

IMPERIAL

Comprehensive Analysis of Natural Carbon Offsetting Solutions

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Declaration

I declare that this project represents my own work. I contributed to developing the dataset from the *Hitachi-Imperial Centre for Decarbonisation and Natural Climate Solutions* between April and June 2024. Additional data used in this work came from the WorldClim database for information on historic climate conditions, Natural Earth for global map shapefiles, the NASA Socioeconomic Data and Applications Center (SEDAC) for information of human land use intensity, and from the Critical Ecosystem Partnership Fund for information on global biodiversity hotspots. I want to thank my supervisor Dr Will Pearse for his assistance in developing the models and analyses used in this project.

Abstract

Humans benefit from many ecosystem functions (EFs), such as pollination and sequestering carbon from the atmosphere. Biodiversity affects the ability of ecosystems to perform EFs because it increases functional diversity and community stability. It is vital to understand the other drivers of variation in biodiversity-ecosystem functioning (BEF) relationships, specifically those of terrestrial carbon sequestration to maximise natural carbon capture as a method of climate change mitigation. Previous research often models these relationships to determine the effects of anthropogenic and climatic variables on BEF. However, there is a lack of large-scale modelling to determine which factors cause the greatest amount of variation in BEF relationships. I demonstrate that the drivers of BEF variation are different between terrestrial carbon sequestration and other EFs. I found biome and EF explain most of the variation in these relationships when all EFs are considered together, suggesting functional diversity is important in BEF. Land use change is responsible for most of the variation in the relationship between biodiversity and terrestrial carbon sequestration, meaning anthropogenic expansion drastically how effectively carbon is captured. Furthermore, I compare patterns of high BEF trends between areas of various land use intensities and biodiversity hotspots, which are regions with high numbers of endemic species. These results confirm that intense land use generally reduces biodiversity and ecosystem function in all EFs considered but increasing the number of endemic species in a region can improve carbon sequestration efficiency. This study also supports two contrasting BEF theories which illustrates the complexity of these systems. In the face of global change and increasing land scarcity, efficient carbon capture projects must effectively sequester carbon using the fewest resources possible. The results of this study suggest that natural carbon capture projects sequester the highest amounts of carbon in areas of limited land use change and high endemic biodiversity.

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Introduction

After several decades of study and debate, it is now widely agreed amongst ecologists that biodiversity is one of the main drivers of ecosystem functioning (Tilman, Isbell & Cowles, 2014). Rapid anthropogenic development has led to a historic loss of biodiversity which can negatively impact ecosystem functions (EFs) in different ways (Pereira et al., 2024). From maintenance of water quality to regulation of invasive pests and diseases, biodiversity loss can have devastating effects on the EFs humans need (Kattel, 2022). The threat of biodiversity loss led to a burst in research of the relationship between biodiversity and ecosystem functions (BEF) in the 1990s (Ehrlich & Mooney, 1983). Tilman (1999) highlighted two theories of how BEF relationships can operate: the sampling effect (where higher biodiversity increases the chances that a species present is highly functional) and the niche differentiation effect (where a heterogeneous habitat prevents one species from dominating but instead promotes complementarity and coexistence of species which increase BEF). These theories have inspired many observational and experimental BEF studies aiming to understand the effects of biodiversity loss on ecosystem functions (Eisenhauer et al., 2016; Godoy et al., 2020). After the detrimental effects of biodiversity loss were highlighted, conservation efforts such as biodiversity hotspots were proposed as a method of protecting areas of high endemic biodiversity while promoting ecosystem functioning (Marchese, 2015). Despite these efforts, it is estimated that 37% of species on Earth will either be threatened or extinct by the year 2100 (Isbell et al., 2023). We must understand the nuances of BEF relationships in order to maintain EFs in the face of massive biodiversity loss.

Carbon sequestration is an EF that is becoming increasingly topical as a link between the climate crisis and biodiversity loss (Weiskopf et al., 2024). With the global push for carbon neutrality as a method for climate change mitigation, there is a growing demand for natural

methods for sequestering carbon from the atmosphere (Hu et al., 2022). Previous carbon capture projects have faced consequences such as displacement of endemic biodiversity and reduction in croplands, primarily because these initiatives involve creating large plantations of monocultures (Di Sacco et al., 2021). Greater biodiversity increases the level of carbon sequestration in ecosystems, meaning there is a need to rethink many carbon projects (Weiskopf et al., 2024). Additionally, carbon capture projects require available land which, with increased anthropogenic expansion and globalisation, is becoming increasingly scarce (Lambin & Meyfroidt, 2011). Therefore, it is imperative to understand how carbon sequestration can be maximised to effectively implement these projects using as few resources as possible.

BEF models tend to vary drastically across studies (Weiskopf et al., 2022). There is generally an asymptotic relationship found in BEF models, where EF will increase with biodiversity to a point where additional species appear to become redundant (Ali, 2023). It is common for BEF models to vary across spatial and temporal scales, making it difficult to compare models and to consolidate global trends (Weiskopf et al., 2022). This variation can lead to drastically different results, as smaller studies may find local biodiversity does not decline at the same rate as global biodiversity, or shorter studies may see less variation in EFs than longer studies that can measure these changes over time (Hagan, Vanschoenwinkel & Gamfeldt, 2021). Additionally, many BEF models have focused on one specific EF or measure of biodiversity at a time while ecosystems are often multifunctional and multiple biodiversity metrics such as species richness, community composition, and functional diversity may affect ecosystem functioning (Hu et al., 2022; Weiskopf et al., 2022). These restricted models fail to capture the complexity of ecosystems and account for the range of possible influences on BEF relationships.

This study uses an extensive BEF dataset to fill these gaps in our knowledge. To capture the complexity of these systems and gain a better understanding of general BEF trends,

I consider multiple EFs and measures of biodiversity simultaneously. I also compare multiple EFs together to terrestrial carbon sequestration to see how drivers of variation differ between EFs. Additionally, I include a data from a range of studies with different lengths of study, spatial extents, and geographic locations to study the effects of these spatial and temporal factors on BEF relationships. I aimed to determine what variables drive the most variation within BEF relationships across ecosystem functions globally, and how changes in these variables maximise BEF. To achieve this, I compared the parameters of BEF models across 12 EFs to model the impacts of anthropogenic, environmental, and geographic factors on these relationships. I then applied this approach specifically to data on terrestrial carbon sequestration. Biome caused more variation in BEF relationships than any other factor, but land use was very important specifically to carbon sequestration. Additionally, in hotspots of high endemic biodiversity, higher levels carbon sequestration could occur with less biodiversity than outside of the hotspots. This study demonstrates the effects of human modification of land, functional diversity, and endemic biodiversity on ecosystem functioning. Effective carbon sequestration projects must take these factors into account to effectively mitigate climate change.

Methods

To understand the drivers of variation in biodiversity-ecosystem function (BEF) relationships, this study used data from a comprehensive literature search to create nonlinear least squares models of biodiversity and ecosystem functioning for each ecosystem function (EF). I then compared the parameters of these models using linear models to determine which factors explained most of the variance in biodiversity ecosystem functioning relationships. I conducted additional analyses of BEF parameters to discover patterns under different land use intensities and biodiversity hotspots to discover patterns between these variables. All analyses were carried out in R version 4.3.3. (R Core Team, 2020).

Literature search and assemblage of BEF data

I conducted a literature search of both observational and experimental BEF studies. I searched the Web of Science and Science Direct databases of peer reviewed publications using combinations of the following search string of keywords in the title or abstract of a publication: ("ecosystem service*" OR "ecosystem function*") AND (biodiversity OR "species richness") AND (carbon OR "soil carbon" OR "carbon capture" OR "carbon sequestration"). In this way I collected data on terrestrial carbon sequestration and other EFs. The protocol for data collection was developed by Drs Pearse and Moffet and is available in the Supplementary Materials. I added my data to an existing dataset developed by the Hitachi-Imperial Centre for Decarbonisation and Natural Climate Solutions (hereafter referred to as the "Imperial data"). The total unfiltered dataset included 227,902 rows of data on 26 distinct EFs from 446 studies. Additionally, I extracted historic climate conditions (1970-2000) by GPS location of each study from the WorldClim version 2.1 database (Fick & Hijmans, 2017). Specifically, mean yearly

temperature (degrees C) and precipitation (mm) were included for each study, as these climatic variables can directly affect ecosystem function and biodiversity (Weiskopf et al., 2020).

Due to the complexity of the large dataset, I cleaned and filtered the data to improve the accuracy of my subsequent analysis. I labelled groups of data by DOI, location, the taxa studied, their biodiversity measurements, and their EF in order to compare unique studies against each other. I removed any biodiversity or EF data with missing values. I then filtered out studies that had less than ten measurements of biodiversity and ecosystem function as this reduced the number of missing values in the results of my further analysis. Additionally, I removed studies from before 1990 as the early 1990s saw a rise in concerns about biodiversity loss and a shift from theoretical biodiversity research to specific studies on biodiversity effects on EF (Tilman, Isbell & Cowles, 2014). I cleaned the data by ensuring dates, units, coordinates, and names were each written in the same format to improve accuracy and address human error in data collection. Finally, I z-standardised the biodiversity measurements and the ecosystem function measurements to compare data measured in different units and improve model interpretability (Schielzeth, 2010). The final dataset used contained 123,172 entries covering 12 EFs across 244 countries.

Modelling BEF relationships

To determine the maximum level of ecosystem functioning and how quickly systems can reach that maximum, I modelled BEF relationships for each study included in the dataset. BEF relationships tend to follow saturating curves but Cardinale et al. (2011) found that the Michaelis-Menten model (Figure 1) portrays this relationship best (Tilman et al., 2001; Ali, 2023). According to Daam et al. (2019), the benefit of using a Michaelis-Menten model for BEF relationships is not ecosystem-specific and is therefore applicable to all the EFs in the dataset. I subset the data by EF and plotted the data to visually check for outliers, which I removed. I

created initial values for the models specific to each EF to improve model accuracy. I then fitted Michaelis-Menten models to each group of data using the function “nls” from the R package “stats” (R Core Team, 2020). From these models I extracted the V_{\max} and the K_m (Figure 1). The V_{\max} represents the horizontal asymptote or maximum level of EF in a system. The K_m represents the value of biodiversity at half the value of V_{\max} . This parameter acts as an explanation of the rate at which a system reaches the maximum level of EF. When describing to a “good” BEF relationship, I imply a high V_{\max} , meaning a high level of EF, and a low K_m , meaning a low level of biodiversity is needed for a high level of EF. I removed any missing or repeated values from the data to reduce Type I error and any non-independence in the data. I organised the data into two data frames for analysis: one with data on all EFs and one with only terrestrial carbon sequestration data.

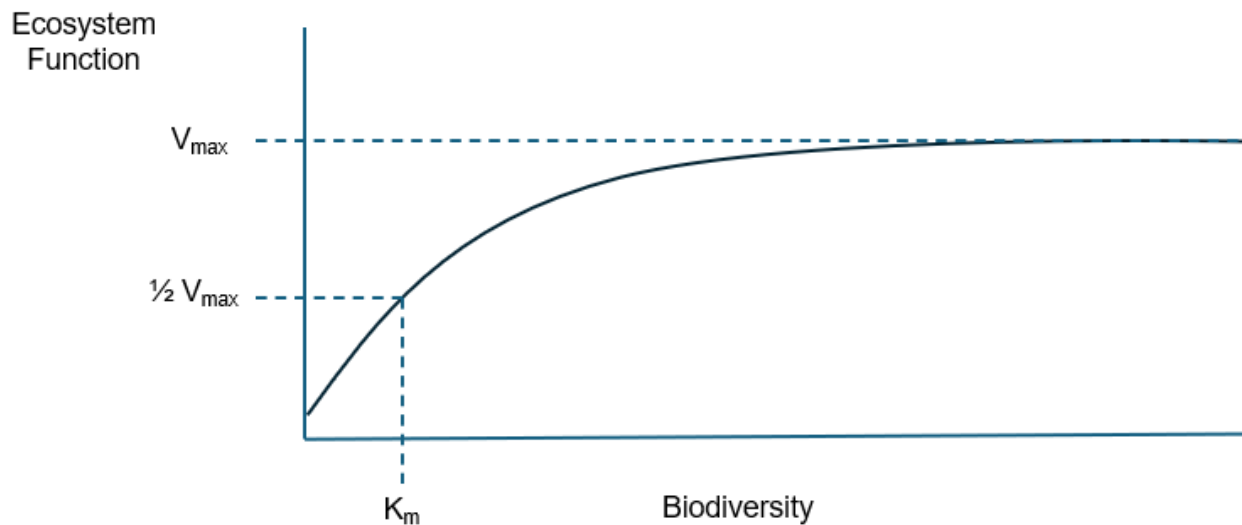


Figure 1. Michaelis-Menten model of BEF relationships. This formula was used to plot a nonlinear least squares model of the relationship between biodiversity and ecosystem function for each study in the Imperial dataset. V_{\max} represents the asymptote or maximum level of ecosystem functioning. K_m is the value of biodiversity at half V_{\max} , which gives an indication of the amount of biodiversity needed to reach a certain level of ecosystem functioning.

Determining relative importance of variables

I assessed the relative importance of variables for four BEF parameters: V_{\max} for all EFs (hereafter referred to by AV_{\max}), V_{\max} for terrestrial carbon sequestration (CV_{\max}), K_m for all EFs (AK_m), and K_m for terrestrial carbon sequestration (CK_m).

Ecological studies often include collinear variables that make it difficult to distinguish the effects between them as the variables (Graham, 2003). To check for multicollinearity between variables, I used the function “collinear” from the package “collinear” (Benito, 2023). This function produces a list of variables with low levels of collinearity and low variance inflation factor (VIF) values. It is particularly useful because it can assess collinearity between categorical and numerical variables. I followed the methods suggested by Benito (2023) and specified the maximum bivariate correlation as 0.75, the maximum VIF as 5, and the encoding method to convert categorical variables to numeric as “mean”. I checked individual correlations and VIF values and removed any variables with high values that the original function missed. I repeated this process with each of the four BEF parameters to produce a list of variables with low collinearity for each one. The variables included in the RWAs are outlined in Table 1.

I determined the relative importance of the variables using a relative weights analysis (RWA). First, I made dummy variables for all categorical variables to be read as numeric so they could be included in the analysis (Hardy & Bryman, 2009). I then conducted the RWA of non-collinear variables using the package “rwa” as outlined by Chan (2019; Tonidandel & LeBreton, 2015). Finally, I ran two linear models to obtain the unstandardised and the standardised regression weights for each variable (Table 2). I conducted this process for each of the four analyses using their respective specified variables.

Table 1. All variables included in RWAs. Variables were used in different combinations to reduce collinearity.

| Variable | Units | Description |
|------------------------|---------------------|---|
| Spatial scale of study | Metres ² | Area of study site |
| Latitude | Decimal degrees | GPS centre of study |
| Longitude | Decimal degrees | GPS centre of study |
| Duration | Years | Length of study from start to end date |
| Start year | Years | When study began |
| Continent | Categorical | Location of study |
| Land use | Categorical | The predominant land use where the study was conducted (i.e. age of vegetation and land use type such as cropland). |
| Land use intensity | Categorical | Categorised by impact and fraction of site affected (i.e. minimal, light, intense) |
| EF | Categorical | Following definitions from IPBES (2019) |
| Biome | Categorical | Predominant biome (i.e. terrestrial, marine, freshwater) |

Analysis of land use and biodiversity hotspots on BEF relationships

To explore patterns in the results from the previous section of analysis, I analysed the relationship between BEF parameters, land use, and biodiversity hotspots. I began by converting the Imperial data into simple features (sf) data using the geographic coordinates from each study and setting the data to a WGS84 projection. I confirmed that this data had no missing or repeated values. I then created a second sf object from this data by filtering for only data on terrestrial carbon sequestration so I could compare carbon sequestration to all other

EFs. These conversions were necessary so my data would be compatible for analysis with other geospatial data.

As the RWA suggested that land use and land use intensity explain significant amounts of BEF variation (Table 2), I used data on global modification of land to see how the relationship applies to human land use intensity (Kennedy et al., 2020). This data, from NASA's Socioeconomic Data and Applications Center (SEDAC), measured human modification of land as a cumulative effect of 13 anthropogenic stressors on a continuous 0-1 metric reflecting the proportion of landscape modified (Kennedy et al., 2020). The data is originally available at a 1km resolution, although I aggregated the data by a factor of 10 by mean value to reduce the resolution to a level more appropriate for this exploratory analysis using the function "aggregate" from the R package "raster" (Kennedy et al., 2020; Hijmans et al., 2023). I used the data in the geographic projection (WGS84) so the scale would match that of the Imperial data. I created a sf object from the raster data to be compatible with the Imperial data. I categorised the SEDAC data into three categories to simplify the analysis following the categories from the Imperial data: values from 0-0.33 was classed as "minimal", from 0.34-0.66 classed as "light", and 0.67-1.0 classed as "intense" (Figure 2A). I joined the data with a simplified sf object from Imperial data containing the EF, V_{max} , K_m , and geometry data. I used the function "st_nearest_feature" from the R package "sf" as this function joins the Imperial points by where they are closest to the SEDAC data in case the two do not perfectly overlap (Pebesma et al., 2024). I then filtered the data to remove any repeated values that may have been made while joining the data and repeated this joining process to create another sf object filtered to only include terrestrial carbon sequestration data.

I conducted a series of Kruskal Wallis tests on the BEF parameters using this data to find any differences in the parameters between the land use intensity categories. For tests that suggested there were significant differences between categories, I conducted a Dunn's test with

a Benjamini-Hochberg adjustments. I then compared the medians of each BEF parameter under different land use conditions to determine which had the highest level of ecosystem functioning.

The final section of this analysis considered the relationship between BEF parameters and biodiversity hotspots. I used data on global biodiversity hotspots as defined by Conservation International (Hoffman et al., 2016). I filtered this data to just include terrestrial data and cleaned it using the function `st_make_valid` from the R package “sf” and removed a polygon denoting Micronesia-Polynesia as it had been corrupted and did not overlap with any Imperial data as displayed in Figure 2B (Pebesma et al., 2024).

To prepare the data for analysis, I created an object containing data from the intersection of the parameter data and the hotspots and another object containing data from the difference between the two. I coded these two objects 1 (study located in a hotspot) and 0 (study not located in a hotspot). I joined the two data frames and conducted another Shapiro-Wilks test to test for any difference in parameter between the two states. I completed this analysis for AV_{max} , AK_m , CV_{max} , and CK_m .

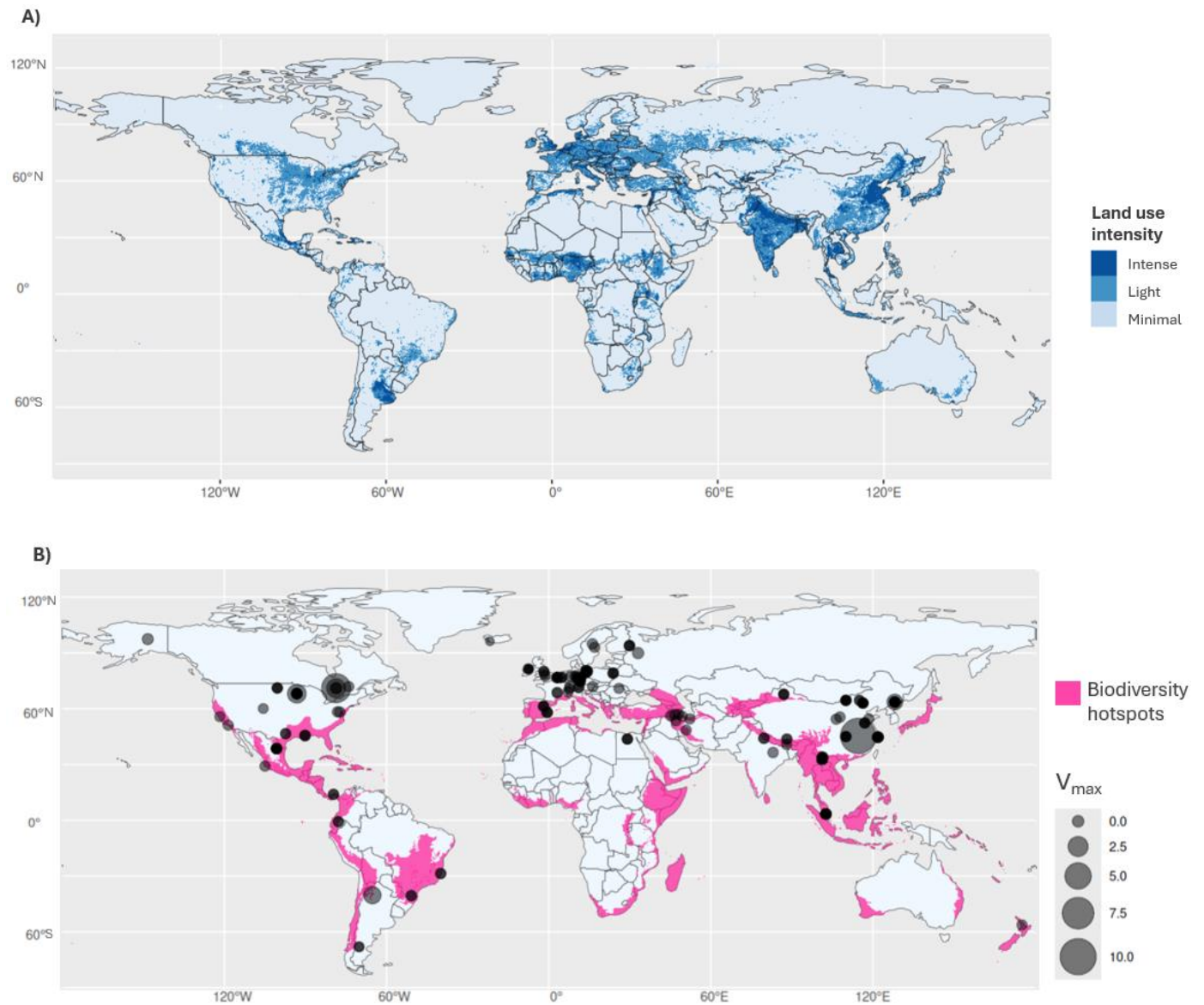


Figure 2. Maps of data used in analyses. A) Map of SEDAC data categorised by land use intensity (minimal, light, and intense. B) Map of biodiversity hotspot data courtesy of Conservation International. Each point represents a study in the Imperial dataset, with the size of the point denoting the V_{max} of the BEF relationship from that study. Base map courtesy of Natural Earth (2024).

Results

I ran a Michaelis-Menten nonlinear least squares model on each study in the Imperial dataset and extracted parameters describing biodiversity and ecosystem function (BEF). These parameters include V_{\max} representing the maximum level of EF and K_m which represents the rate a system reaches V_{\max} . After BEF models had been run and the parameters extracted, I had 54,699 observations of V_{\max} and K_m for 12 different EFs including terrestrial carbon sequestration. I then ran a relative weights analysis and analysed the BEF parameters under different global land use intensity and 35 global biodiversity hotspots.

Relative weights analysis

The RWA for AV_{\max} found that biome was responsible for 43.29% of the variation in the maximum level of ecosystem function in BEF models (Table 2, Figure 3). This result aligns with that of the linear models which predicted that with every shift from the reference level (freshwater to marine to terrestrial), the AV_{\max} will decrease ($b = -0.71$; $\beta = -0.32$; $R^2 = 0.118$; $p < 0.001$, see Table 2). This result suggests that aquatic biomes have higher levels of ecosystem functioning than terrestrial biomes, however the variation within biomes is high. The linear models also found that land use has a significant effect on AV_{\max} and with every shift from the reference level (intense to light to minimal), V_{\max} will increase ($b = 0.02$; $\beta = 0.15$). This result suggests that lower levels of land use intensity result in higher ecosystem functioning. In terms of AK_m , EF explained the most variation (37.77%), suggesting that certain EFs require more biodiversity than others to reach their maximum level. The linear models did support this result ($b = 0.01$; $\beta = 0.03$; $R^2 = 0.035$; $p = 0.081$), however instead found that biome significantly increased AK_m ($b = 0.96$; $\beta = 0.18$). This result suggests that not only do aquatic environments

have higher overall levels of ecosystem functioning, they require less biodiversity than terrestrial systems to reach their maximum level.

Looking specifically at models of biodiversity and terrestrial carbon sequestration, the RWA found that land use explained the largest amount of variation in both CV_{\max} and CK_m . Land use explained 31.63% of the variation in CV_{\max} ($b = 0.04$; $\beta = 0.19$, $R^2 = 0.471$; $p = 0.002$), although the linear models found that land use did not have a significant effect on CV_{\max} . Instead, continent and land use intensity significantly influenced CV_{\max} and explain the next highest amount of variation in CV_{\max} (24.69% and 20.54% respectively). Land use also explained the most amount of the variation in CK_m (40.09%, see Figure 3), with continent and land use intensity following. These results suggest that human modification of land causes significant variation in carbon sequestration globally. However, the linear models for CK_m predicted that none of the variables included had a significant influence on the rate at which ecosystems meet their maximum level of functioning ($R^2 = 0.107$; $p = 0.654$). It is important to note that terrestrial carbon sequestration only takes place in one biome, hence why its results differ from those of all EFs considered together.

Table 2. Summary of relative weight analyses and linear models of BEF parameters for all ecosystem functions (AV_{max} , AK_m) and terrestrial carbon sequestration alone (CV_{max} , CK_m). (*), Statistically significant influence on parameter; b , β , unscaled and scaled linear regression coefficients; RW, raw relative weights which sum to R^2 ; CI-L, CI-U, lower and upper 95% confidence intervals of RWA; RS-RW, rescaled relative weights representing the percentage of variation in BEF explained by the variable. Rows with highest RS-RW are underlined and bold.

| Predictor | b | β | RW | CI-L | CI-U | RS-RW (%) |
|--|-----------------|-----------------|---------------|----------------|---------------|----------------|
| Criterion = AV_{max} ($R^2 = 0.118$; $F[11,499] = 6.049$, $p < 0.001$) | | | | | | |
| Intercept | 0.1740 | | | | | |
| Biome | *-0.7070 | *-0.3169 | 0.1803 | -0.0019 | 0.0169 | 43.2936 |
| EF | -0.0129 | -0.077 | 0.0509 | -0.0081 | 0.0040 | 12.2159 |
| Land use | *0.0235 | *0.1526 | 0.1099 | -0.0015 | 0.0184 | 26.3859 |
| Land use intensity | -0.0300 | -0.0256 | 0.0271 | -0.0051 | 0.2383 | 6.5065 |
| Continent | 0.0054 | 0.1062 | 0.0235 | -0.0013 | 0.0180 | 5.6391 |
| Longitude | 0.0002 | 0.0240 | 0.0044 | 0.0004 | 0.0340 | 1.0594 |
| Study start year | -0.0059 | -0.0529 | 0.0104 | -0.0002 | 0.0267 | 2.5079 |
| Duration (years) | -0.0008 | -0.0611 | 0.0044 | -0.0011 | 0.0356 | 1.0573 |
| Precipitation (mm) | 0.0000 | -0.0745 | 0.0027 | 0.0052 | 0.4859 | 0.6448 |
| Latitude | -0.0007 | -0.0176 | 0.0027 | -0.0013 | 0.0075 | 0.6571 |
| Spatial scale (m ²) | 0.0000 | -0.0085 | 0.0001 | -0.0130 | 0.0018 | 0.0323 |
| Criterion = AK_m ($R^2 = 0.035$; $F[11,499] = 1.654$, $p = 0.081$) | | | | | | |
| Intercept | 0.1172 | | | | | |
| Biome | *0.9625 | *0.1836 | 0.0554 | -0.0065 | 0.2773 | 26.8298 |
| EF | 0.0123 | 0.0333 | 0.0780 | -0.0351 | 0.0242 | 37.7663 |
| Land use | -0.0142 | -0.0392 | 0.0403 | -0.0104 | 0.0125 | 19.5200 |
| Land use intensity | -0.0189 | -0.0069 | 0.0182 | -0.0176 | 0.0143 | 8.8153 |
| Continent | -0.0165 | -0.0138 | 0.0069 | -0.0175 | 0.0134 | 3.3277 |
| Longitude | 0.0011 | 0.0509 | 0.0037 | -0.0165 | 0.0109 | 1.8004 |
| Study start year | -0.0072 | -0.0272 | 0.0004 | -0.0159 | 0.0083 | 0.1856 |
| Duration (years) | -0.0045 | -0.0151 | 0.0012 | -0.0135 | 0.0182 | 0.5796 |
| Precipitation (mm) | 0.0000 | -0.0184 | 0.0015 | -0.0141 | 0.0084 | 0.7221 |
| Latitude | 0.0015 | 0.0158 | 0.0009 | -0.0173 | 0.0125 | 0.4430 |
| Spatial scale (m ²) | 0.0000 | -0.0050 | 0.0000 | -0.0119 | 0.0379 | 0.0103 |
| Land use | -0.0142 | -0.0392 | 0.0554 | -0.0104 | 0.0125 | 26.8298 |
| Criterion = CV_{max} ($R^2 = 0.471$; $F[7,34] = 4.323$, $p = 0.002$) | | | | | | |
| Intercept | *11.2882 | | | | | |
| Land use | 0.0407 | 0.1934 | 0.3088 | -0.0786 | 0.1218 | 31.6308 |
| Continent | *-1.4510 | *-4.8970 | 0.2411 | -0.0228 | 0.2907 | 24.6902 |
| Land use intensity | *-1.5161 | *-1.5350 | 0.2005 | -0.0117 | 0.4730 | 20.5399 |
| Precipitation (mm) | *-0.0013 | *-1.1600 | 0.0902 | -0.0368 | 0.1690 | 9.2370 |
| Latitude | *-0.0324 | *-1.0110 | 0.0560 | -0.0610 | 0.1124 | 5.7372 |
| Duration of study | 0.0132 | 0.2286 | 0.0797 | -0.0699 | 0.3524 | 8.1648 |
| Criterion = CK_m ($R^2 = 0.107$; $F[6,35] = 0.697$, $p = 0.654$) | | | | | | |
| Intercept | 9.9172 | | | | | |
| Land use | -0.0254 | -0.0143 | 0.4000 | -0.1013 | 0.0343 | 40.0878 |
| Continent | -0.6456 | -0.2581 | 0.2163 | -0.0416 | 0.2527 | 21.6736 |
| Land use intensity | -2.1250 | -0.2549 | 0.1620 | -0.0599 | 0.1505 | 16.2363 |
| Precipitation (mm) | -0.0029 | -0.3059 | 0.1145 | -0.0735 | 0.1376 | 11.4777 |
| Latitude | -0.0096 | -0.0355 | 0.0944 | -0.1180 | 0.0668 | 9.4632 |
| Duration of study | -0.0121 | -0.0249 | 0.0106 | -0.1248 | 0.0718 | 1.0614 |

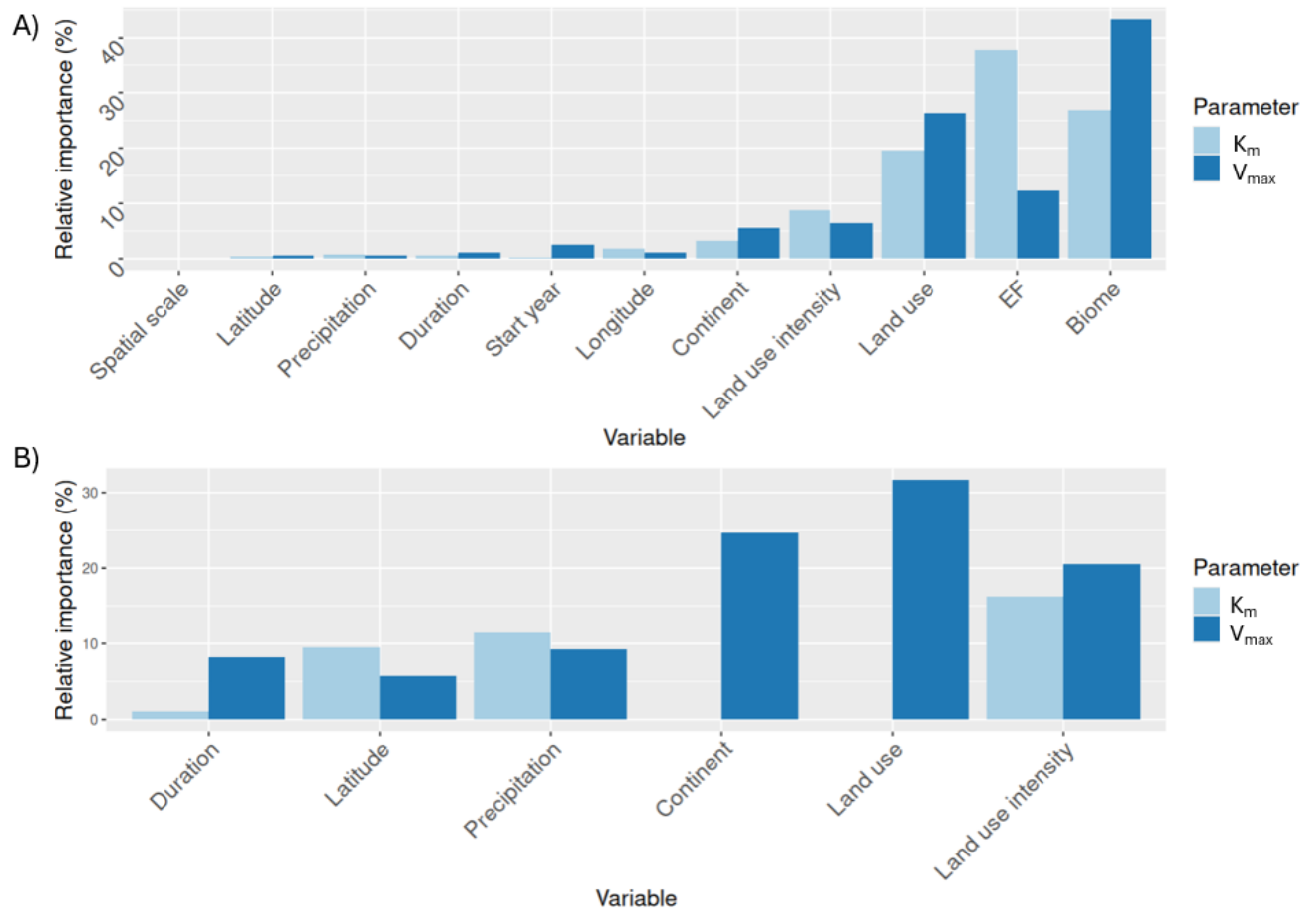


Figure 3. Results of relative importance analyses (RWAs). Bars represent the percentage of total variation explained by each variable within BEF parameters (V_{max} and K_m). The variables included are those controlled for multicollinearity. Plot A) Results of RWA of BEF parameters when all EFs are considered together. Plot B) Results of RWA for parameters of models of biodiversity and terrestrial carbon sequestration.

Analysis of impacts of land use intensity and biodiversity hotspots on BEF

As all BEF parameters were not normally distributed following a Shapiro-Wilk test (all p -values < 0.05 , see Supplementary Materials Table 1), I conducted a series of Kruskal-Wallis tests to find the impact of land use intensity on the BEF parameters. Only AV_{max} and CV_{max} had significant differences between categories of land use intensity (see Supplementary Materials

Table 2). The Dunn's test only found significant differences in AV_{\max} and CV_{\max} between intense and light land use intensity (Supplementary Materials Table 3), meaning the light and minimal categories may overlap. The highest median values for both AV_{\max} and CV_{\max} were in light land use intensity (-0.080, -0.079, Supplementary Materials Table 4), suggesting that less land use intensity increases ecosystem functioning.

The only BEF parameter that significantly differed depending on whether it was located inside of a biodiversity hotspot or not was CK_m ($H(1) = 4.513$, $p = 0.034$, Supplementary Materials Table 5). The median CK_m was higher (-0.025) outside of hotspots than those inside hotspots (-0.160). This result means that in biodiversity hotspots, higher levels of terrestrial carbon sequestration can be reached with lower levels of biodiversity than outside of biodiversity hotspots.

Discussion

This study found that biome, ecosystem function (EF) and land use explain more variation in different biodiversity and ecosystem function (BEF) relationships than any other variable. Additionally, being in a biodiversity hotspot can significantly impact the amount of carbon sequestered in a system. These results predict that the most effective natural carbon sequestration projects would be in areas of high endemic biodiversity with limited human modification of land.

Relative importance of variables in BEF models

When all EFs are analysed together, biome and EF explain the most variation in V_{\max} and K_m . The results of this study suggest that aquatic ecosystems have greater and faster BEF relationships than terrestrial ecosystems. These results align with results of previous research, such as how coastal and marine systems can store more carbon per unit area than terrestrial forests (IUCN, 2017). Additionally, terrestrial ecosystems are more heterogeneous in factors such as temperature than aquatic systems, which may lead to further differences in variation between biomes (Steele, Brink & Scott, 2019). Wu et al. (2023) suggest that differences in functional diversity explain the variation caused by EF. For example, a skew in community composition towards producers or consumers can alter the dynamics of food webs and ultimately ecosystem functioning (Wu et al., 2023). This idea may relate to the discrepancy between biomes, as terrestrial systems have much higher levels of plant biomass than aquatic systems, although it is estimated that 70% of global animal biomass is located in the ocean (Burgess & Gaines, 2018; Bar-On, Phillips & Milo, 2018). It is also likely that the variation in BEF relationships caused by biome and EF is interconnected, as terrestrial and aquatic ecosystems often interact and contain multiple EFs (Dahlin et al., 2021). This complexity makes it difficult to determine whether one biome has better BEF relationships than another. As visualised by Figure 2B, all the data included in this analysis was collected on or relatively close to land,

meaning there is likely some spatial correlation between biomes and EFs. These ideas could be applied to future studies of blue carbon (or aquatic carbon sequestration), which is another important aspect of climate mitigation as, according to the IUCN (2014), a quarter of global carbon emissions are sequestered by the ocean yearly.

It is interesting that variables such as spatial scale and duration of the study did not contribute more to BEF variation because it has been widely found that spatial and temporal changes can drastically change BEF relationships (Thompson et al., 2018; Tilman, Isbell & Cowles, 2014). A study that takes place across a larger area or over a longer period of time provides more opportunity for species to accumulate (Thompson et al., 2021). Qiu and Cardinale (2020) found that biodiversity effects on ecosystem function increase with temporal and spatial scales, and that small scale studies often underestimate these effects. However, the Imperial data covers a wide range of spatial scales and study durations, so the fact that so little of the variation in BEF parameters was explained by these spatial and temporal factors emphasises the importance of biome and EF on BEF relationships.

This study also found that land use explains most of the variation in the relationship between biodiversity and terrestrial carbon sequestration. Chen et al. (2020) found similar results when considering the carbon sequestration levels in afforested ecosystems (a common strategy in many natural carbon capture projects). They found that the previous land use type and the age of afforestation significantly affected the carbon exchange in these ecosystems (Chen, Yu & Wang, 2020). Anthropogenic land use change not only causes biodiversity loss through destruction of habitat, but further reduces many EFs through processes such as destruction of primary vegetation, increased homogeneity of landscapes, and degradation of soil quality (Pereira et al., 2024; Hasan et al., 2020). Young ecosystems, such as those of recent restoration or afforestation efforts, tend to have lower rates of carbon sequestration in their earlier years, but this increases with age and succession (Goulden et al., 2011; Wang et al., 2022). It is evident from these results that land use change and human disturbance have

detrimental impacts on carbon sequestration, suggesting that carbon capture projects should prioritise protecting existing, older ecosystems as these can more efficiently sequester carbon than younger projects (Buotte et al., 2020; Di Sacco et al., 2021).

Effects of land use and biodiversity hotspots on BEF relationships

This study also found that light human land use intensity had the highest V_{\max} values meaning that having less human modification of land increased the total level of ecosystem functioning in a system. It is worth noting that there was no significant difference between minimal and light land use intensities, so light land use is not necessarily better than minimal. Areas of light land use intensity would have greater levels of biodiversity than those of intense land use because of less habitat degradation and fragmentation, allowing higher levels of ecosystem functioning (Semenchuk et al., 2022). Additionally, land use often creates greater homogeneity of habitats which, according to Tilman's (1999) explanation of niche differentiation and BEF, can increase linearity of BEF models. This increase in linearity may relate to why there were no effects of land use modification on K_m parameters as greater amounts of biodiversity would be needed to reach the same level of ecosystem functioning. These results indicate that less human modification of land will benefit BEF.

There are drawbacks in using the SEDAC human land modification data to compare to the Imperial data. The SEDAC data was produced using remote sensing combining multiple data sets with a median year of 2016 (Kennedy et al., 2019). The Imperial data used in this study is from at the earliest 1990, so it would be better to use data on land use intensity from the year of the study as this changes over time. Additionally, there is an added level of spatial uncertainty in the SEDAC data due to the fact it was reprojected from a Mollweide projection (Kennedy et al., 2020). Finally, the Imperial data and the SEDAC data are measured on different scales, with many studies from the Imperial data only taking place in plots of a few

metres-squared in area which is much smaller than the kilometre-squared resolution of the SEDAC data that I further aggregated. To improve these limitations, perhaps the SEDAC data could be used to create models of past and future land use, similar to the historic and future climatic conditions compiled in the Worldclim database (Fick & Hijmans, 2017). Most models so far either only cover certain regions or limited time periods (Chen et al., 2020; ESRI, 2021; An et al., 2024). Having a global dataset on both historic and future land use could improve this study by considering changes in land use over time and possibly at a finer scale. Then, further research could better predict how changing land use will affect BEF relationships in order to create preventative measures for future biodiversity loss.

The presence of a biodiversity hotspot did not significantly correlate with the majority of the BEF parameters, only the K_m of carbon sequestration. This result suggests that when in a biodiversity hotspot, less diversity is required to reach a higher level of carbon sequestration. These biodiversity hotspots were defined partially by their level of endemic plant species, which often have high levels of functionality because they are well adapted to their environment (Hoffman et al., 2016; Keppel et al., 2018). This idea supports the sampling effect theory, which suggests that having a larger pool of species in an ecosystem increases the chances of a dominant, competitive species that is more efficient at using resources and consequently more productive than the other species (Tilman, 1999). Carbon sequestration is highly linked to plant functionality such as productivity, therefore having few, highly functional, dominant plant species may result in higher levels of carbon sequestration than in regions with less adapted species (Chen et al., 2018). This idea aligns with previous research proposing that functional richness is highly linked to ecosystem functioning (Abonyi, Horváth & Ptacnik, 2018; Le Bagousse-Pinguet et al., 2021). It is possible that a significant difference between the presence of a biodiversity hotspot was not found for other BEF parameters because other EFs may not benefit from endemic species as much as carbon sequestration. For example, “food and feed” refers to the production of food for humans and feed for livestock from agricultural land (IPBES, 2019).

Agriculture has been shown to threaten endemic species and reduce biodiversity, suggesting that biodiversity hotspots would not improve production of food and feed (Zabel et al., 2019). The connection between endemism, functional diversity, and ecosystem function is important to consider during conservation efforts.

Implications and conclusions

Despite the growing demand for nature-based solutions in climate mitigation and sustainability, there are numerous challenges faced by conservation and carbon sequestration projects (Seddon et al., 2020). To effectively protect and enhance ecosystem services in the face of global biodiversity loss and climate change, it is necessary to know where to prioritize efforts to maximize efficiency of resources. Since land use intensity is responsible for the most variation in carbon sequestration, it would make sense to organise carbon sequestration projects in places with the least amount of human impact. Additionally, it would be worthwhile to invest in a location that can reach a decent level of carbon sequestration with the least amount of biodiversity as this would require fewer resources to maintain, such as a biodiversity hotspot. Myers et al. (2000) outline how most biodiversity hotspots cover developing countries in the tropics. If these areas are indeed the most efficient places for carbon capture projects, it is essential to ensure that these are conducted with local communities and the socio-economic implications of these projects in mind (Herr et al., 2019). Future work must dive deeper into the connections between terrestrial carbon sequestration, land use intensity, and endemic biodiversity in order to maximise the efficiency of future carbon sequestration projects.

This study evaluated the contribution of a multitude of factors on BEF relationships using multiple extensive and detailed datasets. It is poignant that this study found anthropogenic land use causes significant variation in BEF relationships more than three decades after the fear of consequences of human destruction of ecosystems inspired massive growth in early BEF research (Ehrlich & Mooney, 1983; Myers, 1990; Tilman, Isbell & Cowles, 2014). I found support

for two contrasting theories of BEF relationships (the sampling effect and niche differentiation). Though these theories have different mechanisms underlying BEF relationships, both find that greater biodiversity will increase ecosystem functioning (Tilman, 1999). In the face of historic biodiversity loss, human expansion, and climate change, mitigation strategies like carbon capture projects must be used effectively. The results of this study suggest areas of limited human land modification and high endemic biodiversity are optimal to maximise carbon sequestration. Further work should investigate the impact of future land use change on ecosystem functioning and could apply the methods of this study to carbon sequestration in other biomes in order to increase global carbon sequestration and climate change mitigation.

Data and Code Availability

Supplementary Materials are available at the following GitHub repository:

https://github.com/sineadmoss/2024Project_Supplementary_Materials

Imperial BEF dataset is available on request from Dr Pearse.

References

- Abonyi, A., Horváth, Z. & Ptacnik, R. (2018) Functional richness outperforms taxonomic richness in predicting ecosystem functioning in natural phytoplankton communities. *Freshwater Biology*. 63 (2), 178–186. doi:10.1111/fwb.13051.
- Ali, A. (2023) Biodiversity–ecosystem functioning research: Brief history, major trends and perspectives. *Biological Conservation*. 285, 110210. doi:10.1016/j.biocon.2023.110210.
- An, Y., Tan, X., Ren, H., Li, Y. & Zhou, Z. (2024) Historical Changes and Multi-scenario Prediction of Land Use and Terrestrial Ecosystem Carbon Storage in China. *Chinese Geographical Science*. 34 (3), 487–503. doi:10.1007/s11769-024-1424-y.
- Bar-On, Y.M., Phillips, R. & Milo, R. (2018) The biomass distribution on Earth. *Proceedings of the National Academy of Sciences of the United States of America*. 115 (25), 6506–6511. doi:10.1073/pnas.1711842115.
- Baxter, J.M. (2014) *The significance and management of natural carbon stores in the open ocean*. 2014. <https://iucn.org/resources/publication/significance-and-management-natural-carbon-stores-open-ocean> [Accessed: 20 August 2024].
- Benito, B. (2023) *BlasBenito/collinear*. <https://github.com/BlasBenito/collinear>.
- Buotte, P.C., Law, B.E., Ripple, W.J. & Berner, L.T. (2020) Carbon sequestration and biodiversity co-benefits of preserving forests in the western United States. *Ecological Applications*. 30 (2), e02039. doi:10.1002/eap.2039.
- Burgess, M.G. & Gaines, S.D. (2018) The scale of life and its lessons for humanity. *Proceedings of the National Academy of Sciences of the United States of America*. 115 (25), 6328–6330. doi:10.1073/pnas.1807019115.
- Cardinale, B.J., Matulich, K.L., Hooper, D.U., Byrnes, J.E., Duffy, E., Gamfeldt, L., Balvanera, P., O'Connor, M.I. & Gonzalez, A. (2011) *The functional role of producer diversity in ecosystems*. doi:10.3732/ajb.1000364.
- Chan, M. (2019) *martinctc/rwa*. <https://github.com/martinctc/rwa>.
- Chen, M., Vernon, C.R., Graham, N.T., Hejazi, M., Huang, M., Cheng, Y. & Calvin, K. (2020) Global land use for 2015–2100 at 0.05° resolution under diverse socioeconomic and climate scenarios. *Scientific Data*. 7 (1), 320. doi:10.1038/s41597-020-00669-x.
- Chen, S., Wang, W., Xu, W., Wang, Y., Wan, H., et al. (2018) Plant diversity enhances productivity and soil carbon storage. *Proceedings of the National Academy of Sciences*. 115 (16), 4027–4032. doi:10.1073/pnas.1700298114.
- Chen, Z., Yu, G. & Wang, Q. (2020) Effects of climate and forest age on the ecosystem carbon exchange of afforestation. *Journal of Forestry Research*. 31 (2), 365–374. doi:10.1007/s11676-019-00946-5.

Daam, M.A., Teixeira, H., Lillebø, A.I. & Nogueira, A.J.A. (2019) Establishing causal links between aquatic biodiversity and ecosystem functioning: Status and research needs. *Science of The Total Environment*. 656, 1145–1156. doi:10.1016/j.scitotenv.2018.11.413.

Dahlin, K.M., Zarnetske, P.L., Read, Q.D., Twardochleb, L.A., Kamoske, A.G., Cheruvilil, K.S. & Soranno, P.A. (2021) Linking Terrestrial and Aquatic Biodiversity to Ecosystem Function Across Scales, Trophic Levels, and Realms. *Frontiers in Environmental Science*. 9. doi:10.3389/fenvs.2021.692401.

Di Sacco, A., Hardwick, K.A., Blakesley, D., Brancalion, P.H.S., Breman, E., Cecilio Rebola, L., Chomba, S., Dixon, K., Elliott, S., Ruyonga, G., Shaw, K., Smith, P., Smith, R.J. & Antonelli, A. (2021) Ten golden rules for reforestation to optimize carbon sequestration, biodiversity recovery and livelihood benefits. *Global Change Biology*. 27 (7), 1328–1348. doi:10.1111/gcb.15498.

Ehrlich, P.R. & Mooney, H.A. (1983) Extinction, Substitution, and Ecosystem Services. *BioScience*. 33 (4), 248–254. doi:10.2307/1309037.

Eisenhauer, N., Barnes, A.D., Cesarz, S., Craven, D., Ferlian, O., Gottschall, F., Hines, J., Sendek, A., Siebert, J., Thakur, M.P. & Türke, M. (2016) Biodiversity–ecosystem function experiments reveal the mechanisms underlying the consequences of biodiversity change in real world ecosystems. *Journal of Vegetation Science*. 27 (5), 1061–1070. doi:10.1111/jvs.12435.

ESRI (2021) *Esri Land Cover 2050*. 2021. <https://github.com/vannizhang/land-cover-2050#readme> [Accessed: 21 August 2024].

Fick, S.E. & Hijmans, R.J. (2017) WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*. 37 (12), 4302–4315. doi:10.1002/joc.5086.

Godoy, O., Gómez-Aparicio, L., Matías, L., Pérez-Ramos, I.M. & Allan, E. (2020) An excess of niche differences maximizes ecosystem functioning. *Nature Communications*. 11 (1), 4180. doi:10.1038/s41467-020-17960-5.

Goulden, M.L., Mcmillan, A.M.S., Winston, G.C., Rocha, A.V., Manies, K.L., Harden, J.W. & Bond-Lamberty, B.P. (2011) Patterns of NPP, GPP, respiration, and NEP during boreal forest succession. *Global Change Biology*. 17 (2), 855–871. doi:10.1111/j.1365-2486.2010.02274.x.

Graham, M.H. (2003) Confronting Multicollinearity in Ecological Multiple Regression. *Ecology*. 84 (11), 2809–2815. doi:10.1890/02-3114.

Hagan, J.G., Vanschoenwinkel, B. & Gamfeldt, L. (2021) We should not necessarily expect positive relationships between biodiversity and ecosystem functioning in observational field data. *Ecology Letters*. 24 (12), 2537–2548. doi:10.1111/ele.13874.

Hardy, M.A. & Bryman, A. (2009) Google-Books-ID: GMck2KXHDhOC. *Handbook of Data Analysis*. SAGE.

Hasan, S.S., Zhen, L., Miah, Md.G., Ahamed, T. & Samie, A. (2020) Impact of land use change on ecosystem services: A review. *Environmental Development*. 34, 100527. doi:10.1016/j.envdev.2020.100527.

- Herr, D., Blum, J., Himes-Cornell, A. & Sutton-Grier, A. (2019) An analysis of the potential positive and negative livelihood impacts of coastal carbon offset projects. *Journal of Environmental Management*. 235, 463–479. doi:10.1016/j.jenvman.2019.01.067.
- Hijmans, R.J., Etten, J. van, Sumner, M., Cheng, J., Baston, D., et al. (2023) *raster: Geographic Data Analysis and Modeling*. <https://cran.r-project.org/web/packages/raster/index.html>.
- Hoffman, M., Koenig, K., Bunting, G., Costanza, J. & Williams, K.J. (2016) *Biodiversity Hotspots (version 2016.1)*. doi:10.5281/zenodo.3261807.
- Hu, Y., Zhang, Q., Hu, S., Xiao, G., Chen, X., Wang, J., Qi, Y., Zhang, L. & Han, L. (2022) Research progress and prospects of ecosystem carbon sequestration under climate change (1992–2022). *Ecological Indicators*. 145, 109656. doi:10.1016/j.ecolind.2022.109656.
- IPBES (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. *IPBES Secretariat, Bonn, Germany*. 56.
- Isbell, F., Balvanera, P., Mori, A.S., He, J.-S., Bullock, J.M., et al. (2023) Expert perspectives on global biodiversity loss and its drivers and impacts on people. *Frontiers in Ecology and the Environment*. 21 (2), 94–103. doi:10.1002/fee.2536.
- IUCN (2017) *Blue carbon*. 2017. <https://www.iucn.org/resources/issues-brief/blue-carbon> [Accessed: 23 April 2024].
- Kattel, G.R. (2022) Climate warming in the Himalayas threatens biodiversity, ecosystem functioning and ecosystem services in the 21st century: is there a better solution? *Biodiversity and Conservation*. 31 (8), 2017–2044. doi:10.1007/s10531-022-02417-6.
- Kennedy, C.M., Oakleaf, J.R., Theobald, D.M., Baruch-Mordo, S. & Kiesecker, J. (2020) *Global Human Modification of Terrestrial Systems*. doi:10.7927/EDBC-3Z60.
- Kennedy, C.M., Oakleaf, J.R., Theobald, D.M., Baruch-Mordo, S. & Kiesecker, J. (2019) Managing the middle: A shift in conservation priorities based on the global human modification gradient. *Global Change Biology*. 25 (3), 811–826. doi:10.1111/gcb.14549.
- Keppel, G., Ottaviani, G., Harrison, S., Wardell-Johnson, G.W., Marcantonio, M. & Mucina, L. (2018) Towards an eco-evolutionary understanding of endemism hotspots and refugia. *Annals of Botany*. 122 (6), 927–934. doi:10.1093/aob/mcy173.
- Lambin, E.F. & Meyfroidt, P. (2011) Global land use change, economic globalization, and the looming land scarcity. *Proceedings of the National Academy of Sciences*. 108 (9), 3465–3472. doi:10.1073/pnas.1100480108.
- Le Bagousse-Pinguet, Y., Gross, N., Saiz, H., Maestre, F.T., Ruiz, S., Dacal, M., Asensio, S., Ochoa, V., Gozalo, B., Cornelissen, J.H.C., Deschamps, L., García, C., Maire, V., Milla, R., Salinas, N., Wang, J., Singh, B.K. & García-Palacios, P. (2021) Functional rarity and evenness are key facets of biodiversity to boost multifunctionality. *Proceedings of the National Academy of Sciences*. 118 (7), e2019355118. doi:10.1073/pnas.2019355118.

Marchese, C. (2015) Biodiversity hotspots: A shortcut for a more complicated concept. *Global Ecology and Conservation*. 3, 297–309. doi:10.1016/j.gecco.2014.12.008.

Myers, N. (1990) The biodiversity challenge: Expanded hot-spots analysis. *Environmentalist*. 10 (4), 243–256. doi:10.1007/BF02239720.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature*. 403 (6772), 853–858. doi:10.1038/35002501.

Natural Earth (2024) *Natural Earth - Free vector and raster map data at 1:10m, 1:50m, and 1:110m scales*. <https://www.naturalearthdata.com/>.

Pebesma, E., Bivand, R., Racine, E., Sumner, M., Cook, I., Keitt, T., Lovelace, R., Wickham, H., Ooms, J., Müller, K., Pedersen, T.L., Baston, D. & Dunnington, D. (2024) *sf: Simple Features for R*. <https://cran.r-project.org/web/packages/sf/index.html>.

Pereira, H.M., Martins, I.S., Rosa, I.M.D., Kim, H., Leadley, P., et al. (2024) Global trends and scenarios for terrestrial biodiversity and ecosystem services from 1900 to 2050. *Science*. 384 (6694), 458–465. doi:10.1126/science.adn3441.

Qiu, J. & Cardinale, B.J. (2020) Scaling up biodiversity–ecosystem function relationships across space and over time. *Ecology*. 101 (11), e03166. doi:10.1002/ecy.3166.

R Core Team (2020) *R: A Language and Environment for Statistical Computing*. <https://www.r-project.org/>.

Schielzeth, H. (2010) Simple means to improve the interpretability of regression coefficients. *Methods in Ecology and Evolution*. 1 (2), 103–113. doi:10.1111/j.2041-210X.2010.00012.x.

Seddon, N., Daniels, E., Davis, R., Chausson, A., Harris, R., Hou-Jones, X., Huq, S., Kapos, V., Mace, G.M., Rizvi, A.R., Reid, H., Roe, D., Turner, B. & Wicander, S. (2020) Global recognition of the importance of nature-based solutions to the impacts of climate change. *Global Sustainability*. 3, e15. doi:10.1017/sus.2020.8.

Semenchuk, P., Plutzer, C., Kastner, T., Matej, S., Bidoglio, G., Erb, K.-H., Essl, F., Haberl, H., Wessely, J., Krausmann, F. & Dullinger, S. (2022) Relative effects of land conversion and land-use intensity on terrestrial vertebrate diversity. *Nature Communications*. 13 (1), 615. doi:10.1038/s41467-022-28245-4.

Steele, J.H., Brink, K.H. & Scott, B.E. (2019) Comparison of marine and terrestrial ecosystems: suggestions of an evolutionary perspective influenced by environmental variation. *ICES Journal of Marine Science*. 76 (1), 50–59. doi:10.1093/icesjms/fsy149.

Thompson, P.L., Isbell, F., Loreau, M., O'Connor, M.I. & Gonzalez, A. (2018) The strength of the biodiversity–ecosystem function relationship depends on spatial scale. *Proceedings of the Royal Society B: Biological Sciences*. 285 (1880), 20180038. doi:10.1098/rspb.2018.0038.

Thompson, P.L., Kéfi, S., Zelnik, Y.R., Dee, L.E., Wang, S., de Mazancourt, C., Loreau, M. & Gonzalez, A. (2021) Scaling up biodiversity–ecosystem functioning relationships: the role of environmental

heterogeneity in space and time. *Proceedings of the Royal Society B: Biological Sciences*. 288 (1946), 20202779. doi:10.1098/rspb.2020.2779.

Tilman, D. (1999) The Ecological Consequences of Changes in Biodiversity: A Search for General Principles. *Ecology*. 80 (5), 1455–1474. doi:10.1890/0012-9658(1999)080[1455:TECOCI]2.0.CO;2.

Tilman, D., Isbell, F. & Cowles, J.M. (2014) Biodiversity and Ecosystem Functioning. *Annual Review of Ecology, Evolution, and Systematics*. 45 (1), 471–493. doi:10.1146/annurev-ecolsys-120213-091917.

Tilman, D., Reich, P.B., Knops, J., Wedin, D., Mielke, T. & Lehman, C. (2001) Diversity and Productivity in a Long-Term Grassland Experiment. *Science*. 294 (5543), 843–845. doi:10.1126/science.1060391.

Tonidandel, S. & LeBreton, J.M. (2015) RWA Web: A Free, Comprehensive, Web-Based, and User-Friendly Tool for Relative Weight Analyses. *Journal of Business and Psychology*. 30 (2), 207–216. doi:10.1007/s10869-014-9351-z.

Wang, M., Lu, N., An, N. & Fu, B. (2022) A Trait-Based Approach for Understanding Changes in Carbon Sequestration in Semi-Arid Grassland During Succession. *Ecosystems*. 25 (1), 155–171. doi:10.1007/s10021-021-00646-4.

Weiskopf, S.R., Isbell, F., Arce-Plata, M.I., Di Marco, M., Harfoot, M., Johnson, J., Lerman, S.B., Miller, B.W., Morelli, T.L., Mori, A.S., Weng, E. & Ferrier, S. (2024) Biodiversity loss reduces global terrestrial carbon storage. *Nature Communications*. 15 (1), 4354. doi:10.1038/s41467-024-47872-7.

Weiskopf, S.R., Myers, B.J.E., Arce-Plata, M.I., Blanchard, J.L., Ferrier, S., Fulton, E.A., Harfoot, M., Isbell, F., Johnson, J.A., Mori, A.S., Weng, E., Harmáčková, Z.V., Londoño-Murcia, M.C., Miller, B.W., Pereira, L.M. & Rosa, I.M.D. (2022) A Conceptual Framework to Integrate Biodiversity, Ecosystem Function, and Ecosystem Service Models. *BioScience*. 72 (11), 1062–1073. doi:10.1093/biosci/biac074.

Weiskopf, S.R., Rubenstein, M.A., Crozier, L.G., Gaichas, S., Griffis, R., et al. (2020) Climate change effects on biodiversity, ecosystems, ecosystem services, and natural resource management in the United States. *Science of The Total Environment*. 733, 137782. doi:10.1016/j.scitotenv.2020.137782.

Wu, D., Xu, C., Wang, S., Zhang, L. & Kortsch, S. (2023) Why are biodiversity—ecosystem functioning relationships so elusive? Trophic interactions may amplify ecosystem function variability. *Journal of Animal Ecology*. 92 (2), 367–376. doi:10.1111/1365-2656.13808.

Zabel, F., Delzeit, R., Schneider, J.M., Seppelt, R., Mauser, W. & Václavík, T. (2019) Global impacts of future cropland expansion and intensification on agricultural markets and biodiversity. *Nature Communications*. 10 (1), 2844. doi:10.1038/s41467-019-10775-z.