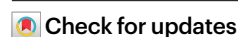


Meta-analysis reveals less sensitivity of non-native animals than natives to extreme weather worldwide

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Extreme weather events (EWEs; for example, heatwaves, cold spells, storms, floods and droughts) and non-native species invasions are two major threats to global biodiversity and are increasing in both frequency and consequences. Here we synthesize 443 studies and apply multilevel mixed-effects metaregression analyses to compare the responses of 187 non-native and 1,852 native animal species across terrestrial, freshwater and marine ecosystems to different types of EWE. Our results show that marine animals, regardless of whether they are non-native or native, are overall insensitive to EWEs, except for negative effects of heatwaves on native mollusks, corals and anemone. By contrast, terrestrial and freshwater non-native animals are only adversely affected by heatwaves and storms, respectively, whereas native animals negatively respond to heatwaves, cold spells and droughts in terrestrial ecosystems and are vulnerable to most EWEs except cold spells in freshwater ecosystems. On average, non-native animals displayed low abundance in terrestrial ecosystems, and decreased body condition and life history traits in freshwater ecosystems, whereas native animals displayed declines in body condition, life history traits, abundance, distribution and recovery in terrestrial ecosystems, and community structure in freshwater ecosystems. By identifying areas with high overlap between EWEs and EWE-tolerant non-native species, we also provide locations where native biodiversity might be adversely affected by their joint effects and where EWEs might facilitate the establishment and/or spread of non-native species under continuing global change.

Climate change and invasive species are two major threats to global biodiversity^{1,2}. Understanding how climate change influences invasions of non-native species is crucial for mitigating their joint impacts in the context of accelerating global change³. In addition to gradual shifts in temperature and precipitation, scientists have recognized that the increasing frequency and magnitude of extreme weather events (EWEs), such as heatwaves, cold spells, storms, floods and droughts⁴,

can result in even greater biological consequences than changes to climate means⁵. Comparison of the responses of native and non-native species to EWEs is crucial for developing early and effective strategies for native species conservation and non-native species prevention under accelerating EWEs associated with climate change⁶.

Considerable evidence from native species has shown that EWEs can cause declines in population abundances and species richness,

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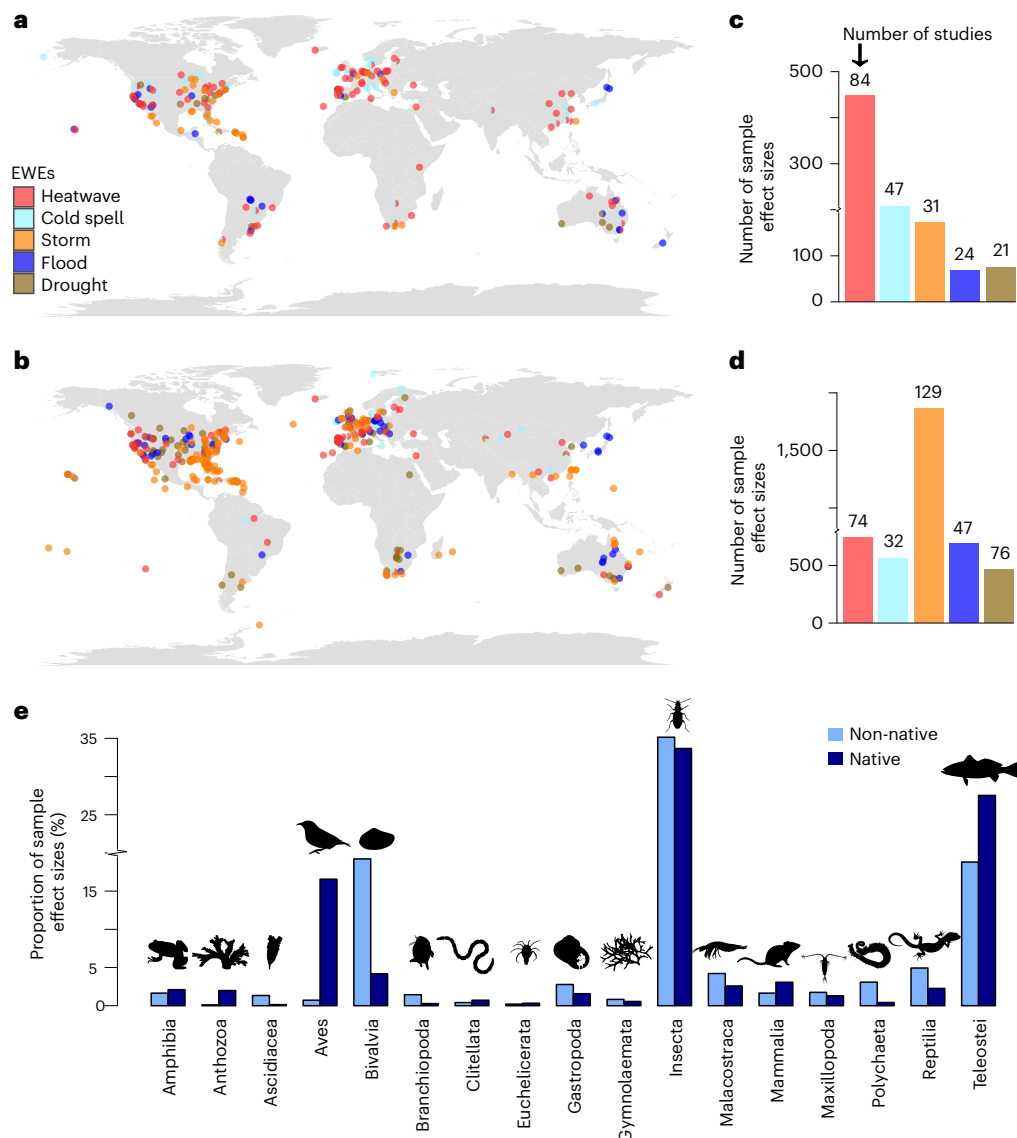


Fig. 1 | Distribution of non-native and native species under EWEs from 443 studies. a–e. Point colours indicate different types of EWE in 235 locations for non-native species (a) and 394 locations for native species (b). The bar chart

shows the number of effect sizes for different EWE groups of non-native (c) and native species (d), and the proportions of sample effect sizes across taxa (e). Animal silhouettes in e were obtained from PhyloPic (www.phylopic.org).

restructure community composition and limit post-event recovery across ecosystems^{7–13}. However, published studies also found that non-native arthropods, mammals, shellfishes and fishes might be relatively tolerant of, or even respond positively to EWEs^{14–17}. There are several possible mechanisms to explain different responses of non-native and native species to EWEs¹⁸. First, EWEs often result in considerable mortality of native species and could thus create more vacant niches to facilitate non-native species invasions^{19,20}. For example, severe drought events decreased native invertebrates and fishes by increasing water salinity, facilitating the establishment of non-native salt-tolerant counterparts^{14,15}. Second, invaders can have more rapid growth rates, stronger competitive abilities, higher phenotypic plasticity, broader tolerance of disturbance and quicker recovery and proliferation than natives^{21–24}. For example, the abundance of most native fish in the Rio Minho estuary, Portugal, declined but abundance of non-native fish increased after extreme droughts and floods, and thus the fish assemblage there was dominated by a few invasive fish species after extreme weather events²⁵. Non-native mesozooplankton species exhibit higher flexibility to marine heatwaves than native species in the

Sevastopol Bay²⁶. Non-native species showed less susceptibility and recovered more quickly than native species in the marine epibenthic fouling community of Bodega Harbor, California, USA²⁷. Despite these striking case studies, a thorough understanding of the general effect of EWEs on non-native and native species across ecosystems, types of EWE and multiple taxonomic groups is still lacking, impeding forecasts of the responses of non-native species to climate change and their joint impacts on native species. It is critical to fill this literature gap because resources for managing and mitigating biological invasions and climate change are limited. Thus, it is crucial to identify the most affected regions and problematic taxa so that those resources are targeted properly.

Here we applied a multilevel mixed-effects metaregression to conduct a global synthesis of non-native and native animal responses to EWEs (Supplementary Fig. 1). These species spanned terrestrial, freshwater (mammals, birds, amphibians, reptiles, fish and invertebrates) and marine ecosystems (surface and benthic fishes and benthic invertebrates). Each measured effect size was assigned to one of eight major response categories: physiology, body condition, behaviour,

life history traits, abundance, distribution, community structure and recovery after EWEs. Our analyses covered five main types of EWEs: heatwaves, cold spells, storms, floods and droughts. Furthermore, on the basis of the results of our meta-analyses, we quantified the spatial overlap between the distributions of EWE-tolerant non-native species and the EWE hotspots. These overlap analyses should identify locations where native biodiversity might be adversely affected by the joint effects of non-native species and EWEs, and where EWEs might facilitate the future establishment and/or spread of non-native species.

Results

Overall EWE distributions

Across the globe, there were a total of 973 measured effect sizes from 177 peer-reviewed studies across 187 non-native species and 4,330 measured effect sizes from 335 peer-reviewed studies across 1,852 native species (Supplementary Fig. 1). These reported studies on the effects of EWEs on animals were mainly distributed in North America and Europe, and sporadically distributed in South America, southern Africa, East Asia and southeast Australia (Fig. 1a,b). Eighty four percent of studies on non-native species (149/177) and 95% of studies on native species (317/335) focused on responses to only one type of EWE (Fig. 1c,d and Supplementary Data 1). Overall, our analyses included effect sizes of EWEs on non-native animals and native animals spanning 6, 7 and 10 classes of terrestrial, freshwater and marine organisms, respectively (Fig. 1e) and three orders of magnitude in body size (for example, smallest mean body size, Insecta: 0.81 ± 0.22 mm; largest Mammalia: $1,531.33 \pm 211.00$ mm).

Species can differ in their exposure to EWEs that may influence selection for EWE tolerance. We assessed exposure differences by comparing the average magnitude of the EWEs within the geographic ranges of each native and non-native species in our database. We found limited evidence that non-native and native species experience significantly different magnitudes of EWE exposures (Supplementary Fig. 2). We also found little evidence in our samples that ecosystem types differed significantly in their magnitudes of EWEs (Supplementary Fig. 2), except that oceans have more days of heatwaves and cold spells than terrestrial and freshwater ecosystems (Supplementary Fig. 2).

Responses of non-native and native animals to EWEs

Overall, we found that non-native species had 24.8% positive, 31.8% negative and 43.4% neutral responses (confidence intervals (CIs) crossing zero) to EWEs. Native species had 12.7% positive, 20.5% negative and 66.8% neutral responses to EWEs. Both non-native and native species exhibited positive, negative and neutral responses to each type of EWE (Fig. 2). Further multilevel mixed-effects metaregression models showed that non-native species only responded negatively to heatwaves in terrestrial ecosystems, whereas native species were adversely affected by heatwaves, cold spells and droughts (Fig. 3a). In freshwater ecosystems, non-native species only responded negatively to storms, but native species responded negatively to heatwaves, storms, floods and droughts. We even observed positive effects of heatwaves and cold spells on freshwater non-native species (Fig. 3b). Marine animal species overall were insensitive to EWEs, regardless of whether they were non-native or native (Fig. 3c). Egger's test indicated limited evidence for publication bias associated with the overall responses of non-native and native animals to EWEs (Supplementary Table 1). In addition, the omnibus Wald-type test showed a good fit of the model to the data (Supplementary Table 4). Hence, the greater tolerance of non-native animals than natives to EWEs does not appear to be artefactual.

To assess whether the responses of non-native and native species were dependent on certain taxa or biogeographic realms (Nearctic, Neotropic, Palaearctic, Indomalayan, Afrotropic and Australasian in terrestrial and freshwater ecosystems; Agulhas, Cold Temperate

Northeast Pacific, Lusitanian, Northern European Seas, Tropical North-western Atlantic, Warm Temperate Northeast Pacific and Warm Temperate Northwest Atlantic in marine ecosystems), we reconducted the analyses above including taxonomic group and realm as independent variables interacting with non-native/native status (Supplementary Figs. 3 and 4). Analyses across taxonomic groups (Supplementary Fig. 3) and biogeographic realms (Supplementary Fig. 4) produced similar results as the overall analyses. One insight revealed from this separate analysis was that the negative response of terrestrial non-native animals to heatwaves was only a product of the sensitivity of non-native insects (mean effect size: -1.188 , $P < 0.001$, Supplementary Fig. 3).

Among response variables, in terrestrial ecosystems, EWEs only had negative effects on abundance of non-native species, but adversely affected body condition, life history traits, abundance, distribution and post-event recovery of native species (Fig. 4a). In freshwater ecosystems, EWEs had negative effects on body condition and life history traits of non-native species, and on community structure of native species (Fig. 4b). Across terrestrial and freshwater ecosystems, we did not observe negative effects of EWEs on the distribution, abundance (except terrestrial insects: mean effect size -0.844 , $P = 0.004$), community structure or recovery of non-native animals (Fig. 4a,b), which thus appear to maintain population stability and community structure during and after EWEs. We even observed a positive response of non-native species' physiology, behaviour and recovery to EWEs in terrestrial and freshwater ecosystems (Fig. 4a,b). In marine ecosystems, non-native species presented overall positive responses to EWEs except for body condition and life history traits (Fig. 4c).

Overlap between non-native species and EWEs

We further conducted spatial overlap analyses between EWE hotspots and suitable habitat for non-native animals to identify where native species might be particularly vulnerable to the combined effects of EWEs and non-native species. To do so, we first applied species distribution modelling to predict those grids with suitable areas for establishment of non-native animals and overlaid these grids with maps of EWE hotspots (see more details in Supplementary Methods). We then calculated the net effect of each non-native animal to EWEs in each overlapped grid as the proportions of positive plus neutral responses minus negative response on the basis of the sample effect sizes in the meta-analyses. The accumulative net effect for each grid was obtained to reflect the overall tolerance of all potential non-native species to EWEs.

Our analyses show that overlapping areas of highly EWE-tolerant non-native species and EWEs hotspots are generally distributed in mid-to-high latitudes, but these patterns did depend on EWE type. For heatwaves, overlapping areas were mainly distributed in mid-latitude regions, including west and east-southern United States, southern Brazil, southern Mediterranean, South Africa, east-southern Asia, south Australia, New Zealand, west-northern coast and islands in the Indian Ocean, and west coast and islands in the Pacific Ocean (Fig. 5a). For cold spells, overlapping areas were mainly distributed in high-latitude regions, including northern areas of the United States and Canada, southern Argentina, northern Europe, western coastal regions of Australia, east coast of the North Atlantic Ocean, south coast of the Baltic Sea and east coast of the Arctic Ocean (Fig. 5b). For storms, overlapping areas were sporadically distributed from low to high latitudes, including Latin America, India, high-latitude European countries (that is, the United Kingdom and Norway), south-western and north-eastern Australia, Northern Atlantic Ocean and the west coast of the Pacific Ocean (Fig. 5c). For floods and droughts, overlapping areas were distributed in mid latitudes of the Mediterranean region, mid-Asia, southern Australia, and East and Southeast Asia. In South America, overlap was associated with floods in western Amazon and southern Brazil but with droughts in northern Amazon and southern Argentina. In Africa, overlap coincided with floods in the middle of Africa but with droughts in northern Africa (Fig. 5d,e).

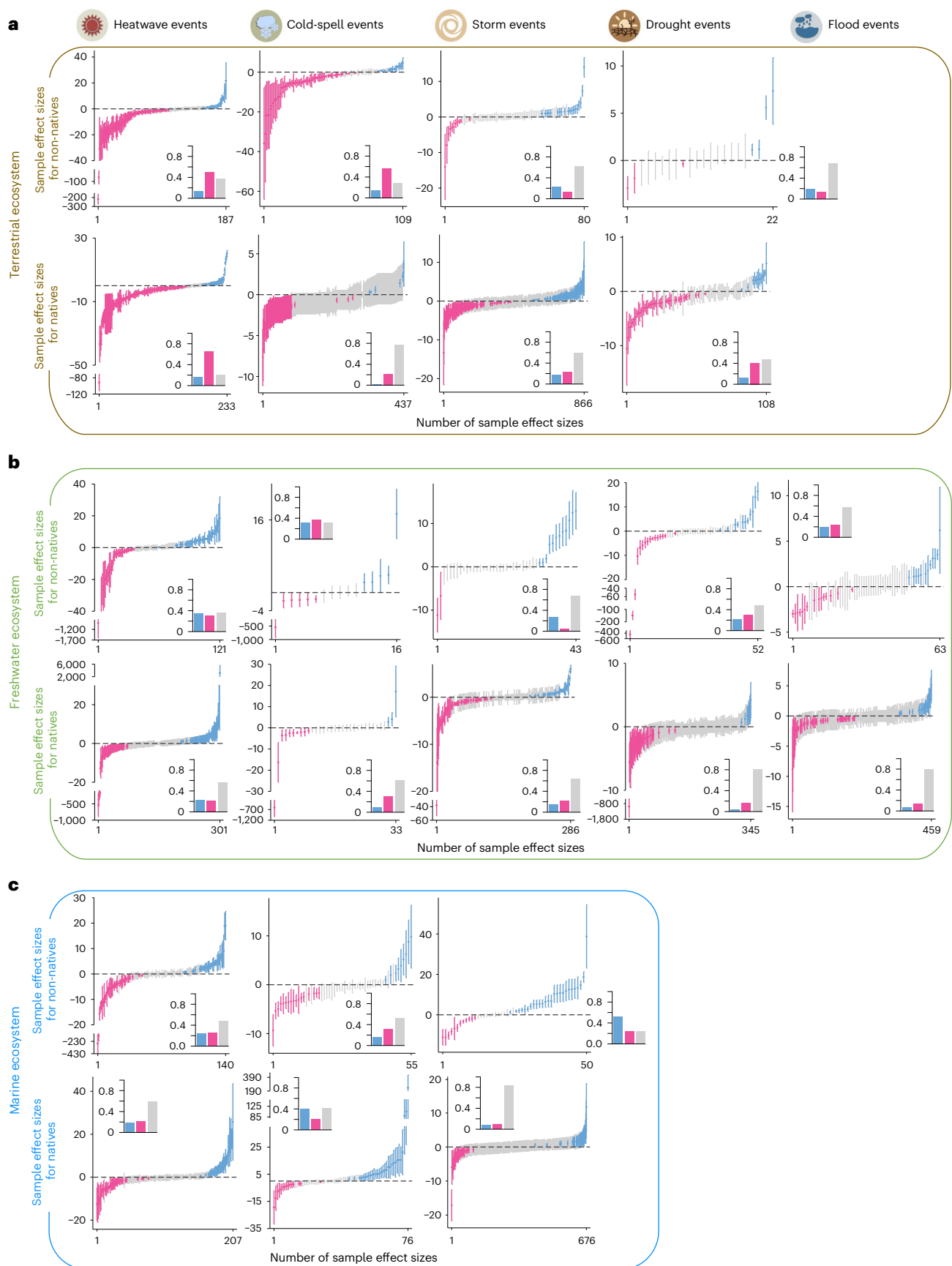


Fig. 2 | Sample effect sizes of non-native and native species in responding to EWEs. a–c, Sample effect sizes in terrestrial (a), freshwater (b) and marine (c) ecosystems. The horizontal dashed lines represent the position where the sample

effect size is zero. The heights of barplots are relative proportions of positive (blue), negative (pink) and neutral (grey) (CIs crossing zero) effect sizes, and were standardized, ranging from 0 to 1.

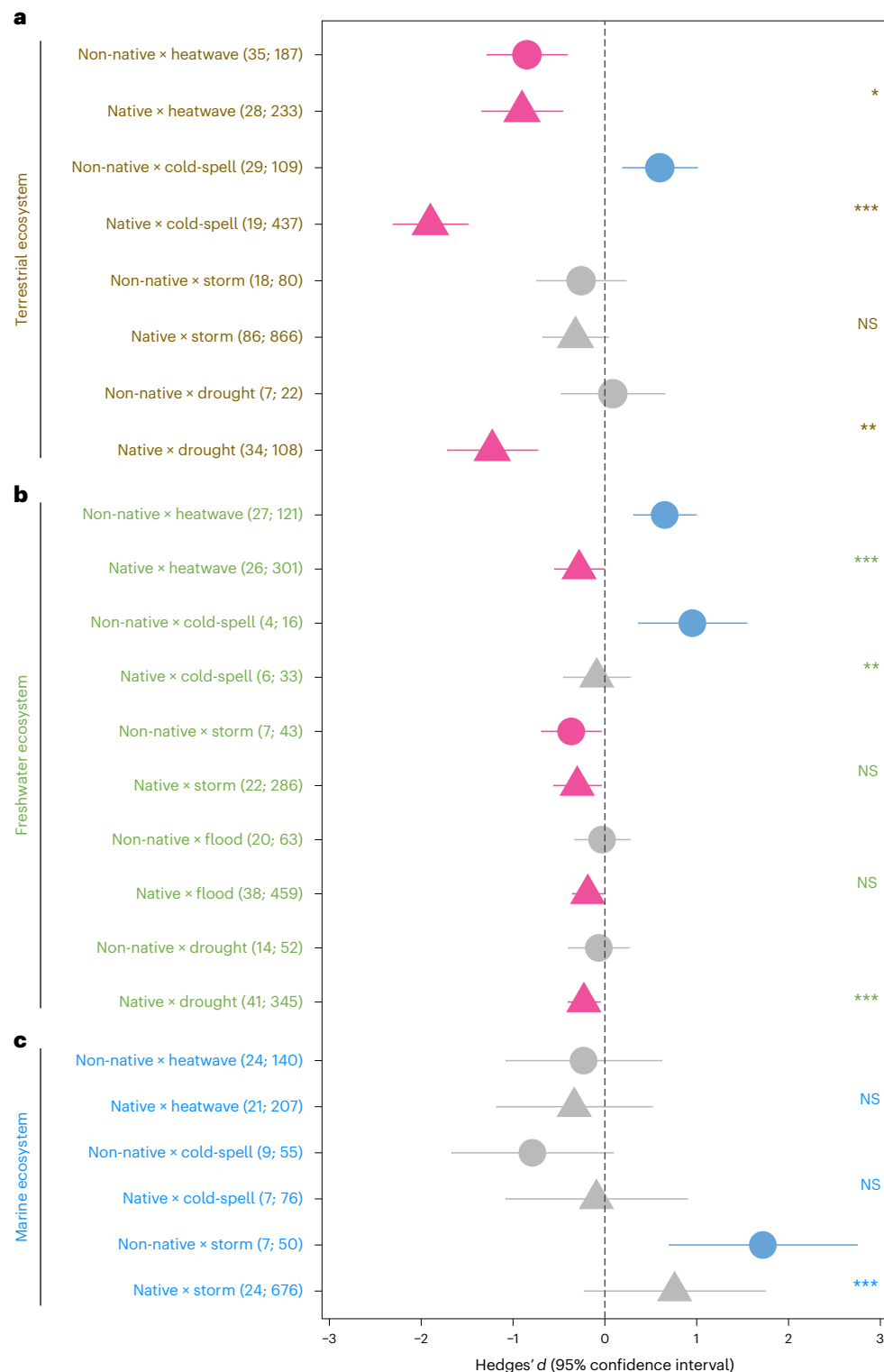


Fig. 3 | A comparison of non-native (circle) and native species (triangle) responses to five different types of EWE. a–c, Effect sizes (Hedges' d) for non-native and native species' responses to heatwave, cold-spell, storm, flood and drought events in terrestrial (a), freshwater (b) and marine (c) environments, estimated from metafor. Error bars are 95% CIs. A Wald-type test was used to detect whether a mean effect size estimate was significant when the 95% CI did not encompass zero. In a, P values of non-native species responses to EWEs were: heatwave (0.0001), cold spell (0.004), storm (0.298) and drought (0.763); P values of native species responses to EWEs were: heatwave (<0.0001), cold spell (<0.0001), storm (0.079) and drought (<0.0001). In b, P values of non-native species responses to EWEs were: heatwave (0.0002), cold spell (0.002), storm (0.027), flood (0.842) and drought (0.698); P values of native species

responses to EWEs were: heatwave (0.042), cold spell (0.635), storm (0.023), flood (0.032) and drought (0.011). In c, P values of non-native species responses to EWEs were: heatwave (0.592), cold spell (0.079) and storm (0.001); P values of native species responses to EWEs were: heatwave (0.442), cold spell (0.856) and storm (0.132). Numbers in parentheses represent the number of studies and measured effect sizes, respectively. Blue, significantly positive mean effect sizes; pink, significantly negative mean effect sizes; grey, non-significant mean effect sizes. The asterisks and 'NS' indicate significant and non-significant differences, respectively, between non-native and native species to the particular EWE; * P < 0.05, ** P < 0.01, *** P < 0.001, performed using an omnibus test (Supplementary Table 2). Multiple comparisons were not performed in data analyses. The two-sided P value was used to judge significance.

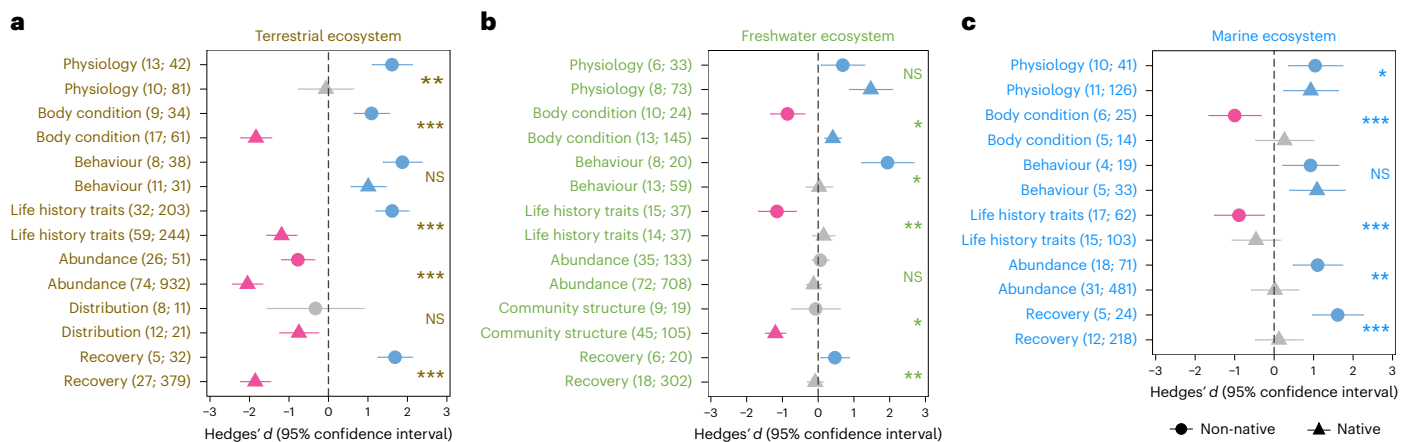


Fig. 4 | A comparison of non-native (circle) and native (triangle) species responses to EWEs for eight response variables. a–c, Effect sizes (Hedges' d) for the non-native and native species responding to EWEs in terrestrial (a), freshwater (b) and marine (c) ecosystems, estimated from metafor. Error bars are 95% CIs. A Wald-type test was used to detect whether a mean effect size estimate was significant when the 95% CI did not encompass zero. In a, P values of non-native species response variables to EWEs were: physiology (<0.0001), body condition (<0.0001), behaviour (<0.0001), life history traits (<0.0001), abundance (0.0003), distribution (0.597) and recovery (<0.0001); P values of native species response variables to EWEs were: physiology (0.854), body condition (<0.0001), behaviour (<0.0001), life history traits (<0.0001), abundance (<0.0001), distribution (0.003) and recovery (<0.0001). In b, P values of non-native species response variables to EWEs were: physiology (0.026), body condition (0.0004), behaviour (<0.0001), life history traits (<0.0001), abundance (0.630), community structure (0.839) and recovery (0.021); P values of native species response variables to EWEs were: physiology (<0.0001), body

condition (0.0004), behaviour (0.882), life history traits (0.337), abundance (0.224), community structure (<0.0001) and recovery (0.463). In c, P values of non-native species response variables to EWEs were: physiology (0.003), body condition (0.003), behaviour (0.011), life history traits (0.005), abundance (0.0005) and recovery (<0.0001); P values of native species response variables to EWEs were: physiology (0.009), body condition (0.487), behaviour (0.003), life history traits (0.143), abundance (0.950) and recovery (0.690). Numbers in parentheses represent the number of studies and measured effect sizes, respectively. Blue, significantly positive mean effect sizes; pink, significantly negative mean effect sizes; grey, non-significant mean effect sizes. The asterisks and 'NS' indicate significant and non-significant differences, respectively, between non-native and native species in their responses to EWEs; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, performed using an omnibus test (Supplementary Table 3). Multiple comparisons were not performed in data analyses. The two-sided P value was used to judge significance.

Our results were robust to different criteria used to define overlap hot-spots (Supplementary Fig. 5, see details in Supplementary Methods).

Discussion

The present study provided a comparative evaluation of the responses of non-native and native animals to historical EWEs across taxa and ecosystems at the global scale. Although there were both 'winners' and 'losers' across both non-native and native species and ecosystems (Fig. 2), proportionally there were more positive responses of non-native than native animals to EWEs, making the mean response to EWEs less negative for non-native than for native species. Our further meta-analyses that controlled for spatial and taxonomic pseudoreplication generally showed that non-native species are less sensitive to most EWEs than their native counterparts, especially in terrestrial and freshwater ecosystems. This high tolerance of non-native species to EWEs compared with native species particularly represented a strong capacity of non-native species to maintain population stability after EWEs across ecosystems. We found limited evidence of publication bias associated with the overall responses of non-native and native animals to EWEs. However, there was detectable publication bias for non-native animal responses to terrestrial cold spells, and for native animal responses to terrestrial heatwaves and cold spells, and freshwater floods and droughts (Supplementary Table 1), which is a common phenomenon in meta-analyses when disciplines are partial to studying certain effects²⁸.

There are several possible explanations for why non-native animals tend to be less sensitive to most EWEs than native species within the same taxonomic class. First, many non-native species exhibit rapid growth rates, long spawning seasons, short longevities, high competitive abilities, rapid population recolonization and trophic preference for detritus that could help them take advantage of limited resources and maintain population sizes during and after EWEs^{18,29,30}. Non-native

species also often have higher plasticity than native species^{18,31,32}. For example, the abundance of the invasive South American tomato pinworm was tolerant of acute and chronic temperature stress because of high thermal plasticity in invaded ranges³³. As another example, an invasive prawn showed higher plasticity of upper thermal limits than native prawns and was thus less vulnerable to extreme thermal events³⁴. Finally, the high propagule pressure and meta-population structure (that is, connectivity) of many non-native species³⁵ often make their populations more resilient to the adverse effects of EWEs than native species^{18,36}. Indeed, population-level response variables of non-native species, such as their abundance, distribution and recovery, were generally insensitive to EWEs (Fig. 4). Nevertheless, we also observed some negative responses of terrestrial non-native animals to heatwaves, particularly for Insecta (Fig. 3 and Supplementary Fig. 3). Additional analyses further showed that heatwaves could negatively impact insect body size, development time, growth rate, longevity, reproduction and survival rate (Supplementary Table 5). These findings support a previous insect study revealing that life history plasticity was weak in insect responses to extreme temperatures³⁷.

Freshwater non-native animals responded positively to heatwaves and cold spells, consistent with some previous studies on freshwater crustaceans³⁸ and mussels^{39,40}. Given that 90.8% (109/120) of non-native freshwater animals in heatwave studies are warm-adapted and cold-adapted fishes and invertebrates (including Bivalvia, Gastropoda and Malacostraca) introduced through aquaculture (Supplementary Data 1)⁴¹, one potential explanation for the positive response of freshwater non-native animals to heatwaves and cold spells is ecological memory theory⁴². This theory predicts that adaptations to environmental change are positively related to the past disturbance events experienced by a species^{43,44}. Future studies should test whether native species exposed to more severe historical EWEs are indeed more tolerant of EWEs.

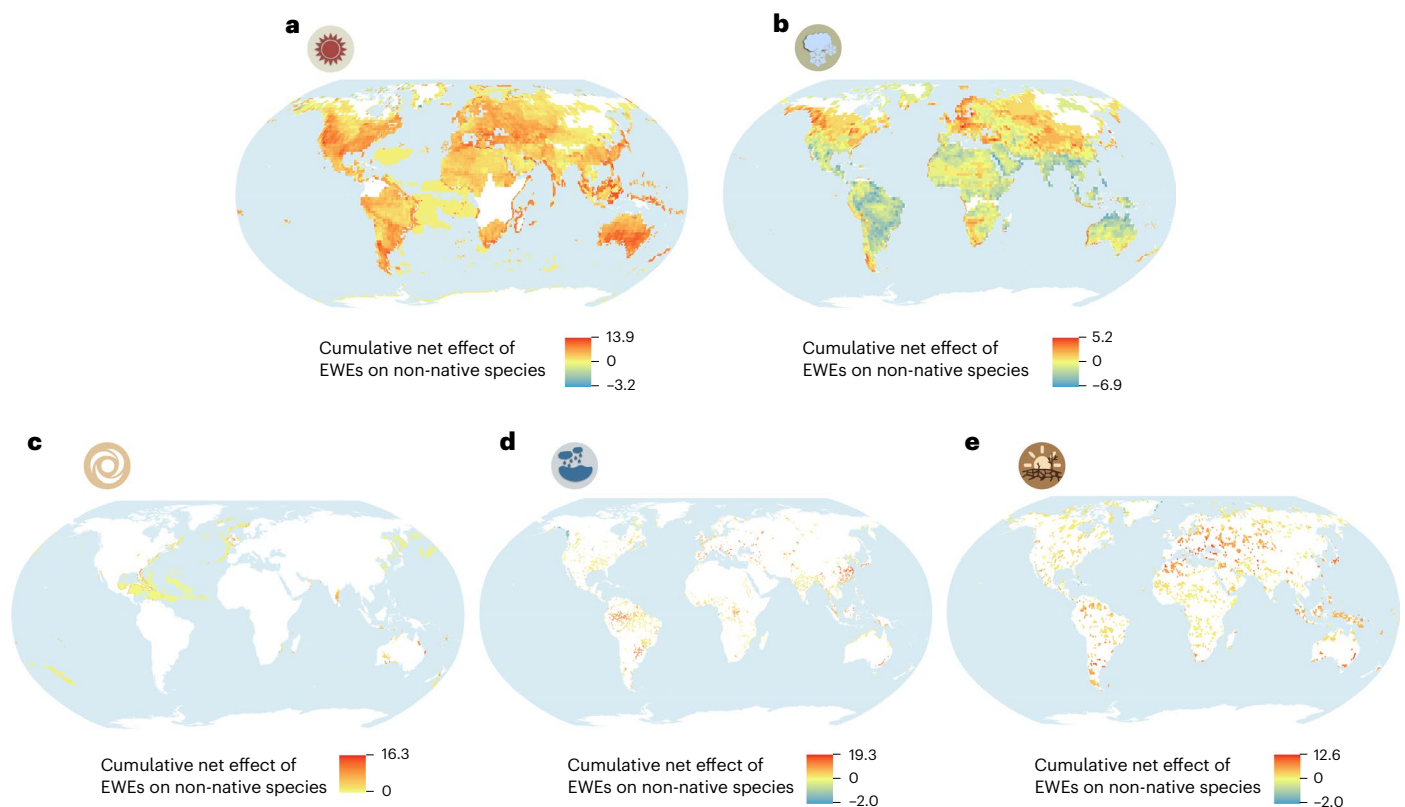


Fig. 5 | Overlapping areas between potential distributions of non-native species that are tolerant of EWEs and EWE hotspots worldwide. a–e. Global maps showing the accumulative net effects of predicted non-native animals in areas with the top 20% occurrences of heatwaves (a), cold spells (b), storms (c), 100-yr floods (d) and extreme droughts (SPI ≤ -1.5) (e) at 5-arcmin resolution. Higher values indicate greater combined risks of invasions and EWEs, and negative values mean that there are more negative responses of non-native species to EWEs than positive and neutral responses in those areas. The 'white' colour in the maps indicates land areas without overlaps between predicted distributions of non-native species and EWEs. Taxonomic information for animals in each corresponding EWE type used in the overlap analyses: for heatwaves, terrestrial (Amphibia, Aves, Eucheilicerata and Insecta), freshwater

(Bivalvia, Branchiopoda, Gastropoda, Malacostraca and Teleostei) and marine (Asciidiacea, Bivalvia, Gastropoda, Gymnolaemata, Malacostraca, Maxillopoda, Polychaeta and Teleostei) species were included; for cold spells, terrestrial (Amphibia, Insecta, Mammalia and Reptilia), freshwater (Gastropoda and Teleostei) and marine (Bivalvia, Malacostraca, Maxillopoda and Polychaeta) species were included; for storms, terrestrial (Amphibia, Aves, Insecta, Mammalia and Reptilia), freshwater (Bivalvia, Clitellata, Gastropoda and Teleostei) and marine (Malacostraca and Teleostei) species were included; for floods, terrestrial (Amphibia and Aves) and freshwater (Bivalvia, Insecta, Malacostraca and Teleostei) species were included; for droughts, terrestrial (Insecta) and freshwater (Bivalvia, Gastropoda, Malacostraca and Teleostei) species were included.

Interestingly, in contrast to terrestrial and freshwater species, both non-native and native marine species were insensitive to EWEs. Importantly, this finding was not a product of the lower magnitude of EWEs in marine than in terrestrial and freshwater environments, as we observed few differences in the magnitude of EWEs among ecosystem types within the geographic ranges of each native and non-native species in our meta-analysis (Supplementary Fig. 2). The only difference we did observe suggested that oceans had significantly more days experiencing heatwaves and cold spells than terrestrial and freshwater ecosystems (Supplementary Fig. 2). The tolerance of non-native marine species to EWEs supports previous findings that marine invaders were generally insensitive to ocean heatwaves^{26,27}, cold spells^{45,46} and storms^{16,47}. For instance, non-native bryozoans and crustaceans maintained their community composition and population abundance, respectively, in response to marine heatwaves^{26,27}. In contrast, it has been reported extensively that marine heatwaves are pervasive stressors to native ocean species, especially anemones and corals (Anthozoa)^{7,48}. Indeed, we observed a negative response of native Anthozoa to marine heatwaves (mean effect size -1.632 , $P < 0.001$), consistent with past studies^{7,48}. In addition, our results support a recent review on the negative response of benthic invertebrates (that is, Bivalvia) to marine heatwaves (mean effect size -0.869 , $P = 0.028$), which was possibly due to their limited abilities

to disperse to more suitable habitats⁷. Regarding the insensitivity of marine native and non-native species to cold spells, Maxillopoda and Polychaeta dominated the effect sizes for this test and the literature reports that these taxa tend to be cold-adapted species and thus have high performance at low temperatures^{45,46}. Finally, we found that marine non-native and native species were also insensitive to storm events. Teleostei and Bivalvia dominated the effect sizes for this test. Our finding is consistent with previous studies that showed that fishes and Bivalvia were insensitive to storms, possibly because they are either mobile enough⁴⁹ or use ocean currents⁵⁰ to seek refuge during storms, respectively.

Our global analysis of spatial overlap between non-native species and EWE hotspots identified several vulnerable areas in mid-to-high latitudes including North America, Europe, Oceania, temperate Asia inland, East and Southeast Asia, South America and Africa and marine regions in low-to-mid latitude areas of the Atlantic Ocean, west-northern coast of the Indian Ocean, south coast of the Baltic Sea, east coast of the Arctic Ocean and west coast of the Pacific Ocean where native species might face joint impacts of invasive species and EWEs. Although the invasion hotspots we identified were only based on habitat suitability for establishment, we found that these predicted hotspots have also been reported as areas with frequent non-native species introductions^{35,51}, which imply a potentially high overall invasion

risk in these regions. Furthermore, our identified EWE epicentres have also been validated by several predictive models^{52–55}.

Our present study also provided some useful directions for future studies. First, this study focused on the direct effect of EWEs to native and non-native species, but EWEs can also have indirect impacts on biota. For example, prolonged heatwaves can promote lethal hypoxic/anoxic conditions⁵⁶. EWEs can cause severe population declines by damaging habitat-forming species, such as corals, forests, mangroves and mussel⁷, or by removing key prey species from food webs⁵⁷. Furthermore, for marine species, the effects of EWEs might be more severe in intertidal and shallow subtidal zones than in deeper/offshore marine waters owing to increased exposure to EWEs. Indeed, we found that non-native species in deeper water (species recorded maximum depth >200 m) exhibited positive responses to EWEs (mean effect size 2.262, $P = 0.009$). However, we did not detect the negative effect of EWEs on either non-native or native species in intertidal and shallow subtidal zones. As we only have 41 samples (3.3% of all marine species samples) for deeper/offshore species, a larger sample size would be useful to more rigorously compare the responses of nearshore vs offshore species. Finally, the invasion and EWE overlap areas in the present study were based on non-native animal tolerance to EWEs. We acknowledge that some EWE-sensitive non-native species might still have the potential to exert ecological forces on existing ecosystems. However, under the limited resources that can be used to manage biological invasions and climate change, we suggest that future studies should prioritize these less-sensitive animals in locations of overlap so that timely mitigation strategies can be implemented if native species exhibit declines associated with biological invasions and intensified EWEs driven by global change. Our present analyses could facilitate early prevention schemes against biological invasions and climate change globally and improve the development of sustainable policies in the era of global change.

Methods

Literature search

We conducted a systematic literature search on ISI Web of Science (all databases) and Scopus to collect published papers from the year 1864 to 24 April 2023. The following search terms were entered into the 'Topic' field in ISI Web of Science and in 'All fields' for Scopus: ('storm' OR 'hurricane' OR 'cyclone' OR 'typhoon' OR 'tornado' OR 'wildfire' OR 'extreme snow' OR 'extreme ice' OR 'extreme heat' OR 'heat wave' OR 'extreme high temperature' OR 'extreme cold' OR 'cold wave' OR 'extreme' OR 'extreme drought' OR 'extreme rainfall' OR 'extreme precipitation' OR 'flood') AND ('abundance' OR 'behaviour' OR 'richness' OR 'reproduction' OR 'mating' OR '*diversity' OR 'composition' OR 'predation' OR 'parasit' OR 'herbivory' OR 'activity' OR 'timing' OR 'physiology' OR 'development' OR 'trophic' OR 'biomass' OR 'survival' OR 'growth') AND ('species' OR 'population' OR 'ecological community' OR 'ecosystem*'). This resulted in a total of 147,212 unique studies that were screened for inclusion in our meta-analysis. We also combined studies from four previous meta-analyses of the animals' responses to EWEs^{8,13,58,59} (Supplementary Fig. 1).

Screening process and data exclusion criteria

First, we screened the title, key words and abstract to determine candidate studies that focused on effects of EWEs on non-native or native species. Review papers and those without quantitative analyses were excluded. We excluded studies on the basis of the following criteria: (1) no statistical comparisons of EWE effects to controls, insufficient information on sample size, mean or variance, or no reporting of the animal species; (2) only lab work simulating the EWE-associated changes in salinity but no direct test of the EWE effects on aquatic or saltmarsh living organisms; (3) intra- or interspecific interactions under changed microclimatic or soil habitats induced by EWEs; (4) sea-level or manipulated water-level rise that resulted in further submergence

or inundation; (5) human burning practices in managed grassland or forests; and (6) comparison of differences in litter or carrion of species along a gradient of EWEs. We excluded these studies because there were either no measured response variables of species to EWEs (2 to 5), or the reported measured variables were only based on the species' litter or carrion but not the living organisms (6). We then divided the studies^{14–16,25–27,38,39,45–47,50,60–490} that passed this screening into those on non-native and native species.

Data extraction and measurable categories of response variables

We extracted sample size, mean and variance values in the control (that is, those samples that did not experience EWEs) and treatment groups (that is, those samples that experienced EWEs) from each study. Particularly, for studies based on successive or long-term observational data, the value at the closest time before EWEs was the control, and the averaged value around the time of EWE was the treatment⁴⁹¹. We only extracted the most extreme EWE level from manipulative experiments testing more than two EWE levels. GetData graph Digitizer (v.2.24) was used to extract values from figures in the studies. We extracted median and interquartile range in boxplots to quantify the mean and deviation values when studies reported statistical results of parametric tests or when the data had been transformed to meet normality in the literature⁴⁹². From each study, we also recorded species name, taxon, ecosystem, type of EWE, coordinates of study/sampling sites and reference information.

We categorized response variables into eight categories. At the population level, categories included life history traits (that is, survival rate, reproduction, longevity, development time, growth rate), abundance (that is, population density or size, capture or encounter rate, number count and relative abundance), distribution (that is, occupancy, home range, spatial distribution, foraging zone, territory size), biodiversity (that is, number of species, richness index, population genetic structure) and recovery (that is, recovery of population abundance and/or community composition after EWEs). At the individual level, categories included physiology (that is, gene expression, immune responses, protein and hormone-related chemical compounds, respiration and critical thermal limits), body condition (that is, body mass and size) and behaviour (that is, activity, dietary, feeding or foraging amount, inter-/intraspecific competition, migration or movement and habitat selection) (Supplementary Table 6). These eight groups were only included in our main analyses if they contained at least 10 effect sizes from multiple studies for each class or biogeographic realm⁴⁹³. The response variables were standardized before the analyses to ensure that all reported responses were in the same direction; that is, larger was always better and smaller worse for each response variable.

Meta-analysis

We used a standardized mean difference with heteroscedastic population variances (SMDH) in the two groups, which is a widely used and robust method to calculate effect sizes⁴⁹⁴. Hedges' d effect sizes were obtained after correcting for sample bias in SMDH using the 'escalc' function in the 'metafor' (v.3.0-2) package⁴⁹⁵. To evaluate responses of mean effect sizes to moderator variables, we ran multi-level mixed-effects metaregression models using the 'rma.mv' function in the 'metafor' (v.3.0-2) package, which allowed us to account for the nested structure and non-independence of observations from a single study. To control for non-independence among variables within a study, we adopted the method used in ref. 28 and set paper ID (a set of numbers used to distinguish different studies) as a random intercept. In addition, we included different taxonomic levels (Class, Order and Family) as a random effect to control for phylogenetic covariance in EWE tolerances among species. We used Family in our main analysis because of its lower Akaike information criterion value than models using Class or Order as random intercept (Supplementary Table 7).

We also included response variable category as a random effect to control for the pseudoreplication issue of different samples among categories of variables. We included interaction between non-native/native status and the occurrence of a given EWE as a fixed effect to test for differences in responses of native and non-native species to EWEs. We considered the mean effect size estimate to be significant when the 95% confidence interval (CI) did not encompass zero. The approximate residual heterogeneity of models was assessed using Cochran's Q (Q_E), and the omnibus Wald-type test (Q_M) was used to assess model performance in explaining the heterogeneity attributed to a given moderator variable⁴⁹⁶. We ran Egger's regression test for publication bias⁴⁹⁷ and an omnibus test to compare the responses of non-native and native species to each EWE⁴⁹⁸.

Sensitivity analyses

Previous studies suggested that sample outliers might influence the results of meta-analyses⁴⁹⁹. To test the robustness of our results to sample outliers, we removed those outliers and re-ran meta-analytic models to check the outcome of mean effect sizes. Outliers were classified as any standardized residual for a study whose absolute value was >3 (ref. 500) and were determined using the 'metaoutliers' function in the 'altmeta' (v.4.1) package⁵⁰¹. Neither the direction nor the significance of mean effect sizes changed when outliers were removed (see details in Supplementary Tables 8 and 9) except for the following: a significant negative response of native species to terrestrial storms became non-significant (Supplementary Table 8), and two significant positive responses (behaviour and life history traits) and one significant negative response (abundance) of native freshwater species to EWEs became non-significant (Supplementary Table 9).

To test whether the overall response to different EWEs was robust across taxa and biogeographic realms (Nearctic, Neotropic, Palaearctic, Afrotropic, Australasian) for terrestrial and freshwater species, and across provinces (Agulhas, Cold Temperate Northeast Pacific, Lusitanian, Northern European Seas, Tropical Northwestern Atlantic, Warm Temperate Northeast Pacific and Warm Temperate Northwest Atlantic) for marine species, we conducted two additional sets of sensitivity analyses specifically focusing only on those taxonomic classes and realms reporting both non-native and native animals (Supplementary Data 1).

Identifying areas of overlap between hotspots of invasions and EWEs

We finally explored overlap areas suitable for establishment of EWE-tolerant non-native animals and frequent EWEs. To achieve this, we first collected occurrence data for each non-native species and predicted their habitat suitability for establishment worldwide. We then overlapped those grids with suitable habitats for non-native species establishment with EWE hotspots (10%, 20% and 30% grids at a spatial resolution of 5 arcmin with the highest frequency of EWEs in history). For these overlapped grids, we calculated the net effect of positive, negative and neutral responses for each non-native animal to focal EWEs (that is, net effect = proportion of positive response + proportion of neutral response – proportion of negative response) on the basis of the sample effect sizes in the meta-analyses above. The accumulative net effect of EWEs on non-native species in each grid was obtained, with higher values indicating greater potential combined risks of invasions and EWEs. Details for predicting non-native species habitat suitability and the distributions of historical EWEs are summarized below.

Habitat suitability for non-native animal establishment. We first generated a non-native species list from the literature used in the meta-analysis (see non-native species list in Supplementary Data 2). Species occurrence records were then gathered from the online database of the Global Biodiversity Information Facility⁵⁰², and we added additional records from the literature (see distribution data source in Supplementary Data 2). We excluded those records without precise

coordinates and without clear establishment status. Next, we applied the 'scrubr' R package to remove duplicate coordinates⁵⁰³. For further spatial modelling analysis, occurrence data were thinned to 5-arcmin resolution (~ 9.2 km at the equator) using the 'spThin' package⁵⁰⁴ to reduce sampling bias from disproportional survey efforts among taxa or regions⁵⁰⁵. We identified the native and non-native ranges for each of species on the basis of the following databases: Global Invasive Species Database (GISD, <http://www.iucngisd.org/gisd/>), Invasive Species Compendium on CABI (<https://www.cabi.org/ISC/>), World Register of Introduced Marine Species (WRiMS, <https://www.marinespecies.org/introduced/>), SeaLifeBase (<https://www.sealifebase.se/search.php>), IUCN (<https://www.iucnredlist.org/>), and extra information from Wikipedia, Google Scholar and published literature (Supplementary Data 3). We further quantified the potential distribution of the non-native species using ecological niche modelling (ENM), which is a widely used method to provide robust predictions of potential distributions of species⁵⁰⁶. ENMs for potential species distributions under current climatic conditions were constructed using MaxEnt⁵⁰⁷ on the basis of a standard protocol following a previous study⁵⁰⁸. Details on modelling steps, predictor selection, method to account for sample bias and assessments of model performance are provided below.

ENM

To quantify potential distributions of non-native species, the MaxEnt algorithm was used to fit the models. The MaxEnt algorithm has generally shown high predictive performance and has been extensively applied in conservation, invasion and biogeography studies, and recent research shows that tuned MaxEnt models can perform comparably to ensemble models⁵⁰⁹. Training data contained both of a species' native and non-native ranges to eliminate biases in evaluating species' realized niches as some non-native species can shift their realized climatic niches in invaded areas^{510,511}. A minimum convex polygon with two-degree buffers was chosen to define the background extent where distribution occurrences of non-native species are located⁵¹². A target-group method was used to account for the potential effect of sampling bias in species occurrence data on results⁵¹³.

For land species, both climate and habitat factors including vegetation and water availability were used to predict their potential distributions, considering the important role of habitat variables in reflecting species' requirements for food and reproduction⁵¹⁴. Details on variable selection differed across taxa on the basis of their main physiological requirements following previous studies (Supplementary Table 10).

For marine non-native species, the Bio-ORACLE database (v.2.2, <https://www.bio-oracle.org/downloads-to-email.php>) was used to collect current environmental data for both surface and benthic species⁵¹⁵. Sea water depth information was accessed from Global Marine Environment Datasets (<https://gmed.auckland.ac.nz/>)⁵¹⁶. The Bio-ORACLE database supplied averaged outputs of predictors on the basis of three atmosphere–ocean general circulation models (AOGCMs) including CCSM4, HadGEM2-ES and MIROC5 at 5-arcmin (~ 9.2 km at the equator) resolution that was then used for further analyses⁵¹⁵. As climate warming effects on marine ecosystems depend on ocean depths⁵¹⁷, potential distributions of benthic and shallow-water species were predicted separately. Water depth, salinity and seasonal water temperature were necessarily used to predict distributions of benthic invertebrates and fishes^{518,519}. Specifically, a total of six candidate predictors were used to predict benthic species distributions, including water depth (m), annual mean current velocity ($\text{m}^{-1} \text{yr}^{-1}$), annual mean sea benthic salinity (PSS yr^{-1}), annual range of sea benthic salinity (PSS yr^{-1}), annual mean sea benthic temperature ($^{\circ}\text{C} \text{yr}^{-1}$) and annual range of sea benthic temperature ($^{\circ}\text{C} \text{yr}^{-1}$). For surface water fishes, water depth, sea surface temperature and salinity, and sea ice were used to predict spatial distributions^{520–522}. Potential distributions of marine surface fishes were predicted by seven candidate predictors, including water depth (m), annual mean current velocity ($\text{m}^{-1} \text{yr}^{-1}$), annual mean ice

thickness (m yr^{-1}), annual sea surface salinity (PSS yr^{-1}), annual range of sea surface salinity (PSS yr^{-1}), annual mean sea surface temperature ($^{\circ}\text{C yr}^{-1}$) and annual range of sea surface temperature ($^{\circ}\text{C yr}^{-1}$). These predictor variables did not show high correlations (Pearson's correlation coefficient $|r| < 0.70$)⁵²³.

Multiple predictor combinations from simple to full models were fitted using the MaxEnt algorithm. Cross-validations for the fitted models were performed on the basis of a spatial partitioning strategy using the 'block' method⁵²⁴. Three representative measures (area under the receiver operating characteristic curve (AUC), true skill statistic (TSS) and Boyce index) were used to evaluate the performance of fitted models^{525–527}. First, AUC is a threshold-independent measure; an AUC value between 0.7 and 0.9 indicates good model performance and a value >0.9 indicates excellent performance⁵²⁸. Second, TSS is a threshold-dependent measure with summing of sensitivity and specificity minus one⁵²⁹; a TSS value from 0.4 to 0.8 indicates good model performance and a value >0.8 indicates excellent performance. Third, the Boyce index is useful for evaluating fitted models with presence-only data to overcome potential overfitting issues. This index ranges from -1 to 1 and a higher value indicates better model performance⁵²⁷. All ENMs analyses were conducted using the 'ENMeval' package in R⁵³⁰. Overall, the ENMs used in our present study had good performance in predicting potential distributions of the non-native species (with minimum values of AUC > 0.75 ; TSS > 0.40 ; more than 83% of species with Boyce > 0.70 ; see details in Supplementary Table 11).

EWEs distribution. Distributions of different types of EWEs were collected from open data sources and publications.

Heatwave and cold-spell events on land

HadEX3 is a newly updated product generated through the coordination of the joint World Meteorological Organization (WMO) Expert Team on Climate Change Detection and Indices (ETCCDI). HadEX3 (<https://www.metoffice.gov.uk/hadobs/hadex3/>) supplies a set of 17 monthly metrics of extreme weather events gridded ($1.875^{\circ} \times 1.25^{\circ}$ longitude–latitude) for global land surfaces from 1901 to 2018 (ref. 531). Four of those metrics were selected owing to their long-term recordings by stations and representation of the frequency and intensity of thermal extremes⁵³¹. Proportions of extreme warm days and duration of warm days are commonly used to evaluate global-scale heatwave conditions^{532,533}. TX90p (percentage of time when daily maximum temperature is >90 th percentile) and WSDI (annual count when at least 6 consecutive days of maximum temperature is >90 th percentile) were used to quantify heatwave events in terrestrial and freshwater systems. TN10p (percentage of time when daily minimum temperature is <10 th percentile) and CSDI (annual count when at least 6 consecutive days of minimum temperature is <10 th percentile) were used to quantify cold-spell events.

Marine heatwave and cold-spell events

Historical marine heatwave events from 1980 to 2019 were recently reported⁵³⁴ as averaged days of heatwaves per decade at $1^{\circ} \times 1^{\circ}$ resolution at the global scale. Reference⁵³⁵ provides mean annual frequency of marine cold-spell (days) from 1982 to 2020 at $0.2498264^{\circ} \times 0.2496528^{\circ}$ resolution globally.

Storm events

The Global Risk Data Platform supplies historical recorded storm events and tracks from satellite remote-sensing from 1970 to 2015 (<https://preview.grid.unep.ch/index.php?preview=data&events=cyclones&evcat=1&lang=eng>). Available polygon layers in this platform contain information on country names, the year of storm events, starting and ending dates and the category per event. In addition, the coordinates of storm tracks per event are provided. Therefore, duration and category data of storm events at $0.5^{\circ} \times 0.5^{\circ}$ resolution were used.

Extreme flood events

Aqueduct Flood Hazard Maps provide global historical flood hazard grid datasets at $5' \times 5'$ resolution (<https://www.wri.org/data/aqueduct-floods-hazard-maps>). The historical dataset supplies times of recorded coastal and riverine floods with returning periods of 2, 5, 10, 25, 50, 100, 250 and 1,000 yr (ref. 536). Sums of times of coastal and riverine flooding events with 100-yr returning periods were used in the data analysis.

Extreme drought events

The global monthly average standardized precipitation index (SPI) dataset is available from the National Center for Atmospheric Research (NCAR)/University Corporation for Atmosphere Research (UCAR) platform (<https://www.ucar.edu/>) at $1^{\circ} \times 1^{\circ}$ resolution for the years 1942–2012. Monthly SPI is a widely used index to describe meteorological drought, and monthly SPI ≤ -1.5 was used to define an extreme drought event⁵³⁷. The SPI data for a 12-month timescale were selected to assess drought events. Furthermore, to better quantify multiple-year averages of drought events, we calculated the frequency of extreme dryness per year (that is, $(1/12) \times \text{number of month(s) with SPI} \leq -1.5$). The annual mean frequency of extreme dryness from January 1950 to December 2012 was used in the data analysis. We standardized all the EWEs layers with different to the same 5-arcmin resolution using the 'resample' function in the 'raster' (v.3.5-21) package⁵³⁸. Animal silhouettes in the PhyloPic database (www.phylopic.org) were accessed and visualized using the 'add_phylopic_base' function in the 'rphylopic' (v.1.1.1) package⁵³⁹. All data⁵⁴⁰ analyses were conducted in R (4.2.1)⁵⁴¹.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

All data have been deposited in a public structured data depository (<https://doi.org/10.6084/m9.figshare.23587695>). Source data are provided with this paper.

Code availability

The R code for running the main analyses is available at <https://doi.org/10.6084/m9.figshare.23587695>.

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Author contributions

X.L. conceived the project. X.L., S.G. and J.R.R. designed the study. X.L. supervised the project. S.G., T.Q. and X.L. collected the data. S.G., T.Q. and X.L. performed data analyses. S.G. and X.L. wrote the manuscript draft and all authors contributed to manuscript revisions.

Competing interests

The authors declare no competing interests.

Additional information

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Data collection

A total of 443 studies used for meta-analysis were collected from two sources. One source comes from conducting a systematic literature search through a variety of search engines such as Clarivate Web of Science and Scopus. Full details of the search terms and filtering criteria were included in the Supplementary Methods. Another source comes from recent reviews and syntheses of Maxwell et al. 2018, Neilson et al. 2020, Thakur et al. 2022, and Sabater et al. 2023. Occurrence records of non-native species were gathered from the online database of the Global Biodiversity Information Facility and added additional records from the literature. Bioclimatic variables were downloaded from the WorldClim-Global Climate Database. Habitat factors included vegetation and water cover variables. The vegetation cover variable referred to the annual normalised difference vegetation index (NDVI) and was collected from the Nasa Earth Observations. The water cover variable was collected from the global lakes and wetlands database. Marine environmental variables were collected from Bio-ORACLE database. Sea water depth information was collected from Global Marine Environment Datasets. Heatwave and cold-spell events on terrestrial and freshwater ecosystems were collected from HadEX3 database. Marine heatwave events were collected from Tanaka and Van Houtan (2022)'s layer data. Marine cold-spell events were collected from Wang et al (2022)'s layer data. Storm events were collected from the Global Risk Data Platform. Extreme Flood events were collected from the Aqueduct Flood Hazard Maps database. Extreme drought events were collected from the National Center for Atmospheric Research (NCAR)/University Corporation for Atmosphere Research (UCAR) platform. Full detail information for all data sources were provided in Supplementary Methods.

Data analysis

All data analysis was completed using R version 4.2.1. All packages used are fully referenced in the Supplementary methods.

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Study description

Extreme weather events (EWEs) and non-native species invasions have devastating impacts on native biodiversity and their joint effects would be a greater threat to native species. However, there is still lack of a general evaluation of the effects of EWEs on non-native species for multiple taxonomic groups across ecosystems and types of EWEs, which is critically important to predict non-native species responses to climate change and evaluate global hotspots of their potential joint effects. Here, we conducted a global synthesis of comparing the responses of non-native and native animal species to extreme weather events. We then calculated the net effect of each non-native animal to EWEs in each overlapped grid as the proportions of positive plus neutral responses minus negative response based on the sample effect sizes in the meta-analyses above. The accumulative net effect for each grid was obtained to reflect the overall tolerance of all potential non-native species to EWEs. A list of EWE tolerant non-native species was determined. Furthermore, we displayed overlaps between hotspots of non-native species and EWEs to identify locations where native species might be adversely affected by their joint effects.

Research sample

Following our criteria, all relevant studies were included and involved mammals, birds, amphibians, reptiles, fish, and invertebrates to five types of EWEs across terrestrial, freshwater, and marine ecosystems. In total we report 5,303 effect sizes for 973 non-native species and 4,330 native animal species from 443 studies.

Sampling strategy

We used terms to search published research literatures from ISI Web of Science (all databases) and Scopus (in "All fields") across all years (last accessed date: 24 April 2023). We removed duplicate publications from different searching sources. The remaining publications were related to research articles, animal species studying system, and available quantifications of extreme weather events (EWEs)' effects on the animal species. As a result, a list of non-native and native animal species could be determined. Based the Class identity and experienced types of EWEs of non-native species, we finally analyzed native species with the same class level and experienced EWEs' type.

Data collection

A total of 443 studies were used for meta-analysis. In those studies, when the data used for calculating sample effect sizes were directly reported in the text, we recorded the data in Excel for next analysis. When the data were not directly reported in the text but in figures, we used GetData graph Digitizer (version 2.24) to extract values. Sample size, mean and variance values in control and treatment groups were extracted from each study. Details of other variables in analysis were also extracted and reported in the Supplementary Methods. Occurrence records of non-native species were downloaded from the Global Biodiversity Information Facility. We used latin names of non-native species to search literatures on ISI Web of Science to add additional records. We further excluded those records without precise coordinates and unclear establishment status. We removed duplicate coordinates. The occurrence data were thinned to 5 arcmin resolution (~9.2 km at the equator) to reduce sampling bias from disproportional survey

efforts among taxa or regions. Distribution layers of different types of EWEs were downloaded from open data sources and publications. Details of available resolution of the layers and cited sources were described in Supplementary Methods.

Timing and spatial scale	The literature was searched by 24 April 2023. Occurrence records of non-native species were downloaded from the Global Biodiversity Information Facility which was last accessed at 21 May 2023. Heatwave and cold-spell events on terrestrial and freshwater ecosystems were collected from HadEX3 database during 1901 to 2018. Marine heatwave events were collected from Tanaka and Van Houtan (2022)'s layer data during 1980 to 2019. Marine cold-spell events were collected from Wang et al (2022)'s layer data during 1982 to 2020. Storm events were collected from the Global Risk Data Platform during 1970 to 2015. Extreme Flood events were collected from the Aqueduct Flood Hazard Maps database during 1979 to 2014. Extreme drought events were collected from the National Center for Atmospheric Research (NCAR)/University Corporation for Atmosphere Research (UCAR) platform during 1950 to 2012. All Literature search and data downloads were conducted on a global scale.
Data exclusions	Papers were excluded where they did not meet our inclusion criteria specified in the Supplementary Methods. We include a detailed PRISMA chart of all exclusion (Supplementary Fig. 1).
Reproducibility	All data sources have been provided in the Supplementary Methods, and we will additionally make all original data public in a structured data depository upon the publication of the work.
Randomization	This is not relevant to this study as the data was collected from existing studies and is already allocated as either treatment or control.
Blinding	Blinding was not carried out as part of this study. All data were extracted from existing treatment and control studies therefore it was not necessary or possible to blind ourselves during this extraction.
Did the study involve field work?	☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging