GLOBAL EVIDENCE OF POSITIVE IMPACTS OF FRESHWATER BIODIVERSITY ON FISHERY YIELDS

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ABSTRACT

Aim

An often-invoked benefit of high biodiversity is the provision of ecosystem services. However, evidence for this is largely based on data from small-scale experimental studies of relationships between biodiversity and ecosystem function that may have little relevance for real-world systems. Here, large-scale biodiversity datasets are used to test the relationship between the yield of inland capture fisheries and species richness from 100 countries.

Location

Inland waters of Africa, Europe and parts of Asia.

Methods

A multi-model inference approach was used to assess inland fishery yields at the country level against species richness, waterside human population, area, elevation and various climatic variables, to determine the relative importance of species richness to fisheries yields as compared to other major large-scale drivers. Secondly, the mean decadal variation in fishery yields at the country level for 1981-2010 was regressed against species richness to assess if greater diversity reduces the variability in yields over time.

Results

Despite a widespread reliance on targeting few species of fish, freshwater fish species richness is highly correlated with yield (R^2 = 0.55), and remains an important and statistically significant predictor of yield once other macroecological drivers are controlled for. Freshwater richness also has a significant negative relationship with variability of yield over time in Africa (R^2 = 0.16), but no effect in Europe.

Main conclusions

The management of inland waters should incorporate protection of freshwater biodiversity, particularly in countries with the highest yielding inland fisheries, as these also tend to have high

freshwater biodiversity. As these results suggest a link between biodiversity and stable, high yielding fisheries, an important win-win may be possible for food security and conservation of freshwater ecosystems. However, findings also highlight the urgent need for more data to fully understand and monitor the contribution of biodiversity to inland fisheries globally.

INTRODUCTION

The degree to which species diversity underpins ecosystem functioning, and ultimately ecosystem services, is a central question in ecology with significant implications for policy and conservation (Mace *et al.*, 2012). It is now well established that biodiversity frequently has a positive effect on ecosystem functioning (Balvanera *et al.*, 2006; Duffy, 2009; Cardinale *et al.*, 2011). However, not all studies support this conclusion (Hooper *et al.*, 2005). Observational studies appear to contradict results from experimental studies, and vary in clarity and direction of relationship (Naeem, 2002). It is therefore possible that biodiversity-ecosystem functioning experiments may not be indicative of realised differences in ecosystem functioning in natural systems. This disconnect may in some cases be due to differences in scale and system (Duffy, 2009), and there is a disparity between the small scales at which these experiments have been performed and the scale at which management and conservation decisions are made (Cardinale *et al.*, 2012).

The use of real-world datasets bypasses some of these issues, yet currently there are only a handful of sufficiently large scale studies with which to examine the effect of biodiversity on ecosystem function in natural ecosystems. To date global studies have examined marine (Worm *et al.*, 2006) and botanical (Maestre *et al.* 2012) systems. To understand whether there is a generalizable relationship between ecosystem function and biodiversity or whether a more idiosyncratic relationship exists there is a need to examine evidence across a range of scales, systems and taxa. Moreover, more work is needed to look beyond questions of generalised functionality and productivity and consider direct links to human-wellbeing. Such work is important because there is a much poorer understanding of the links between biodiversity and the final ecosystem goods that actually confer benefits to humans (Mace *et al.*, 2012).

The question of the extent to which biodiversity underpins ecosystem services is relevant to a range of systems but has perhaps the greatest policy relevance in terms of the provisioning services that underpin food security. Studies of the relationship between ecosystem functioning and biodiversity show that increased species richness may provide i) a buffering effect in fluctuations of productivity and/or ii) an overall performance-enhancing effect (Yachi & Loreau, 1999). However, as these conclusions have been largely drawn from plant community experiments, these mechanisms may have limited generality across systems (Pinto *et al.*, 2013). Although current focus in this area is on examining impacts of biodiversity within human agricultural systems (e.g. as reviewed in Power 2010), people also rely on natural habitats for the provision of food.

At least 2 billion people depend on inland freshwaters directly for the provision of food (Richter *et al.*, 2010), and in many parts of the world inland waters are often the primary source of protein and micro-nutrients (Béné *et al.*, 2007; Dugan *et al.*, 2010). In 2010 global inland capture fisheries yielded over 11 million tonnes, with inland aquaculture yielding up to four times that amount (FAO, 2012). Globally there are hundreds, if not thousands, of freshwater species contributing to food security, yet the relationship between species diversity and yield remains poorly understood in freshwater systems (Balmford *et al.*, 2008). Recent research suggests a performance enhancing effect (Greene *et al.*, 2010; Carey & Wahl, 2011) and a buffering effect (Greene *et al.*, 2010; Franssen *et al.*, 2011) of biodiversity on yield associated with freshwater fish communities, although it is unclear how such results transfer to natural freshwater systems at larger scales (Carey & Wahl 2011). Different species can have a disproportionate contribution to ecosystem functions (McIntyre *et al.*, 2007) but in practise most fisheries concentrate on maximizing biomass – which is highly affected by such factors such as phosphorus levels and macrobenthos biomass in freshwater systems (Hanson & Leggett, 1982) – and have little interest in harvesting a diversity of species. As a consequence, there is no degree of certainty that higher freshwater biodiversity is linked to enhanced livelihoods and increased human well-being. Indeed most fishery managers would prefer the ease of managing a fishery based on fewer species for which stock assessment tools aiming at maximum sustainable yield are more easily applied. Therefore a greater comprehension is needed of how the relationship between biodiversity and ecosystem functioning can influence our understanding of the implications of freshwater biodiversity loss, and contribute to defining management objectives for inland freshwater systems (Dudgeon, 2010).

Beyond food security, understanding the degree to which biodiversity underpins freshwater fisheries has particular policy relevance as freshwater systems have major importance for conservation of biodiversity. Freshwater habitats are disproportionately species-rich given that they cover only 0.8% of the Earth's surface; 10% of species described to date and as much as a third of all vertebrates are confined to freshwater habitats (Dudgeon *et al.*, 2006). Freshwater systems are highly threatened, with many freshwater taxonomic groups facing a significantly higher extinction risk than terrestrial groups (Darwall *et al.*, 2008). As a result, if freshwater biodiversity is shown to generally underpin inland fisheries, the food security implications of this relationship would provide a powerful additional argument to conserve freshwater systems and the biodiversity contained within above and beyond purely conservation objectives.

Here, datasets from the Food and Agriculture Organisation of the United Nations (FAO) and the International Union for Conservation of Nature (IUCN) covering 100 countries are used to provide the first large-scale test of the hypotheses that high freshwater biodiversity has a positive effect on: a) fishery yields, and; b) variability of yield over time. As ecosystem function is a result of more than just the target species (Hensel & Silliman, 2013), the analyses were conducted using fish species richness, and then repeated to include additional freshwater faunal groups: molluscs, odonates and decapods (see Appendix 5).

METHODS

All analyses, unless otherwise specified, were conducted in R version 3.0.2 (R Core Team, 2014).

Freshwater biodiversity and yield

The relationship between inland capture fisheries yields and biodiversity was examined using comprehensive datasets from IUCN (2012) and FAO (2011) along with other macroecological drivers (see Appendix 1 for all data sources). Biodiversity analysis was based on species native range maps of 9,075 freshwater species from IUCN Red List of Threatened Species (IUCN, 2012), including 5,203 species of fish, 1,790 molluscs, 1,329 odonates and 753 decapods. Range maps are compiled by experts in accordance with the IUCN Red List Guidelines (available at www.iucnredlist.org) and derived from a combination of known and expected species localities. The IUCN spatial dataset is the most comprehensive continental scale data available on the distribution of all known freshwater taxa from these groups mapped to the river/lake sub-catchment scale. Species richness (SR) per country was calculated in ArcMap 10 (ESRI, Redlands, California) using the range maps from IUCN Red List assessments for fish alone, and then all available freshwater taxa. For analyses countries for inclusion were restricted to those that have a complete suite of species range maps for the taxonomic groups considered and have been comprehensively assessed by IUCN, namely Africa, Europe and parts of Asia (see Fig. 1B).

The FAO capture database FishStatJ is the most authoritative assessments of the status of world inland fisheries, and reports national annual yield data since 1950 that can be filtered by countries, taxonomy, fishing area and yield measures (FAO, 2011).

Macroecological and human drivers of fisheries yield

Fisheries yield is a product of biophysical drivers and human effort. As such, quantifying the effect of biodiversity (SR) on mean yield (t) was achieved by first building a predictive model of all putative large-scale drivers of fishery yield, and then determining the relative importance of SR compared to the other drivers – area of surface water, fishing effort, productivity and elevation. Mean yield (t) was calculated at the country level from 2001-2010 data to best reflect the time period of the IUCN species assessments (conducted from 2004-2010) (Fig. 1A). The sum of the surface area of inland waters (km^2) per country was extracted from the Global Lakes and Wetlands Database (GLWD) (Lehner & Döll, 2004) to account for available habitat for freshwater species. As no comprehensive data exists on per unit effort of fisheries or number of fishers at the country level, the human population within 10 km of inland waters for each country (hereafter waterside population) was used as a proxy for fisheries effort. Population was extracted from a raster layer of the 2000 global rural population reported by FAO at the 5 arc-minute resolution (Salvatorre *et al.*, 2005), and a range of buffers around each of the waterbodies included in the GLWD applied using ArcMap 10 (ESRI, Redlands, California). Waterside population was validated against primary data on fishing effort available for 28 African lakes (see Appendix 2) with the 10 km buffer yielding the strongest relationship ($r = 0.75$, $n=28$, $p<0.001$). Yield was not standardized by fishing effort or area (sensu

Kantoussan et al. 2014). This is because both fishing effort (waterside population) and area affect the yield relationship at the country-level; considering both as predictor variables accounts for this shared effect. A more in-depth discussion of this issue is included in Appendix 2.

Productivity, or energy available within the system – which is highly correlated with climate at the continental scale (Hawkins *et al.*, 2003) – is a major driver of global freshwater biodiversity patterns (Tisseuil *et al.*, 2012). As no spatial data currently exists on global freshwater productivity, this factor was controlled for by using the principal components from a PCA carried out on nineteen spatial climatic data layers including mean and seasonality for temperature and precipitation variables (see Appendix 3). A broken stick stopping model selected the first two principle components for inclusion in the model; these together account for 79.8% of climate variation. Use of PCA in this way reduces multidimensionality and eliminates collinearity between variables, and is an established approach for controlling for productivity across latitudes in continental scale analyses (Hawkins *et al.*, 2003; Tisseuil *et al.*, 2012). Finally, mean elevation (m) was collated for each country.

Relationship between freshwater biodiversity and yield

All possible linear regression models were built using mean yield (t) as the dependent variable, with fish SR, waterside population, climatic PCA components, inland water surface area (km^2) and mean elevation (m) as explanatory variables. Testing the residuals of the models using Moran's I standard deviate test showed that there was spatial autocorrelation. Therefore a multi-model inference approach using simultaneous autoregressive spatial model (SAR) methods was conducted following Maestre et al. (2012). The type of SAR used was the spatial simultaneous autoregressive error model (SAR_{err}) method, as this is robust to the type of spatial autocorrelation that is present in the data (Kissling & Carl, 2008), calculated within the spdep package in R. Spatial autocorrelation is accounted for by the inclusion of a spatial weighting matrix calculated based on distances between centroid points of countries. This spatial weighting matrix represent an additional term within the SAR model that describes relatedness between individual samples (countries) caused by spatial structure that is not fully accounted for by the other model parameters (Dormann *et al.*, 2007). Where necessary, Box-Cox transformations were used to normalise the distribution of the residuals, equalise the variance and improve the fit of the models (Osborne, 2010). The full SAR models are presented with the results tables (Table 1and Table S3).

From all possible models minimised second-order Akaike information criterion corrected for small sample size (AIC_c) were used to select the best fitting models. The AIC_c of all models selected that included SR as a predictor were compared to the same model without the inclusion of SR. Where AIC_c of models differs by less than 2, they are considered to be indistinguishable (Burnham & Anderson, 2002). The Akaike weights of each model were calculated based on the ΔAIC_c, i.e. the difference between the AIC_c of each model and that of the best model (Burnham & Anderson, 2002) and therefore a set was created from all models where ΔAIC_c was less than 2 from the best model, hereafter known as the top model set. Multimodel averaged parameter estimates of the analysis were calculated using the top model set. The relative importance of each predictor variable was calculated as the sum of the Akaike weights of all models that included the predictor of interest (Burnham & Anderson, 2002). Commonality analysis was then conducted to determine the unique, common and total effects of each of the variables within each of the top model sets (Nimon & Reio, 2011). The variance inflation factor (VIF) was calculated for the top models to check for collinearity between predictor variables.

Relationship between freshwater biodiversity and variability of yield

The coefficient of variation (CV) is a measure commonly used to quantify variation within a system (e.g. Pinto *et al.* 2013). CV of yield (t) was calculated for each country for three decadal increments from the years 1981 – 2010, and the mean CV was compared with linear regression to fish SR per country. Records prior to 1981 were excluded due to the higher chance of inaccuracies and extrapolated figures with older data (Garibaldi, 2012). As before, Box-Cox methodology was used to determine the most appropriate transformation to ensure that data fitted modelling assumptions. Analysis was repeated for country data subset by continent for comprehensive datasets; Africa and Europe.

When examining the link between biodiversity and variation in fisheries yield, CV would not differentiate between a yield which is steadily increasing or decreasing and one which is unstable but fluctuating in similar increments around the mean (see Fig. S3). Therefore a variation measure was adapted to consider differences of year on year yield (see Appendix 4) and calculated alongside CV for comparison.

RESULTS

Freshwater biodiversity and yield

Considered in isolation, there is a strong positive relationship between fish SR and mean annual yield (t) (R^2 = 0.55, F = 122.6, P < 0.001). The relationship between mean annual yield (t) and each of the macroecological drivers used in the models is shown in Fig. 2.

Fish SR is an important predictor of overall fisheries yield in the global SAR models that include it and the other major macroecological drivers of yield. These global models – which explains most of the variation in fisheries yield (R^2 = 0.76 (Table 1)) – shows that all variables considered here are important for predicting fisheries yield with the exception of the second principle component of the climatic variables. SR is present in both of the best fitting models (Table 1A) among the 64 possible models. These top models have the smallest AICc and fewest variables for models with comparable AICc. The residual difference per country for the full model is shown in Fig. S2.

Excluding SR from the models resulted in a reduction in mean adjusted R^2 of 0.02 (Table 1B). SR contributed between 0.03-0.05 in unique effects for each of the top models (Table 2), while area contributed 0.03, and waterside population contributed 0.06-0.07 in unique effects for each model. When shared variation was also considered, SR contributed a total effect of 0.55 (accounting for 72% of pseudo R^2), far greater than the other variables except for waterside population, which contributed 0.60 (79%) (Table 2).The overall contribution of each of the variables within the models are shown in Table 2 and Table S2. With the variance inflation factors between predictor variables in all of the best models well below ten there was no suggestion of undue collinearity between variables (Table 3).

Finally, river fisheries are known to be as much as three times more productive than lakes (Randall *et al.*, 1995) and therefore as a type of sensitivity analysis the models were repeated with river area weighted higher than lake area. This made no difference to the relative importance of fish species richness, or the total effects of fish species richness upon the models and therefore is not considered further within this study.

Freshwater biodiversity and yield variability

Based on data for all countries included in this study there is not a significant relationship between SR and CV of fisheries yield (t) (R^2 = 0.02, F = 4.14, P = 0.07, Fig. 3A). However, independent examination of continent scale data found a significant negative relationship between SR and CV when only African country data is examined (R^2 = 0.16, F = 9.81, P = 0.003, Fig.3B), not present in European data (R^2 = -0.02, F = 0.22, P = 0.65, Fig. 3C). When variability was analysed using an adapted metric which examines year-to-year differences the negative relationship for all countries is significant (Table S5). At the continental scale relationships are similar to those found using CV, although slightly weaker for the African data.

DISCUSSION

This analysis provides the first large-scale analysis of the relationship between freshwater biodiversity and inland fisheries. In showing that there is positive effect on fishery yield at the global scale, these results extend the growing body of work that shows a positive effect of biodiversity on increased productivity (e.g. see reviews in Cardinale *et al.* 2011, 2012) by examining a final ecosystem good utilising large-scale, real-world data. Countries with higher freshwater fish SR report higher mean yield – a finding that mirrors smaller-scale work on freshwater fish in mesocosms (Carey & Wahl, 2011) and reservoirs in the American Midwest (Carlander, 1955) as well as on marine fisheries (Worm *et al.*, 2006). Importantly, this finding holds after accounting for other macroecological and human drivers. Given the scale of the analysis and the number of covariates considered it is unsurprising that the independent effect of fish species richness on yield is small (3-5%), and the effect is comparable to similar studies that have drawn analogous conclusions in different systems (e.g. Maestre et al. 2012).

Previous theoretical and empirical studies have suggested that there are both positive and negative relationships between biomass in fish communities and biodiversity (Hugueny et al., 2010). The two most prominent mechanisms generally responsible for positive relationships between yield and biodiversity are i) the sampling effect, where dominant species increase productivity, and; ii) the complementarity effect, where productivity is higher than would be suggested by consideration of individual species alone due to niche partitioning and facilitation (Loreau *et al.*, 2001). Negative relationships between biodiversity and yield can also occur if one species is able to exploit a limiting resource to such an extent that it is less available to other species (density compensation; (MacArthur *et al.*, 1972)).

The positive relationship between mean yield and species richness revealed in the current analysis provides evidence for either a sampling or complementarity effect. Data on the proportional contribution of species to total yield from the FAO (Table S6) indicates that for many countries over 50% of total yield is attributed to fewer than five species. This might suggest that the sampling effect is acting as a mechanism causing performance-enhancement. If this was the sole mechanism then it cannot be concluded that biodiversity per se is responsible (Loreau *et al.*, 2001) for the relationship described in the current study. However, inland fisheries are not entirely dominated by a handful of species in all countries (Table S6) and socioeconomic factors (e.g. targeted fishing of the most economically valuable species) rather than ecological community structure could contribute to dominance of a few species in catch statistics. As such complementarity effects of biodiversity are still possible, even for a fishery whose yields are largely dependent on a few exploited species. Indeed, previous studies have demonstrated that complementarity and sampling effects may not be mutually exclusive (Loreau *et al.*, 2001), complicating our understanding of the underlying mechanisms.

The analysis here also provides qualified evidence of a positive effect of SR on stability of yield over time, contributing to evidence of the role of biodiversity in regulating aggregate community properties (e.g. Cottingham *et al.*, 2001; Worm *et al.*, 2006). Analysis focused on freshwater systems in Africa demonstrates that stability of yield decreases as SR decreases (Fig. 3). These results add to the evidence from previous, smaller-scale studies that suggest that increased fish SR can lead to an increase in productivity and stability of yields (Franssen *et al.*, 2011; Cardinale et al. 2012). In particular this study suggests that the findings of studies of sockeye salmon in Alaska, which show that diversity in the life-history of populations increase productivity and buffers population fluctuations particularly over long time periods (Greene *et al.*, 2010), may also apply to diversity of fish species. However, these findings do not extend to data covering Europe or to aggregate data across all African and European countries. European freshwater systems have been heavily degraded and suffered dramatic changes and species extirpations (Freyhof & Brooks, 2011); such changes may be the reason for the lack of a relationship between richness and variability of yield observed for Europe, which in turn drives the aggregate pattern across all countries.

The contribution of fish species richness (despite a frequent relience on a limited number of targeted harvest species) to yield and stability of yield (in Africa) in the study highlights the likely importance of non-exploited species in freshwater systems globally. This is probably due to a number of functional processes carried out by species not directly harvested for consumption – such as nutrient cycling, habitat creation, water filtration, their role in the trophic web – all of which work to support the harvested species (Hensel & Silliman, 2013). Although the conclusions drawn here are based on fish SR, it is very likely that it is not just fish, but also other components of freshwater biodiversity are important for fisheries. Unfortunately, it is not possible to disentangle the effects of fish SR and overall freshwater SR in this study due to the extremely high collinearity (88%) between these two variables (see Appendix 5 for detailed Methods and Results for additional analyses based on overall freshwater SR (fish, odonates, molluscs, decapods)).

The very good explanatory power of the global model (R^2 = 0.77) indicates that the results for biodiversity are very unlikely to be an artefact of another macro-scale driver not considered in these analyses, and the residual variation of the model at the country level does not show any striking spatial pattern (Fig. S2). However, as with any large-scale analysis of existing datasets, the findings of the current study are dependent on both the completeness and accuracy of the data underpinning it, and the findings come with a number of important caveats. Firstly, there are no primary datasets for two key drivers of fishery yields (fishing effort and freshwater productivity), meaning that proxy measures which may be imperfect representations of such drivers were utilised. It is therefore possible that some of the effect attributed to biodiversity is actually due to fishing effort or productivity.

Analysis of the variability in fisheries yield over time could also be influenced by a range of factors for which there is limited data. Principal amongst these is a lack of data on variation in fishing effort, which may vary in order to stabilize catches through time. In addition, there is no way to differentiate between types of, or scales of, fisheries; indeed, subsistence catches are vastly unreported (Béné *et al.*, 2007), which may in part explain the high unexplained variance in these analyses. European fisheries in particular may experience more intense management than their African counterparts (such as yield regulations and artificial stocking) and may be expected to provide more accurate reporting. However, differential reporting would not inflate the relationships between yield and fish species richness reported in this study, as there is no reason to suspect a systematic bias of better recording of yields in countries with high than low fish species richness. If anything, biases in management and recording effort will have reduced the observed effects, as in general better management and recording of yields would be expected in countries with relatively low biodiversity (i.e. those in Europe) than in countries with high biodiversity (i.e. Africa).

There are also a number of issues with both the FAO and IUCN datasets. In many cases FAO has had to rely on estimation or extrapolation to determine likely yield sizes. However, if only measured yield data is used for Africa (df=9), the R^2 for the effects of biodiversity on variability in yield increases from 0.16 to 0.21 suggesting more accurate data could indicate an even stronger relationship. FAO yield data is currently only widely available at the country level but it would be beneficial to examine the relationships discussed here at multiple scales (e.g. catchment and sub-catchment levels). Matching catchments to fisheries yields will facilitate the exploration of the link between the health of the river system and the productivity and variability of the yield in further detail. Examining the relationship at a finer resolution would also help to elucidate the role of fish species richness versus other freshwater species richness, as the diversity of the taxonomic groups is not found to correlate at the smaller catchment scale (Darwall *et al.*, 2011). Although the IUCN data is the most comprehensive freshwater dataset available, and indeed could be used for analyses at a finer resolution than country level, it does not provide complete global coverage, omitting important fishing regions such as China and South America.

The findings, but also limitations, of this study have major management implications for freshwater ecosystems for three main reasons. Firstly, as the countries with the most important inland capture fisheries also generally have the highest freshwater biodiversity, it is clear that management of these key fisheries must be sustainable in terms of both yields and conservation. This study therefore provides strong support for efforts to promote multifunctional watersheds, with a focus on sustainable fisheries management and fish conservation initiatives (Dudgeon, 2010). Secondly, results suggest that fish diversity may deliver benefits for human well-being – particularly in terms of maintaining constant yields over time. Capture fisheries are a critical part of food security and livelihoods, particularly in developing countries, where fisheries provide a major source of protein and micro-nutrients, and where they are used as a safety net in times of hardship, such as due to crop failure (Béné *et al.*, 2007; Dugan *et al.*, 2010). As such, these results provide a powerful argument for placing biodiversity conservation centrally within fisheries management. Finally, this study makes it clear that there is a paucity of data for freshwaters, including a thorough understanding of species compositions and distributions worldwide, and for major ecosystem specific macroecological drivers such as productivity measures. Equally, a concentrated effort is required to increase reporting not only of inland fishery yields, but also of fishing efforts (see De Graaf *et al.*, 2012). Only by doing so will we be able to fully understand the extent of the role that biodiversity plays in underpinning inland fisheries.

Inland waters are the most threatened systems globally, with dams, water extraction, pollution and invasive species recognised as some of the biggest threats to freshwater systems and to fisheries, as well as overharvesting of the fisheries themselves (Dudgeon *et al.*, 2006). It is imperative that the relationships explored here should be considered within freshwater and fisheries management; the protection and conservation of species diversity in freshwater systems provides a win-win for human food delivery and conservation efforts to preserve freshwater ecosystems.

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APPENDICES

Appendix 1 Data sources and supporting references

Appendix 2 Controlling for effort in Yield

Appendix 3 PCA of climatic variables

Appendix 4 Variance in yield over time

Appendix 5 Relationship with species richness considering multiple groups

Appendix 6 Supplementary Figures

Appendix 7 Supplementary Tables

BIOSKETCH

This study was completed as part of the PhD thesis of Emma Brooks. It is based on a collaboration between IUCN Gobal Species Programme's Freshwater Biodiversity Unit, who aim to provide the factual basis to conserve and manage freshwater species and support decisions for the benefit of ecosystems and human wellbeing, and the University of Southampton's Centre for Biological

Sciences, taking advantage of their spatial ecology excellence in the understanding of ecosystem services and biodiversity.

Appendix 1 Data sources and supporting references

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TABLES

Table 1 Simultaneous autoregressive spatial models of country-level inland water fisheries yield (t) (quarter root transformed). A) Two best fitting models B) Same models repeated excluding species richness as a variable. Shaded cells indicate which of the biodiversity, climatic and geographic variables were included in the model. SR = species richness of fishes (cubic root transformed), P = human population living within 10km of inland waterbodies (quarter root transformed), C1 = first principle component of climatic variables, C2 = second principle component of climatic variables, A = inland water area in km^2 (quarter root transformed), E = mean elevation (m) (cubic root transformed). ΔAICc = difference between the AICc of each model and that of the best model, Wi = Akaike weights. Full model as calculated in SAR$_{err}$: $\sqrt[4]{Yield} = \sqrt[3]{SR} + \sqrt[4]{P} + C1 + C2 + \sqrt[4]{A} + \sqrt[3]{E}$

A)	SR	P	C1	C2	A	E	La	Lo	Pseudo R^2	AIC_c	ΔAIC_c	W_i
									0.76	545.50	0	0.39
									0.76	547.35	1.85	0.15

B)	SR	P	C1	C2	A	E	La	Lo	Pseudo R^2	AIC_c	ΔAIC_c	W_i
									0.74	552.31	6.81	0.01
									0.74	552.72	7.22	0.01

Table 2 Commonality coefficients of top model set of SAR models of country-level inland water fisheries yield (t). Abbreviations as in Table 1.

Model	Variable (x)	Unique	Common	Total	% of R^2
1					
	SR	0.05	0.50	0.55	72%
	P	0.06	0.54	0.60	79%
	C1	0.01	0.23	0.24	32%
	A	0.03	0.32	0.34	45%
	E	0.01	-0.01	0.002	0.3%
2					
	SR	0.03	0.52	0.55	72%
	P	0.07	0.53	0.60	79%
	C1	0.01	0.23	0.24	32%
	C2	0.003	0.007	0.01	1%
	A	0.03	0.32	0.34	45%
	E	0.01	-0.001	0.002	0.3%

Note: *Unique* = unique effect of x. *Common* = Σcommon effects of x. *Total=Unique+Common*. % of *R^2=Total/Adj. R^2*

Table 3 Variance inflation factors of predictor variables of top model set of SAR models of country-level inland water fisheries yield (t). Shaded cells indicate which of the biodiversity, climatic and geographic variables were included in the model. Abbreviations as in Table 1.

SR	P	C1	C2	A	E
2.48	2.19	1.81		1.86	1.13
3.16	2.36	1.89	1.29	1.90	1.15

Figure Legends

Fig. 1 Data included within the study. A) FAO inland water capture fisheries yield per country (thousands of tonnes) (axis quarter root transformed). B) Freshwater fish species richness per country (axis cube root transformed).

Fig. 2 Relationship between inland water capture fisheries mean annual yield (t) (axes quarter root transformed) and model predictor variables at the country level (N =100): axes for fish species richness and mean elevation (m) are cubic root transformed. Details of the climatic principal components are given in Table S1. Solid lines show $P<0.05$, dashed lines are non significant.

Fig. 3 Relationship between fish species richness and mean coefficient of variation of yield (t) (both axes cubic root transformed). A) All countries within boundaries of this study (N=100). B) African countries (N=48). C) European countries (N=41). Proportion of FAO yield data per country that has been estimated or extrapolated by FAO is graded from white (all years estimated) to black (all actual data).

Figures

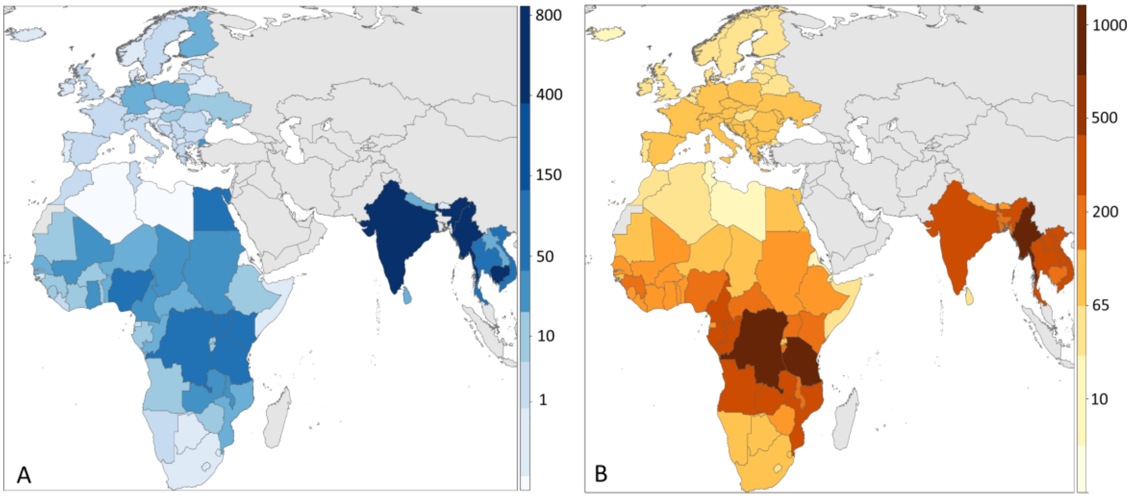

Fig. 1

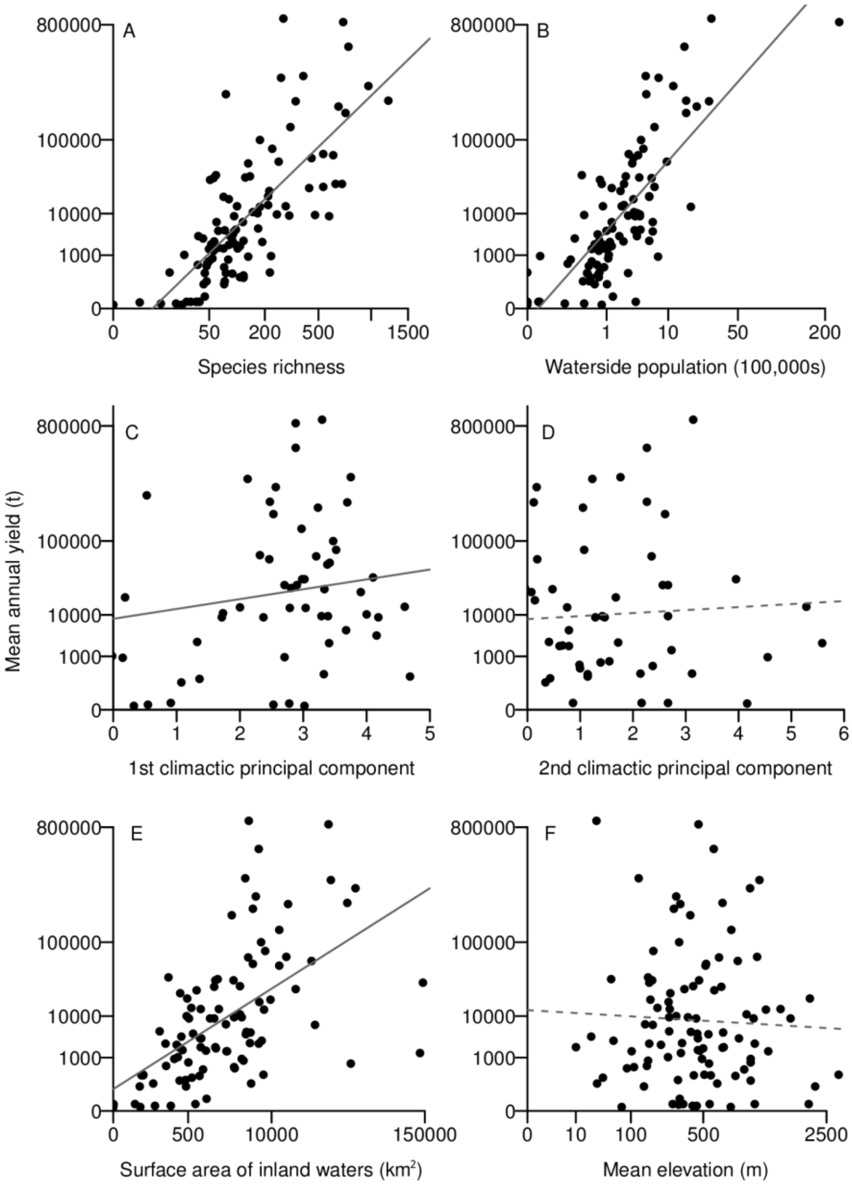
A
B
C
D
E
F
Mean annual yield (t)
800000
100000
10000
1000
0
Species richness
0
50
200
500
1500
Waterside population (100,000s)
0
1
10
50
200
1st climactic principal component
0
1
2
3
4
5
2nd climactic principal component
0
1
2
3
4
5
6
Surface area of inland waters (km2)
0
500
10000
150000
Mean elevation (m)
0
10
100
500
2500

Fig. 2

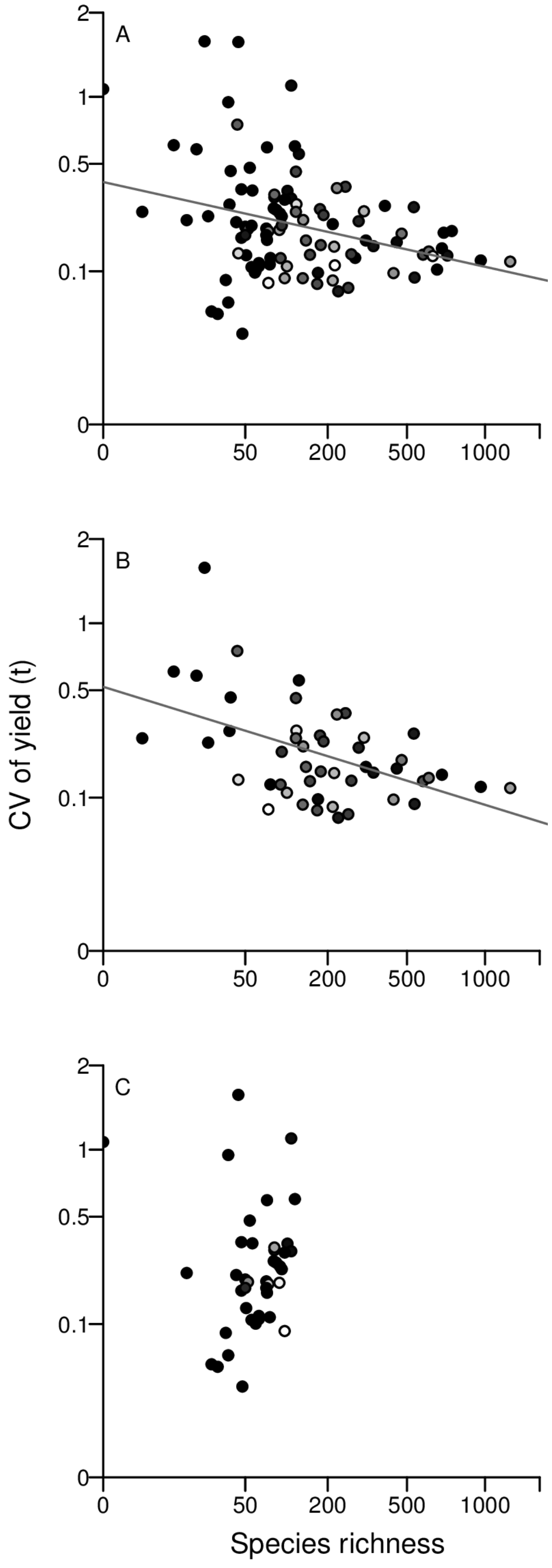

Fig. 3

SUPPORTING INFORMATION

Appendix 2 Controlling for effort in Yield

Yield is a factor not only of fisheries productivity but also of human effort and demand. This is often controlled for by either reporting yield per unit area or yield per unit effort (Kantoussan *et al*. 2014). No per unit effort or number of fishers data is comprehensively available at the country level for inland fisheries. As a proxy measure for fisheries effort we used the sum of the population living within 10km of inland waterbodies for each country. The size of the population surrounding the waterbody would be expected to reflect the reliance upon the waterbody, and thus act as a proxy for fishing effort. In an area with a limited population, yield would be expected to be lower regardless of the amount of fish potentially available.

To test the efficacy of waterside population as a proxy for fishing effort, population within a 5, 10 and 20km buffer (all log transformed) of 28 African lakes for which the number of fisher men and women could be collated (Henderson & Welcomme, 1974; Vanden Bossche & Bernacsek, 1990; Mölsä et al., 1999; van Zwieten & Njaya, 2003; Weyl, 2003; FAO, 2007; Weyl et al., 2010; Marshall & Mkumbo, 2011) was extracted. Population was extracted from a raster layer of the 2000 global rural population reported by FAO at the 5 arc-minute resolution (Salvatorre et al. 2005) using a buffer around each of the sample lakes. The 10km buffer was found to have the strongest correlation with the number of fishers (Pearson's r = 0.75, P<0.0001), compared to the population within a 5km buffer correlation (Pearson's r = 0.74, P<0.0001) or a 20km buffer (Pearson's r = 0.70, P<0.0001). The analysis focused on Africa as: (a) collating fisher data on all lakes globally was not tractable and; (b) Africa has almost half (49) of the countries examined in this study and is a region where inland fisheries are known to be particularly important for rural livelihoods (Dugan *et al*. 2010).

Yield per unit area was not used in these analyses as the surface area of a country's inland waters does not reflect the yield relationship at the country-level; for instance Denmark and Bangladesh contain a similar area of water, yet the yield for Bangladesh far exceeds that of Denmark (Fig. S1A). Fig. S1B shows that population far better correlates with the differences in yield between these two countries. Furthermore, yield per unit area is not regarded as a robust way of controlling for area in this type of ecological analysis (García-Berthou 2001).

Neither surface area nor waterside population are independent as they correlate with each other (Fig. S1C). Similarly, fish species richness also correlates with area (Fig. S1D). There are therefore multiple confounding factors, which are controlled for by including all of them as predictor variables within the multiple regression models. The covariation between variables is likely to reduce the expected size of independent effects, and therefore it is of particular interest to compare the relative importance and effect sizes between variables.

Appendix 3 PCA of climatic variables

It is necessary to control for productivity in the system; however no spatial data of global freshwater productivity currently exists. A surrogate for ambient and productive energy in the system – the two are highly correlated - can be achieved using climatic variables, including water metrics (i.e. precipitation) and seasonality (Hawkins et al., 2003). Climatic variables were derived by performing a principal components analysis (PCA) on a range of climatic data layers. Use of a PCA reduces multidimensionality and eliminates collinearity between variables. Nineteen spatial climatic data layers were accessed from www.worldclim.org, including mean and seasonality for temperature and precipitation variables (Hijmans et al., 2005). Mean values for each of the 19 data layers available were extracted at the country level and used within the PCA (see Table S1). A broken stick model was used as a stopping rule in order to avoid under- or over-estimating the influence of data by including the correct number of non-trivial components (Jackson 1993). These newly derived components were then included as climatic variables within the models. The broken stick stopping model resulted in the retention of the first two principal components for inclusion in further analysis. The eigenvalue of component 1 equalled 10.6, explaining 55.7% of the variance in the data, and component 2 had an eigenvalue of 4.6, explaining 24.1% of the variance. The correlations of the components with each climatic variable are shown in Table S1.

Appendix 4 Variance in yield over time

When examining the link between biodiversity and variation in fisheries yield, CV would not differentiate a difference between a yield which is steadily increasing or decreasing and one which is unstable but fluctuating in similar increments around the mean (see Fig. S3). Therefore a variation metric (V) has been adapted which uses differences of year on year yield to calculate the variability of yield over time within the system, where x_i is fisheries yield for a given year and n is the number of years within the study period:

$$V = \frac{\sqrt{\sum(x_{i+1} - x_i)^2}}{n-1} \div \overline{x}$$

Total fishing yield was extracted per country for each of the years 1981-2010. Records prior to 1981 were excluded due to the higher chance of inaccuracies and extrapolated figures with older data. The variability of yield (t) was calculated for each country for decadal increments from the years 1981 – 2010, and the mean was compared with linear regression to fish SR per country. As before, Box-Cox methodology was used to determine the most appropriate transformation. Analysis was repeated for country data subset by continent for comprehensive datasets; Africa and Europe. A comparison of CV and adjusted variability (V) results is shown in Table S5.

Appendix 5 Relationship with species richness considering multiple groups

A subset of the main analyses detailed in the main text (Fig. 2, Table 1and Table S2) were repeated to incorporate the species richness of other freshwater taxonomic groups. Correlations between spatial patterns of fish SR and SR of the other freshwater faunal groups at the country level were examined using Spearman's Rho due to non-normality of the data, with corrected degrees of freedom calculated using Dutilleul's modified test to account for spatial autocorrelation.

When SR was expanded to include odonates, molluscs and decapods, results were largely concordant with the fish only results, with a 1.35-1.45 increase in AICc (Fig. S4, Table S3-Table S4). The strength of relationship between CV and multiple freshwater taxa species richness is equal to that with fish species richness (Fig. S5). However, in both of these analyses it is not possible to disentangle the effect of overall SR from that of fish richness as there is a strong correlation between fish SR and SR of the other freshwater faunal groups at the country level ($r_{17.15} = 0.88$, $P < 0.0001$).

Appendix 6 Supplementary Figures

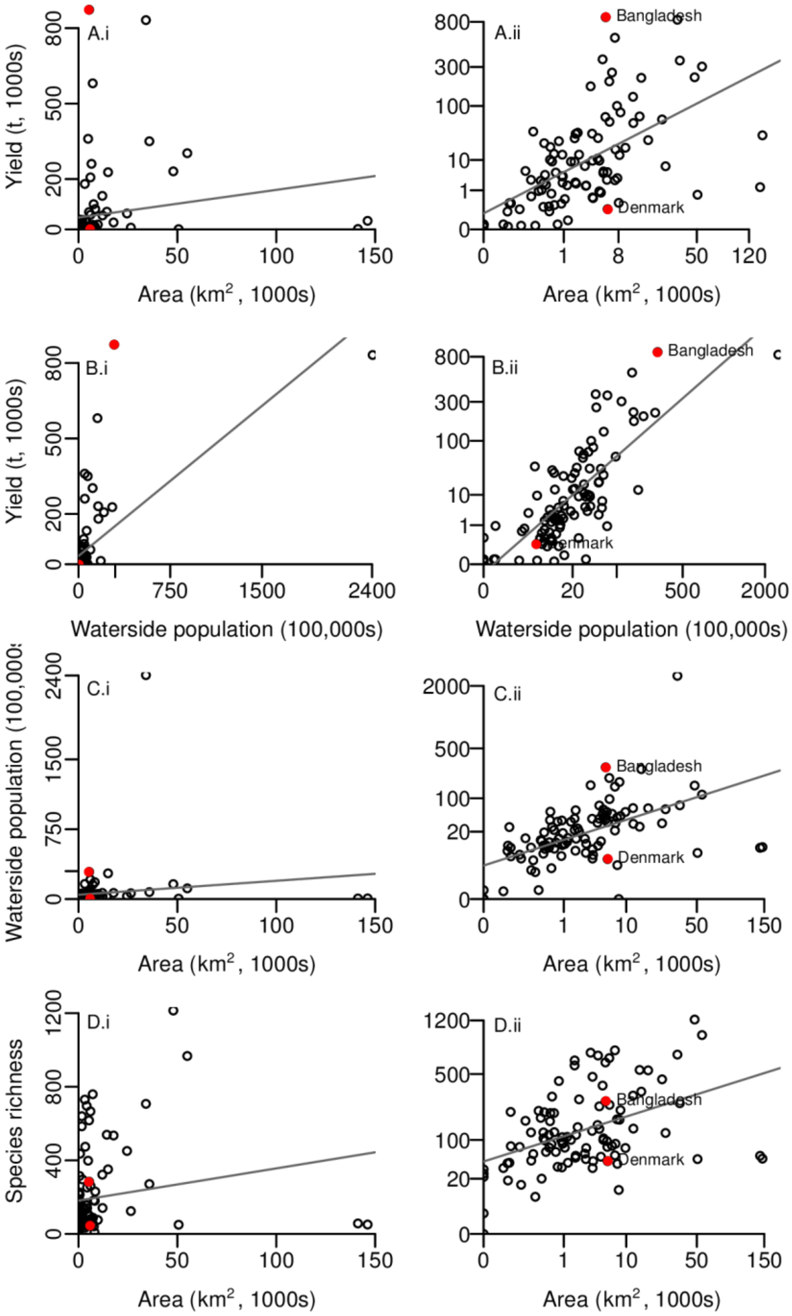

Fig. S1 Relationship between confounding model variables at the country level (N=100), (i) raw data and (ii) transformed data: A) Yield ~ Inland water surface area (cor = 0.59, P<0.0001); B) Yield ~ Mean population (cor = 0.70, P<0.0001); C) Inland water surface area ~ Mean population (cor = 0.53, P<0.0001), and; D) Area ~ Fish species richness (cor = 0.44, P<0.0001). Yield, area and population are quarter root transformed, fish species richness is cubic root transformed. Red dots indicate data from Bangladesh and Denmark for comparison.

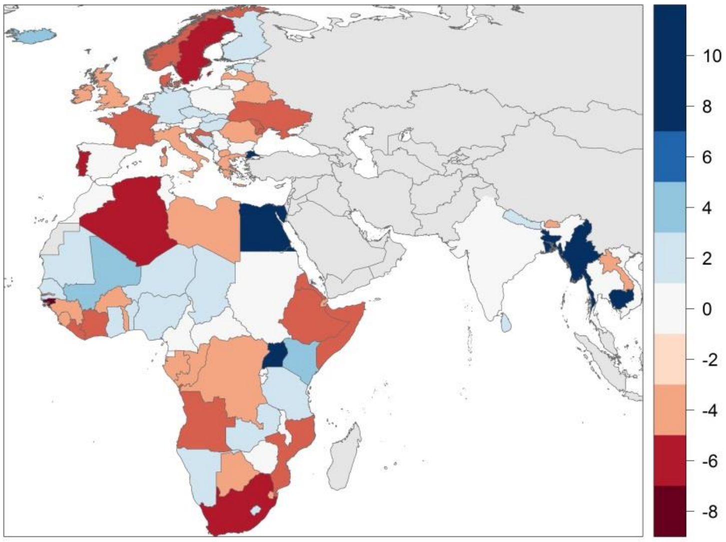

Fig. S2 Residual difference between the observed and expected values from the full spatial simultaneous autoregressive model predicting inland water capture fishery yields per country. Blue countries indicate where FAO reported yield is higher than expected from the model, red countries are where yield is lower than expected. Full model as calculated in SAR_{err}: $\sqrt[4]{Yield} = \sqrt[3]{SR} + \sqrt[4]{P} + C1 + C2 + \sqrt[4]{A} + \sqrt[3]{E}$. SR = species richness of fishes, P = human population living within 10km of inland waterbodies, C1 = first principle component of climatic variables, C2 = second principle component of climatic variables, A = inland water area in km^2, E = mean elevation (m).

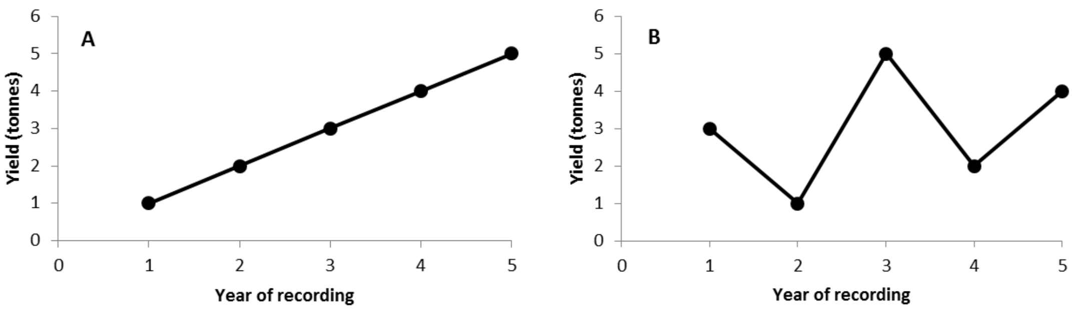

Fig. S3 Hypothetical fluctuations in yield showing that a steady increase in yield over time has the same coefficient of variation as a yield with more fluctuations, but a lower variability in year-to-year differences (V). The mean and CV for A and B are the same at 3 and 0.83 respectively. The adapted variability measure (V) is greater in B (V = 0.48) than in A (V = 0.17).

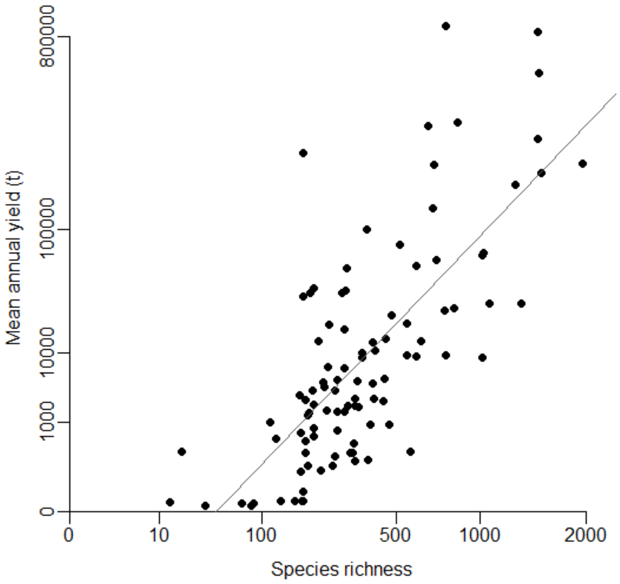

Fig. S4 Relationship between inland water capture fisheries yield (t) (axis quarter root transformed) and freshwater species richness (axis cubic root transformed), R^2=0.54, F= 116.8, df=98, P<0.001.

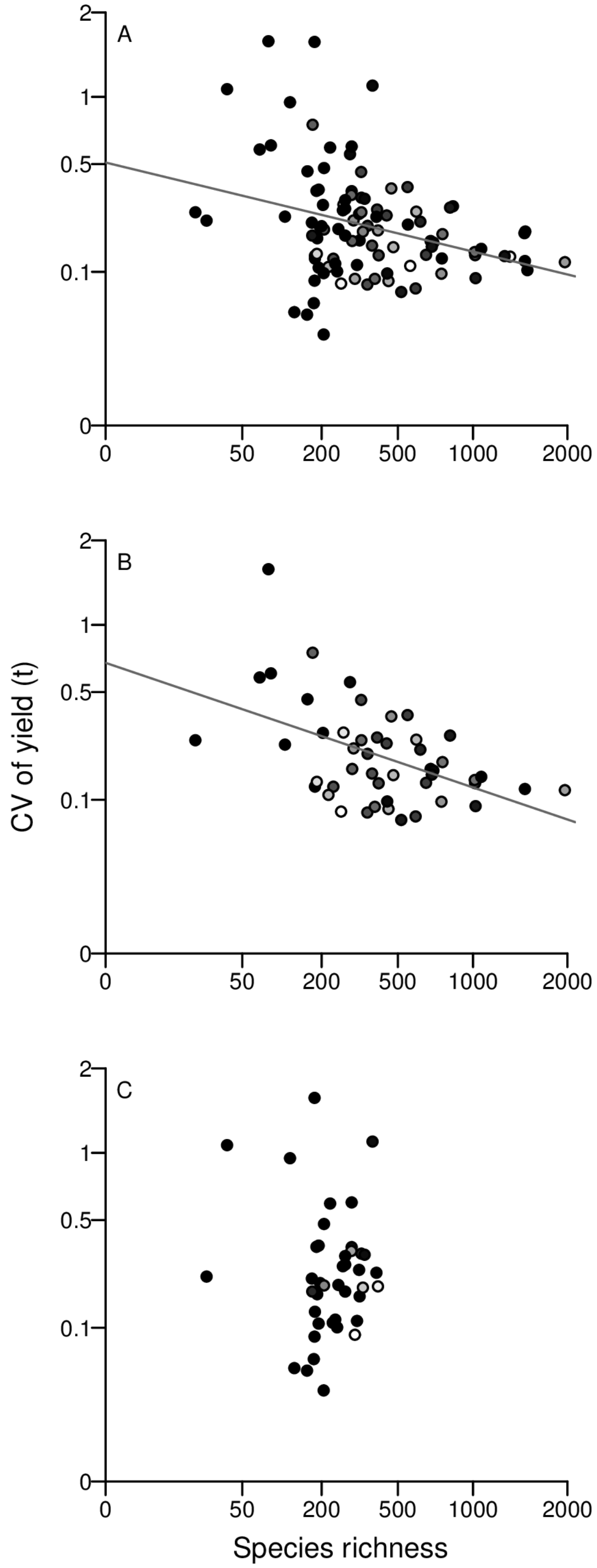

Fig. S5 Relationship between freshwater species richness and mean coefficient of variation of yield (kg) per capita (both cubic root transformed). A) All countries within boundaries of this study, R^2=0.03, F=3.66, df=98, P=0.06. B) African countries, R^2=0.16, F=9.68, df=46, P=0.003. C) European countries, R^2=-0.03, F=0.01, df=39, P=0.92. Proportion of FAO country data that has been estimated or extrapolated by FAO is graded from white (all years estimated) to black (all actual data).

Appendix 7 Supplementary Tables

Table S1 Principal Component Analysis of country climatic variables. The first two PCA axes explained 56% and 24% of the total variability in climate conditions, respectively, and were retained as predictors for inland water fisheries yield models**.**

Variable	**Comp 1**	**Comp 2**	**Comp 3**	**Comp 4**	**Comp 5**
Annual mean temp.	0.98	-0.09	-0.09	0.03	0.13
Mean diurnal range*	0.65	-0.56	0.08	0.04	-0.08
Isothermality†	0.87	0.20	-0.20	-0.27	-0.09
Temp. seasonality‡	-0.85	-0.37	0.20	0.29	0.11
Max temp. of warmest month	0.86	-0.40	-0.06	0.23	0.19
Min temp. of coldest month	0.95	0.14	-0.23	-0.08	0.09
Temp. annual range§	-0.56	-0.66	0.29	0.38	0.07
Mean temp. of wettest quarter	0.87	-0.13	0.20	-0.02	0.24
Mean temp. of driest quarter	0.89	-0.08	-0.30	0.09	0.01
Mean temp. of warmest quarter	0.89	-0.32	-0.05	0.20	0.23
Mean temp. of coldest quarter	0.98	0.05	-0.14	-0.06	0.05
Annual precipitation	0.29	0.93	0.13	0.15	0.02
Precip. of wettest month	0.56	0.72	0.32	0.20	-0.06
Precip. of driest month	-0.77	0.43	-0.27	-0.01	0.28
Precip. seasonality‖	0.84	-0.25	0.28	0.03	-0.11
Precip. of wettest quarter	0.53	0.73	0.34	0.22	-0.07
Precip. of driest quarter	-0.69	0.55	-0.30	-0.01	0.30
Precip. of warmest quarter	0.09	0.72	0.58	-0.16	0.16
Precip. of coldest quarter	0.06	0.59	-0.54	0.50	-0.19
Variability explained	55.73%	24.07%	7.81%	4.26%	2.40%

* Mean diurnal range = (Mean of monthly (max temp-min temp))
† Isothermality = Mean diurnal range/Temp annual range*100
‡ Temp seasonality = Standard deviation*100
§Temp annual range = Max temp of warmest month-min temp of coldest month
‖ Precip. seasonality = coefficient of variation

Table S2 Multimodel averaged parameter estimates of top model set of SAR models of country-level inland water fisheries yield (t). Abbreviations as in Table 1.

Parameter	Estimate	SE	z	95% Lower CI	95% Upper CI	Relative importance	Total effect
(Intercept)	-1.05	1.61	0.65	-4.21	2.11	NA	NA
SR	1.07	0.32	3.36	0.45	1.69	1.00	1.00
P	0.13	0.03	4.12	0.07	0.18	1.00	1.00
C1	0.40	0.18	2.26	0.05	0.75	1.00	1.00
C2	0.15	0.19	0.78	-0.23	0.53	0.28	0.28
A	0.49	0.13	3.76	0.24	0.75	1.00	1.00
E	-0.37	0.17	2.12	-0.71	-0.03	1.00	1.00

Table S3 SAR models of country-level inland water fisheries yield (t) (quarter root transformed) of the four best fitting models (95% confidence model set). Shaded cells indicate which of the biodiversity, climatic and geographic variables were included in the model. SR = species richness of freshwater taxa (cubic root transformed), P = human population living within 10km of inland waterbodies (quarter root transformed), C1 = first principle component of climatic variables, C2 = second principle component of climatic variables, A = inland water area in km^2 (quarter root transformed), E = mean elevation (m) (cubic root transformed). ΔAICc = difference between the AICc of each model and that of the best model, Wi = Akaike weights. Full model as calculated in SAR$_{err}$: $\sqrt[4]{Yield} = \sqrt[3]{SR} + \sqrt[4]{P} + C1 + C2 + \sqrt[4]{A} + \sqrt[3]{E}$

SR	P	C1	C2	A	E	La	Lo	Pseudo R^2	AIC_c	ΔAIC_c	W_i
								0.76	545.42	0	0.44
								0.76	547.24	1.82	0.18

Table S4 Multimodel averaged parameter estimates of top model set of SAR models of country-level inland water fisheries yield (t). Abbreviations as in Table S3.

Parameter	Estimate	SE	z	95% Lower CI	95% Upper CI	Relative importance
(Intercept)	-3.45	1.85	1.87	-7.07	0.16	NA
SR	1.13	0.31	3.60	0.52	1.75	1.00
P	0.12	0.03	3.73	0.06	0.18	1.00
C1	0.45	0.16	2.82	0.14	0.76	1.00
C2	0.15	0.19	0.80	-0.22	0.53	0.29
A	0.52	0.12	4.24	0.28	0.77	1.00
E	-0.37	0.17	2.18	-0.71	-0.04	1.00

Table S5 Comparison of variation in yield against species richness metrics. SR = Fish species richness (cube root transformed), CV = Coefficient of variation (cube root transformed), Y = Yield (t), V = Adapted variability measure (see above for details, cube root transformed). Significant relationships in bold.

Model	All countries				Africa				Europe			
	R^2	*F*	*df*	*P*	R^2	*F*	*df*	*P*	R^2	*F*	*df*	*P*
CV of Y ~ SR	0.02	3.14	98	0.08	**0.16**	**9.81**	**46**	**0.003**	-0.02	0.21	39	0.65
V of Y ~ SR	**0.04**	**5.66**	**98**	**0.02**	**0.14**	**8.71**	**46**	**0.005**	-0.02	0.07	39	0.79

Table S6 Species breakdown of FAO recorded freshwater fish catch harvest per country in 2010 for the countries where this data exists. Percentage of yield (t) produced by number of species, e.g. 90.24% of Denmark's total yield comes from just five fish species, and the total amount harvested from 10 species or fewer. Where yield has not been identified down to species level it is either categorised as grouped (e.g. identified as torpedo-shaped catfishes), or unidentified (identified as freshwater fishes not elsewhere included). Countries are ordered by yield (t), lowest to highest. Data from FAO (2011). Due to the numerical and categorical nature of the data they cannot be statistically analysed, however it is apparent that where catch has been identified down to species level, five species or fewer account for a large proportion of the yield for the majority of countries, and that instances of six or more species identified to contribute significantly to total country yield do not increase as yield (t) increases.

Country	1-5 sp.	6-10 sp.	11+ sp.	Grouped yield	Unidentified
Denmark	90.24%	9.76%	0.00%	0.00%	0.00%
Lesotho	44.44%	0.00%	0.00%	0.00%	55.56%
Botswana	0.00%	0.00%	0.00%	98.33%	1.67%
Ireland	100.00%	0.00%	0.00%	0.00%	0.00%
Slovenia	73.37%	15.98%	7.10%	3.55%	0.00%
Macedonia	53.39%	3.81%	0.00%	40.25%	2.54%
Iceland	100.00%	0.00%	0.00%	0.00%	0.00%
Latvia	79.33%	17.02%	1.22%	0.00%	2.43%
Croatia	87.72%	10.96%	1.32%	0.00%	0.00%
Belgium	73.39%	10.76%	0.00%	15.85%	0.00%
Montenegro	44.01%	0.00%	0.00%	40.45%	15.54%
Norway	100.00%	0.00%	0.00%	0.00%	0.00%
Belarus	62.21%	12.37%	0.22%	25.08%	0.11%
Greece	68.12%	4.13%	0.22%	8.27%	19.26%
Bulgaria	89.20%	6.46%	4.34%	0.00%	0.00%
Sweden	84.21%	15.79%	0.00%	0.00%	0.00%
Lithuania	79.92%	12.37%	4.35%	2.90%	0.46%
Slovakia	85.01%	6.90%	2.18%	5.91%	0.00%
Switzerland	31.40%	1.33%	0.00%	67.15%	0.12%
Netherlands	89.76%	0.00%	0.00%	3.41%	6.83%
Romania	75.95%	12.86%	3.58%	7.45%	0.16%
United Kingdom	93.93%	0.00%	0.00%	6.07%	0.00%
France	53.60%	0.00%	0.00%	4.40%	42.00%
Estonia	94.70%	4.60%	0.66%	0.00%	0.03%
Albania	63.70%	8.60%	0.00%	11.40%	16.30%
Italy	1.14%	0.00%	0.00%	27.41%	71.44%
Czech Republic	91.53%	5.19%	2.03%	0.00%	1.25%
Gambia	0.00%	0.00%	0.00%	25.91%	74.09%
Ukraine	91.55%	5.87%	1.65%	0.94%	0.00%
Spain	41.11%	0.00%	0.00%	0.00%	58.89%
Serbia	47.78%	13.19%	4.41%	0.00%	34.62%
Togo	0.00%	0.00%	0.00%	80.00%	20.00%
Hungary	70.01%	6.11%	0.00%	17.91%	5.97%
Morocco	0.36%	0.00%	0.00%	85.80%	13.84%
Gabon	0.00%	0.00%	0.00%	49.95%	50.05%
Zimbabwe	75.24%	0.00%	0.00%	9.52%	15.24%
Rwanda	100.00%	0.00%	0.00%	0.00%	0.00%

Country	1-5 sp.	6-10 sp.	11+ sp.	Grouped yield	Unidentified
Burkina Faso	0.00%	0.00%	0.00%	65.43%	34.57%
Germany	5.16%	1.48%	0.24%	13.15%	79.96%
Burundi	96.25%	1.37%	0.12%	0.00%	2.27%
Ethiopia	18.55%	0.00%	0.00%	78.29%	3.16%
Poland	9.28%	2.99%	1.16%	0.00%	86.57%
Benin	3.82%	0.00%	0.00%	80.38%	15.80%
Finland	82.36%	12.96%	2.20%	0.00%	2.48%
Laos	0.00%	0.00%	0.00%	15.86%	84.14%
Senegal	25.29%	1.55%	0.12%	13.83%	59.21%
Turkey	74.76%	4.50%	0.25%	19.88%	0.61%
Niger	19.25%	0.00%	0.00%	65.75%	15.00%
Mozambique	28.84%	0.00%	0.00%	0.00%	71.16%
Sri Lanka	0.00%	0.00%	0.00%	53.90%	46.10%
Sudan	62.00%	0.00%	0.00%	0.00%	38.00%
Zambia	10.24%	0.00%	0.00%	0.00%	89.76%
Malawi	0.00%	0.00%	0.00%	95.29%	4.71%
Mali	62.15%	0.00%	0.00%	19.00%	18.85%
Kenya	85.26%	0.00%	0.00%	12.10%	2.64%
Thailand	55.56%	0.30%	0.00%	9.96%	34.19%
Egypt	77.85%	1.16%	0.00%	15.14%	5.84%
Tanzania	70.91%	0.00%	0.00%	23.61%	5.48%
Nigeria	27.82%	1.17%	0.00%	67.38%	3.63%
Uganda	44.47%	0.00%	0.00%	54.83%	0.70%
Bangladesh	11.70%	0.00%	0.00%	0.00%	88.30%
India	0.62%	0.00%	0.00%	62.68%	36.71%