Warming decouples eco-evolutionary feedback between body size and abundance in long term natural ecosystems

Qinghua Zhao[1,5], Yingying X. G. Wang[2,5], Chi Xu[3], George Sugihara[4], Frederik De Laender[1,5]

[1]Research Unit of Environmental and Evolutionary Biology (URBE), Institute of Complex Ecosystems (naXys), Institute of Life, Earth and the Environment (ILEE), University of Namur, Namur, Belgium.

[2]School of Veterinary Medicine, University of California-Davis, Davis, CA, USA

[3]School of Life Sciences, Nanjing University, Nanjing, 210023, China

[4]Scripps Institution of Oceanography, University of California-San Diego, La Jolla, CA, USA

[5]These authors contributed equally

Abstract

Eco-evolutionary feedback, in which abundance influences trait evolution and evolving traits, in turn, affect abundance dynamics, play a critical role in maintaining community structure, function, and stability. A key foundation of this feedback is the bidirectional relationship between body size and abundance. However, the integrity of this relationship is not fixed but varies with climate warming and biotic factors. Using long-term monitoring data from 101 ecological systems spanning over 10-47 years and encompassing multiple generations of plankton, fish, and terrestrial beetles, we provide the first synthetic evidence that warming decouples body size–abundance feedback and this decoupling is stronger in smaller-bodied species. Our findings suggest that warming disrupts trait–demography interactions and indicate that the eco-evolutionary feedback may be vulnerable to anthropogenic pressures.

Keywords: Body size-abundance feedback, Eco-evolutionary feedback, Climate Warming, Species traits.

Introduction

Eco-evolutionary feedback—the reciprocal interactions between ecological and evolutionary processes—are increasingly recognized as a key driver of biodiversity patterns

population stability, species interactions, and ecosystem functioning (Fronhofer *et al.* 2023; Govaert *et al.* 2019; Loreau *et al.* 2023). The feedback arises when traits under selection alter ecological dynamics, which conversely modify selection pressures, creating feedback loops that shape long-term species adaptation to changing environments (De Meester *et al.* 2019; Zamorano *et al.* 2023). This feedback bridges the traditional divide between ecology and evolution, showing that evolutionary change can occur rapidly enough to influence contemporary ecological dynamics (Thrall & Blanc 2023).

At the heart of eco-evolutionary feedback lie functional traits that mediate both ecological performance and evolutionary responses to environmental change (De Meester *et al.* 2019; Pantel & Becks 2023). These traits influence key population processes—such as demographic rates and resource use—and thereby shape ecological dynamics (De Meester *et al.* 2019). The traits often evolve in response to environmental pressures, generating feedback that further modify ecological processes (De Meester *et al.* 2019). Among them, body size is particularly influential due to its pervasive effects across levels of biological organization, and eco-evolutionary feedback often scale with body size, because of shorter generation times facilitating faster evolutionary responses (De Meester *et al.* 2019). Evolutionary shifts in body size affect survival, reproduction, and competitive ability, ultimately shaping population abundance (Pelletier *et al.* 2009). Reciprocally, changes in abundance alter selection on body size: high abundance intensifies resource competition, favoring smaller, more efficient individuals, whereas low abundance can favor larger body sizes due to advantages in competition, mate acquisition, or predator avoidance (Pelletier *et al.* 2009). The bidirectional relationship between body size and abundance thus forms a key foundation of eco-evolutionary feedback operating within and across ecological communities, shaping community structure, buffering ecological systems against environmental fluctuations (Ahti *et al.* 2020; Carlson *et al.* 2011; Edeline & Loeuille 2021; Malerba *et al.* 2018).

Importantly, the strength of body size–abundance feedback is not fixed (Govaert & Klauschies 2024; Han *et al.* 2023). It varies with environmental changes, biotic interactions, and evolutionary dynamics (Fouqueau & Polechová 2024; Kaitala 2021). In stable external environments, tightly coupled body size–abundance relationships can reinforce predictable eco-evolutionary dynamics, as trait shifts propagate through demographic processes and ecological

feedback loops (Fouqueau & Polechová 2024). However, in the context of global change, the robustness of these relationships is increasingly uncertain.

Climate warming, one of the most pervasive anthropogenic stressors, fundamentally alters ecological and evolutionary processes, with body size frequently implicated as a trait sensitive to warming (Gardner *et al.* 2011; Govaert & Klauschies 2024). Numerous studies document shifts toward smaller body sizes in response to rising temperatures—a pattern consistent with metabolic scaling theory, resource limitation, and life-history trade-offs (Gardner *et al.* 2011; Sheridan & Bickford 2011). At the same time, warming can affect population abundance via changes in reproduction, survival, and resource dynamics (Visser 2008; Walsh *et al.* 2019). Despite extensive research on how warming affects body size and abundance independently, whether climate change disrupts the coupling between these two processes—and thus potentially erodes the eco-evolutionary feedback—remains unclear. Furthermore, species diversity and traits can influence these two processes, driving shifts in both body size and abundance. However, whether they disrupt the coupling between these two processes remains unknown.

In this study, we present the first systematic evaluation of how climate warming influences the feedback between body size and population abundance, potential effect on eco-evolutionary feedback. We synthesize a continental-scale dataset encompassing 101 long-term monitoring sites across aquatic and terrestrial systems—including plankton, fish, and ground beetle species—spanning 10 to 47 years and encompassing multiple generations for each species. Using this dataset, we evaluated the presence of bidirectional links between body size and abundance through Convergent Cross Mapping (CCM) (Sugihara *et al.* 2012), a method for detecting causal links (Fig. 1b). Last, we assessed how the proportion of bidirectional links responds to warming and biotic drivers. Taken together, this study provides insight into whether climate warming and biotic factors disrupt body size–abundance feedback, with implications for body size–mediated eco-evolutionary feedback.

Methods

We compiled a long-term dataset encompassing 101 ecosystems: 51 aquatic planktonic systems monitored for 10–40 years, 30 fish systems spanning 31–47 years, and 20 terrestrial systems (beetles) spanning 9–11 years. The duration of these time series captures multiple

generations for each species. The inclusion of multiple generations enables the detection of evolutionary changes in body size, beyond plastic or pure ecological responses. Such temporal resolution captures concurrent shifts in ecological dynamics (e.g., abundance) and evolutionary trait change (e.g., body size), fulfilling the criteria necessary to assess eco-evolutionary feedback.

Aquatic plankton Data. Body size and abundance data were compiled from 51 long-term monitoring sites across aquatic planktonic ecosystems, comprising 20 lakes, 8 rivers, and 23 marine systems (Fig 2a). These datasets were accessed by North Temperate Lakes Long-Term Ecological Research (Magnuson *et al.* 2023a, 2024a, 2022, 2023b), Pangaea (Felden *et al.* 2023), USGS (Nejad *et al.* 2017), Greenland Ecosystem Monitoring (Christensen *et al.* 2017) and Data Observation Network for Earth (Michener *et al.* 2011). The 51 ecosystems have been consistently sampled for 10–40 years. The resident species include phytoplankton and zooplankton, with maximum generation times typically less than a week and two months, respectively (Elbrächter 1976; Gillooly 2000; Litchman 2000). Therefore, the 10–40 years of sampling encompass numerous generations of these planktonic species. For each of the 51 aquatic planktonic ecosystems, 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 51 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 0.05% missing points across the whole planktonic dataset (41 out of 85161 data points). Those missing data points were linearly interpolated using *na.approx* function in the package of zoo (Karakoç *et al.* 2020; Zhao *et al.* 2023). 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), (μm^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 (Chang *et al.* 2020, 2022). 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, μ_{season} is the year mean, and the σ_{season} is the year standard deviation (Chang *et al.* 2020, 2022). 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 30 monitoring sites, including six rivers, five lakes and 19 marines. These datasets were accessed by North Temperate Lakes Long-Term Ecological Research (Magnuson *et al.* 2024c, b), International Council for the Exploration of the Sea (ICES) (Fish trawl surveys 2025), and Reef Life Survey (Edgar & Stuart-Smith 2014). These ecosystems have been consistently sampled for 31–47 years. Among all fish species, Atlantic cod exhibit the longest generation time (≤8 years), medium-sized sportfish range from approximately 5–7 years, and the remaining small, fast-reproducing species have generation times of less than 2 years. Thus, the 31–47 years of sampling encompass numerous generations across all species. 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. 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, all focused on ground beetles. All data were retrieved from BioTIME (Dornelas *et al.* 2018). These ground beetles were consistently sampled for 10–11 years. Given a maximum generation time of 1–3 years, the sampling period encompasses numerous generations across all species. Again, for each site, there were three types of variables: (1) species abundance; (2) species size (i.e. biomass, 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 (GHCN-Daily, Version 3 2012).

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, 0.52% of data points were missing in the dataset. These missing values were subsequently linearly interpolated using the *na.approx* function from the zoo package (Karakoç *et al.* 2020; Zhao *et al.* 2023). Then, long-term linear and seasonal trends were removed from each time series using the same methodology applied to the plankton data. Finally, each time series, including both species abundance and size, was standardized to have a mean of zero and a unit variance.

Detecting the bidirectional link among body size and abundance. To ensure the applicability of empirical dynamic modeling (EDM), we included only species with sufficiently long and continuous time series data (i.e. length $n \geqslant 30$) (Sugihara *et al.* 2012). 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 (Deyle & Sugihara 2011; Sugihara *et al.* 2012) (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) (Sugihara *et al.* 2012). 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 (Karakoç *et al.* 2020). 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 (Hsieh *et al.* 2005).

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 ρ (Ye *et al.* 2019). 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) (Sugihara *et al.* 2012). 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 (Sugihara & May 1990). Convergence can be assessed by evaluating whether there is a significant monotonic increasing trend in cross-mapping skill ρ as library length increases using Kendall's τ test (Chang *et al.* 2020), and whether the ρ at the largest library length is significantly greater than that the ρ at the smallest library length using Fisher's Z test (Chang *et al.* 2020). 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 τ test and Fisher's Z test were statistically significant ($P < 0.05$) for testing convergence (Chang *et al.* 2020).

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 (Chang *et al.* 2020; Mohsin & Gough 2010). This method was chosen due to its widespread use in quantifying warming rates (Pinsky *et al.* 2025; Tong *et al.* 2023), its robustness to episodic extreme events, and its ability to provide stable estimates of long-term trends in the presence of outliers (Mohsin & Gough 2010). 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 (Cohen & Lough 1981; Huntley 1992).

Bidirectional links in responses to climate change and biotic drivers. We employed a generalized linear mixed model (using the glmmTMB function from the glmmTMB package (Brooks *et al.* 2017)) with a binomial error distribution to test the main effects of warming, mean temperature, species richness, mean species body mass, and their pairwise interactions on the proportion of observed links—either from body size to abundance (size →abundance) or from

abundance to body size (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.

All analyses were done with R (ver. 4.1.2). The CCM analysis was examined using the rEDM package (version 1.2.3).

Results

We used a binary response variable to indicate the presence (1) or absence (0) of a link between body size and abundance, with links identified using Convergent Cross Mapping. Across 101 ecological systems monitored over 10 to 47 years—encompassing multiple generations for each of 5858 species—our analysis revealed that warming decouples body size–abundance feedback, as evidenced by a negative association between warming and the proportion of both link types (abundance → size and size → abundance) (Fig 3a-d). This pattern suggests that warming can reduce the potential for body size–abundance feedback, potentially weakening body size based eco-evolutionary feedback.

Notably, the effect of warming body size–abundance feedback varied with species body size and species richness. Warming more strongly decoupled body size – abundance feedback in smaller-bodied species, as evidenced by steeper negative slopes for both abundance → size and size → abundance links (Fig 3a-b). In contrast, this decoupling effect was weaker and in some cases reversed—among larger-bodied species (Fig 3a-b), indicating a potential shift toward feedback coupling. These findings suggest that warming may more strongly weaken body size–mediated eco-evolutionary feedback in smaller-bodied species, while potentially reinforcing it in larger-bodied species. However, species richness showed no consistent effects on body size – abundance feedback. Warming more strongly decoupled the size → abundance link at higher species richness (Fig 3c), while its decoupling effect on the abundance → size link was stronger under lower species richness (Fig 3d). Last, we found mean temperature had no effect on either link of abundance → size or size → abundance (Table S1).

Discussion

Our study provides the first systematic evaluation of body size–abundance feedback—a key foundation of eco-evolutionary dynamics at population and community levels—in response to environmental change, and demonstrates the potential for warming to disrupt these feedbacks. By analyzing long-term field monitoring data from 101 ecosystems—each encompassing multiple generations per species—we captured sufficient temporal resolution to detect potential evolutionary responses. Our results show that warming decouples body size–abundance feedback, suggesting that warming temperatures can decouple body size–mediated eco-evolutionary dynamics. Notably, this decoupling effect can be stronger in smaller-bodied species, indicating that trait dependent eco-evolutionary feedback to climate warming.

Body size evolve rapidly to environmental changes (Merckx *et al.* 2018) and can exert a significant influence on population abundance (Martins *et al.* 2023). Previous experimental studies have documented that the body size and abundance feedback are tightly linked in single-species populations (Gibert *et al.* 2022, 2023), a two-species competitive interactions (Govaert & Klauschies 2024), and a microbial food web (Han *et al.* 2023). Our study further showed that warming tended to decouple body size and abundance feedback (Fig 3). Previous evidence has documented weaker body size–abundance feedback at higher temperatures in an experimental protist food web. (Han *et al.* 2023). This may be attributed to the differing response rates of body size and abundance to warming (Genner *et al.* 2010). Higher temperatures can lead to a significant reduction in species body size (Audzijonyte *et al.* 2020; Terry *et al.* 2022), while it can have slight effect on population abundance (Sebastian *et al.* 2012). Similarly, higher temperatures have shown to accelerate growth, leading to an rapid increase in population abundance (Brandenburg *et al.* 2019; Han *et al.* 2023), while simultaneously either leaving body size unaffected or slightly altered body size (Crozier *et al.* 2010; Genner *et al.* 2010). These different responses rate among size and abundance may weaken the link between them (Han *et al.* 2023).

We found that warming more strongly decoupled body size–abundance feedback in smaller-bodied species, whereas this effect was weaker—and in some cases reversed—among larger-bodied species. This pattern suggests that warming may more strongly weakens body size–based eco-evolutionary feedback in smaller-bodied species, while potentially reinforcing it in larger-bodied species. To date, no empirical evidence has been documented to validate this

trend. Given their shorter generation times and higher sensitivity to environmental fluctuations (Gillooly 2000; Zeuss *et al.* 2017), these species may exhibit more rapid but less stable trait–abundance dynamics under warming, increasing the likelihood of feedback decoupling.

In contrast, at higher levels of species richness, warming more strongly decoupled the link of size → abundance, while exhibiting a weaker decoupling effect on link of abundance → size. Previous experimental studies have demonstrated that increased species richness reduces the proportion of links of size→ abundance (Govaert & Klauschies 2024). Here, enhanced species richness can 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 (Govaert & Klauschies 2024). However, there is currently no empirical evidence documenting the interactive effects between warming and species richness, nor established mechanisms to explain their interactions on both links.

Our analysis further revealed that, unlike indoor experiments where body size and abundance are nearly always linked (Gibert *et al.* 2022, 2023), this feedback is less tightly coupled in natural ecosystems (Fig. S1). Across 101 ecosystems, 25.1% of species exhibited a causal link from size to abundance, while 20.3% showed a link from abundance to size. The weak coupling between body size and abundance suggests that body size based eco-evolutionary dynamics may be loosely linked at natural ecosystems. Moreover, the bidirectional feedback between body size and abundance appears asymmetrical, with a higher proportion of size → abundance links compared to the reverse (25.1% vs. 20.3%, Fig S1). Taken together, these results suggest that body size and abundance may exhibit independent, rather than simultaneous, responses to environmental change in natural systems. Indeed, previous evidence has documented independent shifts in body size and abundance in response to urbanization (Merckx *et al.* 2018) and habitat fragmentation (Warzecha *et al.* 2016; Zastavniouk *et al.* 2017). Species' size can even provide greater accuracy and serve as an earlier warning signals for predicting population collapses than abundance, under environmental deterioration (Clements *et al.* 2017, 2019; Clements & Ozgul 2016).

In summary, long-term field data spanning over 10 years and covering multiple generations provides sufficient temporal resolution to detect evolutionary responses in natural systems. While controlled experiments are well-suited for isolating causal eco-evolutionary feedback, the long-term field studies used in this analysis are essential for capturing these

dynamics in natural ecosystems under sustained environmental change. By revealing that climate warming decouples body size and abundance relationships, this study emphasizes the vulnerability of size-based eco-evolutionary feedback to anthropogenic pressures.

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/link.abundance-size).

Acknowledgements

We thank all participants in each long-term monitoring site. Q.Z. acknowledges funding from the concerted research action (ARC) from the special research fund from the University of Namur, Belgium (ARC grant DIVERCE, Convention 18/23-095).

Figures

Figure 1. **An overview of the methods and sample locations**. **a**, The sample location for plankton, fish and terrestrial beetles. **b**, Conceptual illustration of the bidirectional feedback between body size and abundance. Evolutionary shifts in body size influences key fitness components—survival, reproduction, and competitive ability—that shape population abundance. In turn, changes in abundance modify selection pressures on body size through effects on resource competition, mate acquisition, and predator avoidance. This reciprocal interaction among body size and abundance forms a core mechanism underpinning eco-evolutionary feedback. In this study, we investigate body size-abundance feedback at the individual focal species (e.g. *Gambusia affinis*) rather than across species.

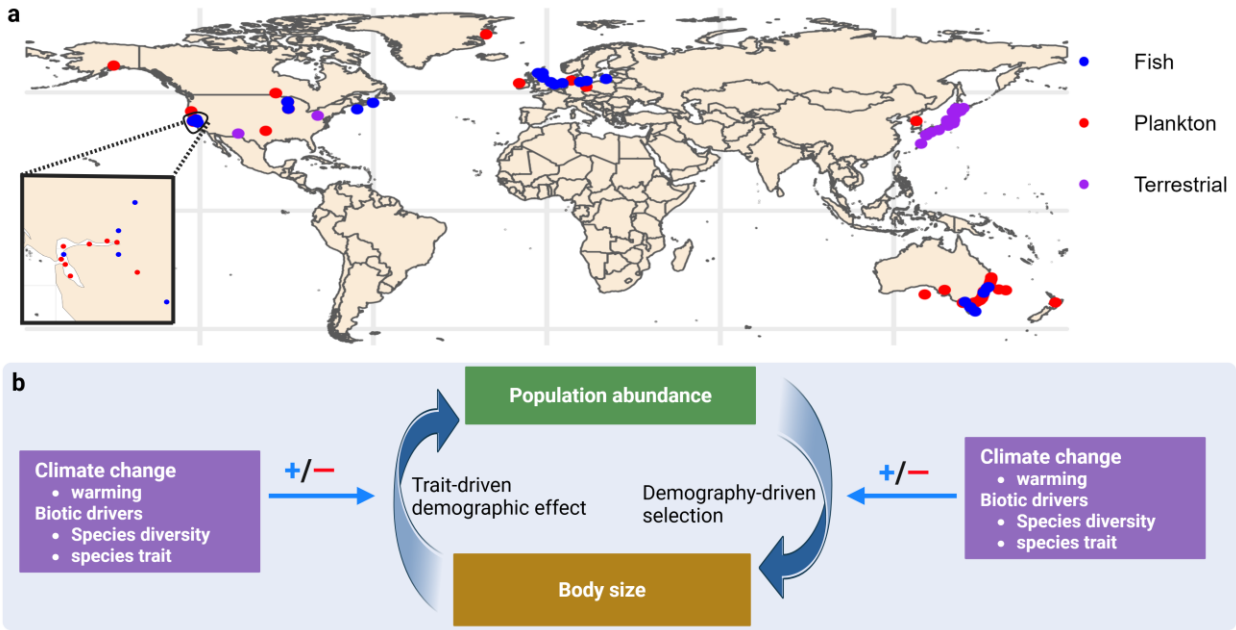


Figure 2. **The body size and abundance feedback in response to warming**. Feedback identified by CCM were coded as 1, and the absence of a link as 0. The solid lines and shaded error bands represent the significant best-fit trendlines and corresponding 95% confidence intervals from two-sided logistic regressions across 101 ecosystems. Black points represent the binary link values (0 or 1) between abundance and body size for each species across 101 ecosystems (total points per panel: n = 5858). Points are vertically jittered to reduce overlapping. A generalized linear mixed model with a binomial error distribution was used to test the effect of warming on the proportion of each link (size → abundance or abundance → size). The response variable was binary, with 1 indicating the presence of a link and 0 indicating its absence. Species groups (e.g., fish) nested within sampling locations (e.g., Trout Lake) were included as random intercepts. The effect of warming is visualized by using the ggpredict function from the ggeffects package. ***P< 0.001, **P<0.01, *P<0.05.

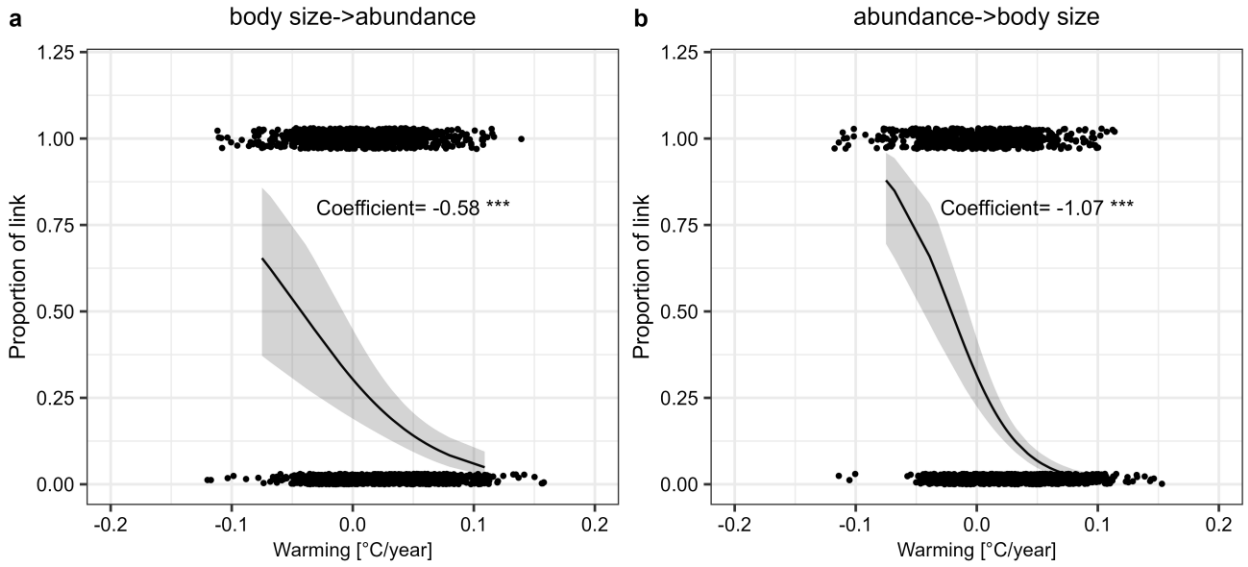
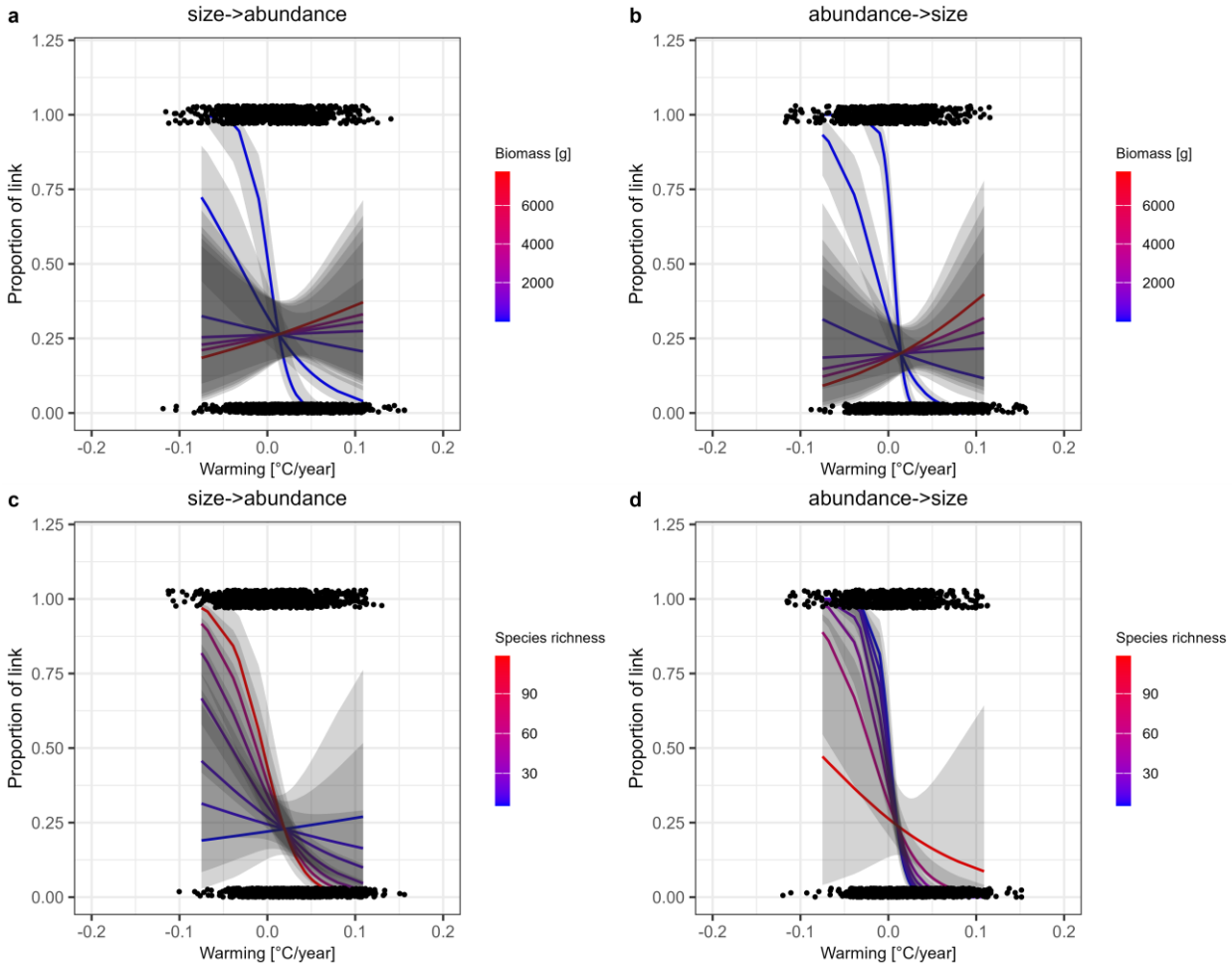


Figure 3. **The body size and abundance feedback in response to biotic drivers. a-d,** The feedback in response to the interactive effects of warming and mean species body mass (**a–b**) and interactive effects of warming and species richness (**c–d**). Feedback identified by CCM were coded as 1, and the absence of a link as 0. The solid lines and shaded error bands represent the significant best-fit trendlines and corresponding 95% confidence intervals from two-sided logistic regressions across 101 ecosystems. Points represent the binary link values (0 or 1) between abundance and body size for each species across 101 ecosystems (total points per panel: n = 5858). Points are vertically jittered to reduce overlapping. The interaction among predictors (**a-d**) is visualized using the ggpredict function from the ggeffects package. For statistical results see table S1.



Supplementary Figures

Figure S1. **Proportion of body size–abundance feedback across 101 ecosystems. a,** At the species level, mean proportions of causal links are shown for aquatic plankton, fish, and terrestrial species. **b**–**c**, At the ecosystem level, frequencies and proportions of causal links from abundance → size (**b**) and size → abundance (**c**) across 101 ecosystems. For detailed proportions of causal links within each ecosystem, see Figures S2–S3.

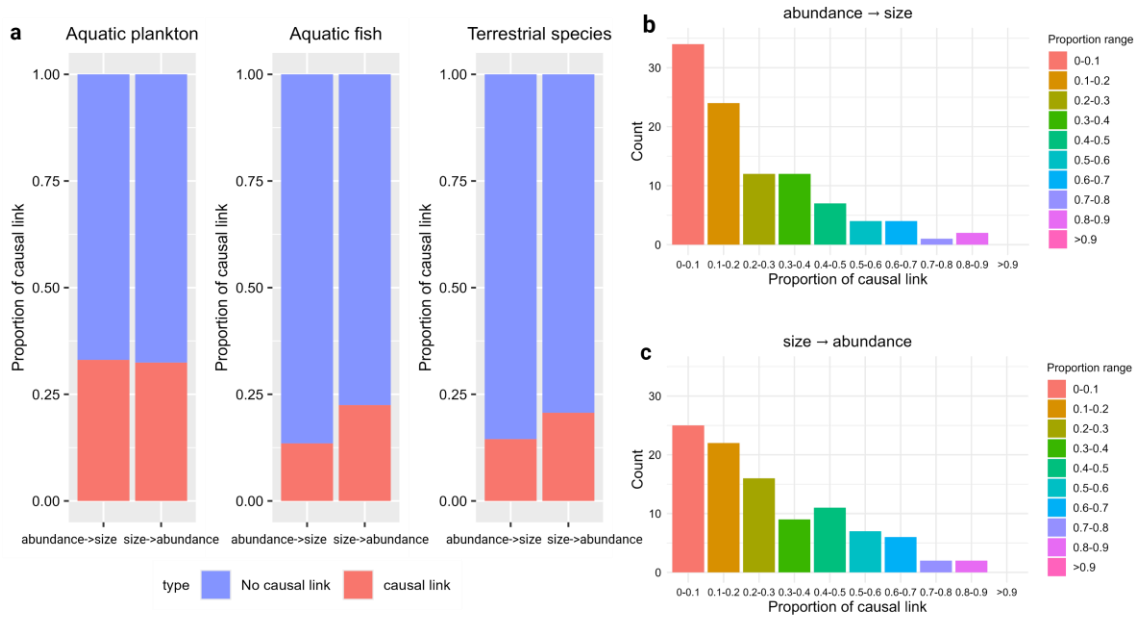


Figure S2. **The bidirectional link between species size and abundance in each of aquatic ecosystems**. Red points indicate causal links identified by CCM, while blue points indicate the absence of a link. Letters on the x-axis represent sampled ecosystems.

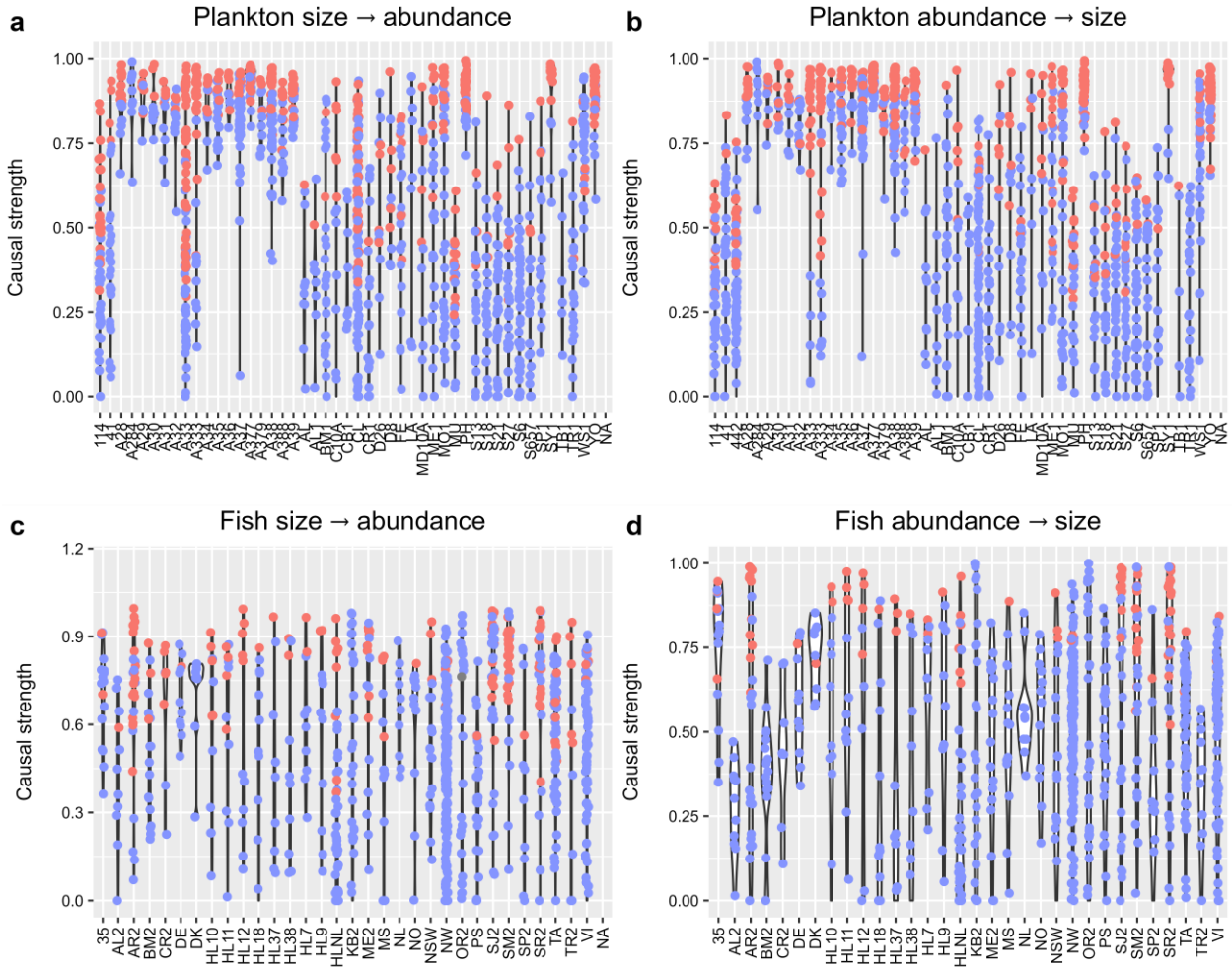
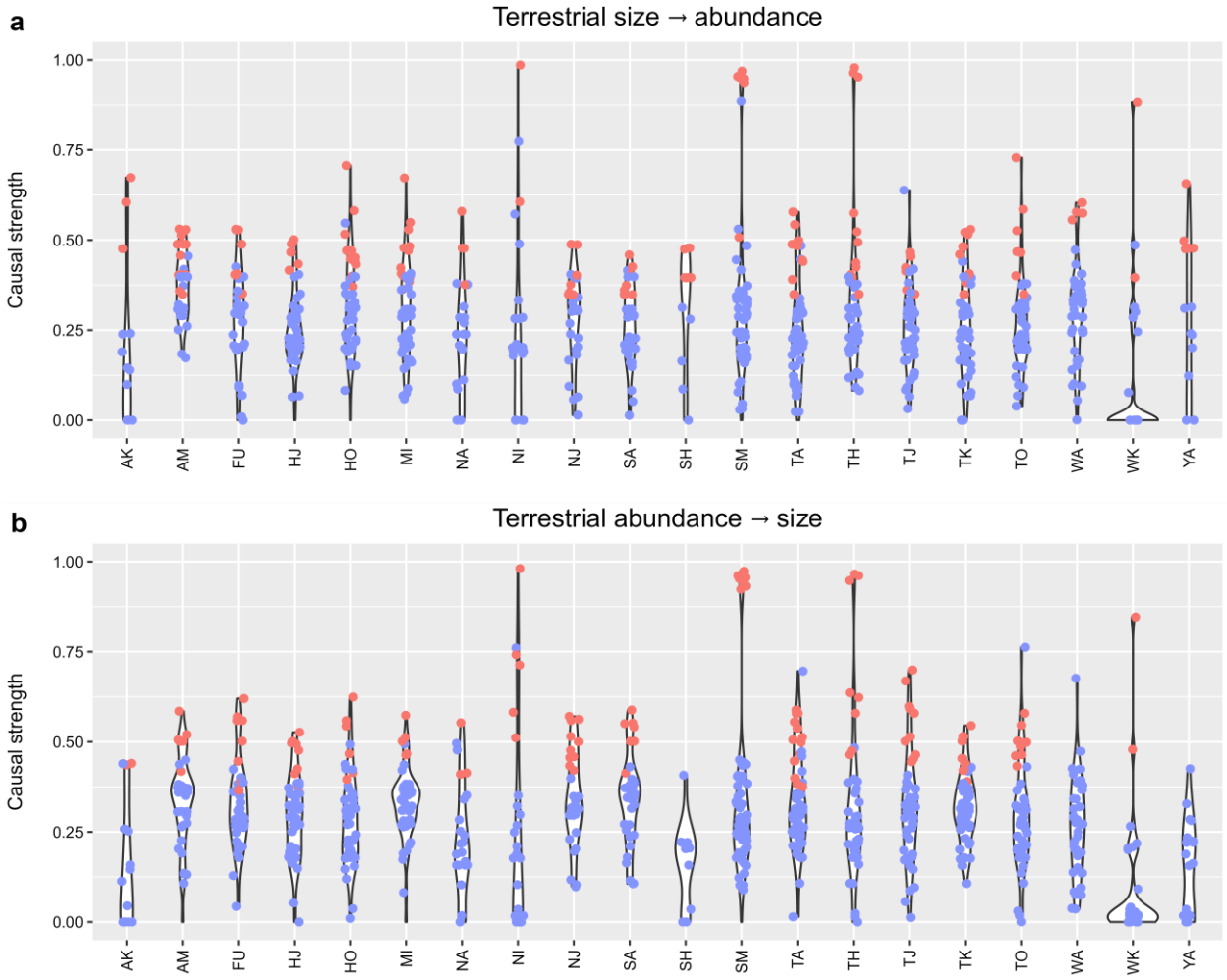


Figure S3. **The bidirectional link between species size and abundance in each of terrestrial ecosystems**. Red points indicate causal links identified by CCM, while blue points indicate the absence of a link. Letters on the x-axis represent sampled ecosystems.



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, species mean body mass and pair wise interaction among warming, species richness and species mean body mass on proportion of either link (size →abundance or abundance →size). In the model, the proportion of each link was treated 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. fish) 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. ***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)	-1.25	-6.95	**<0.001*** **	-1.81	-10.90	**<0.001*** **
Species richness	-0.01	-0.09	0.93	0.31	2.19	**0.03***
Warming	-0.88	-4.90	**<0.001*** **	-1.71	-8.06	**<0.001*** **
Mean body mass	0.18	1.25	0.21	0.35	2.32	**0.02***
Mean Temperature	0.03	0.23	0.82	-0.07	-0.56	0.57
Species richness* Warming	-0.35	-2.25	**0.02***	0.79	3.24	**0.001** **
Warming* Mean body mass	0.73	4.15	**<0.001*** **	1.41	5.79	**<0.001*** **

References

Ahti, P.A., Kuparinen, A. & Uusi-Heikkilä, S. (2020). Size does matter — the eco-evolutionary effects of changing body size in fish. *Environ. Rev.*, 28, 311–324.

Audzijonyte, A., Richards, S.A., Stuart-Smith, R.D., Pecl, G., Edgar, G.J., Barrett, N.S., *et al.* (2020). Fish body sizes change with temperature but not all species shrink with warming. *Nat Ecol Evol*, 4, 809–814.

Brandenburg, K.M., Velthuis, M. & Van de Waal, D.B. (2019). Meta-analysis reveals enhanced growth of marine harmful algae from temperate regions with warming and elevated CO2 levels. *Glob Chang Biol*, 25, 2607–2618.

Brooks, M., Bolker, B., Kristensen, K., Maechler, M., Magnusson, A., Skaug, H., *et al.* (2017). glmmTMB: Generalized Linear Mixed Models using Template Model Builder.

Carlson, S.M., Quinn, T.P. & Hendry, A.P. (2011). Eco-evolutionary dynamics in Pacific salmon. *Heredity*, 106, 438–447.

Chang, C.-W., Miki, T., Ye, H., Souissi, S., Adrian, R., Anneville, O., *et al.* (2022). Causal networks of phytoplankton diversity and biomass are modulated by environmental context. *Nat Commun*, 13, 1140.

Chang, C.-W., Ye, H., Miki, T., Deyle, E.R., Souissi, S., Anneville, O., *et al.* (2020). Long-term warming destabilizes aquatic ecosystems through weakening biodiversity-mediated causal networks. *Global Change Biology*, 26, 6413–6423.

Christensen, T.R., Topp-Jørgensen, E., Sejr, M.K. & Schmidt, N.M. (2017). Foreword: Synthesis of the Greenland Ecosystem Monitoring program. *Ambio*, 46, 1–2.

Clements, C.F., Blanchard, J.L., Nash, K.L., Hindell, M.A. & Ozgul, A. (2017). Body size shifts and early warning signals precede the historic collapse of whale stocks. *Nat Ecol Evol*, 1, 1–6.

Clements, C.F., McCarthy, M.A. & Blanchard, J.L. (2019). Early warning signals of recovery in complex systems. *Nat Commun*, 10, 1681.

Clements, C.F. & Ozgul, A. (2016). Including trait-based early warning signals helps predict population collapse. *Nat Commun*, 7, 10984.

Cohen, R.E. & Lough, R.G. (1981). Length-Weight Relationships for Several Copepods Dominant in the Georges Bank-Gulf of Maine Area. *J. Northw. Atl. Fish. Sci.*, 2, 47–52.

Crozier, L.G., Zabel, R.W., Hockersmith, E.E. & Achord, S. (2010). Interacting effects of density and temperature on body size in multiple populations of Chinook salmon. *Journal of Animal Ecology*, 79, 342–349.

De Meester, L., Brans, K.I., Govaert, L., Souffreau, C., Mukherjee, S., Vanvelk, H., *et al.* (2019). Analysing eco-evolutionary dynamics—The challenging complexity of the real world. *Functional Ecology*, 33, 43–59.

Deyle, E.R. & Sugihara, G. (2011). Generalized Theorems for Nonlinear State Space Reconstruction. *PLOS ONE*, 6, e18295.

Dornelas, M., Antao, L., Moyes, F., Bates, A., Magurran, A., Adam, D., *et al.* (2018). BioTIME: A database of biodiversity time series for the Anthropocene.

Edeline, E. & Loeuille, N. (2021). Size-dependent eco-evolutionary feedbacks in harvested systems. *Oikos*, 130, 1636–1649.

Edgar, G.J. & Stuart-Smith, R.D. (2014). Systematic global assessment of reef fish communities by the Reef Life Survey program. *Sci Data*, 1, 140007.

Elbrächter, M. (1976). Population dynamic studies on phytoplankton cultures. *Marine Biology*, 35, 201–209.

Felden, J., Möller, L., Schindler, U., Huber, R., Schumacher, S., Koppe, R., *et al.* (2023). PANGAEA - Data Publisher for Earth & Environmental Science. *Sci Data*, 10, 347.

Fish trawl surveys. (2025). . Available at: https://www.ices.dk/data/dataset-collections/Pages/Fish-trawl-survey.aspx. Last accessed 30 April 2025.

Fouqueau, L. & Polechová, J. (2024). Eco-evolutionary dynamics in changing environments: integrating theory with data. *Journal of Evolutionary Biology*, 37, 579–587.

Fronhofer, E.A., Corenblit, D., Deshpande, J.N., Govaert, L., Huneman, P., Viard, F., *et al.* (2023). Eco-evolution from deep time to contemporary dynamics: The role of timescales and rate modulators. *Ecology Letters*, 26, S91–S108.

Gardner, J.L., Peters, A., Kearney, M.R., Joseph, L. & Heinsohn, R. (2011). Declining body size: a third universal response to warming? *Trends in Ecology & Evolution*, 26, 285–291.

Genner, M.J., Sims, D.W., Southward, A.J., Budd, G.C., Masterson, P., Mchugh, M., *et al.* (2010). Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Global Change Biology*, 16, 517–527.

GHCN-Daily, Version 3. (2012). Global Historical Climatology Network - Daily (GHCN-Daily), Version 3.

Gibert, J.P., Han, Z.-Y., Wieczynski, D.J., Votzke, S. & Yammine, A. (2022). Feedbacks between size and density determine rapid eco-phenotypic dynamics. *Functional Ecology*, 36, 1668–1680.

Gibert, J.P., Wieczynski, D.J., Han, Z.-Y. & Yammine, A. (2023). Rapid eco-phenotypic feedback and the temperature response of biomass dynamics. *Ecology and Evolution*, 13, e9685.

Gillooly, J.F. (2000). Effect of body size and temperature on generation time in zooplankton. *Journal of Plankton Research*, 22, 241–251.

Govaert, L., Fronhofer, E.A., Lion, S., Eizaguirre, C., Bonte, D., Egas, M., *et al.* (2019). Eco-evolutionary feedbacks—Theoretical models and perspectives. *Functional Ecology*, 33, 13–30.

Govaert, L. & Klauschies, T. (2024). Eco-phenotypic feedback loops differ in multistressor environments. *Ecology*, e4480, e4480.

Han, Z.-Y., Wieczynski, D.J., Yammine, A. & Gibert, J.P. (2023). Temperature and nutrients drive eco-phenotypic dynamics in a microbial food web. *Proceedings of the Royal Society B: Biological Sciences*, 290, 20222263.

Hsieh, C., Glaser, S.M., Lucas, A.J. & Sugihara, G. (2005). Distinguishing random environmental fluctuations from ecological catastrophes for the North Pacific Ocean. *Nature*, 435, 336–340.

Huntley, M.E. (1992). Temperature-Dependent Production of Marine Copepods: A Global Synthesis. *The American Naturalist*, 140, 201–242.

Kaitala, V. (2021). Ecological and evolutionary dynamics under coloured environmental variation. *Trends in ecology & evolution*, 24, 555–563.

Karakoç, C., Clark, A.T. & Chatzinotas, A. (2020). Diversity and coexistence are influenced by time-dependent species interactions in a predator–prey system. *Ecology Letters*, 23, 983–993.

Litchman, E. (2000). Growth rates of phytoplankton under fluctuating light. *Freshwater Biology*, 44, 223–235.

Loreau, M., Jarne, P. & Martiny, J.B.H. (2023). Opportunities to advance the synthesis of ecology and evolution. *Ecology Letters*, 26, S11–S15.

Magnuson, J., Carpenter, S. & Stanley, E. (2023a). North Temperate Lakes LTER: Phytoplankton - Trout Lake Area 1984 - 2006.

Magnuson, J., Carpenter, S. & Stanley, E. (2024a). North Temperate Lakes LTER: Zooplankton - Madison Lakes Area 1997 - current.

Magnuson, J.J., Carpenter, S.R. & Stanley, E.H. (2022). North Temperate Lakes LTER: Phytoplankton - Madison Lakes Area 1995 - current.

Magnuson, J.J., Carpenter, S.R. & Stanley, E.H. (2023b). North Temperate Lakes LTER: Zooplankton - Trout Lake Area 1982 - current.

Magnuson, J.J., Carpenter, S.R. & Stanley, E.H. (2024b). North Temperate Lakes LTER: Fish Abundance 1981 - current.

Magnuson, J.J., Carpenter, S.R. & Stanley, E.H. (2024c). North Temperate Lakes LTER: Fish Lengths and Weights 1981 - current.

Malerba, M.E., White, C.R. & Marshall, D.J. (2018). Eco-energetic consequences of evolutionary shifts in body size. *Ecology Letters*, 21, 54–62.

Martins, I.S., Schrodt, F., Blowes, S.A., Bates, A.E., Bjorkman, A.D., Brambilla, V., *et al.* (2023). 0. Widespread shifts in body size within populations and assemblages. *Science*, 381, 1067–1071.

Merckx, T., Souffreau, C., Kaiser, A., Baardsen, L.F., Backeljau, T., Bonte, D., *et al.* (2018). Body-size shifts in aquatic and terrestrial urban communities. *Nature*, 558, 113–116.

Michener, W., Vieglais, D., Vision, T., Kunze, J., Cruse, P. & Janée, G. (2011). DataONE: Data Observation Network for Earth - Preserving Data and Enabling Innovation in the Biological and Environmental Sciences. *D-Lib Magazine*, 17, 3.

Mohsin, T. & Gough, W.A. (2010). Trend analysis of long-term temperature time series in the Greater Toronto Area (GTA). *Theor Appl Climatol*, 101, 311–327.

Nejad, E.S., Cloern, J. & Schraga, T. (2017). Phytoplankton Species Composition, Abundance and Cell Size in San Francisco Bay: Microscopic Analyses of USGS Samples Collected 1992-2014.

Pantel, J.H. & Becks, L. (2023). Statistical methods to identify mechanisms in studies of eco-evolutionary dynamics. *Trends in Ecology & Evolution*, 38, 760–772.

Pelletier, F., Garant, D. & Hendry, A. p. (2009). Eco-evolutionary dynamics. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 364, 1483–1489.

Pinsky, M.L., Hillebrand, H., Chase, J.M., Antão, L.H., Hirt, M.R., Brose, U., *et al.* (2025). Warming and cooling catalyse widespread temporal turnover in biodiversity. *Nature*, 1–5.

Sebastian, P., Stibor, H., Berger, S. & Diehl, S. (2012). Effects of water temperature and mixed layer depth on zooplankton body size. *Mar Biol*, 159, 2431–2440.

Sheridan, J.A. & Bickford, D. (2011). Shrinking body size as an ecological response to climate change. *Nature Clim Change*, 1, 401–406.

Sugihara, G., May, R., Ye, H., Hsieh, C., Deyle, E., Fogarty, M., *et al.* (2012). Detecting causality in complex ecosystems. *Science*, 338, 496–500.

Sugihara, G. & May, R.M. (1990). Nonlinear forecasting as a way of distinguishing chaos from measurement error in time series. *Nature*, 344, 734–741.

Terry, J.C.D., O'Sullivan, J.D. & Rossberg, A.G. (2022). No pervasive relationship between species size and local abundance trends. *Nat Ecol Evol*, 6, 140–144.

Thrall, P.H. & Blanc, S. (2023). Unravelling eco-evolutionary dynamics: Understanding adaptation to global change. *Ecology Letters*, 26, S3–S4.

Tong, Y., Feng, L., Wang, X., Pi, X., Xu, W. & Woolway, R.I. (2023). Global lakes are warming slower than surface air temperature due to accelerated evaporation. *Nat Water*, 1, 929–940.

Visser, M.E. (2008). Keeping up with a warming world; assessing the rate of adaptation to climate change. *Proceedings of the Royal Society B: Biological Sciences*, 275, 649–659.

Walsh, B.S., Parratt, S.R., Hoffmann, A.A., Atkinson, D., Snook, R.R., Bretman, A., *et al.* (2019). The Impact of Climate Change on Fertility. *Trends in Ecology & Evolution*, 34, 249–259.

Warzecha, D., Diekötter, T., Wolters, V. & Jauker, F. (2016). Intraspecific body size increases with habitat fragmentation in wild bee pollinators. *Landscape Ecol*, 31, 1449–1455.

Ye, L., Chang, C.-W., Matsuzaki, S.S., Takamura, N., Widdicombe, C.E. & Hsieh, C. (2019). Functional diversity promotes phytoplankton resource use efficiency. *Journal of Ecology*, 107, 2353–2363.

Zamorano, L.S., Gompert, Z., Fronhofer, E.A., Feder, J.L. & Nosil, P. (2023). A stabilizing eco-evolutionary feedback loop in the wild. *Current Biology*, 33, 3272-3278.e3.

Zastavniouk, C., Weir, L.K. & Fraser, D.J. (2017). The evolutionary consequences of habitat fragmentation: Body morphology and coloration differentiation among brook trout populations of varying size. *Ecology and Evolution*, 7, 6850–6862.

Zeuss, D., Brunzel, S. & Brandl, R. (2017). Environmental drivers of voltinism and body size in insect assemblages across Europe. *Global Ecology and Biogeography*, 26, 154–165.

Zhao, Q., Van den Brink, P.J., Xu, C., Wang, S., Clark, A.T., Karakoç, C., *et al.* (2023). Relationships of temperature and biodiversity with stability of natural aquatic food webs. *Nat Commun*, 14, 3507.