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Biodiversity mediates relationships between anthropogenic drivers and ecosystem services across global mountain, island and delta systems

Martin Oliver Reader [a,*], Maarten B. Eppinga [a], Hugo Jan de Boer [b], Alexander Damm [a,c], Owen L. Petchey [d], Maria J. Santos [a]

[a] Department of Geography, University of Zurich, Winterthurerstrasse 190, Zürich 8057, Switzerland
[b] Copernicus Institute of Sustainable Development, Environmental Sciences, Universiteit Utrecht, Princetonlaan 8a, Utrecht 3584 CB, Netherlands
[c] Eawag, Swiss Federal Institute of Aquatic Science and Technology, Überandstrasse 133, Dübendorf 8600, Switzerland
[d] Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, Zürich 8057, Switzerland

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ABSTRACT

Global change increasingly threatens nature, endangering the ecosystem services human wellbeing depends upon. Biodiversity potentially mediates these impacts by providing resilience to ecosystems. While biodiversity has been linked to resilience and ecosystem service supply on smaller scales, we lack understanding of whether mediating interactions between biodiversity and anthropogenic drivers are global and ubiquitous, and how they might differ between systems. Here, we examine the potential for biodiversity to mediate anthropogenic driver-ecosystem service relationships using global datasets across three distinct systems: mountains, islands and deltas. We found that driver-ecosystem service relationships were stronger where biodiversity was more intact, and weaker at higher species richness, reflecting the negative correlation between intactness and richness. Mediation was most common in mountains, then islands, then deltas; reducing with anthropogenic impact. Such patterns were found across provisioning and regulating ecosystem services, and occurred most commonly with climate change and built infrastructure. Further, we investigated the contribution of biodiversity and abiotic and anthropogenic drivers to ecosystem services. Ecosystem service supply was associated with abiotic and anthropogenic drivers alongside biodiversity, but all drivers were important to different ecosystem services. Our results empirically show the importance of accounting for the different roles that biodiversity plays in mediating human relationships with nature, and reinforce the importance of maintaining intact biodiversity in ecosystem functioning.

1. Introduction

Biodiversity provides and supports ecosystem services (ES), the many contributions of nature to societies and human wellbeing (Costanza et al., 1997; de Groot et al., 2010). Global change, from land use change to invasive species, is driving dramatic losses in biodiversity and ES – 28 % of assessed species are at risk of extinction, while 12 of 18 ES types are declining (Brauman et al., 2020; Butchart et al., 2010; International Union for Conservation of Nature (IUCN), 2021). The influence of biodiversity on the supply and resilience of ecosystem functions is increasingly established (Isbell et al., 2011; Harrison et al., 2014; Tilman, Isbell and Cowles, 2014; Felipe-Lucia et al., 2018). However, the extent to which biodiversity might dampen or exacerbate the impacts of global change on ES is underexplored, and it is unclear if the relationships between biodiversity and ES are pervasive and tight enough to reveal consistent patterns across global systems. Given the accelerating impacts of global change drivers (Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), 2019), understanding their interaction with biodiversity, and the ability of biodiversity to mitigate these impacts is critical.

ES are founded on a combination of biodiversity, other biotic traits and functions, and abiotic and anthropogenic drivers. High biodiversity can directly supply some ES, such as resistance to invasive species or pathogens (Keesing et al., 2010), while increasing ecosystem productivity and related ES (Tilman, Reich and Isbell, 2012). Biodiversity also provides the range of habitats and food that supports species supplying other ES. In these ways, biodiversity can indicate the variety of ES that a system provides (O'Connor et al., 2021), and typically has positive

* Corresponding author.
E-mail address: martin.reader@geo.uzh.ch (M.O. Reader).

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relationships with the regulating ES that maintain ecosystem processes beneficial to people (Harrison et al., 2014). In contrast, biodiversity often has a negative association with provisioning, material ES, given how intensive agriculture can degrade biodiversity through pesticides, herbicides and monocultures (Dudley and Alexander, 2017). Abiotic drivers, e.g. climate, topography and geology, also directly provide and influence ES, such as water supply and regulation (van der Meulen, Braat and Brils, 2016). These drivers additionally provide the 'stage' for biota to provide ES, defining the potential biodiversity and productivity of an area (Lawler et al., 2015). Finally, anthropogenic drivers are intrinsically related to ES – ecosystem properties and processes become realised ES when people consume or use them (Potschin and Haines-Young, 2011). Humans also directly modify ecosystems, for example through fertiliser input or species dislocation, to develop selected ES. Anthropogenic drivers typically increase material provisioning ES such as crops, while degrading or displacing others (Power, 2010). Thus, while many relationships between biodiversity, anthropogenic and abiotic drivers and ES have been established, we need to better understand the universality of the strength and direction of these relationships, and how they might vary between systems and influence one another (Harrison et al., 2014; Duncan, Thompson and Pettorelli, 2015).

Biodiversity, abiotic and anthropogenic drivers may influence one another's relationships with ES in several ways. Biotic processes can affect the abiotic environment, anthropogenic pressures may degrade biotic integrity, and ES themselves support the human development that drives global change. Synergies and trade-offs also exist between ES, which may mean that the impacts on one ES may influence another (Howe et al., 2014), further complicating the overall effect of these drivers. Anthropogenic drivers, in particular land use change, are key drivers of species loss (IPBES, 2019). Yet biodiversity can, through various mechanisms, mediate the impacts of these drivers on ES supply. Most prominently, high biodiversity can provide an insurance effect: redundant species, with different environmental tolerances, are able to maintain the ecosystem functions providing specific ES, while also underpinning longer-term ecosystem resilience (Yachi and Loreau, 1999; Oliver et al., 2015). This insurance benefit has been shown empirically to maintain ecosystem stability, functionality and resistance to environmental change (Allan et al., 2011; Brittain, Kremen and Klein, 2013; Isbell et al., 2015). Alternatively, in certain circumstances, high biodiversity could amplify the effects of global change – for example, invasive species can exacerbate negative impacts of climate change while increasing local biodiversity (Gallardo et al., 2017). However, much of our knowledge of both the associations between biodiversity and ES, and the resilience of ecosystems to global change, comes from local experiments and relatively small datasets, strongly context dependent, often with contradictory results across scales (Steudel et al., 2012; Duncan, Thompson and Pettorelli, 2015; Oliver et al., 2015). While studying these relationships across multiple ecosystem types might obscure the diversity of relationships that occur within ecosystems (Duncan, Thompson and Pettorelli, 2015), global analyses have the potential to unveil previously undetected broader mediating effects of biodiversity on the relationship between global change and ES.

Here, we assess if a mediating (i.e. weakening, reversing or amplifying) effect of biodiversity on the relationship of global change and ES can be seen across global systems. We use the two globally mapped metrics of biodiversity: species richness and biodiversity intactness (Newbold et al., 2016), and evaluate their interaction with five anthropogenic drivers: population density, built infrastructure, land use change and climate change (temperature and precipitation). With statistical models we estimate the main effects of biodiversity and anthropogenic/abiotic drivers, as well as the interaction term between biodiversity and anthropogenic drivers, on 19 important ecosystem property and service indicators. These interaction terms and main effects may depend on social and environmental context (Duncan, Thompson and Pettorelli, 2015). Therefore, we assess how they differ between three distinct systems, specifically mountains, islands and deltas. The relative levels of biodiversity, abiotic and anthropogenic drivers, and ES in these three systems may help to explain the differences in interactions and associations between them. Consequently, we first ask 'How do levels of biodiversity, anthropogenic and abiotic drivers and ES differ between systems?' and 'Do the correlations between drivers and ES differ between systems?'. We then ask our main question: 'What is the nature of the interaction terms between biodiversity and anthropogenic drivers for each ES?'. We hypothesise that the interaction terms will indicate that biodiversity weakens the driver-ES relationships, and that intactness will have a stronger mediating effect than species richness, as the latter may be diluted by confounding factors. We finally need to know the main effects of these drivers influenced by these interactions. We therefore ask 'What is the size and direction of the association between biodiversity, abiotic and anthropogenic drivers and ES?' (i.e. what are the main effects?). We hypothesise that biodiversity will have a positive correlation with regulating ES, but a negative one with provisioning ES, and that anthropogenic drivers will show the opposite relationships (Harrison et al., 2014). Our findings will highlight the ubiquity of biodiversity as a mediator of the relationships between global change and ES, which is important for projecting the consequences of this change on human well-being.

2. Material and methods

2.1. Study systems

We studied the influence of biotic, abiotic and anthropogenic drivers on ES across a set of mountains, islands and deltas globally. We selected these systems to represent a distinct mixture of ES, biodiversity and anthropogenic and abiotic drivers. We used existing datasets to delineate each of the systems (Fig. 1).

Mountains provide disproportionate ES for their area and occupation, with a net output of water, minerals and climate regulation services (Grêt-Regamey et al., 2012). The varied topography creates higher regional biodiversity in some mountain areas than some tropical forests (Rahbek et al., 2019), while also providing refugia from climate change (Gentili, Badola and Birks, 2015). Mountain ruggedness and isolation limits anthropogenic influences, yet conversely, limited local biodiversity and fragile soils can lack resilience to increasing disturbance (Nilsson and Grelsson, 1995). To delineate mountain systems, we used the Global Mountain Biodiversity Assessment dataset (Körner et al., 2017), which defines mountains using ruggedness (>200 m elevation change within a 2.5′ cell), and divides them into thermal life zones. This subdivision means that individual areas are more coherent for biological analysis, rather than representing entire mountain ranges (Körner, Paulsen and Spehn, 2011).

Islands can supply a wide variety of marine, coastal and terrestrial ES, yet area constraints can limit ES availability on smaller islands (Balzan, Potschin-Young and Haines-Young, 2018). Isolation limits island biodiversity, giving them, alongside mountains, amongst the highest risk of terrestrial extinction (Pörtner et al., 2021), in turn increasing the vulnerability of their ES. Island disturbance is increasing: invasive species and the impacts of tourism are disproportionate (Christ et al., 2003; Russell et al., 2017). While many oceanic islands have a limited history of development, their restricted spatial extent can concentrate impacts of global change, leading to greatly increased species turnover (Nogué et al., 2021). To delineate islands, we used a coastline dataset (www.naturalearthdata.com), excluding continental landmasses.

Deltas are sedimentary features formed around river mouths. They contain some of the richest ES on Earth: fertile flat land alongside plentiful water and fish enabling human settlement and development into modern megacities and globally important food production systems (Seto, 2011). Deltas represent a range of coastal and terrestrial ecosystems and valuable wetland biodiversity hotspots, which are also increasingly under threat (Barbier et al., 2011). Anthropogenic drivers

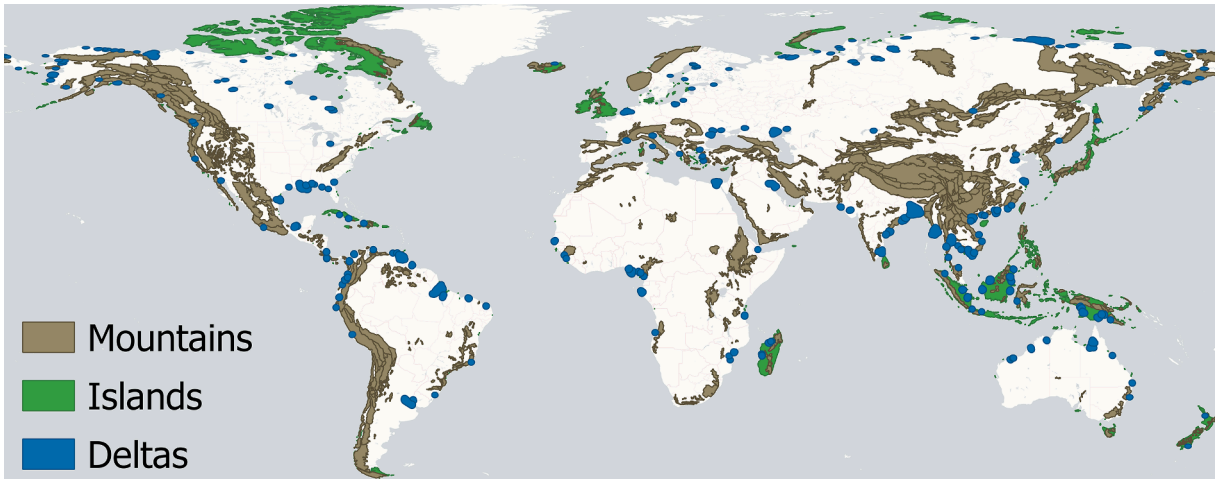


Fig. 1. Mountain (n = 1034), island (n = 912) and delta (n = 235) systems analysed in this study. Deltas are enlarged for visibility. Basemap from https://carto.com.

are likely to be highest in deltas, given their history of extensive and intensive development for housing, agriculture and industry (Renaud et al., 2013). Here, we used the dataset of global delta areas created in our previous work (Reader et al., 2022). We manually mapped deltas from where the distributary network began, along the watersheds either side of the outermost distributaries up to the coastline.

From these datasets, we selected mountain zones (henceforth called mountains), islands and deltas covering >10 km^2 to ensure representative coverage and variability of the ES indicators used. This gave us 1048 mountains, 3451 islands and 236 deltas. We examined which driver and ES datasets were available for as many of these systems as possible (see Data section below), then trimmed indicators and systems until we had a complete set of indicators for 1034 mountains (98.7 % of all large mountains), 912 islands (26.4 %) and 235 deltas (99.6 %). Where overlaps occurred, e.g. mountains on islands, we included the overlapping areas for both systems. Overlaps amounted to 73 deltas on islands (1.2 % of the area of the islands where overlapping occurred), 14 deltas on mountains (0.1 % area) and 287 mountains on islands (34.2 % area), so the potential for non-independence is minor.

2.2. Data

We reviewed publicly available, spatial indicators and selected robust (peer-reviewed or from a recognised agency) indicators relevant

Table 1
Ecosystem property and service indicators. For more details, such as additional processing and download sources, see Supplementary Information Table 1.

Category	Indicator	Description	Unit	Year	Resolution	Citation
Food	Food area	Area of food crops	ha	2010	5 arcmin	IFPRI, 2019; Wood-Sichra et al., 2016
	Food value	Value of food crops	$ per ha	2010	5 arcmin	IFPRI, 2019; Wood-Sichra et al., 2016
	Non-food area	Area of non-food crops	ha	2010	5 arcmin	IFPRI, 2019; Wood-Sichra et al., 2016
	Non-food value	Value of non-food crops	$ per ha	2010	5 arcmin	IFPRI, 2019; Wood-Sichra et al., 2016
	Pasture area	Proportion of pasture area	Proportion	2000	30 arc*sec*	Ramankutty et al., 2008; Ramankutty et al., 2010
Water	Water available	Water runoff available for human use	cm	1948–2010	Catchment	Gassert et al., 2014
	Water withdrawal	Consumptive water use	cm	2010	Catchment	Gassert et al., 2014
	Sediment	Riverine sediment flux	kg/s	2010	6 arcmin	Cohen et al., 2013
Productivity	NPP	Net primary productivity	gC/m^2/yr	2000	5 arcmin	Haberl et al., 2007
	Potential NPP (NPP pot.)	Potential net primary productivity	gC/m^2/yr	2000	5 arcmin	Haberl et al., 2007
	Vegetation biomass (Veg. C)	Vegetation biomass storage	0.01 t/ha	2000	30 arcsec	Ruesch and Gibbs, 2008
	Potential veg. Biomass (Veg. C pot.)	Potential vegetation biomass storage	t/ha	<2010	5 arcmin	West et al., 2010
Habitat	Forest cover	Forest extent	Proportion	2000	1 arcsec	Hansen et al., 2013
	Wetlands	Wetland extent	%	2015	30 arcsec	Lehner & Döll, 2004
Soil	Soil carbon	Soil organic carbon stock	Pg	2019	30 arcmin	Food and Agriculture Organization and Intergovernmental Technical Panel on Soils, 2019
	Soil carbon density	Soil organic carbon density	kg/m^3	<2017	250 *m*	Hengl et al., 2017
	Soil cation-exchange capacity (Soil CEC)	Soil capacity to retain nutrients	cmolc/kg	<2017	250 *m*	Hengl et al., 2017
	Soil nitrogen (Soil N)	Concentration of soil N	g/kg	1950–2015	30 arcsec	Batjes, 2016
	Soil water availability	Soil available water capacity	cm/m	1950–2015	30 arcsec	Batjes, 2016

to and available across all of our study systems. For ES, given the paucity of global indicators, we use indicators across the ES cascade, from ecosystem property and function to supply to service (Potschin and Haines-Young, 2011); we refer to all of these as ES henceforth. We selected 19 ES indicators (Table 1, see SI Table 1 for more information on datasets and SI Note 1 for discussion of potential dependencies). While we list ES each indicator may be related to in SI Table 1, for transparency we will refer to the indicator name rather than any connected service. Recent ES categorisations include cultural and relational services, representing an important and underrepresented part of nature's contributions to people (Díaz et al., 2018). However, the lack of global spatial data excluded the possibility to consider these types of ES, hence we focus on provisioning/material, regulating, and supporting/nature ES.

We selected 15 driver indicators (Table 2): five indicators each of biodiversity, anthropogenic drivers, and abiotic drivers. Biodiversity and its value is difficult to capture using individual metrics (Mace et al., 2014). Therefore, we selected the globally available indicators for both species richness (three taxonomic groups: mammals, birds and amphibians (Jenkins, Pimm and Joppa, 2013; Pimm et al., 2014; IUCN and Center for International Earth Science Information Network (CIESIN), 2015a; IUCN and CIESIN, 2015b) and biodiversity intactness (two metrics: species richness and abundance; Newbold et al., 2016; Sanchez-Ortiz et al., 2019b). These indicators could be expected to differ between the systems, and display different mechanistic links to ecosystem properties and services. Biodiversity intactness combines models of biodiversity and land use pressure to estimate the proportion of intact biodiversity remaining in a landscape, meaning there is some overlap with the anthropogenic drivers. Data availability restricted us to species level indicators, but it should be noted that other important measures and scales of biodiversity exist, such as functional diversity, genetic diversity and habitat diversity (Pereira, Navarro and Martins, 2012).

We represent a range of anthropogenic drivers using five indicators: population, infrastructure, land use change and climate change (temperature and precipitation). Population density represents how human populations occupy and use ecosystems and demand ES. Infrastructure displaces natural ecosystems and degrades ES through associated pollution and fragmentation (Grimm et al., 2008). While population density and infrastructure are connected, areas of high population with lower infrastructure and vice versa exist. Further, ES respond differently to each driver, with infrastructure associated with stronger declines of regulating ES, and population with stronger increases in provisioning ES (Reader et al., 2022; Peng et al., 2017). Land use change is rapidly increasing, affecting almost a third of global land area since 1960, with divergent effects on ES depending on the type of change (Winkler et al., 2021a). Our last anthropogenic driver, climate change, is distinct in its disconnection of source and impacts; the carbon output of industrialised countries altering climate and associated hazards globally. This will directly impact ES such as water provisioning and flood protection, while indirectly affecting all ES through species loss and ecosystem degradation. We finally selected five indicators for abiotic drivers: the average and seasonality of temperature and precipitation, and the ruggedness of the topography. All data were of gridded format, or rasterised from vector data. See SI Table 2 for the method and source used for each indicator (and SI Note 1 for further discussion of data dependencies). For each individual system we calculated the mean of each indicator using zonal statistics in QGIS 3.14 (QGIS.org, 2021) or the equivalent reducer functions in Google Earth Engine (Gorelick et al., 2017).

We tested the pairwise correlation between biodiversity indicators using Spearman's rank correlation coefficient. As the biodiversity indicators were highly correlated, we combined the three biodiversity richness and the two biodiversity intactness indicators into individual richness and intactness indicators using principal component analysis (PCA), a commonly used technique to reduce dimensionality in indicators (e.g. Abson, Dougill and Stringer, 2012). We scaled the data and performed a PCA on the individual mountain, island and delta datasets to obtain a loading for each indicator for each set. We extracted the first principal axis for each group of indicators. For richness, this axis represents 88.8 % of the variability in mountains, 80.2 % in islands, and 83.1 % in deltas; while for intactness it represents 96.7 % of the variability in mountains, 97.2 % in islands, and 96.4 % in deltas. We multiplied each variable by the relevant loading and summed them to create the indicator.

Table 2
Biodiversity, abiotic and anthropogenic driver indicators. For more details, such as additional processing and download sources, see Supplementary Information Table 2.

Type	Driver	Description	Unit	Date	Resolution	Citation
Biodiversity	Amphibian richness	Richness of amphibian species	No. per cell	2013	30 arcsec	IUCN & CIESIN, 2015a
	Bird richness	Richness of bird species	No. per cell	<2018	10 km	Jenkins et al., 2013; Pimm et al., 2014
	Mammal richness	Richness of mammal species	No. per cell	2013	30 arcsec	IUCN & CIESIN, 2015b
	Biodiversity abundance intactness	Species abundance compared to pristine conditions	Proportion	2005	30 arcsec	Newbold et al., 2016; Sanchez-Ortiz et al., 2019a; Sanchez-Ortiz et al., 2019b
	Biodiversity richness intactness	Species richness compared to pristine conditions	Proportion	2005	30 arcsec	Newbold et al., 2016; Sanchez-Ortiz et al., 2019a; Sanchez-Ortiz et al., 2019b
Anthropogenic	Population	Population density	No. per km^2	2020	30 arcsec	CIESIN, 2018
	Infrastructure	Built and electrical infrastructure, roads, rail	Index	2009	30 arcsec	Venter et al., 2016; Venter et al., 2018
	Temperature change	Temperature change in last century	°C	1900–1920 2000–2020	5°	Morice et al., 2021
	Precipitation change	Relative precipitation change in last century	mm	1901–1921 2000–2020	0.5°	University of East Anglia Climatic Research Unit et al., 2008
	Land use change	Number of land use changes over 60 years	No.	1960–2019	1 km	Winkler et al., 2021a; Winkler et al., 2021b
Abiotic	Temperature mean	Annual mean temperature	°C	1970–2000	30 arcsec	Fick & Hijmans, 2017
	Temperature seasonality	Temperature standard deviation × 100		1970–2000	30 arcsec	Fick & Hijmans, 2017
	Precipitation annual	Annual precipitation	mm	1970–2000	30 arcsec	Fick & Hijmans, 2017
	Precipitation seasonality	Precipitation coefficient of variation		1970–2000	30 arcsec	Fick & Hijmans, 2017
	Ruggedness	Terrain Ruggedness Index	Index	2010	1 km	Amatulli et al., 2018

2.3. Statistical analysis

We used R 4.2.1 (R Core Team, 2022) for the statistical analyses. To answer our first question, we used a non-parametric Kruskal-Wallis H test to establish if the mean ranks of each predictor or ES indicator differed between the systems. We then applied a post-hoc Dunn's multiple comparison test to assess if each pairwise combination of indicators differed from the others. We chose alpha 0.05 as the significance level. To answer our second question, we used a pairwise Spearman's rank correlation coefficient to test the correlation of ES and driver indicators for each system and for all systems combined.

To answer our main research questions, we built generalised linear models (GLMs) to assess the interaction between biodiversity and anthropogenic drivers, and the association of biodiversity, and anthropogenic/abiotic drivers on each ES indicator. GLMs can be used to fit complex and non-normal environmental response variables (Bolker et al., 2009). We built models for each ES in each system as a response, and biodiversity and abiotic and anthropogenic drivers as predictors. Variable selection, distribution and link function were kept consistent to maximise the comparability between models. We included interaction terms between the biodiversity and anthropogenic indicators. All predictors were scaled and zero-centred. As data were not normally distributed we used a Tweedie distribution with log link function, which can model continuous variables and zero-inflated data (as Thomas et al., 2020). Parameters describing the distribution were estimated using maximum likelihood. We added an observation-level random effect as this provided the best fit across systems and indicators. We implemented the models with the 'glmmTMB' R package (version 1.1.3, Brooks et al., 2017).

We performed several checks on the models. We checked for multicollinearity using variance inflation factor with the performance package (version 0.9.1; Lüdecke et al., 2021). This was minimal, affecting the temperature mean and seasonality indicators, particularly in deltas (SI Table 3). We checked model assumptions using the 'DHARMa' package (version 0.4.5; Hartig, 2021), which simulates residuals and compares these to the model output. We checked the QQ normality plots and the ordered residuals, alongside tests for normality, overdispersion and zero-inflation (SI Note 2, SI Table 4). While not all models passed every test; visual inspection showed that the distribution of residuals was not heavily biased in the majority of cases. Given that we are examining broad, directional associations, and require similar model construction across systems, this was considered reasonable. Within each model, we used alpha 0.05 to determine the biodiversity and abiotic and anthropogenic drivers with a significant main or interaction effect on an ES; those factors not meeting this criterion were not considered important to the selected ES and not interpreted further. Where interactions are present, interpretation of main effects is limited – these were therefore assessed at mean levels of biodiversity/anthropogenic indicators. We assessed interactions using the 'interactions' package (version 1.1.5; Long, 2019) to plot each driver against each ES at mean and +/- 1 SD levels of biodiversity richness and intactness. We compared these interactions to the overall effect of the anthropogenic driver on the ES at mean biodiversity; if higher levels of biodiversity (+1 SD) increase the trend, we label that an *amplifying* relationship (which can increase a positive or negative trend), if they reduce the trend, we label that *weakening*, and if they reverse the trend, or the direction of the main effect of the anthropogenic driver, we label that *reversing* (Fig. 2).

3. Results

3.1. Mountains, islands and deltas differ in levels of ecosystem services and their drivers

The levels of ES and biodiversity, anthropogenic and abiotic drivers generally differ between systems (Fig. 3 and SI Table 5). For biodiversity, mean and median richness and intactness were higher in deltas, then mountains, then islands. However, while richness and intactness differed across the systems (Kruskal-Wallis $H(2) = 59.33$, $p < 0.001$), mountains and deltas showed little difference (richness Dunn pairwise $z = -1.28$, $p = 0.199$; intactness Dunn pairwise $z = 1.70$, $p = 0.089$). Of the anthropogenic drivers, population density ($H(2) = 4.01$, $p = 0.135$), and infrastructure ($H(2) = 5.71$, $p = 0.058$), were not significantly different between the systems. However, mean and median values were higher in deltas, then islands, then mountains, and the former and latter represent practically the global population of these areas. Land use change differed between systems ($H(2) = 78.53$, $p < 0.001$), and in contrast to population was highest in mountains, then deltas, then islands. Climate change for temperature also differed ($H(2) = 59.33$, $p < 0.001$), and mean change was highest in deltas, then mountains, then islands. Precipitation change again differed ($H(2) = 26.03$, $p < 0.001$), and mean and median change was highest in deltas, then islands, then mountains. Finally, all abiotic drivers differed between the systems ($H(2)$, $p < 0.001$), mean and median ruggedness higher in mountains then islands, temperature higher in deltas then islands, precipitation higher in islands then deltas and climate seasonality highest in mountains.

ES indicator values all differed ($H(2)$, $p < 0.001$) between the systems (Fig. 4 and SI Table 6); excepting soil nitrogen. Food and non-food crop mean area was largest in deltas, then islands. Non-food value was higher in deltas, but food value was higher in mountains (although showing no significant difference with islands; Dunn pairwise $z = 1.14$, $p = 0.255$). Pasture area was highest in mountains, but not significantly different between deltas and islands (Dunn pairwise $z = 1.18$, $p = 0.240$). Mountains had the highest median water availability and withdrawal, and typically showed the largest range across provisioning, material ES. Sediment flux, wetland area and soil indicators were typically highest in deltas, then islands. Forest area and vegetation carbon

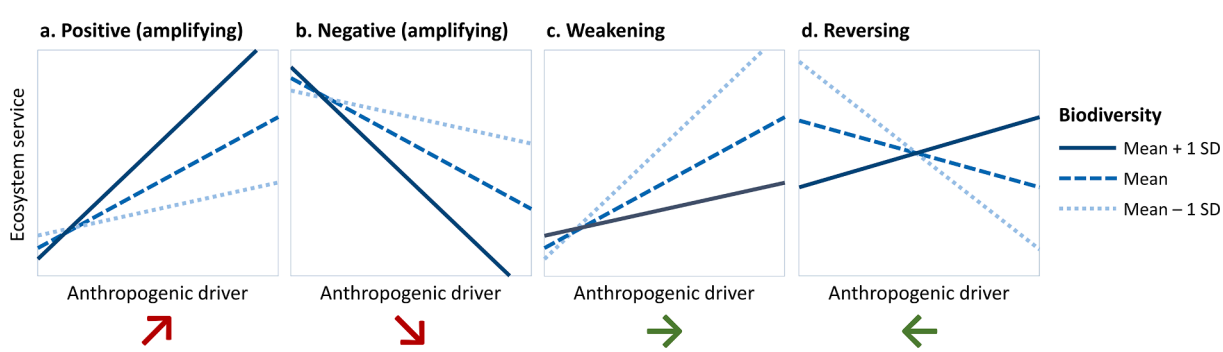


Fig. 2. Potential interaction types. Increased biodiversity may amplify existing relationships, **a.** positively or **b.** negatively. Alternatively, biodiversity may **c.** weaken or **d.** reverse these relationships. The plots show the relationship between an anthropogenic driver and an ecosystem service at different levels of biodiversity – the lightest, dotted line at one standard deviation below mean biodiversity, the dashed line at mean biodiversity and the darkest line at one standard deviation above mean biodiversity. The arrows below the figures are used to indicate the type of interaction on Table 3.

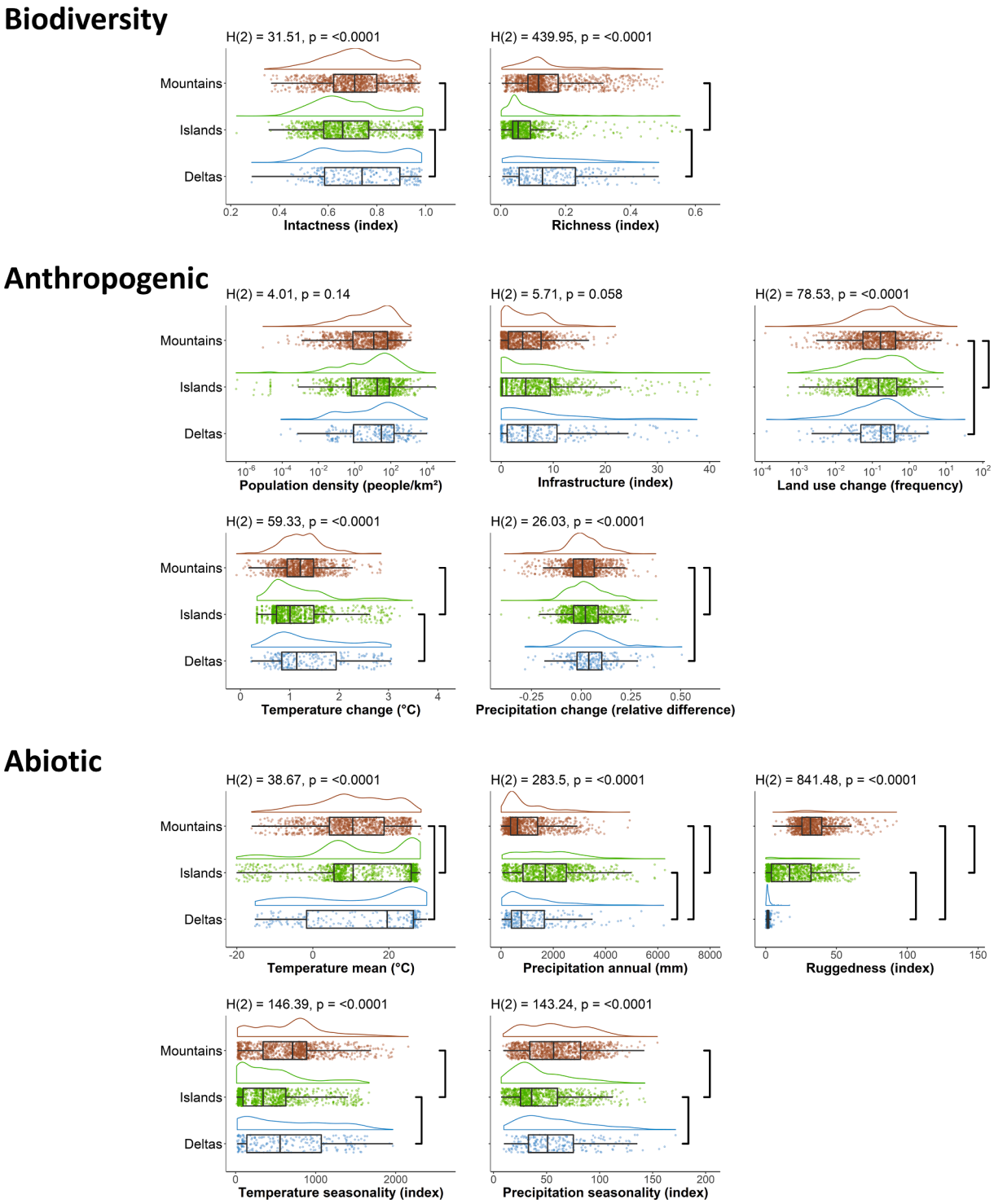


Fig. 3. Differences in biodiversity and anthropogenic and abiotic drivers between systems. The plots summarise the average values of each driver found across mountain, island and delta systems. The statistics show the results of a Kruskal-Wallis H test; the brackets indicate which systems were found to be different by a post-hoc Dunn test ($p < 0.05$). The points shown by the coloured jitter plots represent the average value of the indicator in each individual system. The box plot boxes show the median and interquartile range, the whiskers show 1.5 times the interquartile range of the upper and lower quartiles. The half violin plots above show a smoothed data distribution based on the probability density estimate (y-axis) at each value.

storage was largest in islands, then mountains, while NPP, soil carbon stocks and density were highest in islands, then deltas. Thereby deltas had the highest levels of provisioning, material ES alongside their greater anthropogenic drivers. In sum, we can see the three systems represent different gradients of ES and their drivers, which enables us to explore and explain the interactions and associations between global change and ES.

3.2. *Correlations among ecosystem services and drivers are similar across systems*

The effects of biodiversity, abiotic and anthropogenic drivers may be

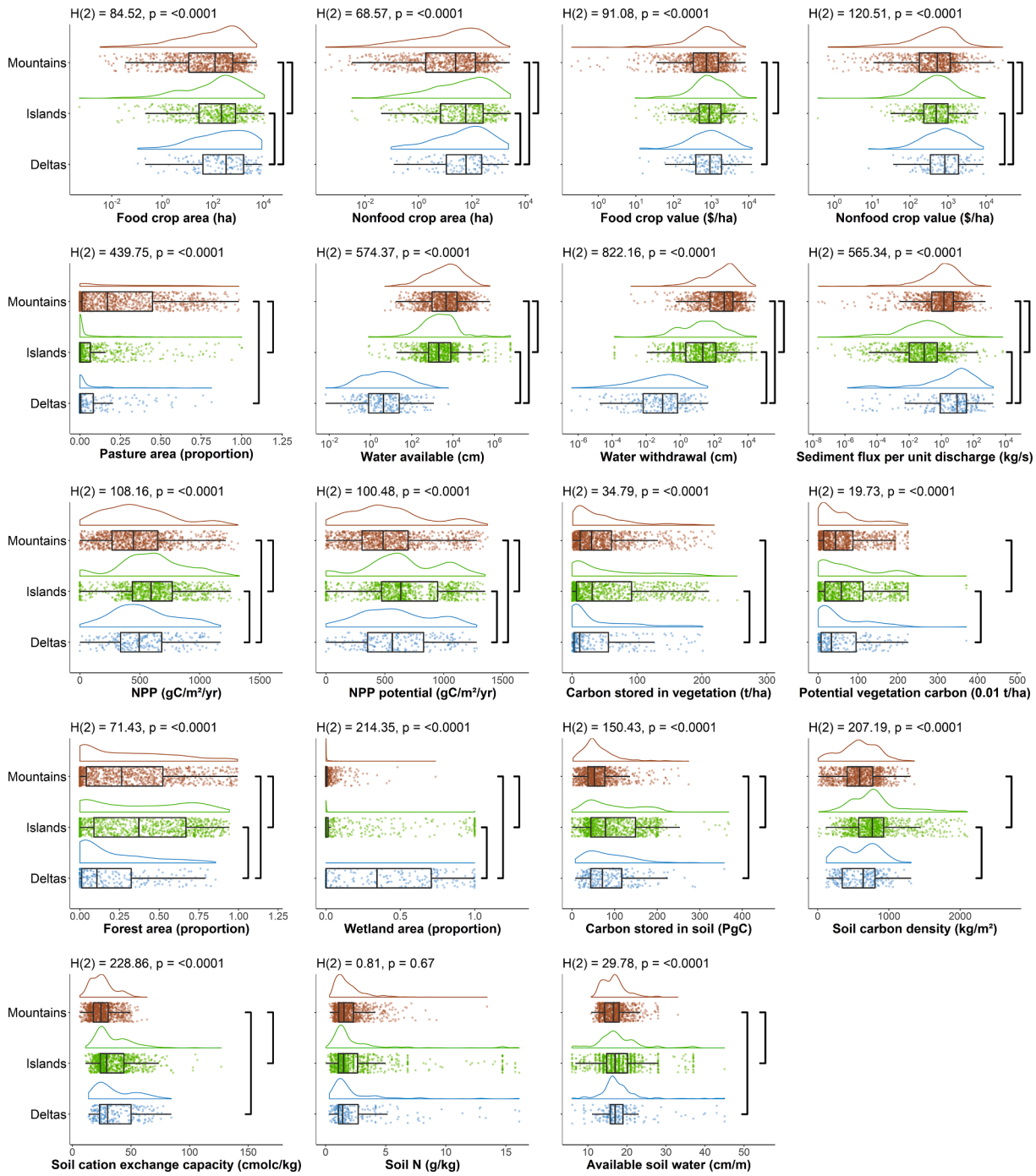


Fig. 4. Differences in ecosystem service supply between systems. The plots summarise the average values per system of each ecosystem service indicator. The statistics show the results of a Kruskal-Wallis H test; the brackets indicate which systems were found to be different by a post-hoc Dunn test ($p < 0.05$). The points shown by the coloured jitter plots represent the average value of the indicator in each individual system. The box plot boxes show the median and interquartile range, the whiskers show 1.5 times the interquartile range of the upper and lower quartiles. The half violin plots above show a smoothed data distribution based on the probability density estimate (y-axis) at each value.

further strengthened or weakened by the synergies and trade-offs between the ES, which can be indicated by their positive and negative correlations. We observed frequent strong positive correlations within three logical groups of ES – provisioning and material ES such as food and water; productivity and habitat ES; and soil ES (Fig. 5, see SI Fig. 1 for correlation coefficients). Across these groups, provisioning ES typically had weak synergies with productivity ES and trade-offs with soil indicators. Individual ES displayed different patterns in each system. In mountains, pasture area and wetlands were negatively correlated with most ES, while crop ES had consistent trade-offs with wetlands and soil indicators. In islands, correlations were very consistent inside the groups, although water availability had a weak negative correlation with crop indicators. In contrast to mountains, island productivity and soil indicators were negatively correlated. Delta ES correlations were the most consistent, with only forests and wetlands showing negative and weak correlations to other carbon and productivity indicators.

Correlations also highlight potential relationships between the drivers, indicating which drivers are likely to operate together. These correlations were moderately consistent, but varied in strength and direction for individual drivers. For the biodiversity indicators, species

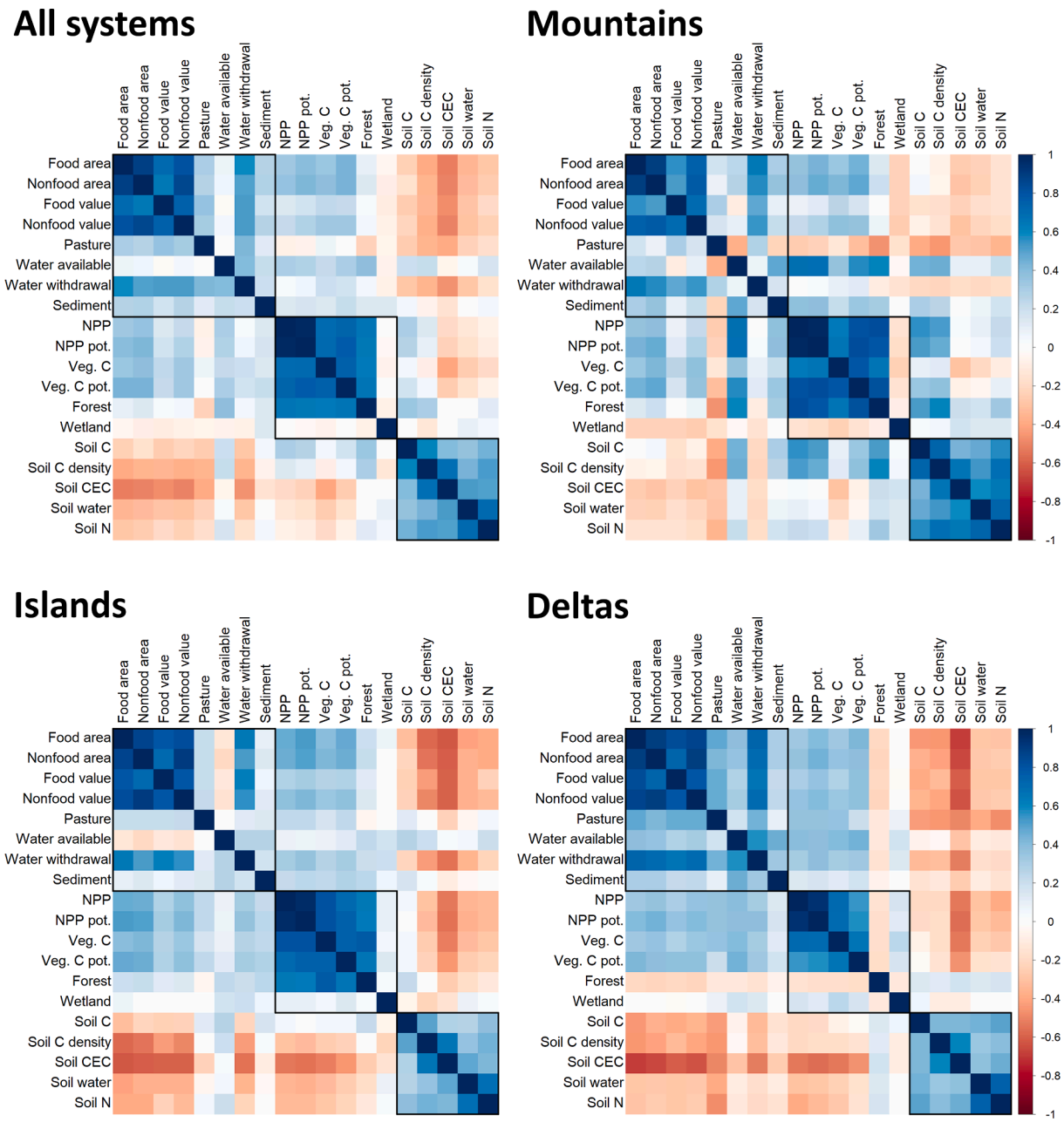


Fig. 5. Trade-offs and synergies between ecosystem services across all systems (top-left), mountains (top-right), islands (bottom-left) and deltas (bottom-right). Blue indicates a positive correlation or synergy, red indicates a negative correlation or trade-off. Correlations were based on a pair-wise Spearman's Rank Correlation Coefficient. The boxes split the ES into logical groups (provisioning, productivity and habitat, and soil). See SI Fig. 1 for correlation coefficients. Plots created using corrplot. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

richness typically had a negative correlation with biodiversity intactness, except in mountains. Within anthropogenic drivers, population and infrastructure were always strongly positively correlated, with a moderate positive correlation with land use change (Fig. 6, SI Fig. 2). These drivers also share a typically negative correlation with biodiversity intactness, and a consistent positive one with species richness. Climate change is weakly correlated with non-climate drivers; except in deltas where temperature change is negatively correlated with other anthropogenic drivers. Abiotic correlations were mostly consistent, although ruggedness showed a weak positive correlation with population and infrastructure in mountains and deltas, but the opposite in islands. Average temperature and precipitation were consistently positively correlated with population, infrastructure and species richness. Correlations appeared strongest for deltas, then islands, perhaps reflecting their relative compactness and consistency in contrast to mountains.

3.3. *Biodiversity mediates anthropogenic effects on ecosystem services across global systems*

Species richness and biodiversity intactness mediated many of the associations between anthropogenic drivers and ES (Table 3, Fig. 7, SI Tables 7 and 8). Of 196 significant interactions between biodiversity and anthropogenic drivers, in 86 cases (44 %) high biodiversity (1 SD above the mean) weakened (n = 53) or reversed (n = 33) the association between the anthropogenic driver and an ES. These are shown on Table 3 by green arrows pointing to the right and left respectively. However, in 110 cases (56 %) biodiversity amplified the association, 72 times

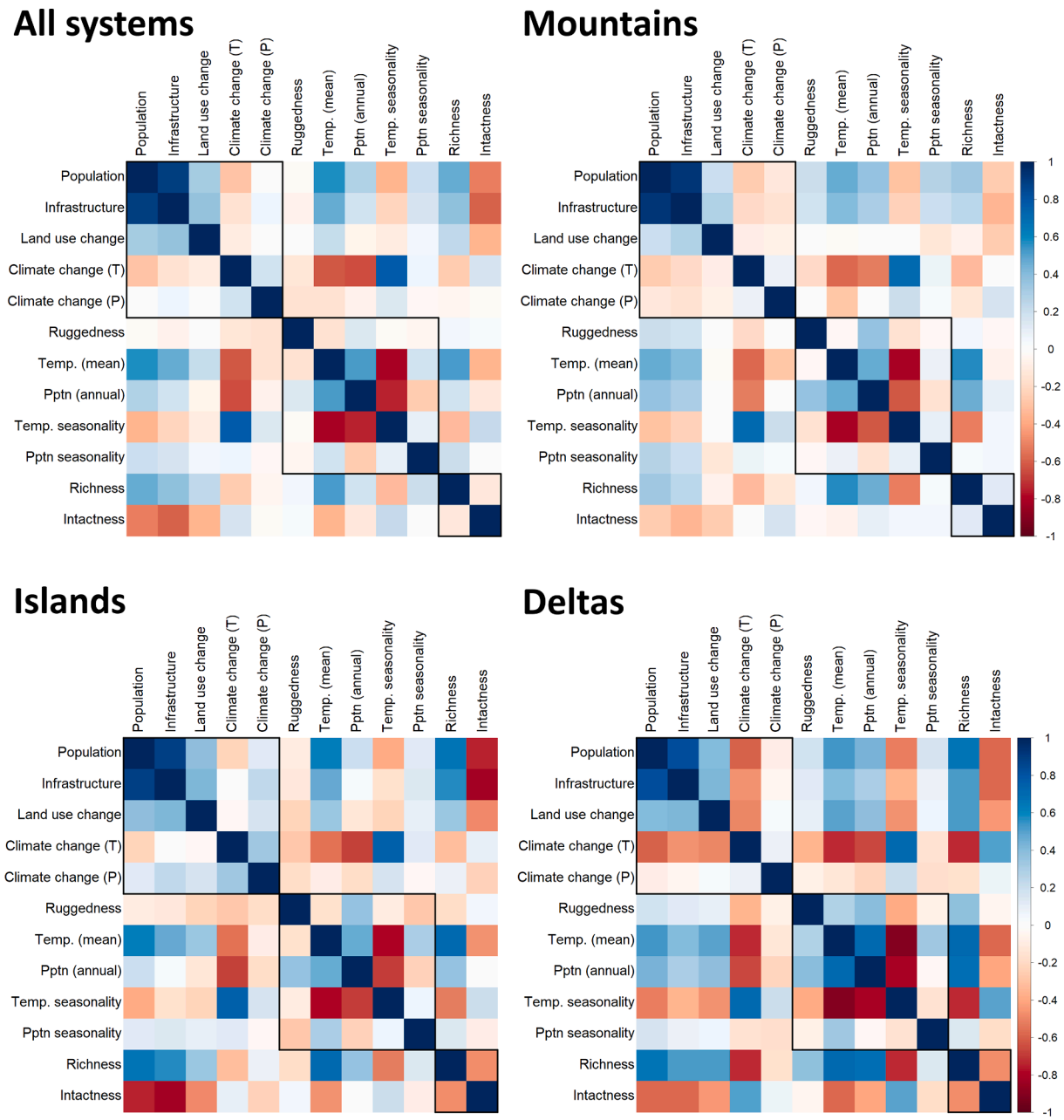


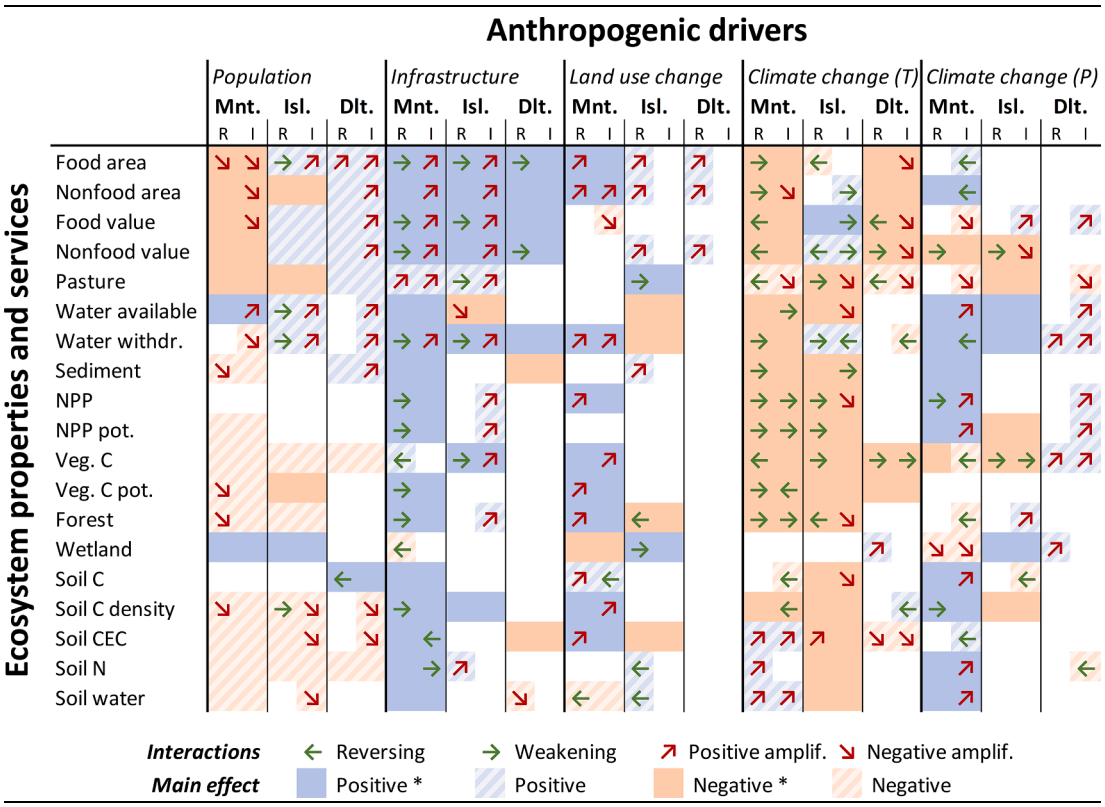
Fig. 6. Correlations between biodiversity and anthropogenic and abiotic drivers. Climate change (T) indicates temperature change and (P) indicates precipitation change over the last 100 years. Blue indicates a positive correlation, red indicates a negative correlation. Correlations were based on a pair-wise Spearman's Rank Correlation Coefficient. The boxes split the drivers into anthropogenic, abiotic and biodiversity groups. See SI Fig. 2 for correlation coefficients. Plots created using corrplot. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

positively, and 38 times negatively, shown by red arrows upwards and downwards. Weakening and reversal were most common with climate change (temperature, 66 % of interactions), while amplification was more common with the other anthropogenic drivers. The total number of interactions were similar between richness (n = 93) and intactness (n = 103), but amplification occurred almost twice as often for intactness (n = 75) as richness (n = 35; $X^2_{1,1} = 14.55$, $p < 0.001$). Interactions between biodiversity and anthropogenic drivers were found across ES, but most commonly for food-related ES (average of 14 interactions, compared to 8 to 9 for other ES). Non-food crop value and productivity and carbon indicators showed more weakening interactions, in contrast to the other ES which showed more amplifying interactions. Most interactions occurred in mountain systems (n = 90), then islands (n = 64), then deltas (n = 42; $X^2_{1,1} = 17.67$, $p < 0.001$). Amplifying interactions were more frequent in particular systems for particular ES, representing 74 % of interactions in deltas, but 50 % in islands. Therefore, the indicator of biodiversity, the ES, and the system all influence the pattern of interactions with anthropogenic drivers.

3.4. *Species richness has broadly positive associations with ecosystem services*

The direction of the main effect (i.e. association) of anthropogenic drivers on ES differed across ES and systems (Table 3, blue indicating positive and red indicating negative associations). These associations will vary given the interactions present, meaning they were assessed at mean levels of species richness and biodiversity intactness. 48 % of 285 potential associations between anthropogenic drivers and ES were

Table 3
Effect of anthropogenic drivers on ecosystem services, and their interactions with species richness (R) and biodiversity intactness (I). Arrows indicate an interaction between richness and intactness and the anthropogenic driver (significant to alpha = 0.05). Left- and right-pointing green arrows indicate a reversing or mediating interaction respectively. Upwards and downwards-pointing red arrows indicate an amplifying interaction, steepening the slope. Main effects of the driver, taken at average levels of richness and intactness, are shown by blue (positive) and red (negative) shading. Where an interaction effect is significant but a main effect is not (alpha = 0.05), or where the slope at average biodiversity differs from the main effect, these backgrounds are lighter and striped. Coefficients and p-values are shown in SI Tables 7 and 8.



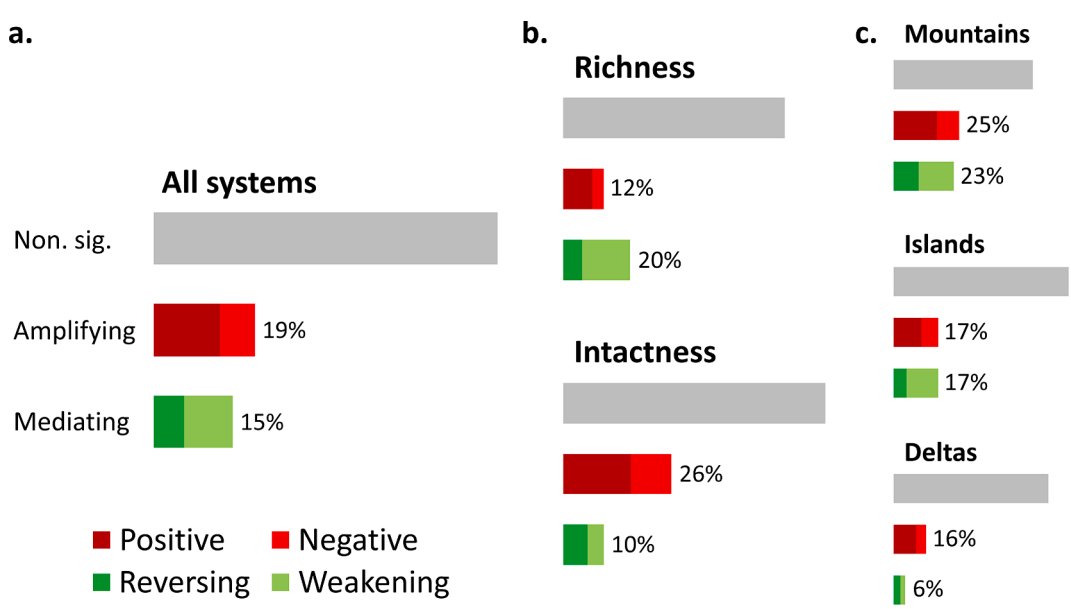


Fig. 7. Interaction types across a. all systems; b. with species richness and biodiversity intactness across all systems; and c. in individual mountain, island and delta systems. 'Non. sig.' indicates no significant interaction effects ($p > 0.05$).

significant. Population had mostly negative associations across ES in mountains, in contrast to positive associations with food ES in islands and deltas. Infrastructure had more consistently positive associations with ES across the systems (89 %), for most ES in mountains and food ES in islands and deltas. Land use change had mixed associations across systems and within ES types. Climate change had the largest proportion

of significant associations with ES for temperature, which had negative associations for most ES across the systems (84 %), excepting some soil indicators in mountains. Precipitation change had more mixed associations, although these were broadly consistent across ES type.

Biodiversity shared a similar amount of significant associations to ES as the other predictors (52 %, Table 4). Intactness had fewer significant associations (17), and these were inconsistent across systems and ES. Richness had more associations (42; $X^2_{1,1} = 10.59$, $p = 0.001$), which were predominately positive, except with some soil indicators. Abiotic drivers had slightly more significant associations with ES (55 %). Ruggedness had broadly negative associations with wetlands and soil ES, and positive ones with productivity indicators, and counter-intuitively food ES in mountains. Average temperature had positive associations with food ES in mountains and islands, although negative ones with soil ES. Temperature seasonality also showed positive associations with food and water ES, but negative ones with others. Annual precipitation however showed negative associations with some food indicators, but broadly positive associations with other ES. Precipitation seasonality had more mixed, but broadly negative, effects. As with interactions, associations of biodiversity and anthropogenic and abiotic drivers were most regular in mountains (161), then islands (130), then deltas (64; $X^2_{1,1} = 41.48$, $p < 0.001$).

4. Discussion

4.1. Biodiversity mediates anthropogenic drivers

We found that biodiversity had an important role in mediating anthropogenic drivers, but contrary to our expectations, amplified interactions were as common as weakened ones, particularly with biodiversity intactness. The different distribution of interactions between richness and intactness indicates different mechanisms or relationships are potentially responsible for the mediation observed. Species richness had more weakened and reversed interactions. Weakened interactions were expected as species rich areas have a larger insurance benefit over space and time (Yachi and Loreau, 1999; Loreau et al., 2003), providing more redundancy in the composition, traits or functions which provide a service (Oliver et al., 2015). A variety of species also has a larger range of responses and tolerances to environmental change (Loreau and de Mazancourt, 2013). Species richness can thereby confer resilience against disturbance, stability of ecosystem functioning, and in turn the long-term maintenance of ES supply (Allan et al., 2011; Isbell et al., 2015; Oliver et al., 2015). Biodiversity intactness, on the other hand, shows to what extent ES are affected by the completeness of the ecosystem, given that extinction can rapidly degrade ecosystem functioning (Larsen, Williams and Kremen, 2005). Intactness showed more amplified interactions, suggesting that relationships between anthropogenic impacts and ES are strongest at maximum intactness, but become weaker as systems lose native species. This shows that extinction can rapidly degrade ecosystem functioning (Larsen, Williams and Kremen, 2005), and corroborates our previous findings that human-ecosystem relationships can shift at relatively low levels of disturbance (Reader et al., 2022). However, confounding factors relate to both biodiversity indicators. A certain level of species richness, alongside a suitable climate and topography, is required for human development, meaning that richness is moderately correlated with many of the anthropogenic drivers, at least at low levels (see Paradis, 2018). Similarly, anthropogenic drivers, primarily land use change, cause much of the loss of biodiversity intactness (IPBES, 2019), and are included in the indicator. However, we argue that correlation between predictor and response would make an interaction less likely to be apparent. Both the mechanisms responsible over these larger-scales, and these potential confounding factors warrant further investigation, but the consistency of our results support a mediating effect of biodiversity on the relationship between anthropogenic drivers and ES.

4.2. Drivers of ecosystem service supply

Species richness had broadly positive associations across ES. Productivity may have been expected to correlate with species richness (Tilman, Reich and Isbell, 2012). However, the association of productivity with food ES, which typically have a negative relationship with biodiversity (Power, 2010) indicates that our results may show a wider association of areas with higher species richness and more suitable conditions for human development. In contrast, intactness had far fewer associations with ES, which could imply that direct impacts of intactness loss have not yet reached the threshold to be visible on this scale, or were diluted by other factors. Associations of the anthropogenic drivers were likewise mixed, suggesting different mechanisms responsible, despite the correlation between some drivers. Population had expectedly positive associations with food crops, although surprisingly not in mountain systems. Infrastructure counter-intuitively had positive associations

Table 4

Association of biodiversity and abiotic drivers with ecosystem services. These are from the same models as Table 3. Numbers show the coefficient of the driver on the ecosystem service using a generalised linear model. Blue indicates a positive association, red indicates a negative association. Given the interaction effects, biotic coefficients may be counter-intuitive as they will depend on the level of anthropogenic driver. Where the model coefficient is in a different direction from the interaction slope at mean levels of the anthropogenic drivers, this is indicated by a lighter, striped background. All estimates shown are significant to alpha = 0.05, * indicates alpha = 0.01, ** indicates alpha = 0.01, *** indicates alpha = 0.00005.

	Biotic						Abiotic																	
	Richness			Intactness			Ruggedness			Temperature (mean)			Temperature (seasonality)			Precipitation (annual)			Precipitation (seasonality)		
	Mnt.	Isl.	Dlt.	Mnt.	Isl.	Dlt.	Mnt.	Isl.	Dlt.	Mnt.	Isl.	Dlt.	Mnt.	Isl.	Dlt.	Mnt.	Isl.	Dlt.	Mnt.	Isl.	Dlt.
Food area	0.9 ***	0.7 ***	1.1 *	-0.2 **	1.3		0.2 **			0.6 ***	3.4 ***		0.7 ***	1 **					0.2 **	-0.2 *	
Nonfood area	0.7 ***	0.4 *	1.2 *	-0.3 ***			0.4 ***	0.4 **		1.5 ***	4.1 ***		0.7 ***				-0.4 *			-0.5 ***	
Food value			0.7 *				0.2 ***			0.5 ***	0.8 ***					-0.3 ***			-0.3 ***		
Nonfood value	0.5 ***		0.8 **	-0.2			0.2 ***			0.8 ***	1.8 ***		0.5 **	0.8 ***		-0.2 **					
Pasture	0.2 **	0.6 **	0.8				0.1 **			0.4 ***	-1.5 ***			-0.9 *		-0.7 ***			-0.2 ***	0.4 **	
Water available	0.7 ***	0.8 ***	0.8 *		2.9 ***	1.5 *	0.1 **	-0.2		-0.2	-1.5 ***		0.5 ***			1 ***	0.7 ***		0.3 ***	0.5 ***	-0.3
Water withdr.	0.6 ***	0.6 ***	1 *		2.8 ***	2.3 ***	0.3 ***	0.2	-0.5 **	0.5 ***		1.7 *	1 ***		1.6 *	-0.5 ***	-0.2		-0.1	0.3 *	
Sediment	0.4 **	1.4 ***	0.7			1.3	0.5 ***	0.7 ***					0.4 *		1	0.5 ***			0.4 ***		
NPP pot.	0.3 ***	0	0.1							-0.3 ***	0.4 ***		-0.1 ***			0.3 ***	0.1 ***	0.1 ***		-0.1 ***	-0.1
NPP	0.3 ***	0.1 **	0.1 *							-0.3 ***	0.4 ***		-0.2 ***			0.3 ***	0.1 ***	0.1 ***	0	-0.1 ***	-0.1
Veg. C	0.3 ***	0.1 *	0.7 ***		-0.4	-0.4	0	0.1 **		0.3 ***	1.2 ***	0.8 *				0.3 ***			-0.1 ***	-0.3 ***	
Veg. C pot.	0.4 ***	0.2 ***	0.4 **					0.1 *			0.7 ***					0.4 ***	0.1 *	0.2	-0.1 *	-0.2 ***	
Forest	0.8 ***	0.2 ***						0.1 ***	-0.3	-0.7 ***	0.7 ***			0.3 *		0.6 ***	0.1 **		-0.1 ***	-0.2 ***	
Wetland			0.4				-0.6 ***	-0.9 ***		-0.8 **	0.7					0	0.6 *			0.5 **	
Soil C				-0.1 **				-0		-0.6 ***	-0.2 **	-0.5 *	-0.3 ***			0.4 ***	0.1 ***	0.2 *	0 *	-0.2 ***	-0.1 **
Soil C density	0.2 ***		-0.1		-0.3 ***	-0.3 *	0.1 **	0 ***		-0.8 ***	-0.4 ***		-0.2 ***	-0.1 ***		0.4 ***	0.1 ***	0.1 **		-0.2 ***	-0.2 ***
Soil CEC		-0.1 ***	-0.2 ***		-0.1	-0.2 **				-0.3 ***	-0.3 ***		0		0.1 *	0.2 ***	0		-0 **	-0	
Soil N	-0						-0	-0		-0.1 ***	-0.1 ***		-0.1 ***	0.1		0.1 ***	0 **	-0.1 *	0 ***		-0
Soil water	0.1 **				-0.5 *		-0	-0.1		-0.5 ***	-0.5 ***	-0.5	-0.1 ***	0.2 *		0.2 ***	0.1 ***		0 **		

with most ES, despite the obvious displacement of ecosystems as infrastructure density increases. Land use change likewise had more positive associations in mountains. Generally, we found both interactions and associations being strongest in mountains, then islands, then deltas. This may reflect that in relatively undeveloped systems, such as mountains, infrastructural development is more likely to occur with high ES supply, and is not yet widespread enough to cause assessable degradation to these ecosystems on a system-wide scale. In deltas, this pattern could show the break down in biodiversity effects on ecosystem functioning found at high levels of environmental change (Steudel et al., 2012). This may also suggest that as anthropogenic influence increases, societies become more disconnected from local ES, able to replace them with trade or technological solutions (Cumming et al., 2014). This matches the change-point in the response of ES at certain levels of modification found in delta systems (Peng et al., 2017; Reader et al., 2022).

Beyond biodiversity, ES supply is also driven by the abiotic environment and human demand and modification. Abiotic drivers shared similar associations with ES to biodiversity and anthropogenic factors. This suggests that abiotic drivers have important direct effects on ES, beyond just providing 'nature's stage' for species and societies (Lawler et al., 2015). Ruggedness had generally positive associations with ES, perhaps indicating how it can be a barrier to global change. The broad positive associations between temperature, NPP and related ES such as food and carbon are intuitive and reported in the literature (e.g. Liu et al., 2021). The differences in associations between systems may reflect to some degree how both climate and topography can mediate the relationship between biodiversity and ecosystem functioning and resilience (Graae et al., 2017; Jactel et al., 2018). Precipitation has broader positive associations with most ES, excepting crops, indicating the decoupling of modern irrigated agriculture from rainfall. Climate seasonality has a more mixed, system-specific association with ES, but is no less important, which matches how seasonality and annual precipitation vary as the main predictor of NPP depending on ecotype (Guo et al., 2012). It is therefore important to include seasonality, and indeed climate extremes, in assessing the impacts of climate change. Given its nonlinear impacts as environmental thresholds are approached (Burkett et al., 2005), climate change may also affect the associations found. In sum, these results reinforce the need to consider abiotic drivers in ES analysis (van der Meulen, Braat and Brils, 2016).

4.3. Synergies and trade-offs between ecosystem services

The effect of drivers on ES may be amplified or weakened by the synergies and trade-offs between the ES. We found synergies and trade-offs were broadly similar between systems, although strongest in deltas, perhaps reflecting the more limited areal extent and higher land-use intensity of these systems. There were consistent synergies between material and productivity related ES, contrasting the reported negative relationship between food ES and carbon storage (e.g. Johnson et al., 2014), but potentially indicating the large areas over which these ES were averaged. There were consistent trade-offs between provisioning and soil-related ES, as may be expected given the impacts of agricultural use (Power, 2010), although higher soil quality could also be expected to correlate with food ES. Non-provisioning ES more often have synergistic relationships among themselves (Howe et al., 2014), but while we found indications for a synergy between productivity and soil ES in mountains, the other systems showed a trade-off. This could be due to the relative pristineness of mountains, where the low level of anthropogenic impact even in areas of higher productivity may have limited soil degradation, or indeed that the low levels of soil ES themselves limit such anthropogenic influence. Interestingly, we find some system-specific differences in individual ES important to each system. In islands, water availability exhibits a trade-off with other provisioning services, perhaps indicating the pressure of agriculture on limited water supplies. In mountains, pastures and wetlands show trade-offs with most other ES, while in deltas forests show consistent trade-offs with other ES. The trade-offs between the area-based ES and other ES in these systems suggests that land use might be the most relevant factor in dictating ES supply at these scales.

4.4. Limitations

Some caution is necessary when interpreting the mediating effects and associations we uncovered. First, we measured interactions as correlations rather than making causal links, and given the two-way nature of these interactions, they can also be interpreted as anthropogenic drivers influencing the response of ES to biodiversity. Second, the associations found may be affected by multicollinearity. Our analysis showed this may have affected some associations with temperature (SI Table 3). Further, while each of our drivers represent distinct facets of ES supply, there are clear correlations between them, for example, climate, species richness and human footprint. In particular, climate change had the most frequent associations of any anthropogenic driver, but is obviously correlated with the abiotic climate drivers, so may instead reflect the consistent effect of the abiotic environment on ES. Our limitation in distinguishing first and second order effects of driver-ES relations means that we may attribute too high direct associations to some drivers where their importance is indirect. Third, recent developments of data aggregation into global datasets allow us to perform global analyses (e.g. Bowler et al., 2020), but often data is unavailable, and challenges remain in the integration of datasets which can differ in nature and overlap in source data. There is also overlap between and among the ES and driver variables, which is an inevitability of exploring drivers for ES, given that ES are based on human interaction with nature (Potschin and Haines-Young, 2011). Some important ES, in particular cultural, and drivers, such as invasive species, were missing, which could have changed the overall pattern of results. Overlaps and data dependencies may have therefore contributed to some of the counter-intuitive associations found, but their exact role is unclear. There was a temporal mismatch between some of the indicators – although we attempted to minimise this by selecting them to maximize overlap. Spatially, averaging values over large areas means that biodiversity will not necessarily be mechanistically linked to the ES or interaction examined; but given the scale mismatches in the data, still captures the broad system-wide patterns. We also only analysed 26 % of islands (912) due to data availability, in contrast to mountains and deltas where we were able to include >98 % of the systems. This likely bias our selection of islands towards those which are less isolated and with larger anthropogenic influences, given data availability appears higher in those closer to continents (Fig. 1). However, the synergies and trade-offs between ES were broadly consistent with the other systems, suggesting a consistent sample. Finally, our methods may introduce some biases. Performing multiple tests (57 models, with 12 predictors and 10 interactions) will increase the likelihood that spurious effects and interactions will be significant by chance. We have selected an unmodified alpha = 0.05, but the majority of associations were significant to much more conservative standards (0.01 (14.1 % of significant associations), 0.001 (14.4 %) and 0.00005 (53.5 %)). Therefore, while interpretation of individual relationships requires caution, the inferred pattern of interactions was robust to variation in the specific assumptions of the statistical framework.

4.5. Future directions

Other metrics of biodiversity, available with new global datasets, or at smaller scales, provide exciting opportunities to examine the mechanisms and implications of the mediating effect found. Firstly, other taxonomic groups, such as plants and insects, may make an important contribution to biodiversity and ES potentially not captured by our indicators. Secondly, investigating different metrics, such as species abundance, functional diversity, genetic diversity (for example Millette et al., 2020) or landscape diversity would show us how different aspects

of biodiversity affect this mediation. There may be compositional change in species traits along a gradient of species richness or intactness, and the average or diversity of these characteristics may be more important to individual ES, and provide us a more mechanistic understanding of the interactions we explore (Harrison et al., 2014). Thirdly, specific indicators may be more relevant to certain systems; for example, aquatic biodiversity and ecosystem services play an important role in delta and island provisioning and sustainability. Exploring these indicators may further highlight the generalisability of our findings. Finally, these established global trends could provide a template to identify regional deviations and smaller-scale processes. These interactions could then be explored and incorporated in the potential outcomes of management strategies or policy decisions at different scales.

4.6. Conclusion

We present a large empirical study that supports the importance of biodiversity in determining relationships between anthropogenic drivers and ES, as well as the importance of abiotic and anthropogenic drivers in determining ES supply. Despite the disparate datasets and local contexts, we find consistent correlations and patterns across the systems alongside logical differences between them. This shows that global datasets can unveil broad patterns within social-ecological systems, and that local context is critical in determining ES relationships. Broadly, we show that high biodiversity can play an important role in the impacts of anthropogenic change on the environment, whether or not those changes are positive. We also found that systems with more modification, such as deltas, tended to have weaker associations between human and biotic factors and their ecosystem service supply, whereas less modified systems, such as mountains, demonstrated more frequent and stronger associations and interactions. Given predicted increases in global change drivers across the three systems, the need for this mediation to be considered will become even more important in the future.

CRediT authorship contribution statement

Martin Oliver Reader: Conceptualization, Methodology, Software, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization. **Maarten B. Eppinga:** Conceptualization, Writing – review & editing. **Hugo Jan de Boer:** Conceptualization, Writing – review & editing. **Alexander Damm:** Conceptualization, Writing – review & editing. **Owen L. Petchey:** Conceptualization, Writing – review & editing. **Maria J. Santos:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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