

## RESEARCH ARTICLE

# Human land use is comparable to climate as a driver of global plant occurrence and abundance across life forms

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## Abstract

**Aim:** Historically, climate has been a dominant driver of global vegetation patterns. Recently, ecological understanding has been updated to acknowledge the influence of human land use (the dominant driver of biodiversity change) in shaping global vegetation patterns. We test whether Raunkiær's life form, a plant classification system designed to reflect climatic drivers, affects how plants respond to both land use and climate.

**Location:** Forty-one countries across six continents.

**Time period:** 1990 to 2013.

**Major taxa studied:** Terrestrial plants.

**Methods:** Combining data from the biodiversity and land use database PREDICTS, and plant trait databases TRY and BIEN, we use generalized linear mixed models with weighted effects coding to test whether Raunkiær's life form affects plant response to land use and climate in over 4800 species at over 300 sites globally.

**Results:** We provide evidence that human land use is comparable to climate in influencing life form occurrence and that land use produces divergent outcomes across life forms.

**Main conclusions:** Combined with climatic suitability, land use acts as a filter contracting the realized niche of trees and expanding the realized niche of disturbance-tolerant species. Our results highlight the fundamental role of human activity in shaping species' distribution.

## KEYWORDS

anthropogenic terrestrial disturbance, biogeography, climate, distribution, global change, human land use, macroecology, plant life forms, Raunkiær, vegetation patterns

## 1 | INTRODUCTION

Globally, biodiversity is in decline (Almond et al., 2020; Díaz et al., 2019). While the global trend is clear, not all species respond to anthropogenic pressures in the same way. Extinction risk differs

across functional traits (Carmona et al., 2021) and land use drives changes in community composition (Allan et al., 2015; Maseyk et al., 2017), indicating nonuniform responses of species. Conflict in the literature (Eriksson & Hillebrand, 2019; Gonzalez et al., 2016) surrounding the rates (Grooten et al., 2018; Le Roux et al., 2019;

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Leung et al., 2020) and directions (Mentges et al., 2020) of trends in biodiversity, as well as the scales (Dornelas et al., 2014; Hautier et al., 2018; Suggitt et al., 2019) and metrics (Hillebrand et al., 2018; McGill et al., 2015) relevant to their measurement, supports differential species' response. What causes some species to thrive in anthropogenic environments and others to decline?

The leading cause of biodiversity loss and ecosystem change is human land use (Brondizio et al., 2019; Díaz et al., 2019). Human activities have influenced terrestrial biodiversity for at least 12,000 years (Ellis et al., 2021). This influence has increased in the last 300 years (Ellis et al., 2010) and further in the last century (Steffen et al., 2015). Currently, 75% of the earth's surface is subject to anthropogenic land use (Ellis et al., 2010; Ellis & Ramankutty, 2008; Venter et al., 2016a). Excluding Antarctica, only 5% of land shows no evidence of modification by human activity (Kennedy et al., 2019). In addition, the rate of land use change is accelerating most rapidly in areas with highest biodiversity (Venter et al., 2016b).

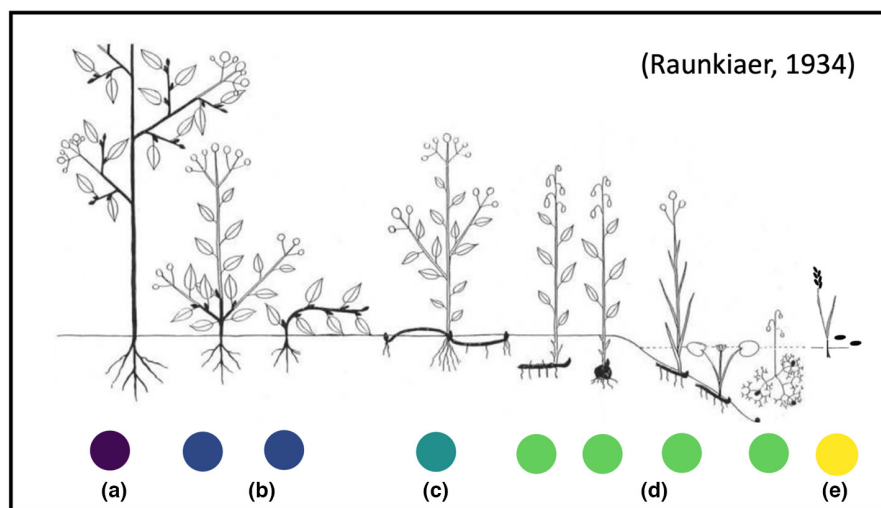
While the main driver of global vegetation patterns has historically been regarded as climate (Whittaker, 1970), how species respond to land use is a determinant of contemporary species distributions and their fate in the Anthropocene. Human use of the earth's terrestrial surface is so pervasive that which biological communities occur is a result not only of climate, biotic interaction and biogeographic legacy but also of human use of the landscape. We therefore consider all types of land use to be human land use, including 'primary' vegetation categorized as 'forest' or 'non-forest'. We use Raunkiær's Life form, a species trait classification describing the

influence of climate on species distributions, to investigate species' differential responses to land use, and to compare the effects of land use to climate in influencing global vegetation patterns.

'The plant itself must be the recorder of the biological value of any climate'—Raunkiær (Smith, 1909).

In the early 20th century, Raunkiær devised a plant classification system to capture the correlation between climate and vegetation (Smith, 1909). He proposed that the biological value (productivity) of a climate could not be accurately measured with physical climate parameters, as (a) different parameter values could produce the same vegetation assemblages or (b) parameter values could have different outcomes depending on other parameters (Smith, 1909). Instead he proposed biogeographers measure 'biological spectra'; the relative abundance of 'life forms' (Figure 1) as manifestations of the biological value/productivity of climate through statistical analysis of biological spectra.

Raunkiær's analysis showed the relative abundance of life forms could be used to describe vegetation assemblage, or 'phyto-climates'. Phanerophytes and therophytes declined with decreasing temperature, hemicryptophytes showed peak relative abundance in temperate zones, and chamaephyte relative abundance increased with falling temperature. Climate had precedence over edaphic factors in driving life form relative abundance. However, successional stage also affected the proportions of life forms, highlighting disturbance as the only factor to compete with climate as a driver of the biological spectra (Smith, 1909). Life form is the most widely available trait-based classification of plant species, enabling differential



**FIGURE 1** Raunkiær's Life forms. Raunkiær classified plant 'life forms' based on the location of the plant's points of regrowth, following local climatic bottlenecks. Plants regrow from apical meristems, that is buds, bulbs and seeds, following climatic bottlenecks least suitable for growth, that is the coldest/hottest/driest/flooded period. Life forms describe the vertical position of apical meristems (degree of meristem exposure) as adaptations to increasingly harsh local climatic bottleneck conditions. Life forms can be subdivided to describe local climate at higher resolutions, but broadly they are characterized as phanerophytes (a), chamaephytes (b), hemicryptophytes (c), cryptophytes (d) and therophytes (e). Phanerophytes (typically trees) have the highest degree of meristem exposure, regrowing from aerial buds suspended well above the soil surface. They are adapted to compete for space and light in warm, wet climates, but less well positioned to cope with extremes of cold and dry. Chamaephytes (typically shrubs) afford more protection to their buds, regrowing from just above the soil surface. Hemicryptophytes (typically herbs) regrow from roots at or near the soil surface, cryptophytes from bulbs below the soil surface, and therophytes solely from seeds, allowing them to survive in climates with extremely harsh bottlenecks. Species can exhibit more than one life form.

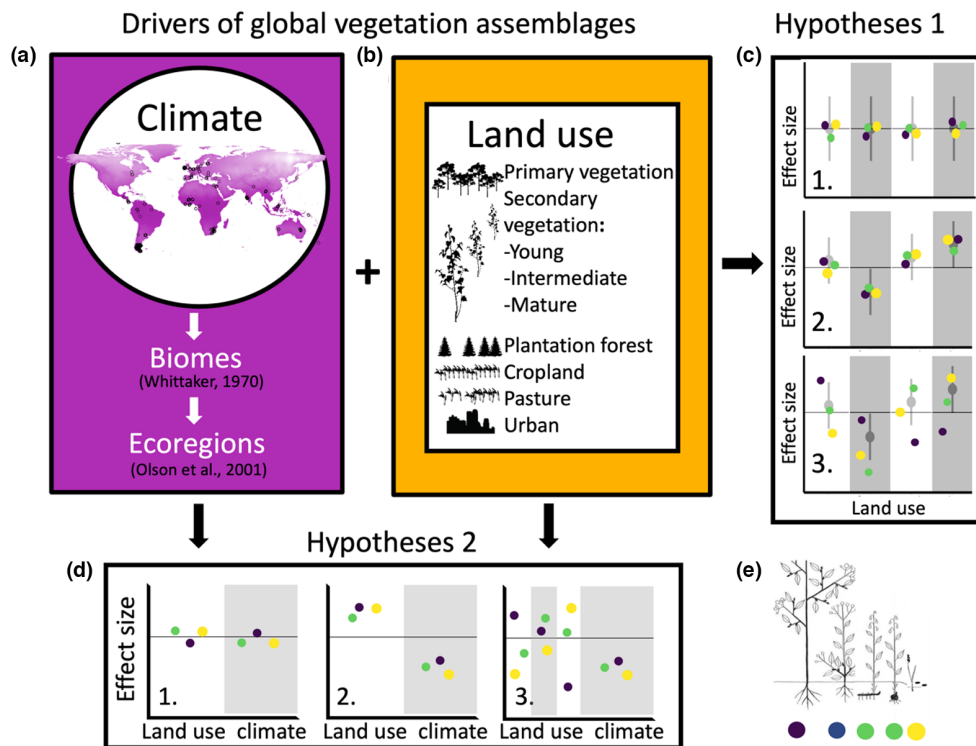
species responses to climate and land use to be analysed at a global scale.

The framework established with Raunkjær's phyto-climates and biological spectra based on the relative abundance of life forms has been developed into terrestrial biomes (i.e. Whittaker (1970)) and further, ecoregions (Olson et al., 2001). However, in the light of the obvious and increasing human modification of the biosphere (Ellis et al., 2010; Grooten et al., 2018; Le Roux et al., 2019; Millennium Ecosystem Assessment, 2005), biodiversity patterns can no longer be studied independently of anthropogenic influence (Ellis et al., 2021; Sullivan et al., 2017). Recognizing land use as an inescapable driver of ecological patterns and processes in the Anthropocene, biomes have now been described in terms of the dual filters of climate and human land use combined (Ellis & Ramankutty, 2008), though there is still a focus on the role of current and future climate (Elsen et al., 2022). We use plant life form to test the differential responses of species to drivers of contemporary biogeography: climate and land use. While climate shapes where species can occur (species' fundamental niche), we show how land use is a dominant factor in determining where they ultimately do occur (i.e. species' realized niche). This realized niche is also influenced by other factors including biotic

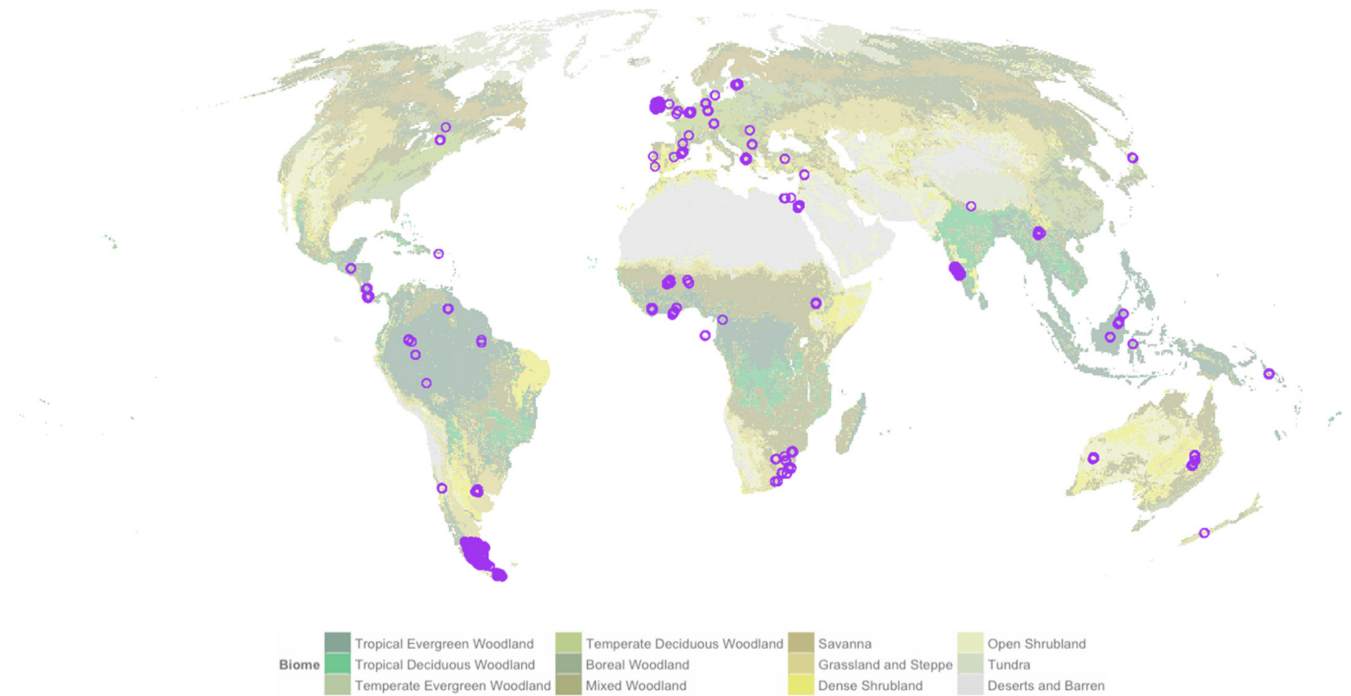
interactions, historic climates and dispersal, which are beyond the scope of this analysis.

## 1.1 | Aims

We determine: (a) whether species differ by life form in their response to land use and climate, and (b) how land use and climate compare as correlates of life form occurrence and abundance (Figure 2). We combine open source databases of plant traits TRY and BIEN (Kattge et al., 2011; Maitner et al., 2018), WorldClim climate data (Fick & Hijmans, 2017), and plant population data from the PREDICTS global dataset of local biodiversity responses to land use (Hudson et al., 2016a) for 4804 species at 323 sites worldwide (Figure 3). We use frequentist mixed effects models with weighted effects coding to test whether plant species occurrence and abundance differ from the data average as a function of the interaction of life form with land use and climate. We compare model effect sizes of climate to climatic differences between biomes and ecoregions to assess whether the modelled effects of land use on species occurrence and abundance are comparable to observed effects of climate on biogeographic patterns. Given the climatic basis



**FIGURE 2** Hypothesis diagram. Raunkjærian life form (e) classifies plant growth strategies in relation to climate. When the classification system was devised, the relative abundance of life forms mainly described local climate (a). Since then, our understanding of what drives global vegetation assemblages has been updated to include human land use (b). Ecology has strong evidence for how life form is structured by climate, but not by land use (c), or how the effects of climate and land use on life form compare (d). We test whether land use, currently the leading driver of biodiversity change, affects life form occurrence and abundance. Additionally, we assess how the relationships between life form and land use and life form and climate compare. (c1) null hypothesis = land use and life form do not affect species occurrence/abundance; (c2) land use affects species' occurrence/abundance and (c3) the response of species occurrence/abundance to land use differs by life form. (d1) Null hypothesis, there is no effect of climate or land use on life form, (d2) the effects of land use and climate on life form are comparable in magnitude, (d3) life form occurrence/abundance is more divergent in response to land use than to climate.



**FIGURE 3** Map of data origins. Site locations are shown with purple empty circles. Colours refer to biomes after Ramankutty and Foley (1999) from Ellis et al. (2010). For colour-free version of this map, see Figure S1.

of Raunkiaer's life forms, we expect that occurrence of life forms will be influenced strongly by climate, that is a strong life form: climate interaction. Given the dramatic effect of land use on vegetation, we also expect life form to interact with land use. We hypothesize that life form will affect species' occurrence and abundance responses to land use and climate, with life forms adapted to be more competitive in productive environments (phanerophytes—mostly trees; Irl et al., 2020) more likely to occur in less disturbed land uses (i.e. primary vegetation or mature forest), and life forms adapted to cope with patchiness of resources (hemicryptophytes, cryptophytes and, in particular, therophytes [annuals]) may be more likely to occur in disturbed land uses (Meers et al., 2008; i.e. cropland or urban land uses). We provide quantitative evidence at an unprecedented scale for the relationship between life form occurrence and abundance, land use and climate, highlighting how these relationships compare to existing climate-based frameworks characterizing global patterns of potential vegetation. This work contributes to a better understanding of the ecological impacts of a key component of global change, building on the work of others incorporating human activity as a pervasive force integral to our understanding ecological patterns in today's world.

## 2 | MATERIALS AND METHODS

### 2.1 | Overview

We used PREDICTS (Hudson et al., 2016b), a global database of local biodiversity, to assess whether plant species' life form, land use in a study site and local climate interact to affect local plant

species' occurrence and abundance. Data were collected, cleaned and merged from different sources and analysed using generalized linear mixed effects models with weighted effects coding in RStudio version 3.6.3 (R Core Team, 2019).

### 2.2 | Data collection

Data on plant occurrence and abundance across land uses and site-level species richness were extracted from PREDICTS; Raunkiaer life form was extracted from TRY and BIEN; and climate data were extracted from WorldClim.

The PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) database (<https://www.nhm.ac.uk/our-science/our-work/biodiversity/predicts.html>) gathers information from papers with occurrence/abundance records for individual species associated with land use, as well as site-level total species diversity. Land uses in this study were as follows: primary vegetation (primary forest and primary nonforest categories combined), unknown secondary vegetation, mature secondary vegetation, intermediate secondary vegetation, young secondary vegetation, plantation forest, pasture, cropland and urban. PREDICTS assumes space-for-time substitution to compare species responses across land uses (Hudson et al., 2016a). All studies contributing data have (a) spatial comparisons of species occurrence/abundance, (b) standardized methodology (sites and species can be compared within the study) and (c) motivation for recording occurrence/abundance of species at each site, that is absences in occurrence data are 'real' zeroes. 'Abundance' data analysed in this study comprised nonzero

per cent cover data: representing local dominance when a species is present. Scales at which the per cent cover data were collected differ between studies, but are comparable within studies. For over 94% of our data, source papers' sampling target was 'entire community', and sampling method and effort were comparable within studies. See [S11](#) for details and Dataset [S1](#) for full list of studies.

TRY (Kattge et al., 2011) and BIEN (Botanical Information and Ecology Network) (<https://bien.nceas.ucsb.edu/bien/>) (Maitner et al., 2018) are open access databases containing plant trait measurements from which we obtained life form data. WorldClim version 1.4 (<https://www.worldclim.org/data/v1.4/formats.html>) is a global climate dataset, from which we obtained statistical summaries of climatic variables as static spatial *bioclimatic* variables at five-minute resolution, calculated using monthly records for temperature and rainfall from 1970 to 2000 (Fick & Hijmans, 2017).

## 2.3 | Data handling

Our final dataset included 4804 species, in 3830 plots at 323 sites, from 73 studies in 41 countries. See [Figure 3](#) for site locations and [Table S10](#) for sample sizes for each land use–life form combination. These studies were conducted between 1990 and 2013. Continuous predictor variables were scaled by subtracting the mean and dividing by one standard deviation. We calculated climate variable averages for each of 12 Biomes (based on data from Ramankutty and Foley [1999] used in Ellis et al. [2010]) and 809 Ecoregions (based on data from Olson et al. [2001]). We calculated the average difference between these values for each climate variable for biomes and ecoregions, respectively. For details of data cleaning and amalgamation processes, see <https://doi.org/10.5281/zenodo.7554843>. See [Figures S3](#) and [S4](#); [Tables S7](#) and [S8](#) for biome and ecoregion climate value summaries.

## 2.4 | Statistical analysis

Generalized linear mixed models (GLMMs) were used to assess the effect of life form on species response to land use and climate. Terms included in the models can be divided into three groups: (a) categorical main effects (land use and life form), (b) continuous main effects (climate variables and site-level species richness) and (c) random effects, included to account for the nested structure of the data, that is within and between group variation in taxonomy, sampling blocks, sites and species. Fixed terms included in the final model dataset were land use, life form, site-level species richness and four climate variables; mean annual temperature, temperature seasonality (SD), mean annual precipitation, and mean annual precipitation seasonality (coefficient of variation). Random terms included in the final dataset related to taxonomy (Class, Order, Family, Genus and Species) and data provenance (Source, Study, Site and Block).

Occurrence and abundance were modelled independently due to the different error structures of the response data. Abundance,

based on nonzero per cent cover data, was logit transformed and scaled and then modelled using a Gaussian error distribution using the lme4 R package (Bates et al., 2015). The occurrence model (based on presence/absence from the full dataset) was modelled using a zero-inflated binomial error distribution from the 'template model builder' (GlmTMB) R package (Brooks et al., 2017).

For both occurrence and abundance, random effects structure was established using null models containing no fixed effects. All random effects were initially included (Barr et al., 2013), and random effects with low attributed variance were removed to prevent issues with model convergence (see [Tables S12a](#) and [b](#) for magnitudes of random effects). Once the random effect structure was established, maximal GLMMs were fitted including all fixed effects.

Model structure;

$$\begin{aligned} \text{Response} \sim & \text{Land use} * \text{Life form} + \\ & \text{Mean annual temperature} * \text{life form} + \\ & \text{Mean annual precipitation} * \text{life form} + \\ & \text{Mean annual temperature variation} * \text{life form} + \\ & \text{Mean annual precipitation variation} * \text{life form} + \\ & \text{Species richness} * \text{life form} + \\ & (1 | \text{Species}) + \\ & (1 | \text{Study}) + \\ & (1 | \text{Class/Order/Family/Genus}) \end{aligned}$$

Model fixed effects terms were as follows: land use, life form and their interaction, climate variables and their interaction with life form, and species richness and its interaction with life form. Species richness was included to account for differences in overall probabilities of occurrence. When accounting for species richness, we therefore compared, for example, mature secondary vegetation and urban land uses from locations of similar biodiversity, to assess the effects of land use on specific life forms directly. We ran models both with and without species richness. Models without species richness were conducted on a version of the analysis where primary vegetation was considered as primary forest and primary nonforest (see [Figures S6a](#) and [b](#)), producing very similar results to the main analysis. Results of models without species richness (see [Figure S6c](#), [Tables S9a](#) and [b](#)) show very similar patterns to those with species richness, with effect sizes of smaller magnitude, that is by accounting for species richness, we determine the effects of land use and life form more clearly.

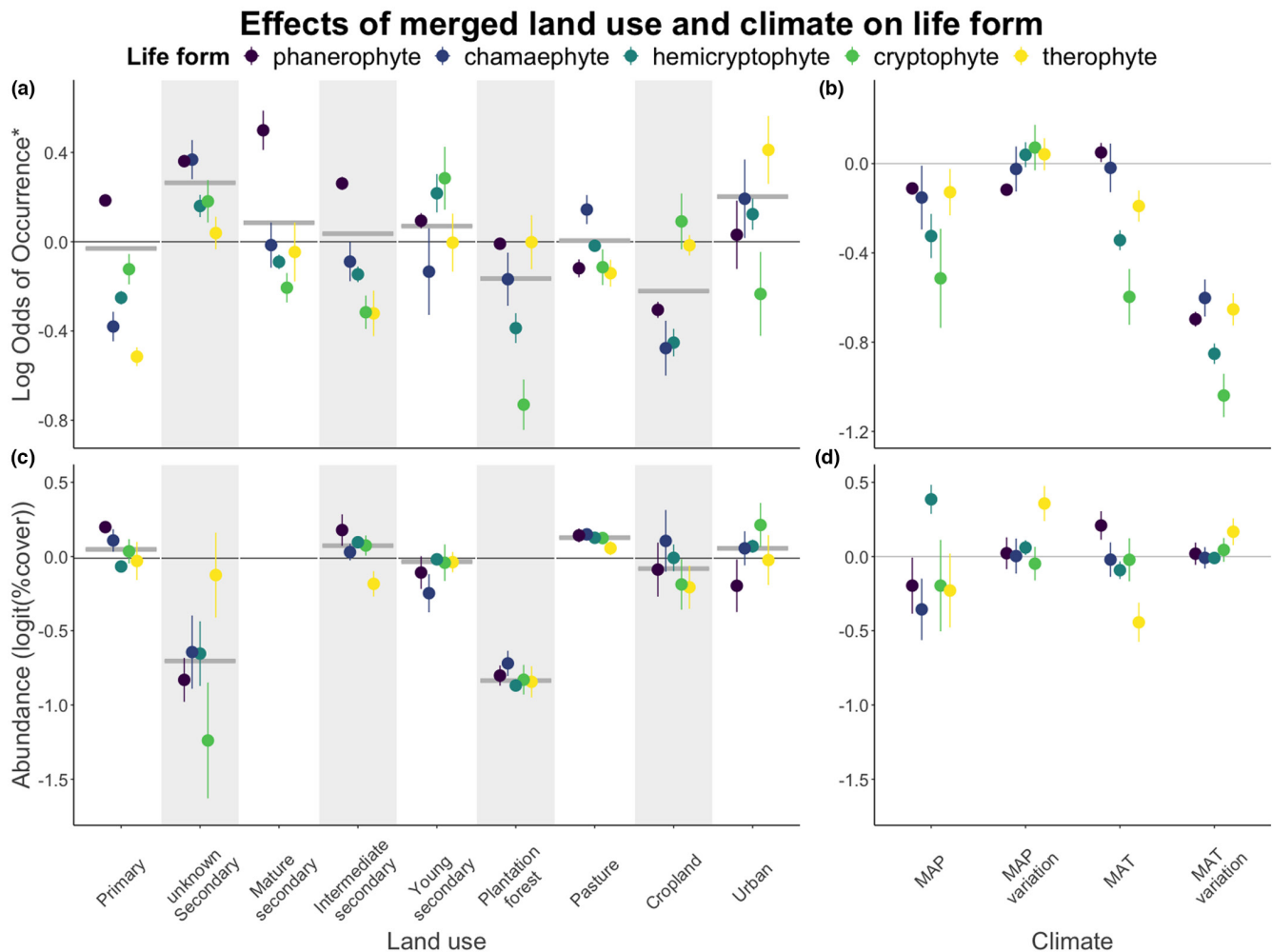
Contrasts in our models were based on weighted effects coding using the 'wec' package (te Grotenhuis et al., 2017a), which is more appropriate than treatment coding in cases where there is no meaningful 'reference' factor level (te Grotenhuis et al., 2017b). Weighted effects coding assesses the difference between factor level means (e.g. land use classes) and the 'grand' mean (i.e. the mean of the means of all factor levels), weighted to account for differences in sample sizes between factor levels. The grand mean is therefore equivalent to the mean of the entire dataset. For weighted effects coding, the interpretation of estimates from continuous variables remains the same as in treatment coding, that is estimates for continuous variables describe the estimated



change in response variable for every 1 unit change in the continuous variable (here 1 SD change, due to variable scaling). For more details, see <https://doi.org/10.5281/zenodo.7554843>. DHARMA (Hartig, 2018) was used for model diagnostics and ggplot2 (Wickham, 2016) for visualizing model outputs. All reported models converged and were deemed of sufficient fit using model diagnostics. All code used in this analysis is available from <https://doi.org/10.5281/zenodo.7554843>.

### 3 | RESULTS

Land use, life form and the interaction between them had significant effects on plant species occurrence globally (Figure 4a and Table S3). Climate also interacted with life form to affect occurrence, with temperature variation (MAT variation) having the strongest effect (Figure 4b and Table S3). With the exception of mean annual temperature variation, the magnitude of effects on species' probability



**FIGURE 4** Species occurrence and abundance by land use and life form. (a) Effects of land use and life form on occurrence. (b) Effects of climate and life form on occurrence. (c) Effects of land use and life form on abundance. (d) Effects of climate and life form on abundance. In (a) and (b), Y axis represents log-odds ratio (probability of occurrence) (y axis in panel (a) represents the log odds minus the grand mean). In (a), continuous horizontal line shows the centred weighted mean log-odds ratio, that is average probability of occurrence when at mean values of continuous variables; in (b), the continuous horizontal line represents zero (no relationship between continuous variable and response). In (c) and (d), abundance data describe species' local dominance when present. Y axis represents scaled and logit transformed nonzero %cover data. In (c), horizontal line shows the weighted mean %cover, that is average transformed %cover when continuous variables are zero, and in (d), the horizontal line represents zero (no relationship between continuous variable and response). In (a) and (c), horizontal line segments show land use means (across all life forms). Circular (coloured) points show 'population' means, as estimated by the model, of the response variable within land uses for each life form. Points lower/higher than the horizontal line indicate that the mean probability of occurrence or abundance estimate of that particular land use\*life form combination is lower/higher than the data average. In (b) and (d), circular (coloured) points represent the slope of relationship (change in log-odds ratio or abundance estimate), associated with 1 SD change in climate for each life form. In (a–d) vertical lines represent 95% confidence interval. CIs overlapping horizontal lines indicate that the probability of occurrence or abundance estimate is not significantly different from average. Total number of observations in occurrence model=624,696 for 4804 species, and abundance model=19,384 for 883 species. Note, abundance data for mature secondary forest were not available.

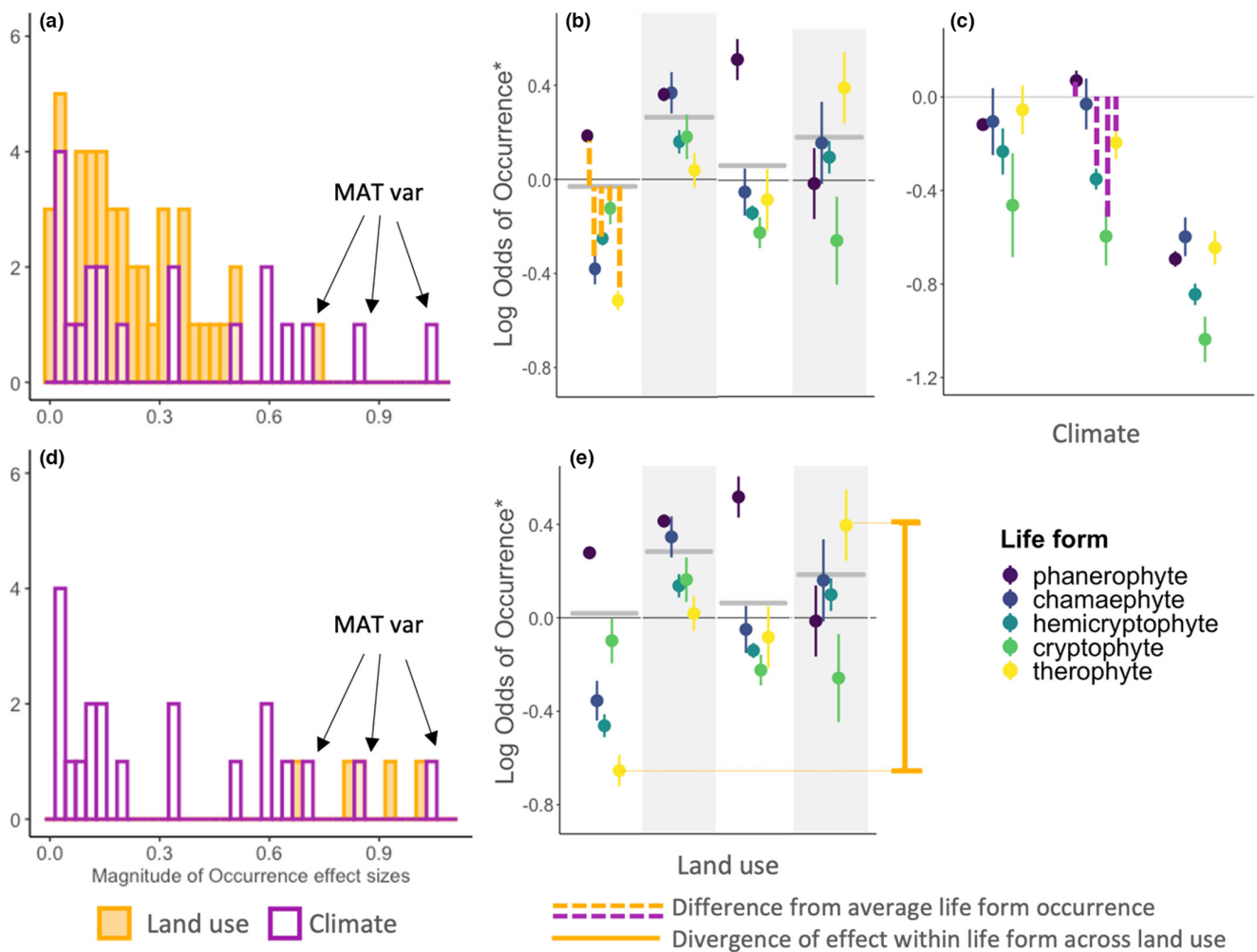
of occurrence associated with land use was comparable with those associated with a 1 standard deviation change in climate variables (Figure 5a; Tables S5a and b). Land use and climate also interact with life form to affect species abundance (Figures 2d and 4c; Table S4). As with occurrence, the largest effects of land use on abundance are comparable to, or larger than, the effects of a 1 standard deviation change in climate (Figure S5a; Tables S6a and b). Here, a 1 SD change in most climate variables was comparable to the average difference in climate variables between biomes or ecoregions (Figure 6; Tables S7 and S8).

The divergent effects of land use on the probability of occurrence within individual life forms (Figure 5d) are comparable to the magnitude of the effects of individual climate variables (Figures 4c and 5e; Tables S5c and b). For individual model estimates, *p*-values,

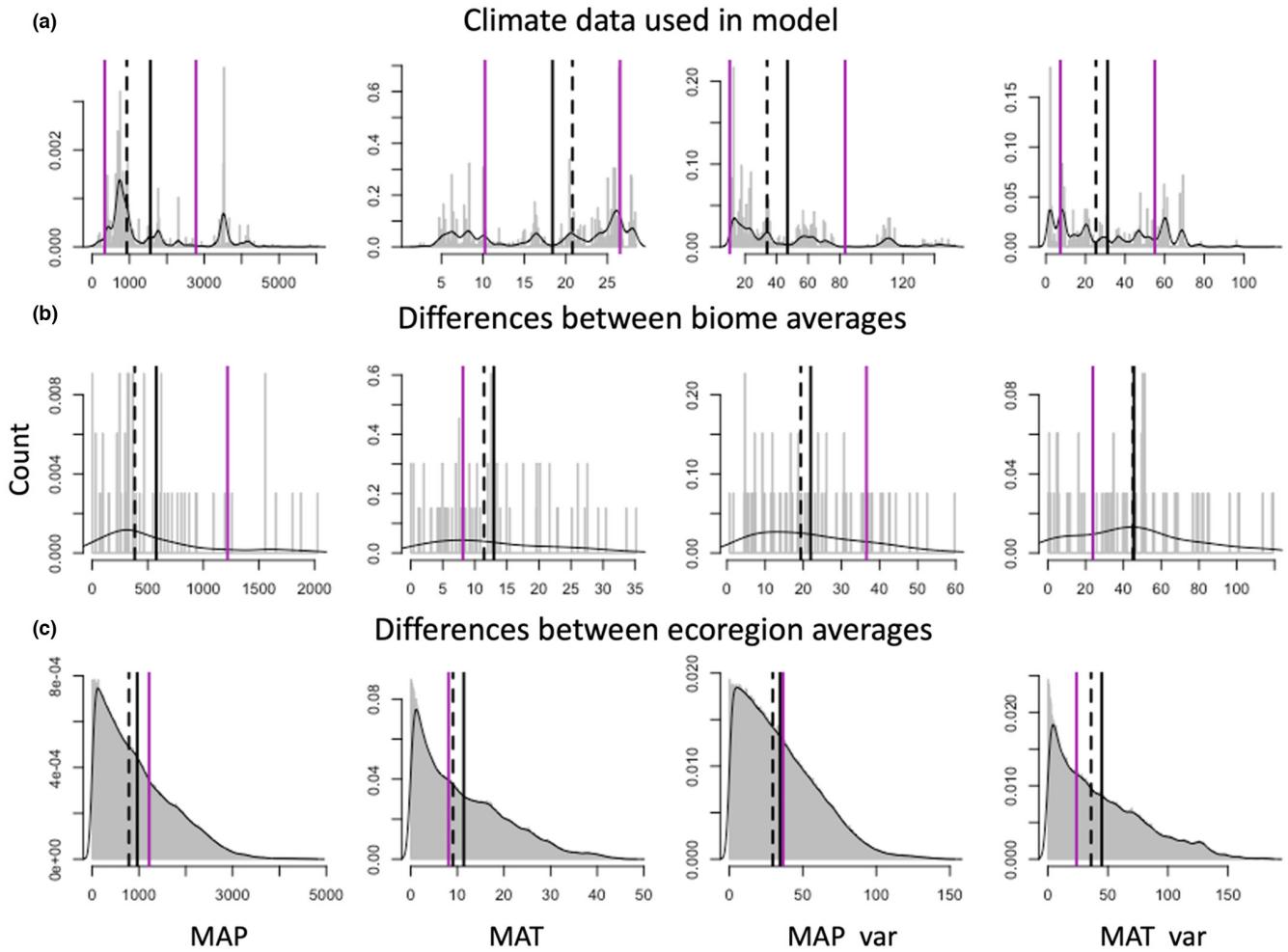
biome climate averages and climate variable summary statistics, see Tables S5–S9.

### 3.1 | Land use

Species' probability of occurrence differs by life form across land uses. Phanerophytes had higher probabilities of presence in less disturbed land uses, that is primary vegetation, mature and intermediate secondary vegetation, compared with mean probability of occurrence at mean climate and species' richness values (Figure 4a and Table S3). Though higher than average, phanerophyte probability of occurrence decreases in young secondary vegetation relative to less disturbed land uses (Figure 4a, 95% CIs do not overlap with



**FIGURE 5** Comparison of Climate and Land use Occurrence effects. In histograms (a) and (d), orange bars represent magnitude of land use effects and purple bars represent magnitude of climate effects. Panels (b), (c) and (e) show illustrative effect sizes of land use (primary forest, unknown secondary vegetation, mature secondary vegetation and urban) and climate (MAP, MAT and MAT var) to enable interpretation of (a) and (d). (a)—the distribution of effect sizes for life form by land use (dashed orange lines in [b]), compared with the effect of 1 SD change in climate variables (dashed purple lines in [c]). (d)—the distribution of effect size range within life form across land uses (solid orange line in [e]), compared with effect on life form occurrence of a 1 SD change in climate variables (dashed purple lines in [c]). For a similar figure comparing climate and land use on abundance, see Figure S5. The largest climate effect sizes were due to Mean Annual Temperature Variation (MAT var) shown in panels (a) and (d).



**FIGURE 6** Climate variable effect size in real-world terms. Comparison of standard deviations of climate variables used in our models to differences between real-world classifications of climate-based vegetation assemblages. Grey histograms represent (a) climate variable data used in occurrence models, and differences between climate variable averages in (b) biomes, and (c) ecoregions. Purple lines represent (a)  $\pm$ one standard deviation of a particular climate variable in the model data, or (b) and (c) magnitude of sd in model data. Solid black lines represent the mean value of each histogram (i.e. mean difference between average temperature in biomes), and dashed black lines represent median value of each histogram (i.e. median difference between average rainfall in ecoregions). Biomes based on Ramankutty and Foley (1999) from Ellis et al. (2010) and ecoregions based on Olson et al. (2001).

estimates in other nonplantation forest land uses). Phanerophytes had lower than average probability of occurrence in more frequently disturbed land uses (pasture, cropland and urban land uses; 95% CIs do not overlap with overall mean). The probability of occurrence of therophytes was higher in some of the more disturbed land uses, that is higher than the land use average in plantation forest and cropland (Figure 4a and Table S3). Therophyte probability of occurrence was lowest in primary vegetation and highest in urban land uses (with 95% CIs far from the overall and land use-specific mean occurrences).

The abundance results show some similarities to the occurrence results. Phanerophyte abundance when present was higher than the data average in primary vegetation, the least disturbed land use, and lower in urban environments (Figure 4c and Table S4). The differences between land uses were more pronounced than the differences within land uses for abundance data. Abundance was lower

than the overall data average for all life forms in plantation forest and lower for all life forms except therophytes in secondary vegetation of unknown age. Abundance was higher than the data average in less disturbed land uses (primary vegetation and intermediate secondary vegetation).

### 3.2 | Climate

As expected, life forms differed in their responses to climate variables (Figure 4b,d; Tables S3 and S4). The effect (slope) of a climate variable is the change in occurrence or abundance associated with a change of one standard deviation in that variable. In the occurrence data, there was a consistent pattern in the response of life form to increasing precipitation, temperature and temperature variation (Figure 4b). Broadly, mean annual precipitation



(MAP) and mean annual temperature (MAT) have negative or non-significant effects on probability of occurrence (with the exception of a small positive effect of temperature on phanerophytes; Figure 4b). Mean annual temperature variation has the largest, negative effect on probability of occurrence across all life forms. Mean annual precipitation variation has a small negative effect on phanerophyte occurrence and has no effect on other life forms. For abundance data, responses to climate are more similar across life forms, with some exceptions, mainly for therophytes (Figure 4d and Table S4).

### 3.3 | Climate–Land use comparisons

#### 3.3.1 | Differences from average life form occurrence

The largest differences from average life form probability of occurrence were associated with mean annual temperature variation (Figure 4b; Table S5a and b). For other climate variables, the effects of particular land uses on life form occurrence and abundance are similar to or greater than 1 SD changes in climate variables (Figure 5a; Figure S5; Tables S5a,b, and S6a,b). For example, the negative effect of plantation forest on cryptophyte occurrence ( $-0.73$  Log Odds) is slightly greater than the effect of mean annual temperature ( $-0.597$  Log Odds) on cryptophyte occurrence, meaning the difference between average cryptophyte occurrence and cryptophyte occurrence in plantation forest is similar to the effect of a mean temperature difference of  $8.14^{\circ}\text{C}$  (1 SD MAT), or in terms of biomes between open shrubland and tropical evergreen woodland biomes (delta  $7.93^{\circ}\text{C}$ ) (see Figure 6; Tables S5a,b, S7, and S8 for comparisons in terms of biomes).

#### 3.3.2 | Range in occurrence within life form across land use

The differences in probability of occurrence *within* life forms across land uses are similar to the differences in probability of occurrence associated with a one SD change in mean annual temperature variation (Figure 5d). For cryptophytes, the difference between the land uses with highest and lowest probability of occurrence ( $\Delta 1.01$  Log Odds) is comparable to the effect of a 1 SD change in mean annual temperature variation ( $\Delta 1.04$  Log Odds; Figure 5d; Tables S5b,c, S7, and S8). For phanerophytes, the decrease in probability of occurrence between mature secondary vegetation and cropland ( $\Delta 0.80$  Log Odds) is slightly greater than the negative effect of mean annual temperature variation ( $\Delta 0.70$  Log Odds) (1 SD MAT<sub>var</sub> =  $23.84^{\circ}\text{C}$ ), that is difference in phanerophyte occurrence between Mature secondary vegetation and cropland is slightly greater than the difference in occurrence associated with the change in temperature variation between open shrubland and Savanna biomes (delta  $25.8^{\circ}\text{C}$ ) (Figure 5d; Tables S5c, S7, and S8).

## 4 | DISCUSSION

Here, we show for the first time at a global scale, life form occurrence and abundance between and within land uses is comparable to, and sometimes greater than, differences between biomes or ecoregions. Land use has a divergent effect on life form occurrence comparable to the effect of climate, with particular life forms more strongly affected than others by land use. The productivity of environments is driven mainly by climate, but which species succeed in them is also a result of land use. Humans are therefore in direct competition with plant species for highly productive environments, and we find that species that have historically dominated these climates are the least able to cope with human disturbance; that is, human pressure in highly productive climates leads to deforestation driving a lack of phanerophytes in these areas. Human land use is acting as a filter, expanding the realized niche of disturbance-tolerant life forms and contracting the realized niche of others. Land use change is comparable in strength to a 1 SD change in temperature, rainfall and rainfall variation as a driver of plant life form occurrence and abundance.

Individually, both land use and climate are expected to have a strong influence on species occurrence and abundance (Allan et al., 2015; de Chazal & Rounsevell, 2009; Huang et al., 2021; Smith, 1909; Thuiller et al., 2006). The effect sizes of land uses were typically similar to, or greater than, the effect sizes of climate (the exception being the effects of temperature variation, the strongest environmental driver of global vegetation patterns [Huang et al., 2021]). A one standard deviation difference in climate variables is broadly equivalent to the average differences in climate between ecoregions (Figure 6 and Figure S3) or Biomes (Figures S4 and S5; Table S8). We show that land use is comparable to climate in driving distribution patterns in plant life form. The divergent effect of land use on life forms (i.e. the difference in probability of occurrence between trees in primary vegetation and cropland) is comparable to the probability of occurrence associated with a 1 SD change in climate. Land use therefore acts as an additional filter, determining successful and unsuccessful types of species in the Anthropocene.

Intensification of human land use is not uniform across different biomes. Forest biomes (temperate broadleaf and mixed forests, tropical and subtropical dry broadleaf forests, Mediterranean forests, woodlands, and scrub, and mangroves) are the most highly impacted by human modification, while the lowest levels of modification are now in the coldest and driest, least productive biomes (Ellis et al., 2010) (tundra, boreal forest and taiga and desert and xeric shrubland; Kennedy et al., 2019; Venter et al., 2016a). Concerningly, productive environments, in particular primary forest, support a disproportionate amount of the world's existing biodiversity (Barlow et al., 2007; Mannion et al., 2013; Newbold et al., 2015; Shvidenko et al., 2005; Willig et al., 2003), with less than 3% of the biodiversity hotspots showing no human pressure (Venter et al., 2016b). From phyto-climates through biomes to ecoregions, ecologists have developed an understanding of how climate interacts with species intrinsic characteristics to produce vegetation assemblages. This understanding has been updated to

consider how human land use changes climate based models. We contribute a more explicit understanding of which types of species are increasing and which are declining in today's climate and land use-driven assemblages.

Phanerophytes were expected to have the highest relative abundance in climates with mild climatic bottlenecks (Raunkiaer, 1934; Smith, 1909), where there is a weaker trade-off between competing for light and shielding buds from periods of harsh climate. In productive habitats, phanerophyte occurrence is high, but decreases with increasing disturbance; that is land use is contracting phanerophytes' realized niche. Therophytes (and to a lesser extent hemicryptophytes and cryptophytes) are adapted to patchiness of resources (conditions suitable for growth and reproduction). These life forms historically had their highest relative abundances in climates unsuited to phanerophytes, and species with strategies adapted to resource patchiness are able to take advantage of human disturbance. Cryptophytes followed by therophytes had the largest range in probability of occurrence, indicating that human disturbance expands habitat suitable for these disturbance-tolerant life forms. A disproportionate increase in intra-annual climate variability is projected in more productive habitats (i.e. the Amazon; Bathiany et al., 2018). With phanerophytes unsuited to disturbance and hemicryptophytes unsuited to increased variability, therophytes may be best positioned to cope with the dual filters of land use and climate.

We show that life form affects species response to land use and provide strong evidence for land use as comparable to climate in moulding species' realized niche and creating the vegetation assemblages that contribute to the broad patterns of terrestrial life on Earth. By including both climate and land use in the same model, we obtain estimates for each variable where all other values are held constant at the average values of the other variables. Locations of biodiversity samples within studies were all within the same region, and in all except three studies, within the same biome (or further information on sites within studies, see Figures S8–11). As sites with different land uses are nested within study identity, by including study as a random effect we are comparing the effects of land uses within similar climatic contexts. However, explicitly testing the interaction between climate and land use, that is the effects of life form within land use and climatic contexts in a three-way interaction, was outside the scope of the data available for this study. Given that we are not seeking to use our model to predict relationships between land use, climate and life form on another dataset with different structures of nonindependence, that we do not have a small sample size (so are not limited by the degrees of freedom in our analysis) and that the nonindependence between climate and land use in our data is weak (land use accounts for less than 20% of variance in climate), we are confident that the structure of our data does not affect the interpretation of the results of our statistical analysis.

The effects of temperature in our occurrence model are associated with a change of over eight degrees Celsius, a magnitude which exceeds maximum global temperature changes projected in IPCC scenarios for the rest of the twenty-first century (Masson-Delmotte

et al., 2021). However, it is not meaningful to extrapolate species responses to future climate conditions based on patterns observed here. Effects associated with temperature in our models describe changes in probability of occurrence in comparison to the mean temperature, so our results describe increases in tree occurrence observed when moving (for example) from temperate to tropical climates, that is the *current* relationship between temperature and occurrence. An increase in temperature in temperate zones to that of a rainforest is not likely to produce an equivalent increase in tree species occurrence, as vegetation in both areas is also a product of current and historic land use, along with other historic and evolutionary factors.

This study used some of the largest available datasets of species occurrence/abundance, traits (life form) and human land use, and yet coverage remains patchy, and highly correlated with areas of intensive, historical human activity (Figure 3). These biases are present across data collections, both ecological (Boakes et al., 2010; Dennis & Thomas, 2000; Pyšek et al., 2008) and otherwise (Arora, 2016), but must be addressed. In this study, a broader range of site locations, particularly towards the colder climates, may have enabled us to detect clearer patterns in chamaephyte occurrence and abundance. Coordinated distributed data collection projects similar to NutNet (Borer et al., 2014) could be set up to supplement the continued collation of existing land use and life form data carried out by TRY, BIEN and PREDICTS, in particular to target undersampled areas. With this work, we provide quantitative evidence for the expected relationship between land use and life form at a broad spatial extent and show that this relationship is in some cases comparable in magnitude to the relationship between life form and climate. Though we consider the available data sufficient for testing our hypothesis, it was not extensive enough to explore the complex feedback between land use and climate, or any nonlinear relationships between them. Furthermore, to obtain as broad a spatial and taxonomic coverage as possible, we did not investigate time-lagged responses of plants to land use and climate conditions through, for example, land use history. Our findings therefore act as a snapshot of life forms in existing land uses and do not relate to vegetation succession or population viability following land use change. Population viability in particular is not well described by occurrence data, meaning our results have the potential to underestimate the strength of some land use–life form relationships. Abundance data reflected local dominance when present (see methods), rather than the habitat or landscape level relative abundance (i.e. commonness). Future work should use relative abundance data at a broader scale, capable of reflecting the vegetation composition of sampling sites or ecoregions rather than smaller-scale transects and quadrats.

While Raunkiaerian life form data are readily available, ecologically informative multidimensional trait data (Bohn et al., 2014; Funk et al., 2017; Herron et al., 2007; Lavorel, et al., 2002) and demographic data (Hemrová et al., 2017; Ramula et al., 2008; Salguero-Gomez et al., 2016) are sparser (Coutts et al., 2016; Kattge & Knöll, 2020; Kelly et al., 2021; Salguero-Gómez et al., 2014). A unique advantage of life form is its relationship with climate, enabling a strong test of

differences between land use and climate as drivers of biodiversity patterns. We show that life form is a useful lens through which to view biodiversity changes due to both climate and land use, including in future scenarios generated with dynamic vegetation models; however, expanded multidimensional trait datasets will undoubtedly prove useful in future analyses.

Ecological understanding of the drivers of vegetation patterns has developed immensely since Raunkjær's life forms were first described. 'Phyto-climates' have been refined into biomes, and ecoregions, and these climate-based frameworks have been updated to include the influence of human land use. Our work contributes to an emerging understanding of species divergent responses to the forces currently shaping their realized niches.

Here, we provide quantitative broad-scale evidence for the effect of nine dominant categories of land use on all major plant life forms. This work formalizes our understanding of which species are most vulnerable to the dominant force of global change. Land use changes towards more intensive use (i.e. away from primary or mature vegetation) in productive environments disproportionately affecting large, relatively long-lived species (e.g. phanerophytes). Furthermore, we show how human land use is associated with more divergent outcomes in species occurrence across life forms than climate, highlighting the disproportionately negative potential outcomes on species vulnerable to land use change. Climate change and its impact on species rightly receives huge research interest and investment. By providing quantitative evidence for both the obvious and surprising impacts of land use on occurrence of different life forms, and by showing how this impact can be considered comparable to the impacts of current climate, this work highlights land use as a key driver of species biogeographic distributions.

#### AUTHOR CONTRIBUTIONS

Research was conceived and designed by Caroline M. McKeon, Ruth Kelly, Yvonne M. Buckley and Luca Börger. Caroline M. McKeon conducted the data analysis and wrote the first draft. Ruth Kelly and Yvonne M. Buckley provided advice on analyses. Data were contributed through TRY, BIEN and Worldclim and through PREDICTS by Luca Börger and Adriana De Palma. Results were initially interpreted by Caroline M. McKeon with advice from Yvonne M. Buckley and Ruth Kelly. All authors provided intellectual input and edited the MS.

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#### CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

#### DATA AVAILABILITY STATEMENT

All code and data used in this analysis will be available on Zenodo at <https://doi.org/10.5281/zenodo.7554843> on publication.

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## BIOSKETCHES

**Caroline McKeon** obtained her PhD in Macroecology from Trinity College Dublin, Ireland, studying anthropogenic pressure as an ecological and evolutionary filter on species across the globe through the lens of scale, and trait-based ecology. She is currently a postdoctoral researcher building a size-based food web model to inform Ecosystem Based Fisheries Management in the Irish Sea. The Buckley laboratory investigates fundamental drivers of population processes to support sustainable environmental decision-making in a rapidly changing world.

## SUPPORTING INFORMATION

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

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