# Warming is associated with temporal decoupling of species' body size and abundance

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**Abstract**

Across species, body size and population abundance are often assumed to be tightly linked, with smaller species reaching higher abundance. Consequently, either size or abundance is commonly used as a proxy to assess responses to abiotic and biotic environmental changes and to inform conservation strategies. However, whether the tight relationship holds within species remains unclear. Here, we analyzed 41 natural ecosystems spanning 10 to 48 years and found that species abundance and size are not tightly linked over time. Only 14.0% of species had their abundance causally linked to size, while 21.5% had their size causally linked to abundance. Only 7.7% of species had bidirectional causal links among size and abundance. Warming was associated with decoupling between abundance and size. Our findings suggest that species' abundance and size tend to be decoupled over time under climate change. Thus, abundance and size time series can provide distinct insights into species' responses to climate change and should be considered separately in ecosystem conservation and stability assessments.

**Keywords**: Body size, Population abundance, Climate change, Ecosystem conservation, Stability assessment

## Introduction

Body size as one of the most crucial functional traits is typically closely linked to population abundance[1–3]. Much evidence shows that species with larger body sizes tend to result in lower abundances, following an inverse power law[1,2]. Essentially, this relationship is often attributed to differences in metabolic rates among organisms of varying sizes[1,2,4]. Larger species generally have lower metabolic rates and invest more energy in growth and maintenance[1,2]. This life-history tradeoff results in lower reproductive frequency, and thus longer generational intervals, which limits population size[5,6]. Larger producer species, such as phytoplankton, has lower nutrient conversion efficiency due to their surface-area-to-volume ratio, resulting in lower population abundance[7]. In the context of food webs, both theoretical and empirical work has well demonstrated that species at higher trophic levels tend to have larger body sizes and smaller population sizes[8–12] with limited dietary niche breaths and higher extinction risk[13]. However, the effect of body size on abundance has predominantly been documented across species, mostly based on snapshot samples. It is unclear whether a similar effect exists within species, across time series. In addition, while experiments have shown that body size changes over time can strongly influence population density over time within protist species[5,14–16], it remains uncertain whether the effect of size on abundance holds tightly in natural ecosystems.

The body size-abundance relationships could be *bidirectional* through time, and both directional effects may not be of equal strength[5,14]. Plastic or evolutionary shifts in body size can influence fitness and therefore population abundance, which in turn can affect size, creating feedback loops[5,17]. However, compared to the well-documented influence of size on abundance, the effect of abundance on body size time series are not well understood[5]. Such effect can in principle occur through eco-evolutionary feedback[17], phenotypic plasticity[5,14], and demographic processes[18,19]. For example, high population abundance can result in crowding and increased intraspecific competition[20,21]. Stronger competition can reduce resource availability, potentially resulting in growth limitation and smaller body sizes[22,23]. Indeed, changes in abundance affecting body size have been documented in indoor experiments[5,14]. However, this evidence has not yet been fully translated to natural ecosystems. Recent field studies suggest declines or increases in species abundance either had no consistent association with changes in body size[24] or showed complex associations[25,26]. However, these field studies focus on trends in body size across entire communities which thereby obscures the putative size-abundance relationships within species.

Therefore, it remains unclear whether abundance time series can influence body size time series. Addressing this question is essential, as it determines whether species abundance time series alone can reliably represent its body size dynamics in assessing species' responses to environmental changes.

In nature, changes of abundance and body size often co-occur with environmental shifts or community changes[5,27–29]. Factors such as warming[30–32], species diversity, and species traits can potentially alter both body size and abundance. This raises the question if these factors will change the established relationships between body size and population abundance. In this study, we investigated whether body size and abundance were bidirectionally linked by analyzing data from 41 natural ecosystems. The presence of bidirectional links (size → abundance, as well as abundance → size) was evaluated using convergent cross mapping (CCM), a technique to detect causal links (Fig. 1a). Then, we examined the proportion of bidirectional links in responses to warming and biotic drivers. Our findings suggest that body size and abundance are only weakly linked within species, and that warming further weakens this coupling. These results underscore the importance of incorporating both species size and abundance into monitoring and conservation efforts.

**Results**

Our results from CCM showed that bidirectional link between species' abundance and size were not common within individual species (Fig 1b). Across 41 ecosystems, including aquatic plankton and fish, and terrestrial species (primarily beetles)—a total of 1269 species were analyzed. Of these, 21.5% ± 2.8% (mean ± s.e.) of the species had link from size to abundance (size → abundance), while 14.0% ± 2.3% had link from abundance to size (abundance → size) (Fig 1b). Only 7.7% of species had bidirectional causal links between size and abundance. In addition, within plankton, 11.5% ± 3.6% of the species had size → abundance, and 16.1 % ± 5.1% had abundance → size (Fig 1b). Within fish (and terrestrial species), the proportions were 30.8% ± 7.4% (21.1% ± 3.1%) and 16.4% ± 6.5% (13.2% ± 1.8%), respectively (Fig 1b).

The link between size and abundance was system-dependent (Fig 1c-d). In four out of all 41 ecosystems, the proportion of link size → abundance exceeded 50% (Fig 1d; FigS1-S2). Among the four systems, the three were aquatic fish ecosystems (i.e. Smokelumne River-

Georgiana Slough, Sacramento River-Koket, and American River), while the remaining one was a terrestrial beetle ecosystem. In contrast, in just one system out of 41 systems, the proportion of link abundance → size surpassed 50% (Fig 1c; FigS1-S2) and the one was again a fish ecosystem (i.e. Smokelumne River-Georgiana Slough). These results indicate that species' body size and abundance tend to be temporally decoupled rather than tightly linked. These conclusions were not affected by including rare species—which are normally excluded from similar analyses (Fig. S3-S5), and neither when only using the dominant species for analysis (Fig. S6-S8).

Across 41 systems, warming was negatively correlated with the proportion of both links of abundance → size and size → abundance (Fig 2a, d). In contrast, mean species body mass was only positively associated with the proportion of links of size → abundance (Fig 2c, f), whereas species richness only had negative correlation with the link (Fig 2b, e). In addition, we found mean temperature had no effect on either link of abundance → size or size → abundance (Table S1). Within species group (plankton, fish or terrestrial species), the species richness and mean body mass on proportion of link size → abundance were system dependent (Fig. 2). In most species groups, species richness had negative effects on link of size → abundance (Fig. 2b). Conversely, mean species body mass was positively correlated with link of size → abundance in one out of three groups (Fig. 2c). Warming had negative effects on both links within each species group (Fig. 2a, d).

**Discussion**

In the studied ecosystems, the bidirectional links between abundance and body size were weak, with 14.0% of species exhibiting link of abundance → size and 21.5% exhibiting link of size → abundance. Moreover, warming was associated with lower proportions of both links of abundance → size and of size → abundance. These results suggest that species abundance and size are not tightly linked over time, but tend to be independent under warming.

Body size responds rapidly to environmental changes[33] and can exert a significant influence on population abundance[25]. Previous experimental studies have demonstrated that temporal changes in species' body size are tightly associated with abundance in single-species populations[5,14], a two-species competitive interactions[34], and a microbial food web[16]. However, in natural ecosystems, we found the proportion of link size → abundance to be weak. The weakening of the link was associated with warming and increased species richness (Fig 2).

Experimental evidence had documented weaker causal link of size → abundance at higher temperatures[16]. This may be attributed to the different responses of size and abundance to warming[26]. Higher temperatures can lead to a reduction in species body size[35], while it can have no significant effect on population abundance[36]. Similarly, higher temperatures have shown to accelerate growth, leading to an rapid increase in population abundance[16,37], while simultaneously either leaving body size unaffected or slightly altered body size[26,38]. These different responses among size and abundance can weaken the link between them[16]. Increased species richness also reduced the proportion of the link of size → abundance. Enhanced species richness may subject organisms to a broader spectrum of ecological interactions, such as intensified interspecific competition and predation, which can disrupt the link of size → abundance within species[34]. Indeed, evidence has documented that adding interspecific competition can weaken the link strength of size → abundance[34]. We also found mean species body mass increased the proportion of link size → abundance. To date, no direct empirical evidence has been documented to validate this trend. However, evidence documented that species with larger body mass exhibit longer generation times and slower population turnover[1,39], allowing both body size and population abundance to respond more gradually to environmental changes. This extended adaptation period may facilitate the temporal coupling relationship between body size and population abundance. In addition, we found that the proportion of link abundance→ size is also weak, and warming is associated with a lower proportion of the link. This contrasts with previous experimental studies that demonstrated a strong relationship within protist species[5]. Again, the weakening of the link driven by warming may be attributed to different responses of size and abundance to warming[26,34].

The bidirectional feedback loop between body size and abundance dynamics can be asymmetric. Indeed, previous experimental evidence has shown a stronger causal link of size → abundance than the other way around[5,14]. Our results showed that the proportion of body size → abundance is slightly higher than the reverse (21.5% vs. 14.0%). These findings suggest that changes in body size may occur independently of changes in abundance rather than tightly coupled. Indeed, body size and abundance have showed independent changes, particularly in responses to environmental changes such as urbanization[33] and habitat fragmentation[40,41]. Species' size can even provide greater accuracy and serve as an earlier warning signals for predicting population collapses than abundance, under environmental deterioration[42–44].

Furthermore, the proportion of link among size and abundance was species dependent (Fig. S9). 84.7% of species exhibited a proportion of links among size and abundance below 50%, while only 4.1% had a proportion of links equal to 100%, including beetle species within the *Geotrupidae* taxon (Fig. S9).

In summary, our findings reveal that species size and abundance time series are decoupled over time and warming tends to accelerate this decoupling. The conventional paradigm positing a robust cross-species association between size and abundance is not upheld within species. Our results underscore the potential limitation of relying on either body size or abundance time series alone to examine species' responses to warming and measure ecosystem resilience.

## Methods

**Aquatic plankton Data**. Species size and abundance data were compiled from a total of 10 long-term monitoring sites in aquatic planktonic ecosystems, including nine lakes and one marine system, as detailed in Supplementary Table S2: (1) Wadden sea, EU, 2001-2010; (2) Lake Mendota, USA, 1995-2005; (3) Lake Monona, USA, 1995-2005; (4) Lake Allequash, USA, 2009-2018; (5) Lake Big Muskellunge, USA, 1991-1999; (6) Lake Crystal Bog, USA, 2008-2018; (7) Lake Crystal, USA, 1990-1999; (8) Lake Sparkling, USA, 1990-1999; (9) Trout Lake, USA, 1990-1999; (10) Lake Trout Bog, USA, 2009-2018. For each aquatic planktonic ecosystem, there were three types of variables: (1) species abundance; (2) species size (i.e. body length, biovolume, or biomass); (3) water temperature. For species size (2), a single metric is reported for each species and subsequently used for further analysis.

Next, for consistency, each species' time series were standardized to seasonal sampling frequencies (if multiple samplings were conducted per season, e.g., monthly and bimonthly sampling data sets, those were averaged). Here, the seasonal resolution (trimonthly) is the shared consensus that can be applied to all 10 data sets, and the seasonal average here is also the most representative measure across all data sets, because the equal sampling interval is necessary for Convergent cross mapping (CCM) analysis. After the seasonal average, there were 0.31% missing points across the whole planktonic dataset (41 out of 17032 data points). Those missing data points were linearly interpolated using *na.approx* function in the package of zoo[45,46]. Then, the species abundance across all data sets was scaled to the same unit (individuals per litre).

Species length, biovlume and biomass were standardized to the same unit (μm), ($\mu m^3$) and ($mg/m^3$) respectively.

Last, we removed the long term linear and seasonal trend from each time series. Specifically, we first removed the long-term linear trend from each time series by using the residuals from a linear regression against time[47,48]. Next, we removed seasonality by scaling against the mean and standard deviation of values occurring in the same year, $D_{season}(t) = (O(t) - \mu_{season})/\sigma_{season}$, where $D_{season}(t)$ is the deseasoned time series, $O(t)$ is the original time series, $\mu_{season}$ is the year mean, and the $\sigma_{season}$ is the year standard deviation[47,48]. Then, we selected species time series with number of zeros <60% because too many zero values may cause statistical problems in time series analysis. Finally, each time series (both species abundance and size) was scaled to zero mean and unit variance.

**Fish Data**. Fish size and abundance data were compiled from 11 monitoring sites (Supplementary Table S3), including six rivers and five lakes, as detailed below: (1) American River, USA, 1976-2023; (2) San Joaquin River (Elkhorn), USA, 1981-2023; (3) Sacramento River (Koket), USA, 1976-2023; (4) Keller Beach, USA, 1980-2023; (5) Smokelumne River (Georgiana Slough), USA, 1976-2023; (6) Old river (Franks Tract), USA, 1993-2023; (7) Lake Allequash, USA, 1981-2018; (8) Lake Big Muskellunge, USA, 1981-2018; (9) Lake Mendota, USA, 1981-2018; (10) Lake Sparkling, USA, 1981-2018; (11) Trout Lake, USA, 1981-2018. Again, for each Fish ecosystem, there were three types of variables: (1) species abundance; (2) species size (i.e. body length); (3) water temperature.

For consistency each species time series of abundance and size were standardized to the yearly sampling frequency (if multiple samplings were conducted per year, e.g., quarterly sampling data sets, those were averaged). Again, the yearly resolution is shared across all data sets. After the yearly average, there were no missing points across the fish dataset. Then, the fish abundance across all data sets was standardized to the same unit (caught per effort). Species length was standardized to the same unit (mm). As all fish data were standardized to yearly intervals, there was no need to remove long-term linear or seasonal trends from each time series. Therefore, the original data were utilized for further analysis. Again, we selected species time series with number of zeros <60%. Finally, each time series (both species abundance and size) was scaled to zero mean and unit variance.

**Terrestrial species.** Terrestrial species size and abundance data were compiled from 20 monitoring sites (Supplementary Table S4). Of these, 18 sites are ground beetles, while one site monitored lizard populations and another monitored rat species. Again, for each site, there were three types of variables: (1) species abundance; (2) species size (i.e. biomass, $\mathrm{mg}/m^3$); (3) surface temperature. Each site reports both abundance and size. The daily temperature and precipitation for each site were retrieved from NOAA's National Centers for Environmental Information[49].

Next, to ensure consistency, each species' time series were standardized to seasonal sampling frequencies (if multiple samplings were conducted per season, those were averaged). After calculating seasonal averages, 5.4% of data points were missing in the dataset. These missing values were subsequently linearly interpolated using the na.approx function from the zoo package[45,46]. Then, long-term linear and seasonal trends were removed from each time series using the same methodology applied to the plankton data. Again, species time series with less than 60% zero values were retained for analysis. Finally, each time series, including both species abundance and size, was standardized to have a mean of zero and a unit variance.

**Quantifying the bidirectional causal link**. For each species (plankton, fish or terrestrial species), we identified the bidirectional causal link among species size and its abundance (i.e. size →abundance, abundance →size) using convergent cross-mapping (CCM) (Fig 1). CCM is based on Takens's theorem for dynamic ecosystems, which infers the causal relationship among variables from their empirical time series[50,51] (see three brief videos for a summary introduction: http://tinyurl.com/EDM-intro). If the causal variable X (e.g. species abundance) and affected variable Y (e.g. species size) belongs to the same dynamical system, information on the causal variable X is encoded in the affected variable Y. Thus, one can predict the states of causal variable X using the affected variable Y. CCM infers causality by measuring the extent to which the causal variable X has left signatures in the time series of the affect variable Y; a procedure known as cross mapping (cross-prediction)[50]. In this study, the appropriate embedding dimensions for cross-mapping E were determined by the optimized the hindcast cross-mapping in which X(t) projected one-step backward to Y(t-1), examining values of E from 2 to square root of $n$, where n is the length of the time series[46]. Thus, we computed $n$ as the geometric mean time series length across all data sets. E was finally examined from 2 to 7 across all data sets. We used simplex projection to select the best E that gave the highest prediction skill[52].

To accommodate the fact that the causal variables (e.g., species abundance) can exhibit time-delayed effects on the affected variables (e.g., species size), we carried out 0 to 1 year (i.e. 0~4 time point for plankton and terrestrial species but 1 time point for fish) lagged CCM analyses, in which we retained the CCM with the time lag resulting in the highest cross mapping skill $\rho$[53]. The criterion for testing causality is the convergence toward higher cross-mapping skill with increasing library length (i.e., the number of points used for state space reconstruction)[50]. An increase in library length enhances the density of points in the reconstructed attractor, facilitating more precise identification of nearest neighboring points for predictions. This, in turn, leads to improved predictive accuracy[54]. Convergence can be assessed by evaluating whether there is a significant monotonic increasing trend in cross-mapping skill $\rho$ as library length increases using Kendall's $\tau$ test[48], and whether the $\rho$ at the largest library length is significantly greater than that the $\rho$ at the smallest library length using Fisher's Z test[48]. In this study, library length was set from the minimum (E) to the maximum length (i.e., the length of the entire time series). Throughout this study, an interaction link (e.g., X→Y) was considered causal if both Kendall's $\tau$ test and Fisher's Z test were statistically significant ($P < 0.05$) for testing convergence[48].

Finally, the warming rate, representing the long-term warming trend of water temperature or land surface temperature in each ecosystem, was measured using the Theil–Sen median-based trend estimator, implemented via 'sens.slope' from 'trend' package[48,55]. This method was chosen due to its widespread use in quantifying warming rates[56,57], its robustness to episodic extreme events, and its ability to provide stable estimates of long-term trends in the presence of outliers[55]. Species mean body mass was computed as average across whole time series, estimated from biovolume, assuming that organisms have the same density as water, if unavailable, was obtained from published sources[58,59].

**Bidirectional links in responses to climate change and biotic drivers**. We employed a Zero-inflated Generalized Linear Mixed Model (glmmTMB function in glmmTMB package[60]) with a binomial error distributions to test the main effects of warming, mean temperature, species richness, and mean species body mass on proportion of either link (size →abundance or abundance →size). To ensure normality, mean temperature, species richness, and mean species body mass were log-transformed using base 10. In the model, the proportion of each link was used as the response variable, consisting of binary values: 1 indicating the presence of a causal

link and 0 indicating the absence of a link. Last, we set species groups (e.g. plankton) nested within sample locations (e.g. Trout Lake) as random intercepts. Details of statistics see Table S1.

**Sensitivity analysis.** Given that low-frequency rare species or dominant species may alter bidirectional link between species abundance and size, we extended the analysis to: 1) include a large number of rare species (number of zeros 60%~80%) into analysis; these were species excluded in analysis in main text, and 2) only use the very dominant species into analysis (number of zeros <50%, that is species presence once per two samplings). The extended analysis (1)-(2) did not change the conclusions (Fig. S3-S8). All analyses were done with R (ver. 4.1.2). The CCM analysis was examined using the rEDM package (version 1.2.3).

## Competing interests

The authors declare no competing interests.

## Author Contributions

Q.H.Z., F.D.L. and Y.X.G.W designed the research. Q.H.Z. and Y.X.G.W performed the study and analyzed the data. Q.H.Z and G.S performed the CCM analysis. Q.H.Z., F.D.L. and Y.X.G.W led the writing, with contributions from C.X. and G.S.

## Data and code availability

The data reproducing all the results in this study are available on GitHub (https://github.com/QZhao16).

## Acknowledgements

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## Figures

**Figure 1**. **Proportion of bidirectional link among species' abundance and size**. **a**, An overview of the methods. The bidirectional link among abundance and body size can be modulated by climate change and biotic drivers. In this study, we investigate the link within individual species rather than across species. **b**, The average proportion of causal links for aquatic plankton, fish, or terrestrial species across 41 ecosystems. The frequency and proportion of causal links abundance → size (**c**) and size → abundance (**d**) across 41 ecosystems. The details of proportion of causal link within each of the 41 ecosystems see Fig. S1–S2.

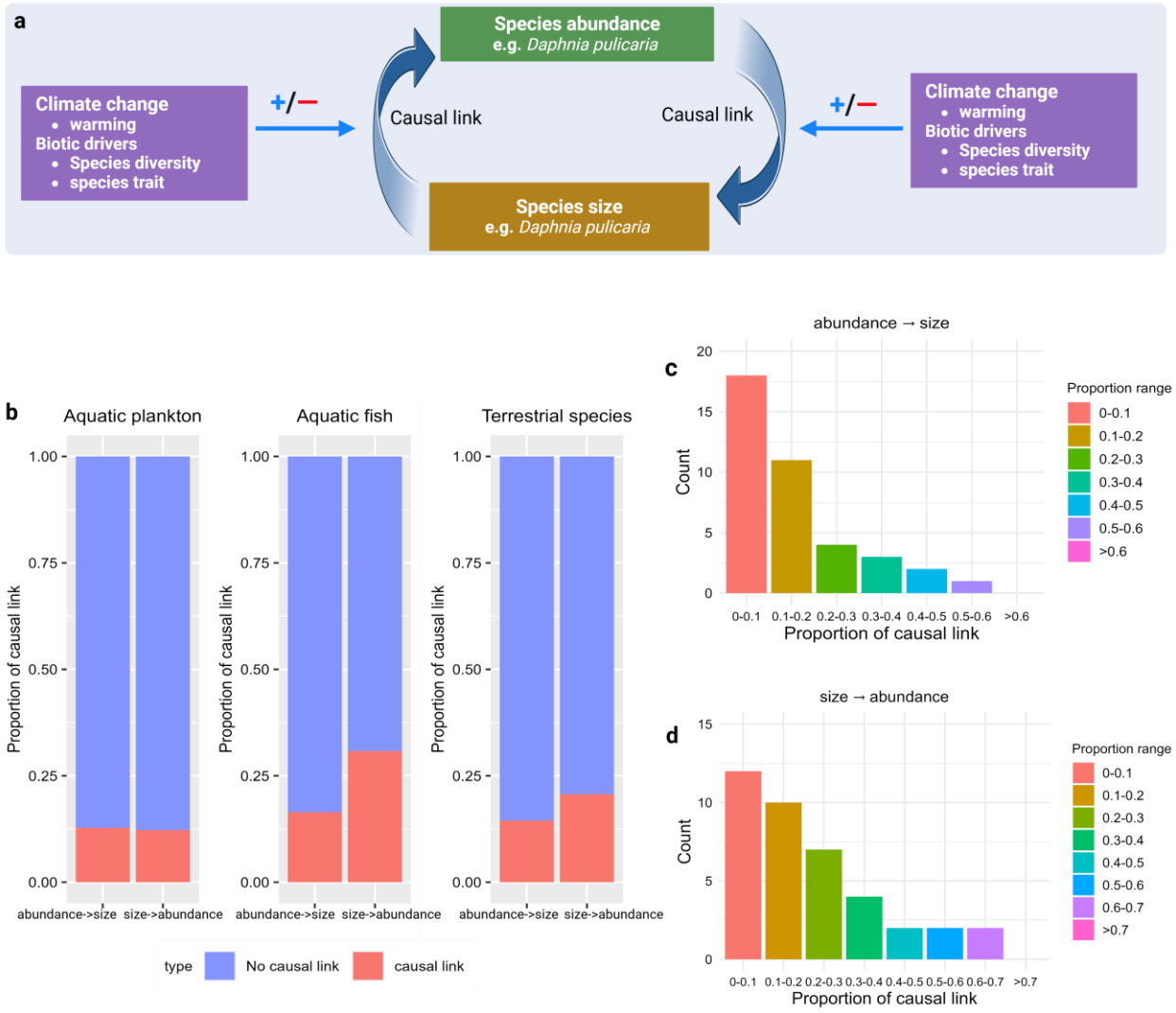
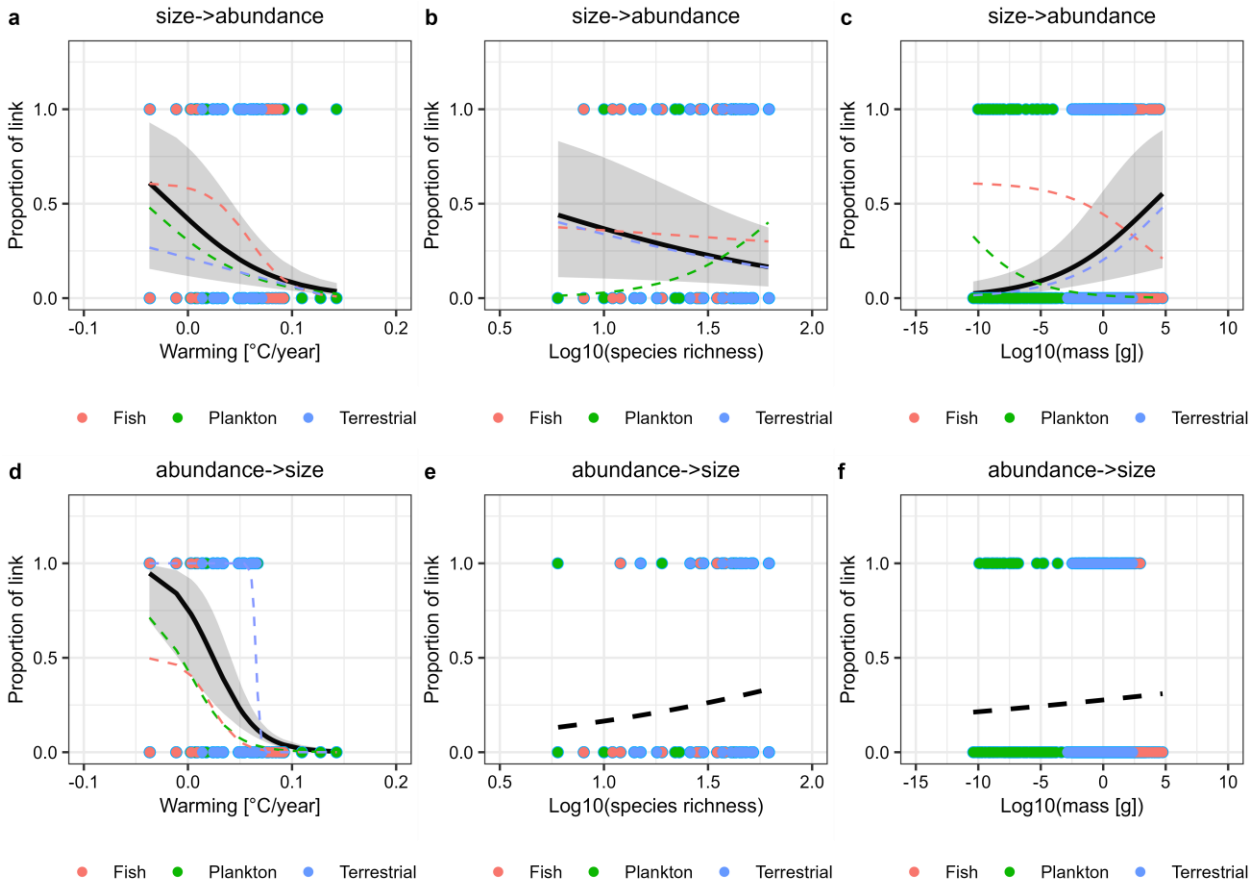


**Figure 2**. **The bidirectional link between abundance and size in response to warming and biotic drivers.** Proportion of casual link from size to abundance (size →abundance) and from abundance to size (abundance →size) in responses to warming (**a, d**), species richness (**b, e**), and mean individual body mass (**c, f**). **a-f,** Causal links identified through CCM are coded as 1 and non-causal link as 0. The bold black lines and error bands depict the significant best-fit trendline and the 95% confidence interval in the logistic regressions (two-sided) across 41 ecosystems, respectively, while the dashed bold black lines indicate nonsignificant fit across 41 ecosystems. The non-bold dashed colored lines indicate the best-fit trendline in the logistic regressions (two-sided) within each group (plankton, fish or terrestrial species). Colored points represent the values of causal links between abundance and size within each species across 41 ecosystems (total points in each figure, $n$ = 1269). For statistical results see table S1.



## Supplementary Figures

**Figure S1**. **The bidirectional causal link between species size and abundance in each of aquatic ecosystems**. Red points indicate causal link identified by CCM, while blue points indicate non-causal link. The numbers in parentheses above each violin plot represent the number of causal links (blue) and the total links (black). The percentage above each violin plot indicates the proportion of causal links to total links. The abbreviations of the sites see Table S2-S3.

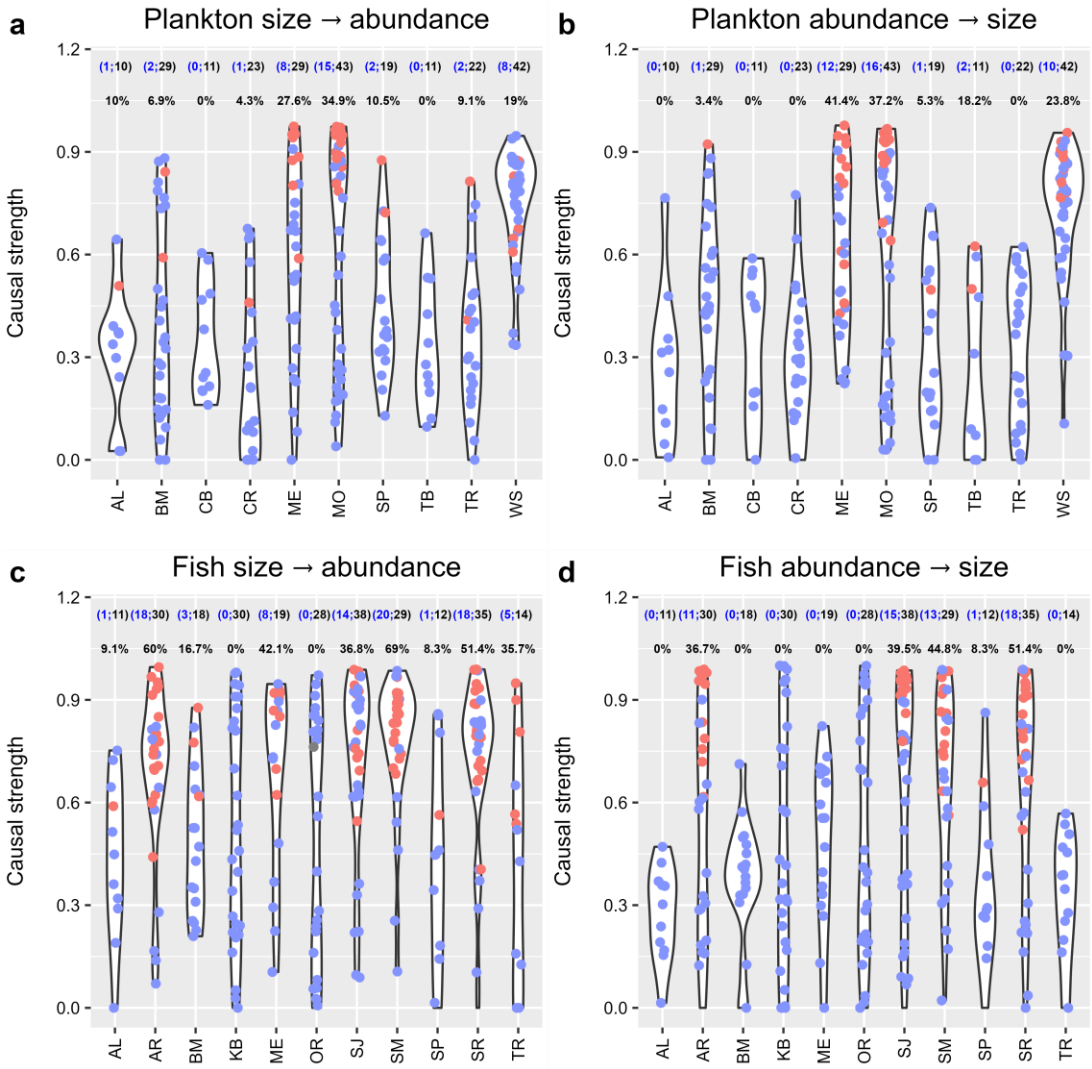


**Figure S2**. **The bidirectional causal link between species size and abundance in each of terrestrial ecosystems**. Red points indicate causal link identified by CCM, while blue points indicate non-causal link. The numbers in parentheses above each violin plot represent the number of causal links (blue) and the total links (black). The percentage above each violin plot indicates the proportion of causal links to total links. The abbreviations of the sites see Table S4.

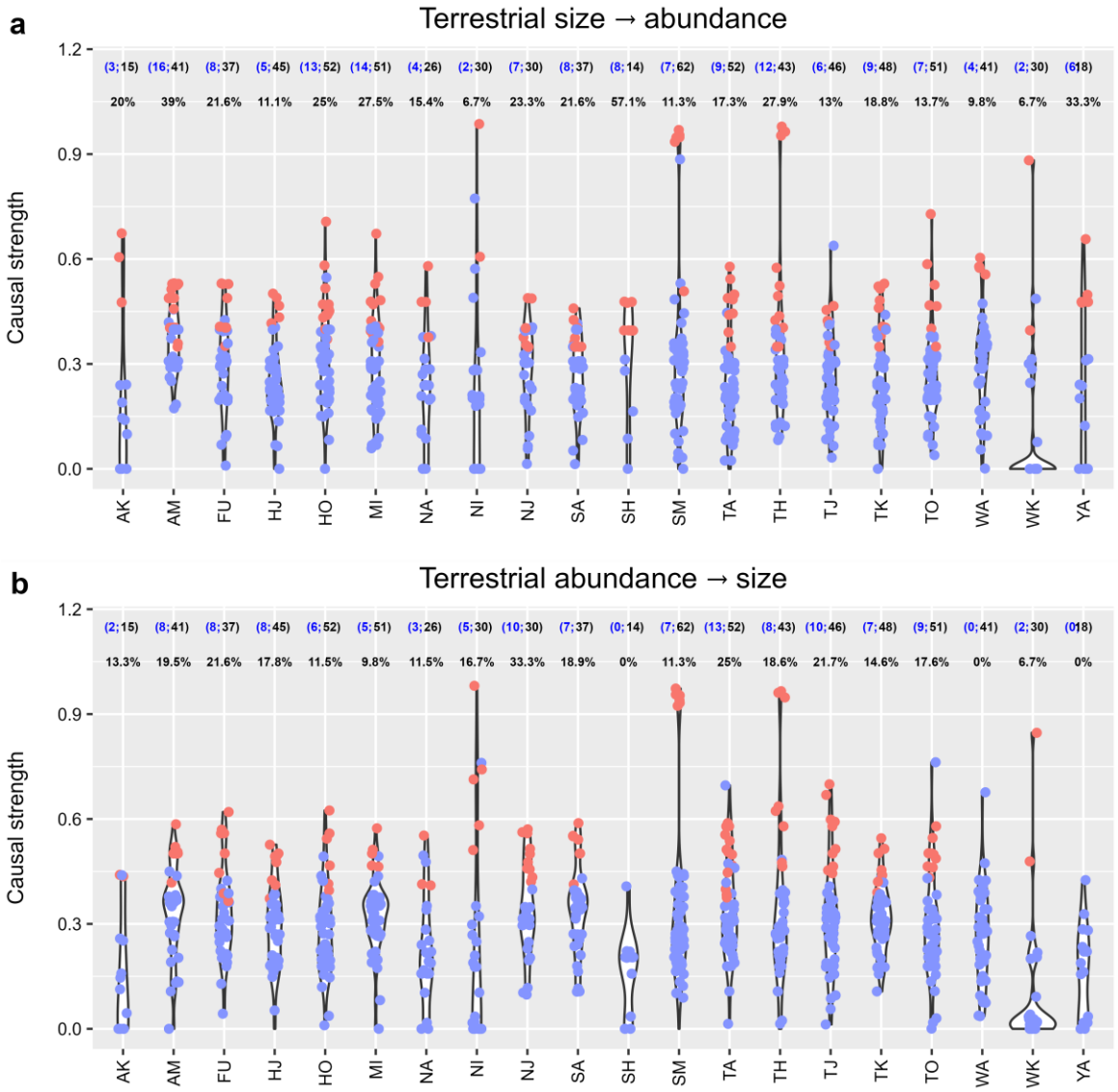


**Figure S3. The average proportion of causal links for aquatic plankton, fish, and terrestrial species across 41 ecosystems, by including rare species (number of zeros 60%~80% in species time series) into analysis**. Within each system, the proportion of the bidirectional causal link see Figure S4-S5.

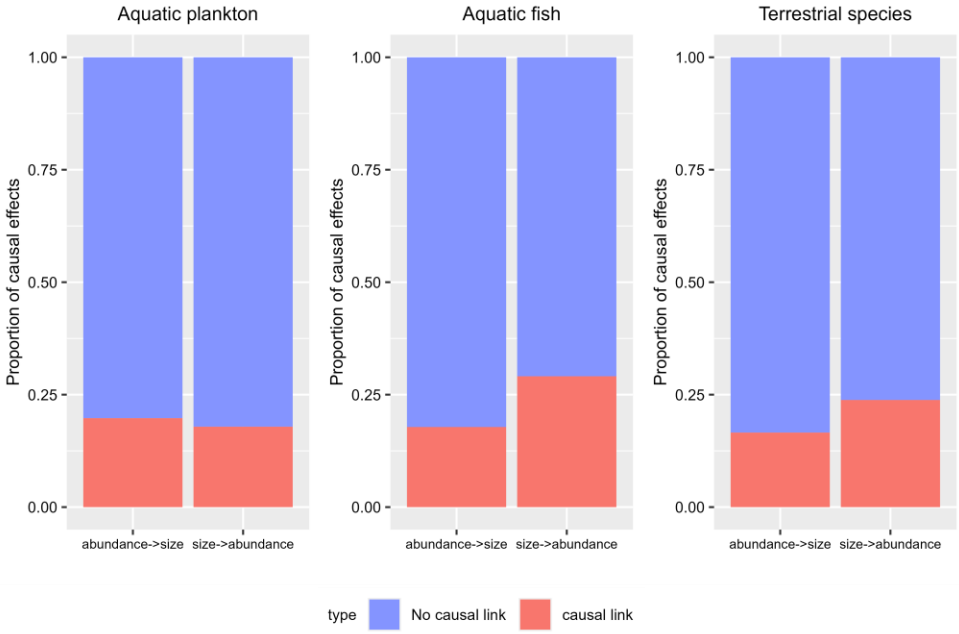


**Figure S4**. **The bidirectional causal link between species size and abundance in each of aquatic ecosystems, by including rare species (number of zeros 60%~80% in each species time series) into analysis**. Red points indicate causal link identified by CCM, while blue points indicate non-causal link. The numbers in parentheses above each violin plot represent the number of causal links (blue) and the total links (black). The percentage above each violin plot indicates the proportion of causal links to total links. The abbreviations of the sites see Table S2-S3.

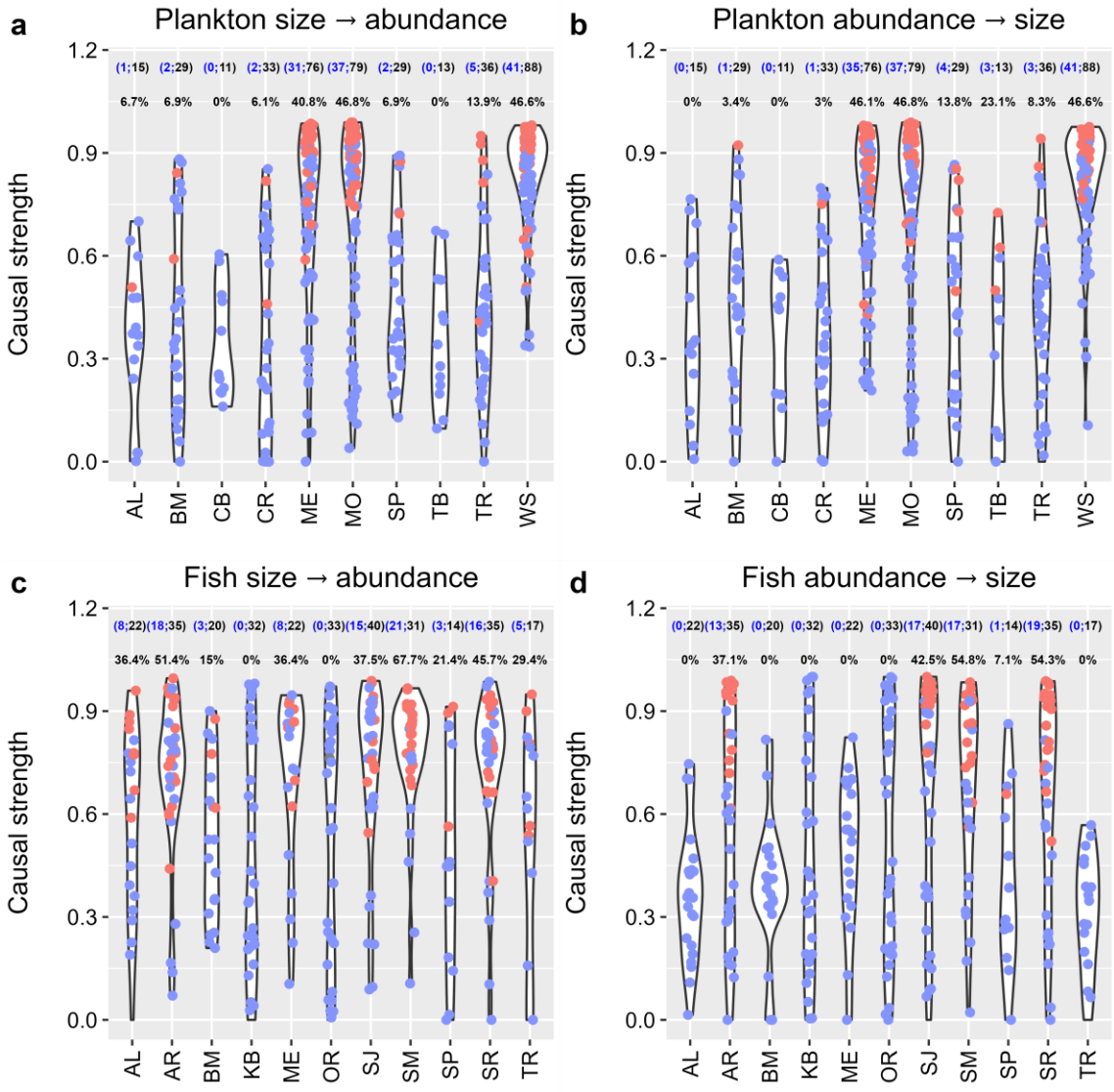


**Figure S5**. **The bidirectional causal link between species size and abundance in each of terrestrial ecosystems, by including rare species (number of zeros 60%~80% in each species time series) into analysis**. Red points indicate causal link identified by CCM, while blue points indicate non-causal link. The numbers in parentheses above each violin plot represent the number of causal links in CCM (blue) and the total links (black). The percentage above each violin plot indicates the proportion of causal links to total links. The abbreviations of the sites see Table S4.

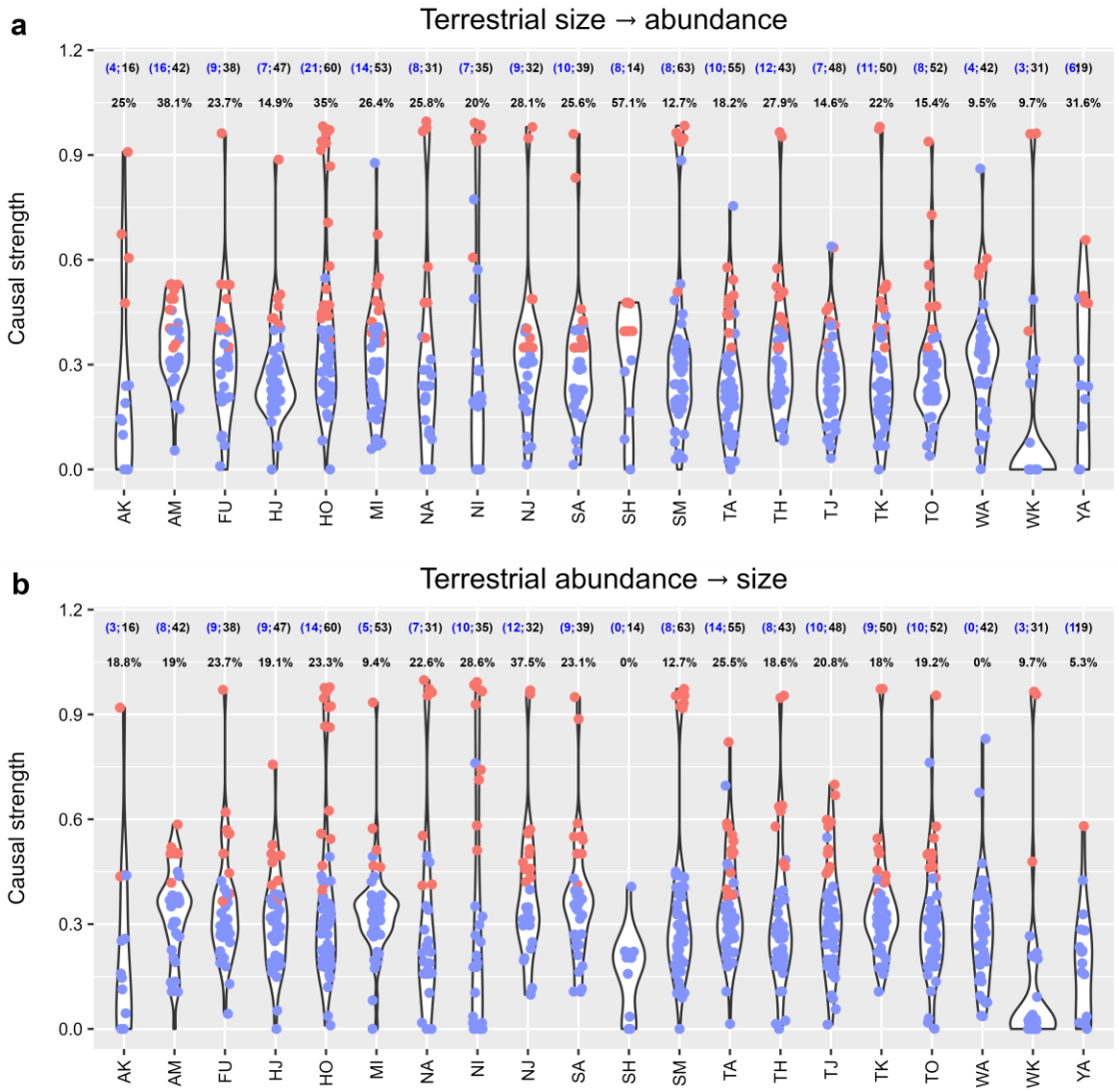


**Figure S6. The average proportion of causal links for aquatic plankton, fish, and terrestrial species across 41 ecosystems, by only using very dominant species (number of zeros <50% in each species time series) into analysis**. Within each system, the proportion of the bidirectional causal link see Figure S7-S8.

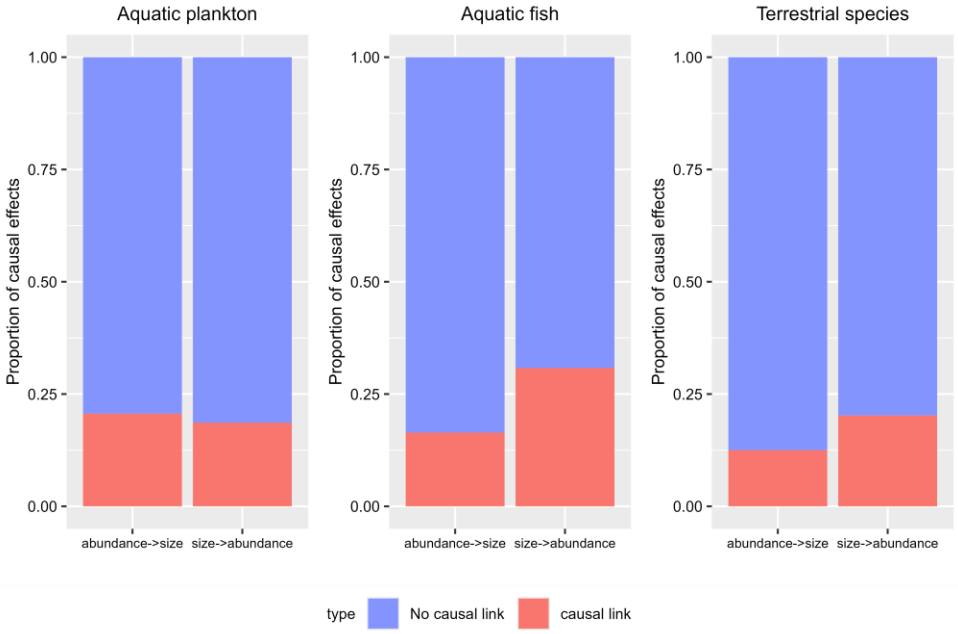


**Figure S7**. **The bidirectional causal link between species size and abundance in each of aquatic ecosystems, by including rare species (number of zeros <50% in each species time series) into analysis**. Red points indicate causal link identified by CCM, while blue points indicate non-causal link. The numbers in parentheses above each violin plot represent the number of causal link (blue) and the total links (black). The percentage above each violin plot indicates the proportion of causal links to total links. The abbreviations of the sites see Table S2-S3.

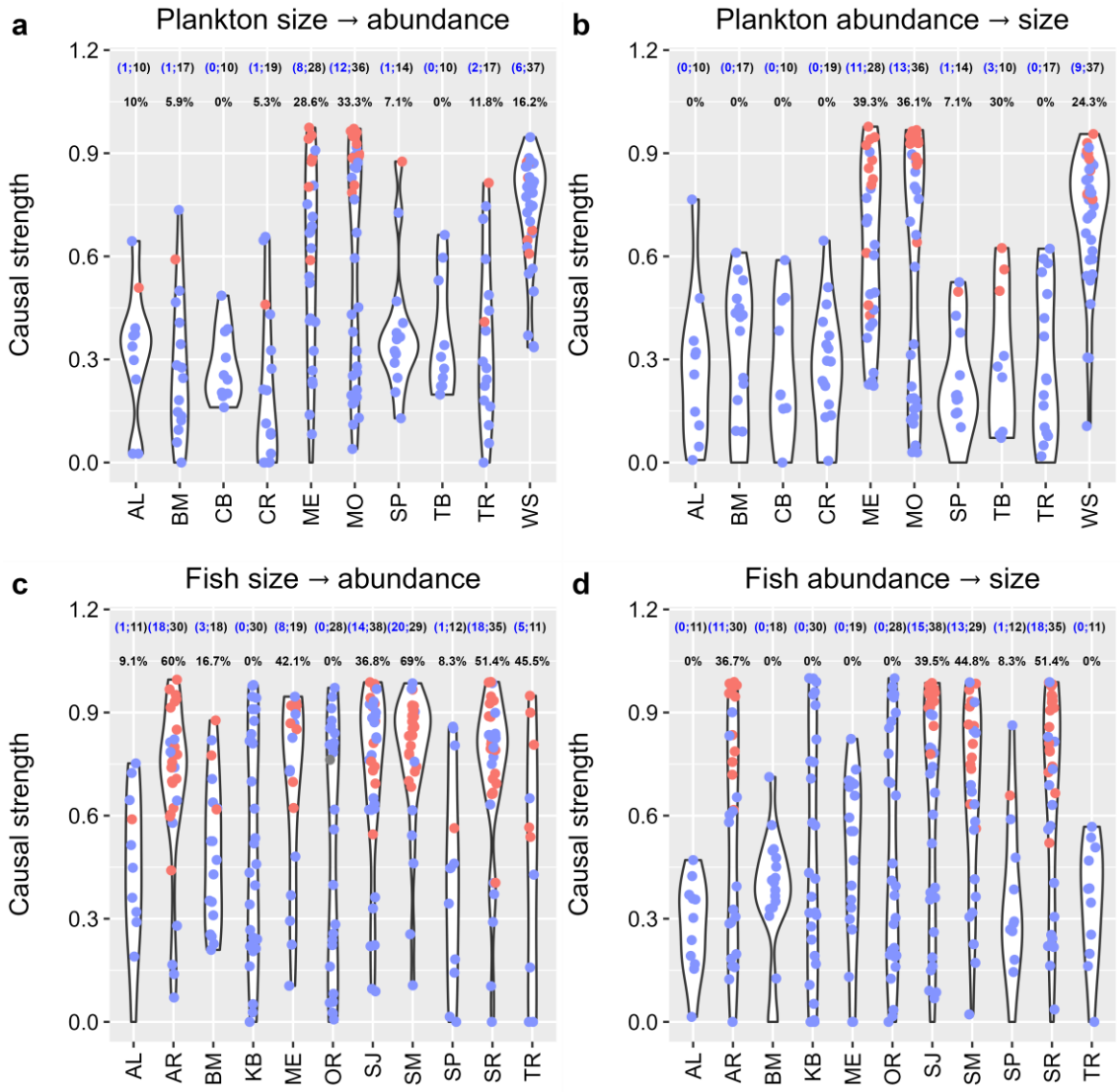


**Figure S8**. **The bidirectional causal link between species size and abundance in each of terrestrial ecosystems, by including rare species (number of zeros 60%~80% in each species time series) into analysis**. Red points indicate causal link identified by CCM, while blue points indicate non-causal link. The numbers in parentheses above each violin plot represent the number of causal links (blue) and the total links (black). The percentage above each violin plot indicates the proportion of causal links to total links. The abbreviations of the sites see Table S4.

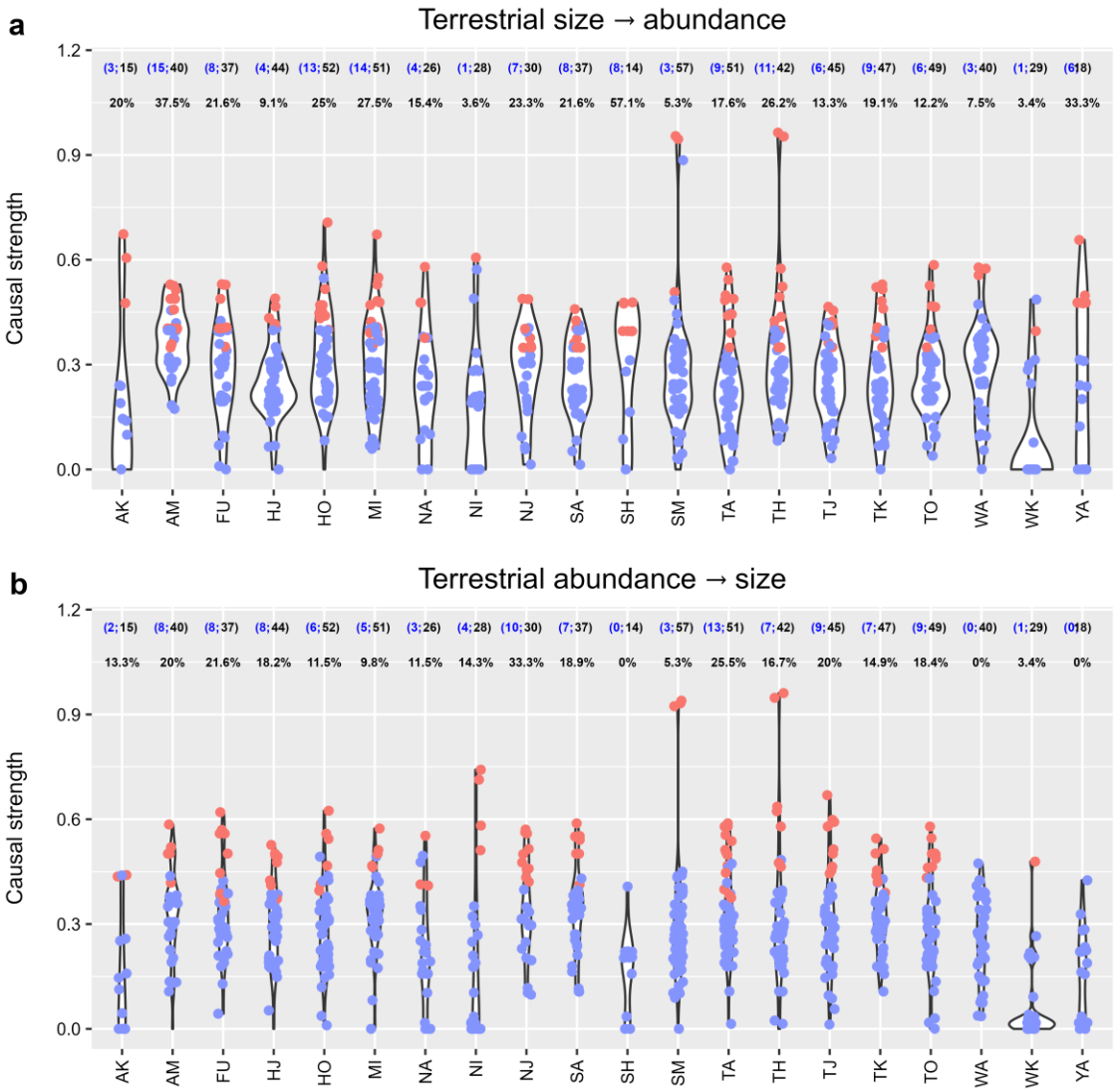
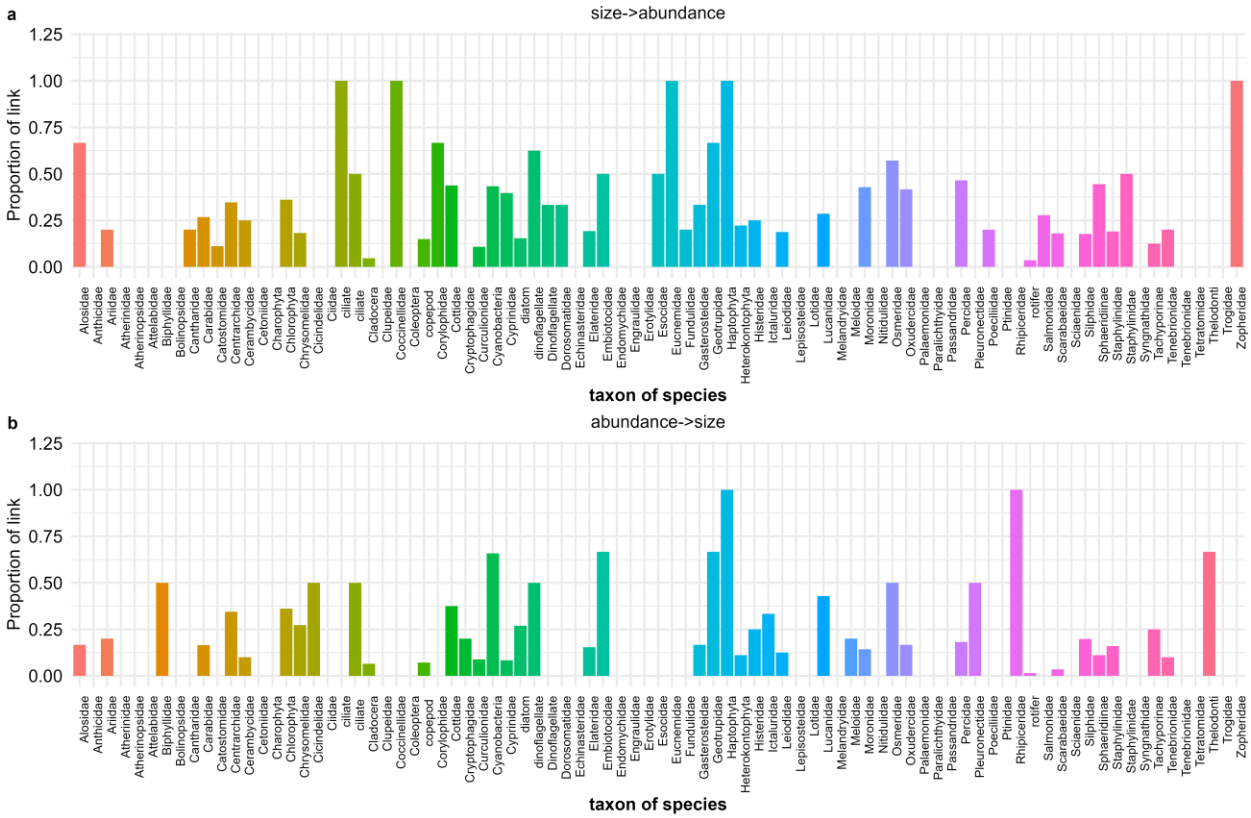


**Figure S9**. **Species-dependent casual link across 41 ecosystems**. The absence of bars corresponding to a specific taxon (e.g., Atherinidae) indicates a proportional value of zero for the associated link.



## Supplementary Tables

**Table S1**. Generalized Linear Mixed Model (glmmTMB function in glmmTMB package) with a binomial error distribution was employed to test the main effects of warming, mean temperature, species richness, and mean species body mass on proportion of either link (size →abundance or abundance →size). In the model, the proportion of each link was used as the response variable, consisting of binary values: 1 indicating the presence of a causal link and 0 indicating the absence of a link. This model set species groups (e.g. plankton) nested within sample locations (e.g. Trout Lake) as random intercepts. Mean temperature, species richness, and mean species body mass were log-transformed using base 10 to ensure normality. For the model testing the link proportion of size → abundance, model's marginal and conditional $R^2$ are 0.15 and 0.22 respectively. For the model testing the link proportion of abundance → size, the $R^2$ is 0.14 and 0.24, respectively. ***$P$< 0.001, **$P$<0.01, *$P$<0.05.

| | proportion of size → abundance | | | proportion of abundance → size | | |
|---|---|---|---|---|---|---|
| | coefficient | Z | P value | coefficient | Z | P value |
| (Intercept) | 1.84 | 0.88 | 0.38 | -1.42 | -0.72 | 0.47 |
| Species richness | -1.61 | -2.13 | **0.03*** | 1.18 | 1.43 | 0.15 |
| Mean body mass | 0.10 | 2.17 | **0.02*** | 0.03 | 0.79 | 0.43 |
| Mean Temperature | 0.61 | 0.60 | 0.55 | 0.76 | 0.80 | 0.43 |
| Warming | -22.93 | -2.88 | **0.004**** | -47.08 | -5.21 | **<0.0001***** |

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