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Consistent ecosystem service bundles emerge across global mountain, island and delta systems

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ABSTRACT

Ecosystem services are often analysed individually, but are intertwined with one another and the social-ecological systems they occur in. As a response, ecosystem service bundles, i.e. co-occurring sets of ecosystem services, can be used to simplify complex relationships between nature and society, and in turn aid understanding. Typically bundles are studied on the local to regional scale, given the importance of local context to bundling, but wider scale analysis may help highlight broader ecosystem service balances for sustainable management. However, it remains uncertain if the relationships between ecosystem services are strong enough to describe coherent bundles at the global scale, and the extent to which these bundles are robust across different social-ecological systems and within different biogeographical realms.

Here, we examine whether coherent bundles emerge from a set of 25 ecosystem property and service indicators across regional mountain, island and delta systems around the world. We analyse differences between bundle composition and correlation structure based on system, latitude and biome. We find consistent bundles broadly representing 'food', 'productivity' and biodiversity 'intactness/soil' ecosystem properties and services emerge across mountains, islands and deltas globally. These bundles show strong positive correlations internally, and consistent negative correlations between 'food' services and 'intactness/soil' ecosystem properties across bundles. The bundles weakened at higher latitudes and individual biomes where the division between ecosystem properties and services broke down. In sum, while islands, mountains and deltas are distinct social-ecological systems, we found ecosystem bundles robustly described synergies and trade-offs between ecosystem services across these systems. This suggests that bundling has a role in simplifying wider scale interactions between humans and ecosystem services.

1. Introduction

One of the key scientific challenges of the Anthropocene is to identify pathways to sustainability (Cork et al., 2023; Sachs et al., 2019). Such pathways demand sustainable resource management; securing the supply of different ecosystem services (ESs) that contribute to human wellbeing (Wu, 2013; Yang et al., 2020). Coherent resource management in turn requires an understanding of the potential synergies and trade-offs between different ESs (Chisholm, 2010; Ellis et al., 2019). However, ESs are often analysed individually, limiting the potential contribution of such assessments to informed policy making (Chisholm, 2010; Rau et al., 2020). Identification of ES bundles, groups of ESs co-occurring in space and time (Raudsepp-Hearne et al., 2010), provides a promising and increasingly used means to address these challenges (Saidi & Spray, 2018). Specifically, bundling can implicitly account for synergies and trade-offs, highlight the co-benefits of prioritising a particular ES, identify hot and cold spots of ES supply, and provide guidance where information is missing (Meacham et al., 2022). Bundling is usually performed at local and regional scales (Meacham et al., 2022; Saidi & Spray, 2018). This makes sense, as smaller scales will mean tighter mechanistic relationships between people and nature, and ESs and bundles will differ between different social-ecological contexts and scales (Grêt-Regamey et al., 2014; Madrigal-Martínez and Miralles i García, 2020; Qiu et al., 2018; Raudsepp-Hearne and

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Peterson, 2016). However, this focus on smaller scales, typically with disparate ES indicators, and with substantial geographical gaps (Howe et al., 2014), makes comparison between studies difficult, and so limits wider inferences which the global decline of ESs and interconnectedness of systems may demand (Brauman et al., 2020; Meacham et al., 2022). The increasing number of global indicators of ecosystem properties and services provide an opportunity to identify whether coherent bundles and ES relationships can be formed at wider scales, and further, whether they remain consistent across different biogeographical contexts.

Social-ecological systems represent units of interacting biophysical and human systems (Berkes & Folke, 1998) that provide a natural scale of observation for ES bundles and relationships, given ESs represent the intersection between ecosystem properties and functions and the societies which use them (Potschin & Haines-Young, 2011). Yet, it is still an open question as to whether consistent bundles and ES relationships can be found across different social-ecological systems. Of the studies that go beyond the national scale, our previous work found three bundles of services across large river delta systems around the world, which broadly represented provisioning ESs, productivity and species richness, soil quality and biodiversity intactness (Reader et al., 2022). Meanwhile, a study of global urban hinterlands identified seven archetypes of ES supply, one combining crops and water ESs, others water and recreation, and carbon storage and air quality (Haberman & Bennett, 2019). Wider scale relationships between ESs have also been inferred by *meta*-analyses. These have consistently found some broad relationships, specifically trade-offs between provisioning and other ESs (Howe et al., 2014), and synergies between regulating and cultural services (Lee & Lautenbach, 2016). Within regions, ES relationships and in some cases bundles have been shown to persist at different scales (Hamann et al., 2015; Qiu et al., 2018; Raudsepp-Hearne & Peterson, 2016). However, it remains to be seen whether these relationships will persevere across larger, more varied systems.

Ecosystem services and their bundles are driven and limited by their biotic, abiotic and socio-economic context (Bennett et al., 2009; Cavender-Bares et al., 2015; Duncan et al., 2015). Therefore, analysing ES associations across systems with similar geographical contexts can provide a means for establishing the consistency of such bundles and relationships. Latitude and biome represent two simple metrics to classify these geographical contexts. Latitude affects biodiversity, primary productivity and human occupancy (Gaston, 2000; Kummu & Varis, 2011), and specific ESs fluctuate across latitudinal gradients (Sato et al., 2021), which may mean that associations between ESs and the subsequent bundles will differ with latitude. For example, in less intensively used systems at higher latitudes, trade-offs between biodiversity and provisioning services may be less pronounced at wider scales (Reader et al., 2022). Biomes represent biogeographic units with distinct biotic communities and climate. These differences will affect the ecological traits and functions, and abiotic processes that act as drivers for ESs and their interactions (Mace et al., 2012; Renard et al., 2015) – meaning that biomes understandably have been found to represent markedly different individual and summed ES supply (de Groot et al., 2012). Latitudes and biomes therefore represent a broad range of biogeographical contexts over which the consistency of bundles and relationships can be established.

Here, we investigate whether we can find coherent bundles and relationships of ESs across global systems, and assess the robustness of these findings across different systems, latitudes and biomes. Our first research question asks which bundles of ESs form across global systems, and what are their synergies and trade-offs. Based on our previous work on deltas, we would expect provisioning ESs to bundle together, alongside bundles representing soil quality and biodiversity intactness, and productivity and species richness (Reader et al., 2022). However, given potentially looser links between indicators over larger, less homogenous systems, weaker or incoherent bundles may occur. Our second research question asks which bundles form in different systems, latitudes and biomes, and to what extent these differ from the combined system bundles. If synergies and trade-offs are commonly structured across systems, latitudes and biomes, which may be the case when aggregating regional-scale data, we can expect similar bundles. Alternatively, the different bioclimatic properties and population densities may affect the association between ESs and generate different bundles. More specifically, we could expect the clear trade-offs between provisioning and other services to break down in less populated systems.

To answer these questions, we collected 25 spatial ES indicators across three systems: mountains, islands and deltas, at the global extent. We used five clustering algorithms, selecting our bundles using majority vote, and examined the consistency of bundling and the correlations within and across these bundles when clustering was performed on the level of system, latitude and biome. In doing so, we aim to highlight the ES relationships that can be observed on a global scale, and the extent to which these relationships and associations can be generalised.

2. Methods

2.1. Study systems

We studied large mountain, island and delta systems distributed globally. We chose these systems because they represent relatable, delineable social-ecological systems with biophysical boundaries, in which we could expect a wide gradient of ecosystem properties and services (Balzan et al., 2018; Martín-López et al., 2019; Nicholls et al., 2018). We used the global datasets of mountain, island and delta boundaries gathered for our previous work (Reader et al., 2023). Mountain zones (henceforth called mountains) were taken from the Global Mountain Biodiversity Assessment dataset (Körner et al., 2017; Payne & Snethlage, 2018), which delineates mountains using ruggedness (> 200 m elevation change within a 2.5′ cell), splitting them into thermal life zones. Islands were based on a coastline dataset (www.naturalearthdata.com), excluding continental landmasses. Finally, deltas were based on a dataset of delta distributary networks we manually constructed (Reader et al., 2022). We selected mountains, islands and deltas > 10 km^2 to ensure representative coverage and variability of ES indicators. We examined which ES datasets (see next section) were available for as many of these systems as possible, selecting 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 %), in combination representing 22 % of global land area. Overlapping areas, e.g. mountains on islands, were kept in each dataset. There were 73 deltas on islands (average proportion per island covered by deltas of 5.9 %), 14 deltas on mountains (0.001 %) and 287 mountains on islands (25.4 %).

2.2. Ecosystem service indicators

We reviewed publicly available spatial ecosystem property and service datasets from peer-reviewed papers or recognised agencies, selecting the most recent global scale indicators relevant to our study systems (Table 1, Supplementary Information Figs. 1–3). Given the limited number of global realised ecosystem service indicators, we selected indicators from across the ES cascade (as for example Raudsepp-Hearne et al., 2010). This means we selected indicators for ecosystem properties and functions, ecosystem service supply, realised ecosystem services, and their benefits to society (Potschin & Haines-Young, 2011). An advantage of this wider selection is that it can illustrate where different parts of this cascade might align or diverge (Schirpke et al., 2019). Therefore when we refer to ES bundles, we mean bundles of ecosystem properties, services and benefits. Further, while cultural and relational services are an important part of nature's contributions to people (Díaz et al., 2018), data availability limits us to provisioning/material, regulating, and supporting/nature indicators. Although some indicators can be proxies for more specific ESs (SI Table 1), the relationship between an indicator and an associated service may

Table 1
Ecosystem property and service indicators. For more details e.g. additional processing and download sources, see Supplementary Information Table 1. Modified from Reader et al., 2023.

Category	Indicator	Description	Unit	Year	Resolution	Citation
Food	Food area	Area of food crops	ha per cell	2010	5 arc-min	IFPRI, 2019
	Food value	Value of food crops	$ per ha	2010	5 arc-min	IFPRI, 2019
	Non-food area	Area of non-food crops	ha per cell	2010	5 arc-min	IFPRI, 2019
	Non-food value	Value of non-food crops	$ per ha	2010	5 arc-min	IFPRI, 2019
	Pasture area	Proportion of pasture area	Proportion	2000	30 arc-sec	Ramankutty et al., 2008; Ramankutty et al., 2010
	Livestock	Livestock density	kg per km^2	2010	km^2	Gilbert et al., 2018
Water	Water available	Water runoff for potential use	cm	1948–2010	Catchment	Gassert et al., 2014
	Water withdrawal	Consumptive water use	cm	2010	Catchment	Gassert et al., 2014
	Sediment	Riv. sediment flux	kg/s	2010	5 arc-min	Cohen et al., 2013
Productivity	NPP	Net primary prod.	gC/m^2/yr	2000	5 arc-min	Haberl et al., 2007
	Potential NPP	Potential net primary prod.	gC/m^2/yr	2000	5 arc-min	Haberl et al., 2007
	Carbon vegetation	Vegetation biomass storage	0.01 t/ha	2000	30 arc-sec	Gibbs & Ruesch, 2008
	Potential carbon veg.	Pot. vegetation biomass storage	t/ha	< 2010	5 arc-min	West et al., 2010
Biodiversity	Amphibian richness	Richness of amphibian species	No. per cell	2013	30 arc-sec	IUCN, 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 arc-sec	IUCN, 2015b
	Biodiversity intactness (abundance)	Species abundance vs. pristine conditions	Proportion	2005	30 arc-sec	Newbold et al., 2019; Sanchez-Ortiz et al., 2019
	Biodiversity intactness (richness)	Species richness vs. pristine conditions	Proportion	2005	30 arc-sec	Newbold et al., 2019; Sanchez-Ortiz et al., 2019
Habitat	Forest cover	Forest extent	Proportion	2000	1 arc-sec	Hansen et al., 2013
	Wetlands	Wetland extent	%	2015	30 arc-sec	Lehner & Döll, 2004
Soil	Soil carbon	Soil organic carbon stock	Pg	2019	30 arc-min	FAO, 2019
	Soil carbon density	Soil organic carbon density	kg/m^3	< 2017	250 m	Hengl et al., 2017
	Soil cation-exch. 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 arc-sec	Batjes, 2016
	Soil water availability	Soil available water capacity	cm/m	1950–2015	30 arc-sec	Batjes, 2016

vary from one area to another. For example, the indicator forest area may be strongly correlated with the service timber yield in plantations, but not at all in protected old-growth forests. Therefore we refer to the indicator only. We selected 24 indicators across the systems (from Reader et al., 2023). To these, we added an indicator for livestock production (Gilbert et al., 2018), given its global importance for nutrition and livelihoods, and trade-offs with other ESs (Herrero et al., 2009). All data were of gridded format, or rasterised from vector data. For further description of the indicators and their processing, see SI Table 1. We calculated the mean of each indicator for each individual system using zonal statistics in QGIS 3.14 (QGIS.org, 2021) and the equivalent reducer function in Google Earth Engine (Gorelick et al., 2017). We then normalised each indicator to maximise comparability between one another.

2.3. Analysis

To construct ES bundles we firstly identified the suitable number of bundles for our datasets, then used an ensemble of clustering algorithms. We then examined the internal and external correlation structures of these bundles. We repeated this for the combined systems, and then for what we refer to as 'subsets' of the overall dataset: the individual mountains, islands and deltas, and different latitudes and biomes. We finally compared the bundles formed in each subset using the proportion of similarly clustered ES indicators and Fisher's exact test, and their correlations using a Mantel test. We used the diceR package to perform the clustering (version 1.2.2; Chiu & Talhouk, 2018), and R 4.2.2 (R Core Team, 2022) to perform the analyses. We further explain each step below.

2.3.1. Number of clusters (k)

To construct bundles, we firstly needed to assess the number of clusters, *k*, to which our clustering algorithms would resolve. We used consensus clustering which performs multiple runs (1000) over subsets of 80 % of the data, and then used the 'elbow' method to indicate at which point diminishing returns in cluster consensus began (Monti et al., 2003). We repeated this across the three systems using the commonly used k-means, partitioning around medoids and hierarchical clustering approaches to examine if different algorithms affected the *k* value (ConsensusClusterPlus package version 1.50.0, Wilkerson & Hayes, 2010). We finally examined bundle composition and consistency as *k* increased to observe the effect of changing this value on our findings.

2.3.2. Clustering

Various methods have been used to identify bundles, most typically clustering algorithms or principal component analysis (Saidi & Spray, 2018; Spake et al., 2017). However, different methods can produce different outputs, and a harmonised methodology has not been established, and may be inappropriate, given different methods may capture different aspects of the relationships between ESs (Madrigal-Martínez and Miralles i García, 2020). Most typically localities (from pixels to regions) are clustered together, and these clusters represent locations with similar ES values, then subjectively assigned a bundle label (following Raudsepp-Hearne et al., 2010). Where sufficient ES indicators are available, clustering by ES (as Martín-López et al., 2012; Reader et al., 2022) can provide an alternative approach that shows which ESs are consistently found with one another, with the benefit of being able to assign multiple bundles to an area (Meacham et al., 2022).

Different clustering algorithms prioritise different mathematical relationships between the ES indicators to create the clusters, and can therefore significantly affect bundle formation (Reader et al., 2022). Hence, we adopted an ensemble approach using five clustering algorithms, which take distinct approaches to group data: k-means, hierarchical clustering, affinity propagation, Bayesian Gaussian mixture models, and fuzzy c-means (see SI Note 1 for more details). We used Euclidean (straight-line) distance as the metric to cluster the observations within the algorithms, given it is very commonly used and performs reasonably well across different datasets (Shirkhorshidi et al., 2015). Clustering within the algorithms can also depend on initial conditions; we therefore ran each one 500 times, and selected the most frequently occurring clustering. We relabeled the clusters for consistency between the algorithms using the diceR 'relabel_class' function, manually relabeling where it would further improve the average proportion of indicators clustering together.

2.3.3. Establishing combined system bundles and correlations

To answer our first research question, we formed bundles from the combined systems, based on which cluster each indicator was most commonly grouped within across the five algorithms. We then calculated the robustness of each bundle, by taking the average robustness of the bundle component indicators, i.e. the number of times each algorithm agreed with the majority vote (with a maximum of five when all algorithms classified the indicator within the same cluster). To assess the strength of internal positive and negative correlations within the bundle, we calculated the pairwise correlations between the indicators using Spearman's ρ. To show the correlations between bundles we took the average correlations between each indicator from one bundle with those of another. To reduce any bias introduced when averaging correlations, we first transformed the Spearman's ρ values using a Fisher transformation, averaged them per bundle, then back transformed to a Spearman's ρ (Corey et al., 1998).

2.3.4. Assessing differences between bundles

To answer our second research question, we repeated the bundling process for each system (mountain, island and delta), latitude and biome (see SI Fig. 4 for observations per subset and the proportions of biomes found per system and latitude). We divided all systems and the individual systems into latitudinal groups selected to ensure enough observations within each subset – those where the area centre-point lies between the Equator and 15° north and south ($n = 163$ mountains, 282 islands, 65 deltas), from 15° to 30° ($n = 181, 72, 46$), 30° to 60° ($n = 639, 380, 56$) and 60° to 90° ($n = 51, 178, 68$). We then used the Terrestrial Ecoregions of the World mapping (Dinerstein et al., 2017) to subset the systems into one of 14 biomes. For individual systems the ensemble of clustering algorithms worked well, but clustering was less consistent in the biomes and latitudes, and ties occurred where two sets of two algorithms disagreed (occurring in 100 of 850 indicators, i.e. 25 indicators across all systems, mountains, islands and deltas; four groups of latitudes across each of these, and fourteen biomes; $850 = 25(4 + 16 + 14)$). As these subsets focused on identifying deviations from the main trends, we treated these ties conservatively, and grouped indicators according to the main trends where possible.

To assess differences between the bundles, for each subset we calculated the proportion of indicators occurring in the same bundle as the bundles formed for each system and for the combined systems. For example, a bundle calculated for the Temperate Grassland biome subset may contain five out of six of the same indicators as the most similar combined system bundle. We also calculated the number of times each indicator was selected in each bundle across the subsets. We measured the difference between bundles in the subsets versus all systems using a Bray-Curtis dissimilarity metric and Fisher's exact test, which will report a $p < .05$ where counts of indicators in each bundle differ significantly. We tested the difference in the correlation structures using a Mantel test on the pair-wise indicator correlation matrices. Finally, bundling could potentially be affected by sample size – fewer points would be more affected by noise, meaning the bundles could be less consistent. We therefore repeated the bundling process across the systems using 10 random samples each of 10 %, 25 % and 50 % of the complete dataset.

3. Results

3.1. Four bundles were identified across global systems

We found that across our systems, latitudes and biomes, our ecosystem property and service indicators most readily clustered into four bundles (SI Note 2). For the combined systems, these bundles broadly represent 'food' – containing indicators of crops, livestock and water withdrawal, 'intactness/soil' – measures of biodiversity intactness and soil quality; 'productivity' – net primary productivity, carbon storage, species richness and forest area; and 'water' – available water, sediment flux and wetland area (Table 2). Moving forward, we highlight these bundles using quotation marks. Whereas the 'food' indicators broadly represent ecosystem services, the other bundles include indicators of ecosystem properties or potential services. These bundles were consistent and recognisable across different numbers of clusters (SI Note 2), and were consistently selected together across the different clustering algorithms (Table 2, SI Note 3). 'Food' indicators clustered together most often, with an average robustness of 0.91, 'intactness/soil' had an average robustness of 0.86, 'productivity' had an average robustness of 0.85, while the 'water' indicators had a robustness of 0.6, just above that occurring when random data was clustered (0.57; Reader et al., 2022).

We can see these bundles reflected by the pairwise correlations of their indicators – there are clear positive correlations within the bundles, which are stronger than between bundles correlations, with the exception of the less robust 'water' bundle (Figs. 1 and 2). There are broad negative correlations between the 'intactness/soil' components and the other indicators, most prominently 'food' (Figs. 1 and 2). Surprisingly, 'water' indicators correlated more with 'productivity' than themselves, but the separation of this weaker bundle increases the robustness of the others.

3.2. Bundles remained consistent across mountains, islands and deltas

The four combined system bundles remained consistent within mountain, island and delta systems (Fig. 3), with 85 % of the ecosystem property and service indicators remaining in the same bundle as the combined system result. Composition was not significantly different from combined system bundling for either mountains (overlap of indicators = 76 %, Fisher's exact test $p = .93$), islands (overlap = 88 %, $p = .83$), or deltas (overlap = 92 %, $p = 1.00$). 'Productivity' and 'intactness/soil' bundles were most consistent with the combined system pattern, with 96 % and 90 % of the same indicators respectively. Mountain areas displayed the least similar bundles, with the 'food' bundle splitting and 'water' indicators joining the other three bundles. Intactness split from soil indicators in island systems, and pasture split from the food bundle in every system. These results again reflect the correlation patterns between their ES indicators: correlations within the systems were broadly similar in direction (Mantel $p < .05$, meaning as indicators became more correlated across the systems, they also became more correlated in the individual systems; SI Table 2). These correlations were weaker in mountains, and the individual indicators which bundled differently such as pasture area in mountains and forest area in deltas displayed correlations opposing the general pattern of the bundle (Fig. 1). Across bundle correlations were also similar, with only 'water' and 'intactness/soil' differing in direction, with a positive correlation between these in mountains, and a negative one in deltas (Fig. 2).

3.3. Bundle composition across latitude

The 'intactness/soil' and 'productivity' bundles based on ecosystem

Table 2

Four bundles were identified across global systems. The number beside each ecosystem property or service indicator shows the robustness of its selection (the number of times they were clustered within the same group by the five different algorithms) for the combined systems. The average robustness at the bottom shows the mean of this robustness per bundle. The colours around each bundle name are used to highlight these bundles in the other figures.

Intactness/soil		**Productivity**		**Food**		**Water**	
Indicator	*Robust*	Indicator	*Robust*	Indicator	*Robust*	Indicator	*Robust*
Biodiv. intactn. (A.)	0.6	Amphibian richn.	0.6	Food crop area	1	Water availability	0.6
Biodiv. intactn. (R.)	0.6	Mammal richn.	0.6	Nonfood crop area	0.8	Sediment flux	0.6
Soil carbon	1	Bird richn.	0.6	Food crop value	1	Wetland area	0.6
Soil carbon density	1	NPP actual	1	Nonfood crop value	1		
Soil CEC	0.8	NPP pot.	1	Livestock density	1		
Soil water	1	Carbon veg.	1	Pasture area	0.6		
Soil nitrogen	1	Carbon veg. pot.	1	Water withdrawal	1		
		Forest area	1				
Average robustness	0.86		0.85		0.91		0.6

properties remained relatively consistent across different latitudes in the different systems, with 73 % and 69 % overlap with the indicators from the combined system bundles respectively (Fig. 4). However, the 'food' (30 % overlap) and 'water' (19 % overlap) bundles were far less consistent, tending to split and cluster with the 'productivity' bundle. Biodiversity intactness and species richness indicators also tended to split from the combined system bundle, as did soil indicators at higher latitudes. Five indicators, including pasture area, and the 'water' indicators clustered extremely inconsistently, and clustered with the combined bundles below 25 % of the time. Compared with the global combined system set, latitudes across all systems were more different (average Bray-Curtis dissimilarity = 0.42, Fisher's exact test $p < .05$),

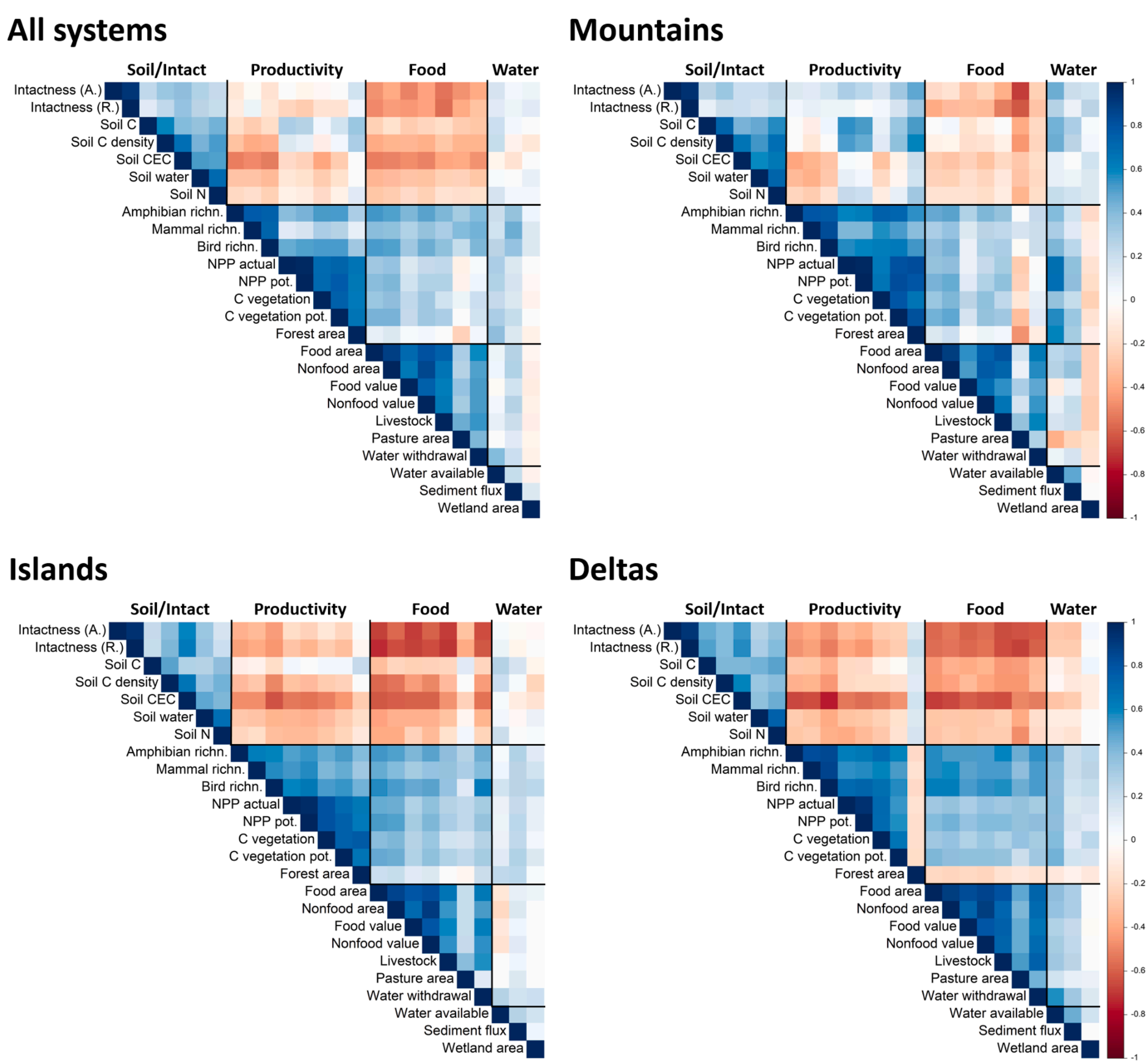

Fig. 1. Ecosystem service pairwise-correlations across all systems (top-left) and for individual mountain, island and delta systems. Blue indicates a positive correlation, or synergy, red a negative correlation, or trade-off. Correlations calculated using Spearman's ρ. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

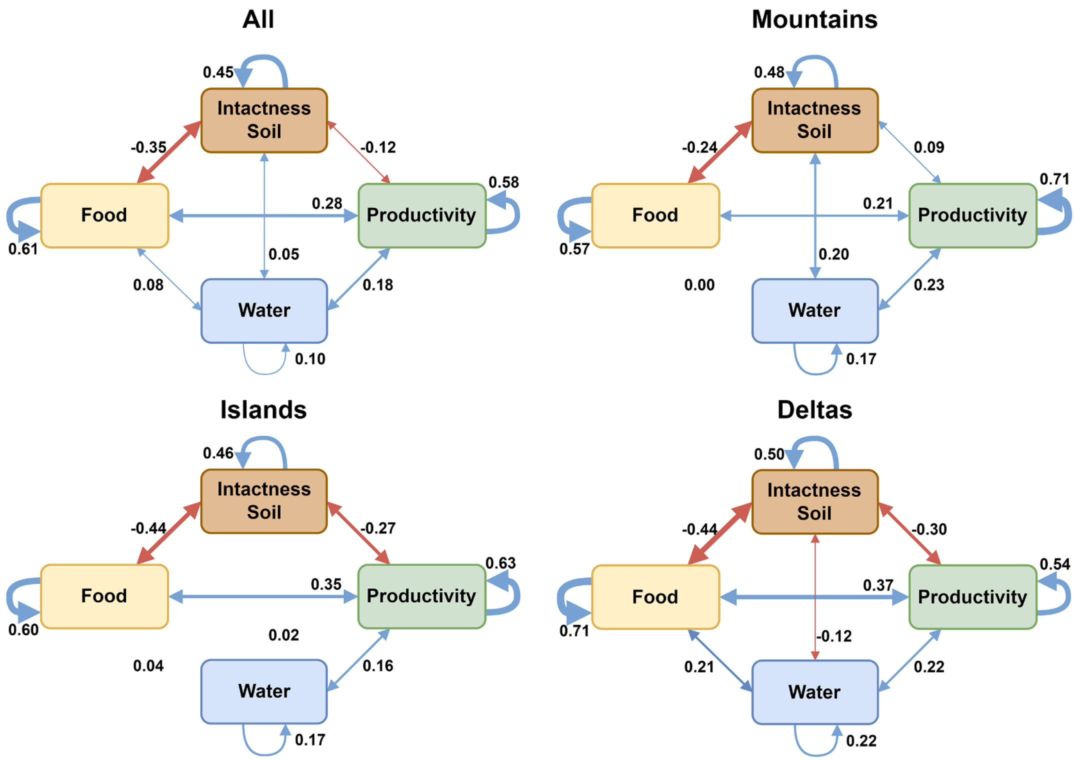

Fig. 2. Average within and across bundle correlation across all systems (top-left) and for individual mountain, island and delta systems. Numbers indicate correlation between the indicated bundles (Spearman's ρ). Arrow width is proportional to the strength of correlation, blue indicating a positive correlation and red a negative correlation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

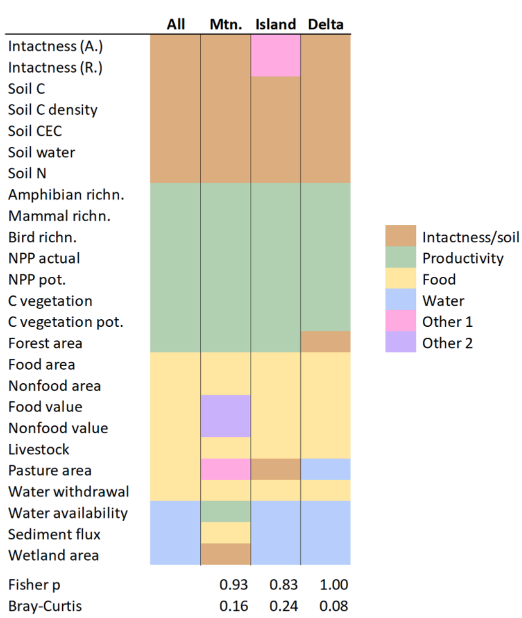

Fig. 3. Bundle consistency over mountains, islands and deltas. Colours indicate which cluster ecosystem service indicators were grouped with across the systems (see Table 2, where not consistent with these clusters, additional colours were used). Fisher p indicates the Fisher's exact test p-value (two-sided) for each system and the combined bundles (All); $p < .05$ indicating a statistically significant association between system and bundle composition. Bray-Curtis indicates the Bray-Curtis dissimilarity metric between bundle composition of each system and the combined bundles, 0 indicating zero dissimilarity, 1 indicating complete dissimilarity.

than latitudes across mountains (average Bray-Curtis dissimilarity = 0.32, $p > .05$), islands (average Bray-Curtis dissimilarity = 0.36, $p < .05$ for those over 30°) or deltas (average Bray-Curtis dissimilarity = 0.26, $p > .05$).

Average between and within bundle correlations were similar to those of the combined system bundles, although at lower latitudes there was a weakening of the negative correlation between 'intactness/soil' and 'food', and the positive correlation between 'productivity' and 'food' (Fig. 5). At high latitudes (60-90°) correlations between the indicators were broadly similar, excepting the weaker correlations within the 'intactness/soil' bundle. At low-latitudes (0-15°), correlations between many 'productivity' and 'food' indicators reversed, while richness and other productivity indicators exhibited negative correlations (SI Fig. 5). The correlation matrices between the latitudinal and combined system bundles remained correlated, although weaker in comparison to the whole systems (r 0.36-0.75, $p < .001$; SI Table 2).

3.4. Bundle composition across biome

Across the biomes we found a similar, if weaker broad pattern to the different latitudes: the general maintenance of 'intactness/soil' (58 % clustered similarly to the combined system bundle) and 'productivity' (67 %), but the division of 'food' (43 %) and 'water' (17 %) bundles, the latter again more frequently clustering with 'productivity' (Fig. 6). Most similar biomes to the combined system bundles were mangroves (60 %) and tropical moist broadleaf forest (64 %). Most dissimilar were temperate grassland (44 %, Bray-Curtis = 0.32, Fisher's exact test p = .00), tundra (44 %, Bray-Curtis = 0.4, p = .04), Mediterranean (40 %, Bray-Curtis = 0.28, p = .19) and desert (40 %, Bray-Curtis = 0.32, p = .00). Smaller sample sizes in the biome and latitude subsets may partially explain these differences: bundles became less consistent over smaller random samples of the combined system dataset (SI Note 4). However, both biome and latitude appear to have greater effect on the

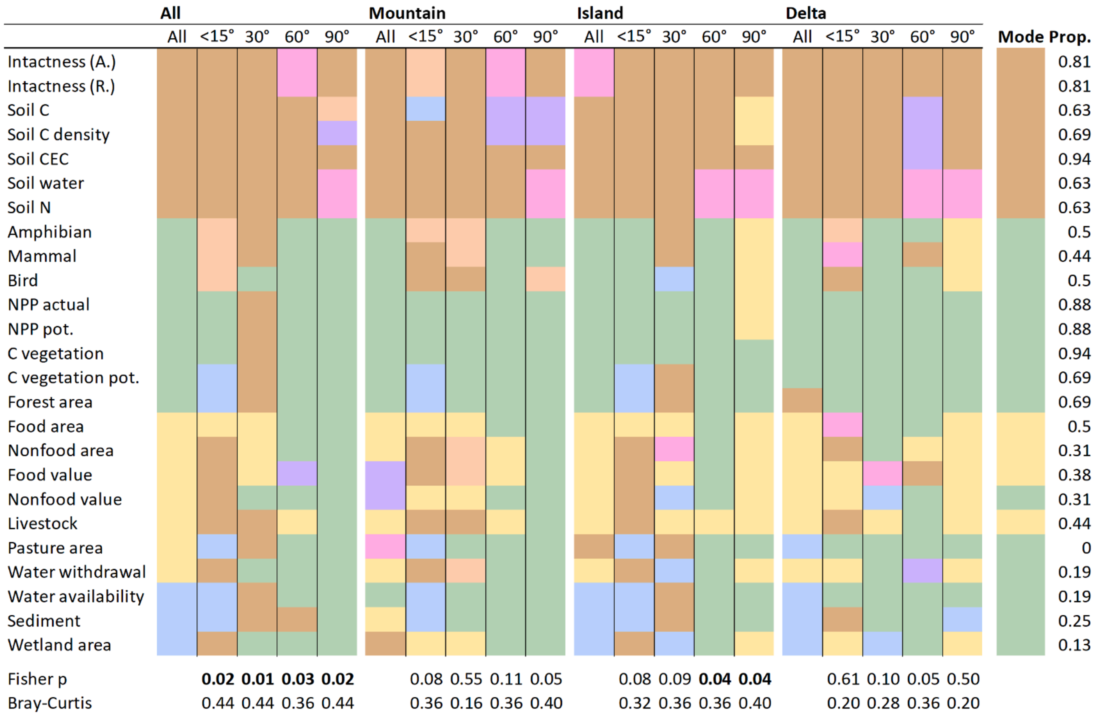

Fig. 4. Bundle consistency over different latitudes. Colours indicate which cluster ecosystem service indicators were grouped with across the latitudes and systems (see Fig. 3). Latitude, indicated by degrees, is both above and below the Equator. 30° indicates between 15 and 30°, 60° indicates between 30 and 60°, and 90° indicates 60-90°. On the right, Mode shows the most frequently selected bundle for each indicator, and Prop. shows the proportion of times this was selected (of 16). Fisher p indicates the Fisher's exact test p-value (two-sided) for each latitude and the combined system bundles (All); p < .05 indicating a statistically significant association between bundle composition across systems and for the latitudinal subset. Bray-Curtis indicates the Bray-Curtis dissimilarity metric between bundle composition of each latitude and the combined bundles, 0 indicating zero dissimilarity, 1 indicating complete dissimilarity.

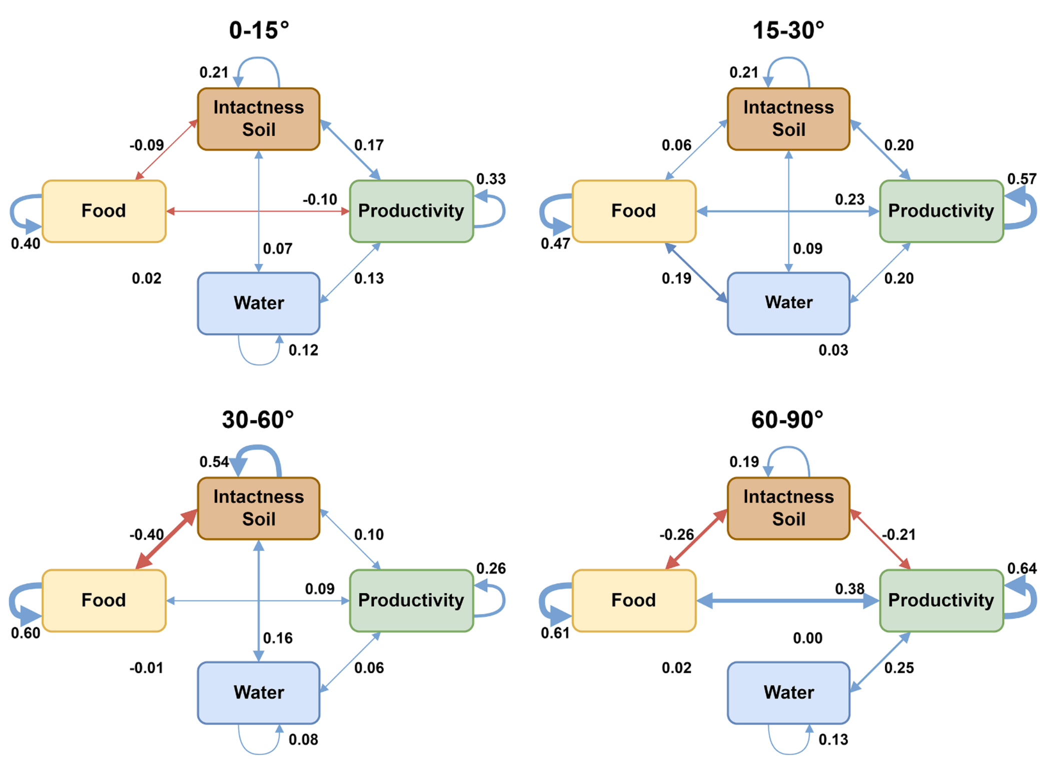

Fig. 5. Average within and across bundle correlation across different latitudes for all systems. Numbers indicate correlation between the indicated bundles (Spearman's ρ). Arrow width is proportional to the strength of correlation, blue indicating a positive correlation and red a negative correlation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

bundles found – all bundles are less consistent than the random subsets, particularly the ‘intactness/soil’ and ‘productivity’ bundles, and ‘intactness/soil’ indicators are bundled more frequently with ‘food’. Typically, correlations are strong within the bundles, even within ‘food’, and the trade-off between ‘intactness/soil’ and ‘food’ remains (Fig. 7). However, correlations weaken in the tundra, desert, mangrove and Mediterranean biomes (Fig. 7, individual indicators shown in SI Figs. 6–8), although all correlation matrices remained positively correlated with the combined system bundles (r 0.14-0.68, $p < .02$, SI Table 2).

4. Discussion

We identified three coherent, strongly correlated, bundles of ecosystem property and service indicators across the mountain, island and delta systems studied. In sum, we observe the well-established division between provisioning and non-provisioning ESs (Howe et al., 2014; Lee & Lautenbach, 2016) in the split between provisioning ecosystem services and benefits in the ‘food’ bundle and ecosystem properties and non-provisioning services in the other bundles. The most robust and internally correlated bundle, ‘food’ represented crops, livestock and water withdrawal, which is consistent with agriculture being the largest water user globally (FAO, 2022). A crop, livestock and water archetype has previously been established across rural areas surrounding cities around the world (Haberman & Bennett, 2019), and we find this is broadly observable across the three systems. The clear link between agricultural productivity and primary productivity is shown by the strong correlation between ‘food’ and ‘productivity’. The ‘productivity’ bundle combined net primary productivity with carbon vegetation stocks, which have an established relationship (Keeling & Phillips, 2007), alongside forest, which is also logical, given that the predominant broadleaf forest found across our systems tends not to be climate limited (Churkina & Running, 1998; SI Fig. 4). Similarly, broad global positive correlations have been observed between latitude, productivity and biodiversity (Gillman et al., 2015), and our findings show that these relationships were strong enough for species richness to bundle together with productivity. This bundle perhaps then represents the direct influence of climatic factors. The final consistent bundle, ‘intactness/soil’ represented biodiversity intactness alongside soil quality indicators; note that intactness, the proportion of original species and abundance remaining, often correlates negatively with species richness (Reader et al., 2023). These indicators may appear less obviously connected, but intactness is sensitive to habitat degradation and land use change (Newbold et al., 2019; Rouget et al., 2006), which would also impact soil quality (Ludwig et al., 2004). This mirrors the observed negative correlation between ‘intactness/soil’, and ‘food’, which highlights the large role of agriculture in driving habitat degradation and land use change (Dudley & Alexander, 2017; Power, 2010). A fourth bundle, ‘water’, containing indicators of water and sediment flow, was logical and relatively robust, but had weaker internal correlations. One bundle will always be weaker than the others however, and isolating these less consistent indicators strengthens the other bundles. The internal coherency of this bundle can indicate if it warrants further analysis. Overall, the bundles found were very similar to those produced from our work on deltas (Reader et al., 2022), despite the different methodology, number of indicators and the different systems. While the bundles we observed do not denote mechanistic linkages between services, our bundling approach shows that the associations between ESs are nevertheless strong enough to be consistently visible across thousands of different social-ecological systems across the globe.

Within individual systems, while overall composition and correlations of the combined system bundles persisted, some differences became apparent. In mountains, ‘food value’ separated from the other ‘food’ indicators, perhaps showing a division between more profitable crops in some areas and others with more extensive agriculture. This may have further weakened the ‘water’ bundle, the indicators here divided among other bundles. Alternatively, this could be explained by the high availability of water in mountains (Viviroli et al., 2020), which may weaken its interactions with other indicators, or the relatively small wetland area, which interestingly clusters with ‘intactness/soil’, perhaps due to its sensitivity to modification (Gibbs, 2000). Pasture bundled

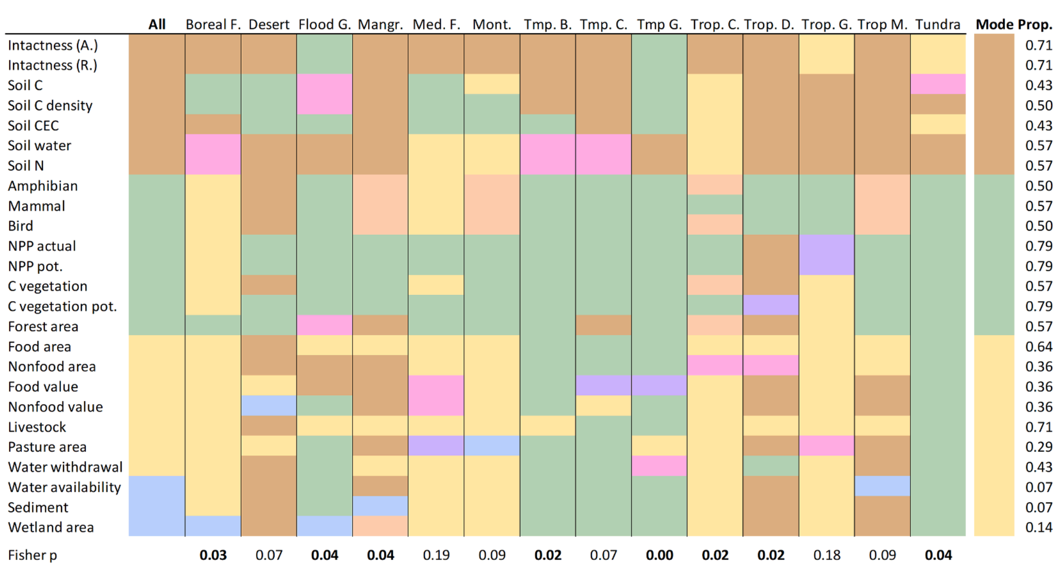

Fig. 6. Bundle consistency over different biomes. Colours indicate which cluster ecosystem service indicators were grouped within across the biomes and systems (see Fig. 3). Biomes are combined across the systems. Boreal F. – Boreal Forest, Flood G. – Flooded Grassland, Mangr. – Mangroves, Med. F. – Mediterranean Forest, Mont. – Montane Grassland, Temp. B. – Temperate Broadleaf, Temp C. – Temperate Coniferous, Temp. G. – Temperate Grassland, Trop. C. – Tropical Coniferous, Trop. D. – Tropical Dry Broadleaf, Trop. G. – Tropical Grassland, Trop. M. – Tropical Moist Broadleaf. On the right, Mode shows the most frequently selected bundle for each indicator, and Prop. shows the proportion of times this was selected (of 14). Fisher p indicates the Fisher’s exact test p-value (two-sided) for each biome and the combined system bundles (All); $p < .05$ indicating a statistically significant association between bundle composition across systems and for the biome. Bray-Curtis indicates the Bray-Curtis dissimilarity metric between bundle composition of each biome and the across system bundles, 0 indicating zero dissimilarity, 1 indicating complete dissimilarity.

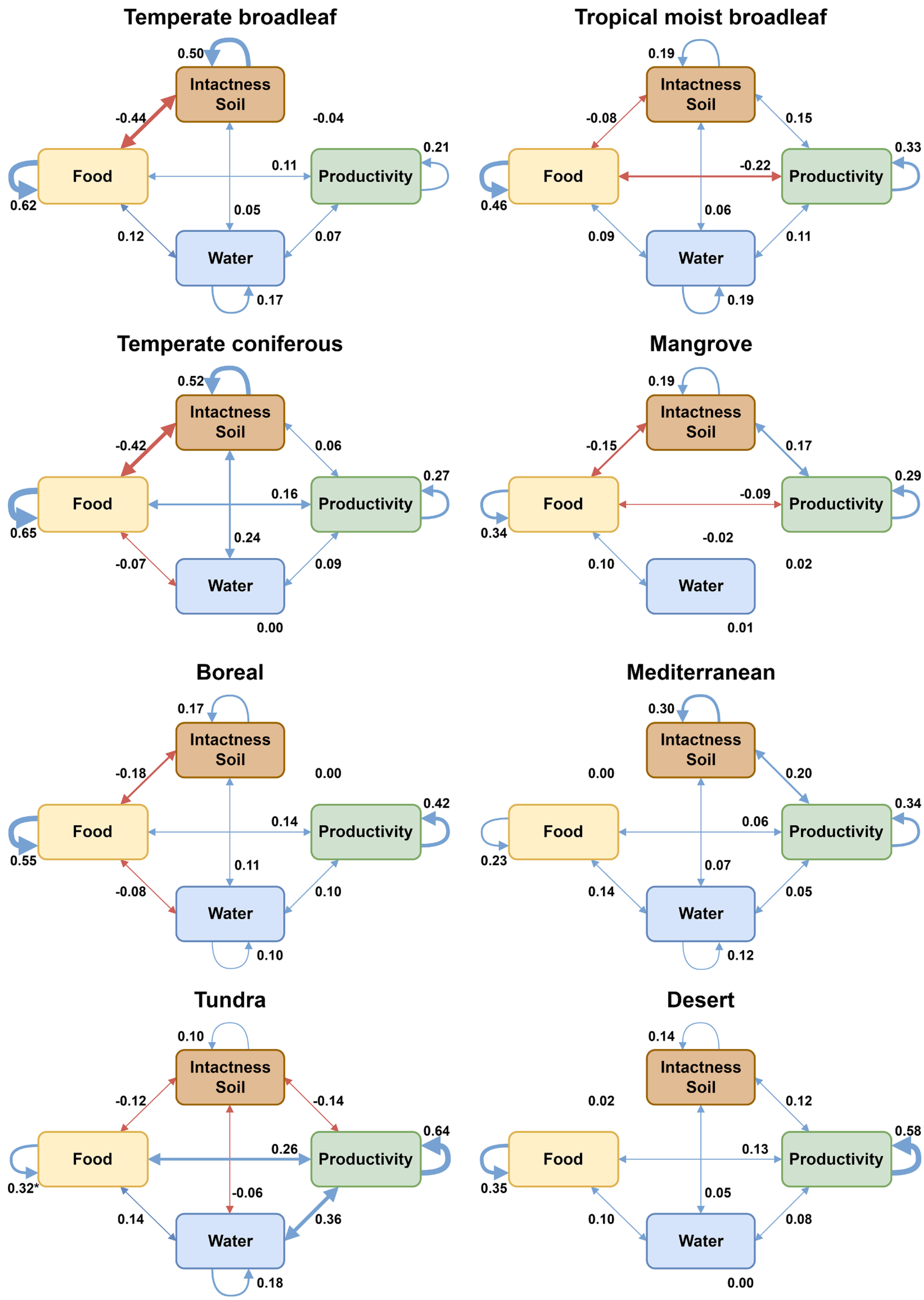

Fig. 7. Average within and across bundle correlation across biomes for all systems. Numbers indicate correlation between the indicated bundles (Spearman's ρ). The within bundle correlation for food in Tundra (marked *) was not Fisher transformed which could bias the result negatively, as the very high correlation between two of the indicators led to a spuriously high result (0.86). Arrow width is proportional to the strength of correlation, blue indicating a positive correlation and red a negative correlation. Biomes displayed have > 100 observations across all systems. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

differently in each system, and indeed tended to have weaker or oppositional correlations compared to other 'food' indicators. This could be due to it being a land cover-based indicator, which represents a wider range of agricultural intensity than the crop area indicators, meaning it will have less clear relationships with the other indicators. Likewise, wetland area is also land cover-based, and exhibited similarly weak correlations, potentially because it covers diverse wetlands from intensively-farmed rice paddies to relatively pristine mangroves (Lehner & Döll, 2004), while forest area in deltas correlated negatively with its 'productivity' bundle, being more related to 'intactness/soil'. However, the high agreement across and between the systems show that these broad associations and bundles still persist at such large extents despite substantial differences in population, global change drivers and overall supply of ESs between the systems (Reader et al., 2023).

The combined system bundle make-up and correlation structure weakens and breaks down when examining different latitudes and biomes. The ecosystem property bundles – 'intactness/soil' and 'productivity' weaken in consistency, but still maintain the majority of the same indicators, while the 'water' bundle breaks down completely in every biome, underlining its position as the 'other' bundle. However, the ecosystem service 'food' bundle, while remaining the most common grouping of its indicators, more frequently divides amongst itself and joins the other bundles, perhaps illustrating the different relationships between agriculture and other ecosystem properties depending on biogeographical context. For example, soil loss is driven by cropland in the Tropics, but this relationship weakens elsewhere (Borrelli et al., 2017). At higher latitudes and less habitable biomes such as tundra, desert, and boreal forest, 'food' and 'productivity' related indicators are more frequently bundled. This potentially shows how in these environments the simple relationship between crop production and better growing conditions is stronger than the habitat degradation caused by intensive agriculture which may contribute to the combined system bundles (Reader et al., 2022). The large differences in overall and individual ES supply between biomes (de Groot et al., 2012) perhaps explain why bundle composition in individual biomes was on average the furthest from the combined system bundles, reflecting that specific associations based on biogeographical conditions are often stronger than broad global associations between ESs. This was particularly the case in less habitable biomes, which may again reflect climate as a limiting factor on agricultural production, but surprisingly the temperate biomes also differed substantially. It should be remembered that system, biome and latitude will also have interacting effects – particular biomes will be more typical of particular systems and latitudes – and across systems lower latitudes have a higher proportion of broadleaf forest, and higher latitudes of tundra (SI Fig. 4). Similarly, while biome and latitude have distinct effects on bundles, the smaller sample sizes in these subsets will also weaken overall clustering, which may explain some of the more unexpected results (SI Note 4). Together, these results suggest that ES management needs may differ based on biogeographical factors, rather than the type of social-ecological system in particular.

When interpreting the bundles and relationships we uncovered, some caution is necessary. Firstly, our bundles are based on a mix of indicators of ecosystem properties, services and values. While this reflects global data availability, and these groupings and correlations are still informative, synergies and trade-offs may differ if purely realised ecosystem services were considered (Schirpke et al., 2019). More generally, bundle composition will clearly also be affected by the indicators selected (Saidi & Spray, 2018). In particular, we lack global indicators for cultural and relational ESs (although see Braun et al., 2018; Paracchini et al., 2014), meaning these important services and their influence on the clustering process are missing from our analysis. Data quality issues are also apparent. Even with a relatively large number of datasets, individual biases in particular indicators may skew the clusters emerging, which will be more pronounced in subsets of our systems. While often founded on impressive numbers of observations or remotely-sensed imagery, global datasets can extrapolate from relatively few samples, particularly in less populated areas. Inputs for several of these datasets also overlap, which could potentially strengthen correlations found; e.g. land cover classifications and human population density is used to model crop data and water usage (SI Table 1). Data restrictions also limited our selection of islands to those which were typically more populated or closer to larger landmasses, potentially with different ES relationships to more remote islands. Finally, there are methodological considerations. Investigation of the sensitivity of bundling to the method employed is urgently required (Meacham et al., 2022), and ideally the clustering approach should fit the data, with a mechanistic basis for the selection of algorithm, distance metric, weighting and other coefficients. Given the variable and multi-dimensional nature of ES indicator data, however, our ensemble of clustering approaches may be useful to highlight where ESs are not so easily clustered and minimise the possibility that clusters are emerging from the biases of a single algorithm.

Several avenues for future research are suggested by our analyses. Critically, this study explores and describes patterns, and any attribution of these patterns requires further analysis of the drivers of bundling, in particular human factors such as population density, infrastructure or land use (Reader et al., 2023). Finding balances between ES supply, use and demand is critical and more indicators are necessary to gain an appreciation of these differences at wider scales (Baró et al., 2015; Crouzat et al., 2015; Zoderer et al., 2019). Our analysis averages interactions across many landscapes; establishing direct mechanisms behind the synergies and trade-offs and bundles found will require multi-scale work to disentangle (such as Qiu et al., 2018). Longitudinal studies, as more time series data becomes available (e.g. Iizumi & Sakai, 2020), may also help identify drivers, and allow us to further assess the consistency of the patterns we find. Temporal differences have been found to influence both bundles and associations (Jaligot et al., 2019; Renard et al., 2015). By using numerous observations, our approach has the advantage of avoiding the pitfall of an individual area representing an ungeneralisable 'snapshot' of shifting ES relationships (Rau et al., 2020).

Our study examined bundle consistency, intra and across bundle correlations, and their relationships across global systems, latitudes and biomes. We discovered that associations between ecosystem property and service indicators were strong enough at global and system-wide extents to overcome local contextual differences, leading to three consistent and logical bundles which replicate relationships found at local and regional scales (Lee & Lautenbach, 2016). These findings illustrate the global impact of humans on ecosystems, and represent an initial step in informing the large-scale decision-making required to find sustainable balances of ESs, potentially reducing information requirements and simplifying management. However, at smaller extents, at particular latitudes and in particular biomes, specific local relationships between the ES indicators meant these larger bundles broke down, although the division between 'productivity' and 'intactness/soil' indicators remained. Given the increasingly connected nature of global social-ecological systems, and the global decline of ESs (Brauman et al., 2020), the need for wider scale analysis and management of ESs is clear. In turn, while bottom-up approaches and local contexts remain critical to sustainable ecosystem service management, appraising and managing at wider scales requires knowledge of ES relationships and responses at these extents.

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CRediT authorship contribution statement

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

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

The datasets used in this study are publicly available (see Table 1). For processed data and scripts, see https://github.com/ESS-uzh/ES-Bundles, doi: 10.5281/zenodo.10492768.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecoser.2023.101593.

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