Huntley et al., 2016), and especially at times of high overall rates of global climatic change (Brown et al., 2020), is hypothesised to result in relatively low extinction rates, thus allowing species numbers to increase over time as evolutionary processes generate new, and often more specialised, species. In contrast, where climatic conditions, and especially the biome, are not stable over such relatively long time scales, then the environmental changes, especially changes in biome, will lead to extinctions of species that are unable to shift their ranges so as to track areas of suitable conditions, and also are unable to adapt to the changed conditions (Huntley et al., 2010). The progressive extinction of many tree genera in Europe during the Quaternary (Magri et al., 2017) exemplifies this, each successive glacial stage leading to most of the area occupied by the Temperate Summergreen Forest and Temperate Broad-leaved Evergreen Forest biomes during interglacial stages being instead occupied by Steppe, Tundra or various boreal forest biomes (Allen et al., 2020). Even where temperate forest biomes were present during glacial stages in parts of southern Europe, they were so much reduced in extent that this likely also contributed to extinctions, not only of trees and other forest plants (Huntley, 1993), but of forest animals such as *Palaeoloxodon antiquus* (Straight-tusked Elephant) and *Stephanorhinus hemitoechus* ('Narrow-nosed Rhinoceros'; Stuart & Lister, 2007). Biome changes occurring in response to changes towards warmer and/or moister climatic conditions have similarly led to extinctions, both regionally and globally, of species or species populations. This is especially the case where forest biomes have replaced open biomes, leading to the extinction of species adapted to the open conditions such as *Coelodonta antiquitatis* (Woolly Rhinoceros, Stuart & Lister, 2012) and *Panthera spelaea* (Cave Lion, Stuart & Lister, 2011). Unless the rate of proliferation of new species through evolutionary processes is sufficiently rapid to more than offset such losses through extinction, which will rarely be the case, then areas of past environmental instability will have lower levels of current species diversity.

Our results show that only a small fraction of the overall global land surface has supported the same biome throughout the past 140 ky. Furthermore, not unexpectedly, areas of biome constancy are not distributed evenly but are concentrated at lower latitudes. The widespread coincidence of areas of biome constancy with areas of high species diversity, and especially of high concentrations of endemic and range-restricted species, such as has recently been reported for the flora of New Guinea (Cámara-Leret et al., 2020), adds support to the hypothesised importance of the role of biome stability in the development of biodiversity 'hotspots'. Our analysis of the relationship between present species richness and past biome constancy shows a consistent pattern across the four taxonomic groups of terrestrial vertebrates that we investigated. In areas with less than the median species richness (0.1–0.5 quantiles, see Table S1), linear quantile regressions indicated that species richness is generally unrelated to past constancy of the current biome, or even, in the case of birds, shows a relatively weak negative relationship. In areas higher than the median species richness, however, there is a positive relationship, this relationship being strongest for the highest quantile (0.9). Quantile generalised additive models supported the visual impression of nonlinearity of these relationships (Figure S3), with the strongest effects seen at higher biome constancy values; this was apparent even for the median and lower quantiles, the relationships for which showed peaks at high biome constancy, although with a downturn at the highest constancy values. These results suggest that in regions with high present species diversity, more consistent availability of a particular biome has, as hypothesised, led to relatively low extinction rates, while at the same time allowing lineages to radiate, thus generating higher species diversity than in areas where biome constancy was low. The form of the relationship between species richness and biome constancy in low-diversity regions of the world suggests that in most of these areas current species number may be determined primarily by ecological filtering acting to prevent the development of high species diversity. However, even in low-diversity regions, a species richness peak at the highest values of long-term biome constancy likely indicates a role for reduced extinctions, with the notable exception of the subtropical desert areas that have very high constancy but low species richness. The, albeit relatively weak, negative linear relationships seen for lower values of *tau*, especially for birds, reinforce this conclusion, reflecting the correspondence between areas with very low numbers, or even absence, of species (Figure 2) with areas constantly occupied by the Desert biome (Figure 1a) that is characterised by a combination of highly stressful environmental conditions and consequent low primary productivity that together limit the diversity of species that can be supported.

The apparent role of high biome stability in the development of centres of high species diversity, with their concentrations of range-restricted and endemic species, brings into sharp focus the question of the vulnerability of these areas to future climatic change, as well as to the range of ongoing anthropogenic activities that already have transformed many areas into what have been referred to as ‘anthromes’ (Ellis et al., 2010). Our results project that the climatic conditions to be expected by 2100 will lead to an eventual change of biome across one fifth (RCP4.5) to one third (RCP8.5) of the land area where the biome previously has been constant, increasing to one third (RCP4.5) to more than half (RCP8.5) if the constant areas of Desert are excluded. We also project eventual biome replacement across between two fifths (RCP 4.5) and more than half (RCP 8.5) of the areas currently identified as EBAs. The eventual transformation of the biome over such high proportions of the Earth's most biodiverse areas as a consequence of anthropogenic climatic change, compounded with biome transformations resulting from a range of human land uses, has profound implications for biodiversity conservation strategies. Unless stringent measures to limit anthropogenic climatic change are rapidly adopted and implemented, then it will no longer be effective simply to focus upon providing protection for areas that currently support high levels of biodiversity. Such protection will need to be extended to much greater areas, especially those adjacent to current ‘hotspots’, in order to enable species to make the adjustments of range necessary if they are to continue to be able to occupy the environmental conditions, and biome, to which they are adapted. Even then, the evidence of the importance of past biome stability for the accumulation of diversity raises the prospect that some, perhaps even many, species may be unable to shift their ranges sufficiently to adapt to the committed eventual biome transformations. The widespread transformation of biomes as a result of human land use substantially magnifies this problem.

The implications of extensive biome replacement for human society are also profound. Biome replacement, in common with many ecosystem dynamic processes, will often be initiated by some form of environmental disturbance, for example extreme drought or wildfire, that causes the death and/or destruction of members of the dominant PFT, if not of most of the plants present (Brando et al., 2014; Phillips et al., 2010). Prior to such a disturbance, ecological inertia may enable the biome to persist even though climatic conditions are progressively changing, and if the change has been sufficient then the disturbance will be followed by the development of a different biome. In many cases, and especially in the case of forest biomes, completion of this development will require between one and several centuries (Prentice et al., 1991). During that time, there will generally be a major reduction or even loss of many of the ecosystem services provided by the biome, including carbon storage and sequestration. Even where the replacement biome is eventually able to supply the same level of ecosystem services, these will only be restored fully when the replacement biome has developed to maturity. In many cases, however, the ecosystem services may not return to their previous levels. For example we simulate mean carbon mass for the present day of 16.4 kg/m^2 for Tropical Evergreen Forest, and 7.5 kg/m^2 for Tropical Raingreen Forest. We also simulate 43% (RCP4.5) to 57% (RCP8.5) commitment by 2100 to the eventual replacement of Tropical Evergreen Forest by Tropical Raingreen Forest, resulting in a 23% (RCP4.5) to 32% (RCP8.5) reduction in carbon storage in areas thus transformed, even when the replacement biome has fully developed. Avoiding the negative consequences of such potential losses of ecosystem services requires urgent steps to be taken to limit anthropogenic climatic changes. Failure to do so is likely to lead to extensive biome transformations, with associated losses of ecosystem services, at least temporarily but often persisting at least for decades or even centuries. In some cases, because of hysteresis in the response to a climatic change of at least some global systems (Garbe et al., 2020), these losses may even be irreversible, at least on time-scales of relevance to humanity.

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DATA AVAILABILITY STATEMENT

The following files have been deposited in the Data Dryad repository (https://doi.org/10.5061/dryad.f4qrfj6w6): (1) Five pairs of files in.csv format, one pair for the 'present', and one pair each for the 2050 and 2100 RCP4.5 and RCP8.5 scenarios, each pair comprising one file each for the LPJ-GUESS simulated LAI and C-Mass values for all half-degree grid cells. (2) One.csv format file giving the biome assignments for the 'present' and for the 2050 and 2100 RCP4.5 and RCP8.5 scenarios for all half-degree grid cells, along with two files giving, respectively, the biome extents and the carbon mass of PFTs for each biome. (3) Two.csv format files, the first giving the % constancy values, and the second giving frequency counts, for the present biome, the most frequent biome, and all other biomes, as well as the total number of biomes, for each grid cell, for the present vegetation simulation plus 88 palaeovegetation simulations. (4) A metadata file describing the contents and formats of these data files. Other associated files relating to our previous work presenting the past biome inferences that underpin this study can already be found in the Dryad Data repository (https://doi.org/10.5061/dryad.2fqz612mk).

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BIOSKETCH

Brian Huntley is a palaeoecologist, ecologist and biogeographer with research interests in the interactions between species, ecosystems and their changing environment. His work encompasses studies of the palaeoecology and palaeoenvironments of the Quaternary, of present ecosystems and biogeographical patterns, and of the potential impacts of anthropogenic global change on species and ecosystems. His research has considered a range of taxonomic groups, from plants to extinct Quaternary mammals, and various ecosystems, from Arctic tundra to fynbos. He has particular interest in birds and climatic change, and in the development of conservation strategies informed by research into how species and ecosystems respond to environmental changes.

Author contributions: B.H. conceived the study, developed the biome inference approach and wrote the program to implement this, mapped the simulated biomes, analysed the simulation results, prepared the Figures and Supporting Information, and drafted the manuscript. P.J.V. and J.S.S. performed the climate modelling experiments; MF and TH advised on running the palaeovegetation simulations; MF developed and implemented code to incorporate the climatic anomalies, extend simulations to the shelf areas and specify the varying obliquity; MF, TH and JRMA parameterised the PFTs; J.R.M.A. performed the palaeovegetation simulations; and RO processed the biodiversity data and performed the quantile regressions. All authors commented upon and contributed to the final version of the manuscript.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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