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Climate-driven impacts of exotic species on marine ecosystems

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Abstract

Aim: Temperature is fundamental to the physiological and ecological performance of marine organisms, but its role in modulating the magnitude of ecological impacts by exotic species remains unresolved. Here, we examine the relationship between thermal regimes in the range of origin of marine exotic species and sites of measured impact, after human-induced introduction. We compare this relationship with the magnitude of impact exerted by exotic species on native ecosystems.

Location: Global.

Time period: 1977–2017 (meta-analysis).

Major taxa studied: Marine exotic species.

Methods: Quantitative impacts of exotic species in marine ecosystems were obtained from a global database. The native range of origin of exotic species was used to estimate the realized thermal niche for each species and compared with the latitude and climatic conditions in recipient sites of recorded impact of exotic species. The difference in median temperatures between recipient sites and the thermal range of origin (i.e., thermal midpoint anomaly) was compared with the magnitude of effect sizes by exotic species on native species, communities and ecosystems.

Results: Recorded impacts occurred predominantly within the thermal niche of origin of exotic species, albeit with a tendency toward higher latitudes and slightly cooler

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conditions. The severity of impacts by exotic species on abundance of native taxa displayed a hump-shaped relationship with temperature. Peak impacts were recorded in recipient sites that were 2.2°C cooler than the thermal midpoint of the range of origin of exotic species, and impacts decreased in magnitude toward higher and lower thermal anomalies.

Main conclusions: Our findings highlight how temperature and climatic context influence ecological impacts by exotic species in marine ecosystems and the implications for existing and novel species interactions under climate change.

KEYWORDS

alien, climate change, environmental matching, invasive, non-native, temperature

1 | INTRODUCTION

Human transport systems (e.g., via ballast waters) are redistributing marine species beyond their original ranges (Seebens et al., 2013), allowing exotic species to settle and, in many instances, proliferate and impact native species and ecosystems (Anton et al., 2019b). Determining the mechanisms that influence the successful establishment and magnitude of ecological impacts by exotic species on recipient ecosystems is therefore crucial. Several factors have been reported to influence the success of establishment of introduced species and their impact. High species richness in the recipient community, for example, can lead to greater biotic resistance to the introduction and abundance of exotic species, which might affect their long-term establishment and impacts (Kimbro et al., 2013). Likewise, high richness of exotic species in the recipient community can lead to “invasion-meltdown”, whereby facilitation between introduced species increases their likelihood of establishment and impact (Simberloff & Von Holle, 1999). In marine systems, the impacts of exotic species generally display a poor relationship to global anthropogenic stressors, such as cumulative human impact, distance to market, exotic species richness and rates of ocean warming (Geraldi et al., 2020). However, performance might depend not only on the characteristics of the recipient site per se, but also on the relative difference between the origin of the exotic species and the recipient site that it moves into.

Temperature is a fundamental driver of the physiological performance of species across all biological realms, and environmental matching between source and recipient climates has been observed to be an important determinant of the performance of exotic species in freshwater and terrestrial systems (Hulme, 2017; Iacarella et al., 2015). To date, however, the role of temperature and climate in shaping the impacts of exotic species in marine systems has not been examined at a global scale.

Physiological and ecological performance of individuals typically display a strong response to temperature, broadly characterized by a hump-shaped curve (Angilletta, 2006; Waldock et al., 2019), with peak fitness at optimal temperatures and decreasing fitness toward minimum and maximum thermal tolerance limits (Dell et al., 2011; Valladares et al., 2014). In the marine realm, fundamental thermal niches of individuals often closely resemble realized thermal distributions of species (Sunday et al., 2012), with the maximum population abundance for many species occurring around the thermal midpoint (Stuart-Smith et al., 2015; Waldock et al., 2019), although not always (Sagarin & Gaines, 2002). The realized thermal niche of a species could, therefore, be indicative of the physiological limitations of exotic species and the strength of their ecological impacts. For instance, tropical species are unlikely to become established if introduced to polar marine ecosystems and vice versa, and species with broad thermal niches might be more likely to become established when introduced into new habitats than thermal specialists (Bates et al., 2013). Therefore, exotic species might have a greater likelihood of establishing in recipient sites that fall within their thermal range of origin and might be expected to have greater fitness and potentially larger ecological impacts in recipient sites that resemble their thermal optima, compared with sites that are close to or outside their upper or lower thermal limits.

In this study we test this idea, first by examining the latitudinal and thermal displacement of marine exotic species from their range of origin into recipient sites where ecological impacts have been recorded; and second, we quantify how temperature modulates the magnitude of impact by marine exotic species. First, we predict that impacts by exotic species will have been recorded in locations that fall within the thermal range of origin of each exotic species. Second, we predict that the magnitude of impacts recorded by exotic species will be greatest around the centre of a species' thermal distribution (i.e., thermal midpoint) and diminish with increasing difference between the median temperature in a recipient site and median temperature observed across an exotic species' range of origin (herein defined as a thermal midpoint anomaly). Finally, we discuss our findings in light of how ocean warming might influence the trajectory of the impacts of exotic species over the coming decades. As climate regimes are shifting owing to ocean warming, human-mediated species redistributions might lead to species being established in habitats that are warming up to either resemble or exceed the thermal regimes in the range of origin of the exotic species (Hulme, 2017). This, in turn, could affect the physiological and ecological performance of exotic species, their competitive ability, trophic interactions and, potentially, their impact on recipient communities (Iacarella et al., 2015).

We base our analysis on a quantitative global database of more than half a century of impacts of marine exotic species (Anton et al., 2019b) and couple it with geographical and thermal distribution data for exotic species within the database. Our findings relate specifically to established marine exotic species in sites around the world where ecological impacts on native species and communities have been tested quantitatively. In doing so, this work provides a framework for understanding of how exotic species and, indeed, species undergoing climate-driven redistribution might perform in new "foreign" habitats in the future.

2 | MATERIALS AND METHODS

2.1 | Impact of exotic species on the invaded ecosystem

The quantitative impacts of exotic species in marine ecosystems were obtained from a public database (Anton et al., 2019a), which includes a detailed description of the methods in the paper by Anton et al. (2019b). Briefly, a search was performed for all papers that quantified the ecological impacts of exotic marine species before 4 May 2016, using the Web of Science (Thomsen Reuters) search engine from the King Abdullah University of Science and Technology server (Dallas et al., 2018). The search resulted in 1,012 studies, of which 159 were eventually used in a meta-analysis, following screening and eligibility criteria (Anton et al., 2019b). Effect size Hedges' g and the variance for Hedges' g were calculated following Koricheva et al. (2013) and were used as the effect size to estimate the differences in the response variable between control and experimental treatment. Hedges' g ranges from $-\infty$ to $+\infty$ and can be interpreted as (Koricheva et al., 2013): $|g| \leq 0.2$, a small impact; $0.2 \leq |g| \geq 0.5$, a medium impact; $0.5 \leq |g| \geq 0.8$, a large impact; and $|g| \geq 0.8$, a very large impact.

In the study by Anton et al. (2019b), quantitative impacts of exotic species were measured on 10 metrics, which were classified as individual-, community- or ecosystem-level impacts. Individual-level impacts included survival (including mortality), growth (including percentage growth), fitness and behaviour. Community-level impacts included effects on the abundance and richness of native taxa, and ecosystem-level impacts included biogeochemical elements (stocks or fluxes of carbon, nitrogen, phosphorus and silicate), rate processes (net community production, photosynthesis, respiration and decomposition), pollution (including heavy metal concentration and water clarity) and sediment changes (Anton et al., 2019b).

2.2 | Patterns of redistribution of exotic species

The effect size of exotic species and the location of studies were then used to examine thermal performance relationships of marine exotic species by comparing the location and magnitude of ecological impacts with the thermal range of origin of exotic species. We focused our analysis on species that are influenced primarily by seawater temperatures and therefore included only studies within marine systems, below the high tide line (i.e., eulittoral zone and below). Studies involving species that reported impacts from above the high tide line were removed from the database ($n = 3$ species; Supporting Information Figure S1). Mangrove and marsh plant species from intertidal habitats were also removed from analyses owing to the greater influence of air temperatures than sea temperatures on their ecological performance (Ball, 1988; Gedan & Bertness, 2010; Lovelock et al., 2016) ($n = 7$ species). Also, we included only studies that specified the role of direct human vectors as the cause of introduction. Any climate-driven range-expanding species were not included in the study ($n = 1$ species; Supporting Information Figure S1).

We estimated the geographical range of origin for all exotic species in the database by searching for primary literature on the "native range" or "native distribution" in Web of Science (Thomsen Reuters) search engine from the Spanish National Research Council (CSIC) server (Dallas et al., 2018) (10 April 2017), to distinguish it from the introduced range of the species. Species from the impacts database were used only if their range of origin could be distinguished from their introduced range in the literature (e.g., through molecular studies). This was important, particularly for species with impact sites in close proximity to their native range of origin. Species whose range of origin could not be verified were excluded ($n = 15$ species). In total, 50 of the 76 species in the original marine exotic species database were used in this study (Supporting Information Table S1), corresponding to 108 of the 159 studies used in the original database by Anton et al. (2019a) (a list of data sources is given in Supporting Information Appendix S1). After the range of origin of each species had been verified manually, we downloaded occurrence records for the verified species from the Global Biodiversity Information Facility [GBIF.org (6 November 2019) GBIF Occurrence Download]. GBIF occurrence records do not distinguish between the introduced and native range of species. Therefore, global GBIF occurrence records were retained only if they fell within a marine province (Spalding et al., 2007) corresponding to the manually verified range of origin of each exotic species. Occurrence sites that fell outside the reported range of origin were deemed to be introduced sites and therefore discarded. Additional occurrence sites were included from the literature if they differed from the available GBIF occurrences, and only documented occurrence sites were included. A minimum of three occurrence sites, representing the leading edge, trailing edge and central distribution, was required for a species to be included. Species with a small range of origin (e.g., *Caulerpa cylindracea*) had relatively few points compared with species with broad distributions (Supporting Information Table S1). Likewise, species with native distributions in east Asia tended to have fewer recorded occurrences than species in North America or Europe. In total, 5,700 occurrence sites were identified, spanning the range of origin for 50 exotic species (Supporting Information Figure S2). The number of occurrences varied between species (145 ± 25 mean ± *SE* occurrence sites) depending largely on the geography of their range of origin (Supporting Information Table S1). This represents a small subset of the total number of sites where exotic species have been observed, and 4% of exotic species listed in the Global Register of Introduced and Invasive Species (GRIIS; http://www.griis.org/).

The range of origin for each exotic species was used to characterize its realized thermal niche of origin. Realized thermal niches are typically smaller than a species' fundamental niche based on physiological tolerances, but arguably provide a better reflection of real-world limits where species need not only to survive, but also to establish and persist in a competitive environment. Moreover, in the marine realm, where most organisms cannot escape or modify ambient thermal conditions (cf. terrestrial organisms), realized thermal niches generally resemble fundamental thermal niches and can therefore provide a useful proxy of a species' thermal tolerance breadth (Sunday et al., 2012).

For each native occurrence site extracted from GBIF, we extracted mean sea surface temperature (SST), and the first, 10th, 90th and 99th percentile SST recorded between 1981 and 2017. These temperatures were then compared among all native occurrence sites within the range of origin of each species to characterize realized upper and lower thermal limits. The same temperature metrics from recipient sites were also extracted for each species. Thermal midpoint anomalies were calculated by subtracting median temperatures in the range of origin ($\mathrm{Tmed}_{\mathrm{RO}}$) from median temperatures at recipient sites ($\mathrm{Tmed}_{\mathrm{RS}}$), such that negative and positive values represent recipient sites that are cooler and warmer than the range of origin, respectively. The midpoint between the upper and lower limits of the realized temperature distribution occupied by each species was used as a measure of central tendency of the realized thermal distribution in its range of origin. Given that not all locations within a species' range of origin could be identified, this was considered to be a more accurate reflection of the thermal midpoint than the mean of the extracted data. Likewise, lower and upper temperature anomalies were calculated as $\mathrm{Tmin}_{\mathrm{RS}} - \mathrm{Tmin}_{\mathrm{RO}}$ and $\mathrm{Tmax}_{\mathrm{RS}} - \mathrm{Tmax}_{\mathrm{RO}}$, respectively. All SST data were based on daily SST maps with a spatial resolution of ¼°, obtained from the National Center for Environmental Information (NCEI, https://www.ncdc.noaa.gov/oisst; Reynolds et al., 2007). These maps have been generated through the optimal interpolation of Advanced Very High Resolution Radiometer (AVHRR) data for the period 1981–2017. For each reported site, we selected the nearest point from the SST maps.

2.3 | Relationship between effect size and thermal midpoint anomalies

Absolute effect sizes of individual response variables were compared with thermal midpoint anomalies experienced by exotic species in the recipient site of impact, relative to its range of origin. Impacts of exotic species on community-level response variables, namely native taxa abundance ($n = 420$) and species richness ($n = 130$), accounted for 73% of total case studies recorded in the database. The remaining case studies on individual- and ecosystem-level response variables accounted for 11% and 16% of total observations, respectively. Case studies within each response variable were averaged to the mean effect size per species per site, to reduce the weight of highly studied species on the analysis. After this step, taxa abundance ($n = 65$) and species richness ($n = 30$) accounted for 63% of species and site averaged cases, individual-level response variables ($n = 32$) collectively accounted for 21%, and ecosystem-level response variables ($n = 25$) collectively accounted for 16% of the data. Of the 10 response variables recorded, eight could be evaluated individually, but water quality ($n = 1$) and sediment stability ($n = 1$) could not, owing to low sample size. All 10 response variables were subsequently pooled within individual, community or ecosystem levels to examine overall impacts at the organizational level.

To test the hypothesis that the impact of exotic species was highest when temperatures at recipient sites reflect the thermal midpoint of the range of origin of the exotic species, we compared effect sizes (Hedges' *g*) and thermal midpoint anomalies (TMAs) using a Gaussian function:

$$g = k e^{\left[-0.5(\mathrm{TMA}-\mu)^2/\sigma^2\right]},$$

where k = amplitude, μ = mean and σ = standard deviation of the curve. The best-fitting values for each parameter were determined using a nonlinear least squares regression in R. The 95% confidence intervals (CI) for each of the parameters were calculated using nonparametric bootstrapping of the mean centred residuals. The relationship between observed effect sizes and the overall best-fitting model was determined by bootstrapping the data set and comparing the sum of squared deviations (SS) of the observed data from the model with the SS of 10^4 resampled data. Observed effect sizes were considered to display a significant relationship to the best-fitting model if the observed SS was smaller than the fifth percentile of bootstrapped SS.

To account for differences in sample sizes of impacts under the different anomalies, we also re-ran analyses using bootstrapped mean effect sizes for each thermal midpoint anomaly to compare SS from the observed distribution of effect sizes with SS from randomized distributions.

2.4 | Temporal trajectory of thermal midpoint anomalies

To examine the trajectory of thermal midpoint anomalies through time, we used the multi-model CMIP5 ensemble of sea surface temperature (SST) simulations forced by RCP4.5 and RCP8.5 Intergovernmental Panel on Climate Change (IPCC) scenarios for greenhouse gas emissions (Taylor et al., 2012). All available models and ensembles (from 25 to 37 ensembles, depending on the scenario) were used to compute the mean projections. The SST change projected for each impact site was computed as the difference between the average monthly SST in the period 2030–2049 and 1981–2000 or 2080–2099 and 1981–2000. Projected thermal midpoint anomalies were then calculated for each site as the difference between projected temperatures at the recipient site and thermal midpoint of the range of origin. Thermal midpoints in initial conditions at the time of experiments were computed by standardizing recipient site temperatures by the year experiments were conducted in each publication. The median thermal midpoint anomaly across all case studies in current conditions, and projected median anomalies in 2050 and 2100, were compared with the best-fitting relationship of effect sizes on native taxa abundance to examine the trajectory of recorded impacts in response to warming.

3 | RESULTS

3.1 | Latitudinal and thermal displacement of marine exotic species

Across all case studies where ecological impacts were recorded, species introductions typically involved a poleward latitudinal shift, with 41% of reported cases occurring poleward of the cool edge of the range of origin of the exotic species (i.e., positive latitudinal anomalies of blue line), whereas only 5% of the introductions occurred equatorward of the warm edge of their range of origin (i.e., negative latitudinal anomalies of red line; Figure 1e). Overall, species introductions involved a poleward latitudinal shift of (mean ± *SE*) 6.8 ± 1.14° latitude calculated from the latitudinal midpoint of the range of origin (Figure 1e).

In terms of thermal displacement, a total of 64% of the introductions in the data set occurred into sites with thermal midpoints cooler than the thermal midpoint at the range of origin for exotic species (Figure 1g), slightly higher than the predicted 50% of case studies (Figure 1c). That is, thermal midpoints in recipient sites were, on average, 1.2 ± 0.39°C cooler than the thermal midpoint from a species' range of origin. Temperature minima in recipient sites were cooler than observed throughout the range of origin of exotic species in 28% of recorded impact sites (Figure 1f). In comparison, 14% were established in sites experiencing maximum temperatures warmer than any location within the range of origin (Figure 1h; Supporting Information Table S1). Overall, maximum temperatures (i.e., 99th percentile SST between 1981 and 2017) experienced at the recipient site were 6.5 ± 0.5°C (mean ± *SE*) cooler than maximum temperatures experienced in the range of origin (Figure 1h), and average minimum temperatures were 4.1 ± 0.6°C warmer than the coolest temperatures experienced at the range of origin of the exotic species (Figure 1f). Macroalgae had the majority of the recorded ecological impacts outside of their thermal range of origin, accounting for nine of 14 cases where maximum temperatures in recipient sites exceeded maximum temperatures in the range of origin and 20 of 27 cases where minimum temperatures were below the lower limit of the range of origin (Figure 1v). Mobile invertebrates accounted for five of 14 and five of 27 of the recorded impacts outside upper and lower thermal limits, respectively. Sessile invertebrates recorded the remaining two of 27 impacts below lower thermal limits, and fish recorded no impacts outside their thermal range of origin (Figure 1).

Patterns of thermal displacement with respect to depth zonation showed a subtle trend, whereby impacts occurring in shallow sites more frequently conformed to the range of origin of the exotic species than observed in deeper sites (Supporting Information Figure S3). Impacts in the intertidal zone ($n = 43$) occurred in recipient sites with cooler minimum temperatures than cold limits of the species' range of origin in 9% of observations, compared to 32% at 1–5 m ($n = 31$), 50% at 6–30 m ($n = 20$) and 66% at depths > 30 m ($n = 6$). Impacts in recipient sites that were warmer than the warm range edge of origin for exotic species were observed in 7% of intertidal case studies, 9% at 1–5 m, 25% at 6–30 m and 50% of cases at sites > 30 m depth (Supporting Information Figure S3).

3.2 | Effect of environmental temperatures on ecological impacts of exotic species

Absolute effect sizes of individual response variables were compared with thermal midpoint anomalies experienced by exotic species in the recipient site of impact, relative to its range of origin. Impacts on the abundance of native taxa displayed a significant relationship with temperature, characterized by a Gaussian distribution of effect sizes across a 19°C range of thermal midpoint anomalies ($n = 65$, SS = 6.32, $R^2 = .06$, $p < .01$; Figure 2a). Maximum effect sizes on taxa abundance (Hedges' $g = 0.96 \pm 0.13$ mean ± *SE*) were identified at thermal midpoint anomalies = −2.2 ± 2.3°C and declined with increasing anomaly size away from optimal conditions (Figure 2a). This pattern was consistent with bootstrapped mean effect sizes across species per 1°C thermal midpoint anomalies ($n = 17$, SS = 0.45, $R^2 = .28$, $p < .01$), indicating that the hump-shaped pattern in impacts was robust to differences in sample size across thermal midpoint anomalies. The best-fitting relationship of absolute effect sizes and thermal midpoint anomalies was consistent when divided between both positive and negative impacts on native taxa abundance (Figure 2b). Bootstrapped mean negative impacts displayed a significant Gaussian relationship, with maximum effect sizes on native taxa abundance (Hedges' $g = -0.75 \pm 0.09$) at thermal midpoint anomalies of −2.26 ± 0.95°C ($n = 11$, SS = 0.36, $R^2 = 0.389$, $p < .05$). Bootstrapped mean positive impacts on native abundance reflected a similar relationship with respect to thermal midpoint anomalies ($n = 10$, SS = 0.29, $R^2 = .37$, $p < .05$), albeit with maximum impact at anomalies of −4.4 ± 4.7°C (Figure 2b). Interestingly, when separated by depth zonation, the pattern held for intertidal case studies, but not for subtidal cases. Bootstrapped mean effect sizes of intertidal impacts on native taxa abundance displayed a significant relationship with thermal midpoint anomalies ($n = 11$, SS = 1.04, $R^2 = .41$, $p < .01$), with maximum impact (Hedges' $g = 1.28 \pm 5.2$) at thermal midpoint anomalies of −1.05 ± 3.6°C. In contrast, subtidal case studies on their own showed a non-significant relationship with thermal midpoint anomalies ($p = .10$).

Impacts on native species richness displayed a non-significant relationship with thermal midpoint anomalies ($p = .13$), but a similar distribution to taxa abundance, resulting in a significant overall relationship of community-level impact with respect to thermal midpoint anomalies ($n = 17$, $SS = 1.78$, $R^2 = .22$, $p < .05$).

At the individual level, impacts on the fitness of native species displayed a negative linear relationship with thermal midpoint anomalies ($F_{1,3} = 426.8$, $R^2 = .991$, $p < .001$); however, the small sample size limited the analysis to a narrow range of thermal midpoint anomalies (Figure 2c). All remaining individual- and

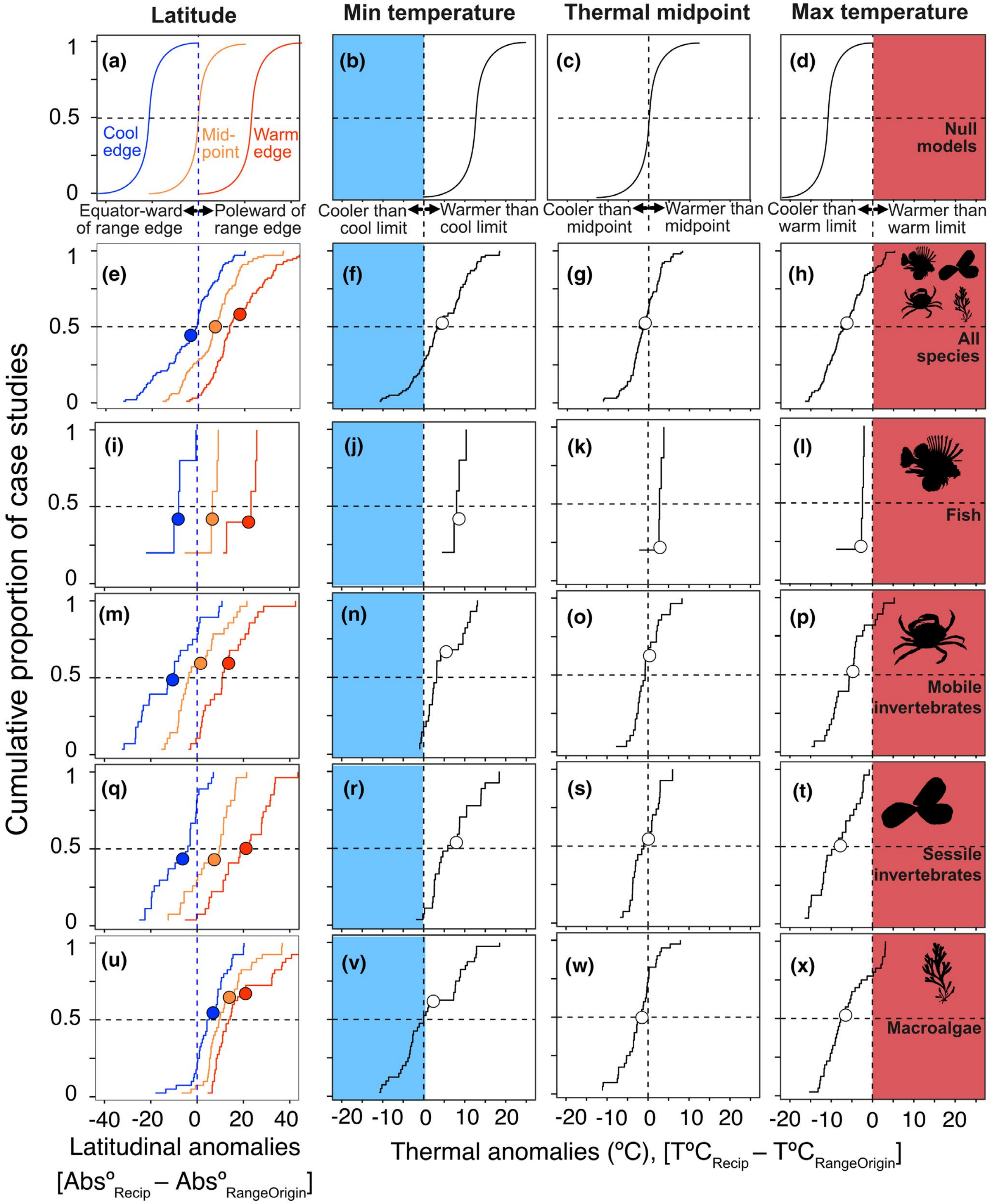

FIGURE 1 Cumulative distribution functions of the latitudinal and temperature displacement of exotic species with respect to their range of origin. Latitudinal and thermal displacement represents the latitudinal position and thermal conditions of impacted recipient sites minus the cool, median or warm latitudinal and thermal limits in the corresponding range of origin of the exotic species. (a–d) Null models for each column of panels. The null model is that recipient sites of exotic species fall within the absolute latitudinal and thermal range of origin for the species. (e–h) Empirical results for all species combined (*n* = 100 unique species–recipient site combinations). (i–x) The subsequent rows of panels represent the four major taxonomic groups of marine exotic species: fish (i–l; *n* = 5), mobile invertebrates (m–p; *n* = 28), sessile invertebrates (q–t; *n* = 27) and macroalgae (u–x; *n* = 40). The left column of panels (a,e,i,m,q,u) represents the difference in absolute latitude between recipient sites and the cool edge (blue), midpoint (orange) and warm edge (red) of the range of origin of each exotic species, respectively. Remaining columns (e.g., represented with a black line) show the difference in minimum temperatures (b,f,j,n,r,v), thermal midpoint temperatures (c,g,k,o,s,w) and maximum temperatures (d,h,l,p,t,x) in recipient sites compared with the range of origin of each exotic species. Positive and negative anomalies correspond to latitudes and temperatures that are higher or lower, respectively, in recipient sites than the range of origin. The width of the curve indicates the range of thermal anomalies where impacts have been recorded. The vertical dashed lines in the plots show the lower thermal limit (b,f,j,n,r,v), thermal midpoint (c,g,k,o,s,w) and upper thermal limit (d,h,l,p,t,x) in the range of origin of the exotic species. The circle on each line represents the mean anomaly. Horizontal dashed lines demarcate 50% of case studies in each respective panel [Colour figure can be viewed at wileyonlinelibrary.com]

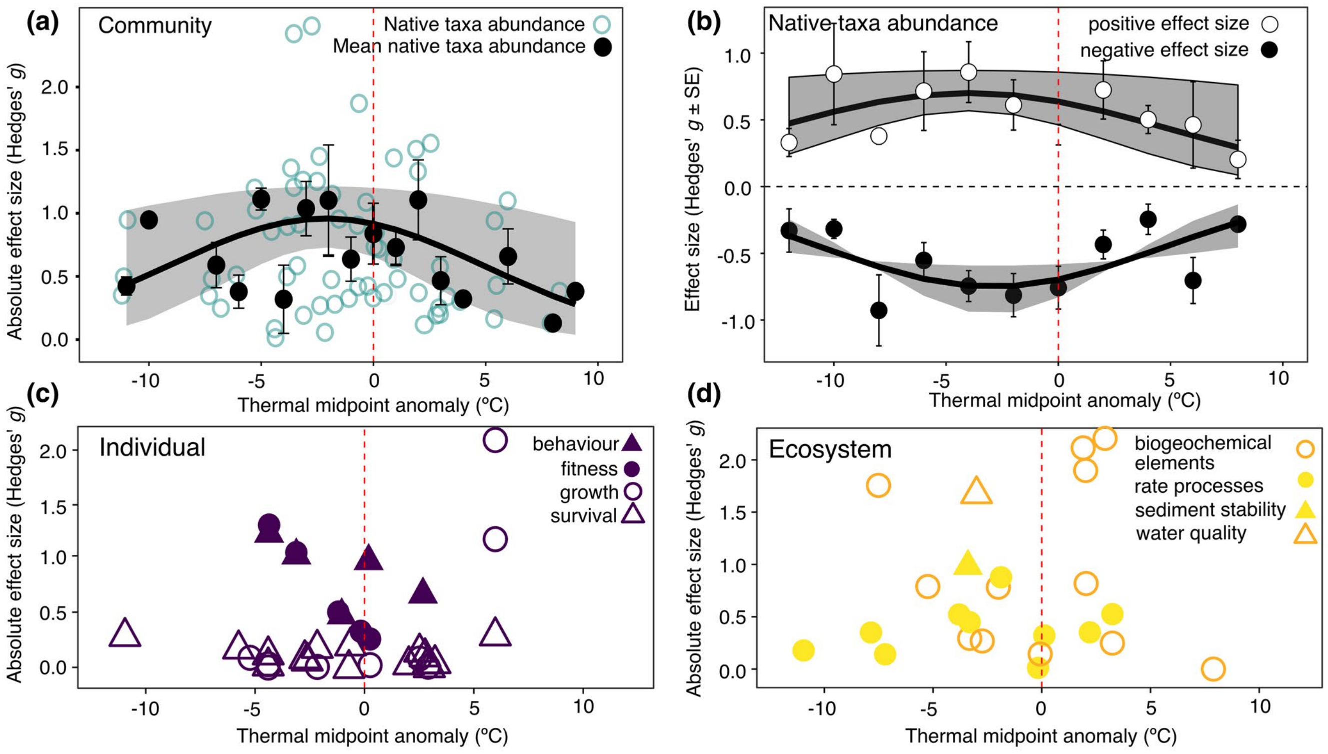

FIGURE 2 Relationship between the magnitude of effect size of impacts of exotic species and thermal midpoint anomalies. (a) Absolute effect sizes by exotic species on native taxa abundance. (b) Positive and negative impacts on native taxa abundance. (c) Absolute effect sizes of individual-level response variables. (d) Absolute effect sizes of ecosystem-level response variables. Coloured points (in a,c,d) represent absolute effect sizes averaged per species per recipient site. Black filled circles (in a,b) represent the mean (±*SE*) across species within 1°C thermal midpoint anomalies. The line of best fit (continuous black line) ±95% confidence interval (grey band) for absolute impacts (a) and positive and negative impacts (b) was fitted for impacts on abundance of native taxa using a Gaussian equation. For absolute impacts (a), peak ecological impacts were observed at Hedges' $g = 0.96$ and a thermal midpoint anomaly = −2.2°C. The vertical dashed red line reflects 0°C anomaly, corresponding to the hypothesized optimal temperature of exotic species. Thermal midpoint anomalies represent the difference (in degrees Celsius) between sea surface temperature (SST) midpoints experienced across the range of origin of an exotic species (averaged across 1981–2017 baseline) and a recipient site where its impact was recorded (between 1981 and 2017). Negative and positive anomalies represent recipient sites that are cooler and warmer than the thermal midpoint of range of origin of the exotic species, respectively [Colour figure can be viewed at wileyonlinelibrary.com]

ecosystem-level response variables displayed non-significant relationships to thermal midpoint anomalies, and the overall impacts of exotic species on individual and ecosystem levels were also non-significant ($p > .05$; Figure 2c,d).

The magnitude of effect size by exotic species displayed no relationship with either the number of exotic species with a recorded impact at the same site or the total number of exotic species reported from the local area (Supporting Information Figure S4). Likewise, we found no relationship between the elapsed time since arrival of an exotic species at a recipient site and the magnitude of its impact (Supporting Information Figure S4). The average time since arrival for exotic species was 27.9 ± 3.4 years.

3.3 | Trajectory of impacts of exotic species on native taxa abundance

The observed relationship between the impacts of exotic species on native taxa abundance and thermal midpoint anomalies suggests that as ocean temperatures warm in recipient sites, the magnitude of impact by exotic species might also change along a trajectory of increasing or decreasing impacts, depending on the position of current thermal midpoint anomalies with respect to the optimum. Climate change projections under RCP8.5 emissions scenarios project that ocean warming will alter the median thermal midpoint anomalies at recipient sites from −1.2°C at present to 0.88°C by 2050 and 2.8°C above the current thermal midpoint in the range of origin by 2100 (Figure 3). These changes correspond to a steady decline in the median projected impact of exotic species on the abundance of native taxa, assuming no immigration, emigration or adaptation of native and exotic species, or a decline in the performance of native species within recipient sites over the same period (Figure 3). Temporal changes in ecological impacts, however, are unlikely to respond to ocean warming in isolation. Instead, impacts are likely to emerge from a suite of climate- and non-climate-associated processes acting on native and exotic species over the coming decades (Figure 3). These processes might sustain, increase or decrease net impacts in any given location. In the following discussion, we describe how some of these processes might influence the temporal trajectory of the impacts of exotic species on marine ecosystems.

4 | DISCUSSION

4.1 | Influence of temperature on impacts of marine exotic species

Our results reveal the relationship between temperature and the magnitude of impacts by marine exotic species. Consistent with expectations, the global distribution of ecological impacts by exotic species broadly matched their thermal range of origin, albeit with a tendency toward more impacts at sites of higher latitude, at the cooler end of species' thermal distributions. Within recipient sites, the magnitude of impacts by exotic species on the abundance of native taxa displayed a hump-shaped relationship with thermal midpoint anomalies, whereby maximum impacts were observed 2.2°C below the thermal midpoint of the average species range of origin. The hump-shaped pattern of the impacts of exotic species is analogous to temperature-dependent performance profiles of individuals, a long-standing tenet of thermal biology (Angilletta, 2009), but seldom observed to result in indirect impacts on community levels of organization (Pörtner & Farrell, 2008). Observed patterns of redistribution and impact highlight the influence of climate on marine communities, with strong relevance for the hundreds of exotic species whose impacts remain to be measured and the thousands of species currently undergoing climate-change-driven redistribution into ecosystems outside of their range of origin.

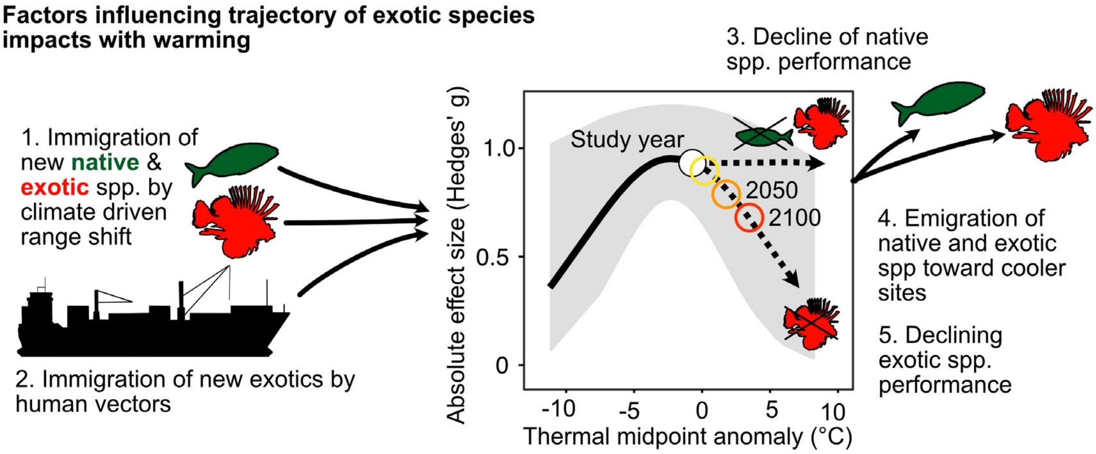

FIGURE 3 Heuristic model of factors influencing the trajectory of impacts of exotic species through time, in response to warming. The graph illustrates the best-fitting model of impacts on the abundance of native taxa in response to thermal midpoint anomalies (Figure 2). The white-filled circle represents the median thermal midpoint anomalies experienced by exotic species at the time studies were conducted. The yellow, orange and red open circles represent median midpoint anomalies in 2020, 2050 and 2100 under RCP8.5 warming projections and the corresponding median projected effect size, based on changes in temperature. However, temporal dynamics of the impacts of exotic species might be influenced by several factors in addition to temperature that might cause impacts to increase, remain stable or decrease through time. These include but are not limited to: immigration of new thermally tolerant native and new exotic species into the recipient site (1, 2); relative differences in thermal sensitivity between interacting native and exotic species in response to warming (3, 5); and poleward movement of established native and exotic species from recipient sites toward cooler sites (4) [Colour figure can be viewed at wileyonlinelibrary.com]

From the 10 response variables examined, the impact on abundance of native taxa was the only metric observed to show a significant hump-shaped relationship with temperature. For several response variables, small sample sizes prevented a robust examination of effect sizes, whereas impacts on taxa abundance accounted for > 42% of case studies in the data set. In addition, the direct link between thermal performance of exotic species and impacts on native taxa abundance aligns with current ecological constructs. Temperature can have a strong influence on the distribution and abundance of marine species, such as fishes, for example, where ≤ 75% of species display hump-shaped patterns in abundance across their thermal distribution (Waldock et al., 2019). High abundances of exotic species in favourable conditions would have direct trophic (e.g., predator, prey) and non-trophic (e.g., competition, facilitation) implications for the abundance of native species. Other common response variables, such as impacts on species richness, would be influenced by similar processes, but depend on more extreme impacts that reduce detection (e.g., complete removal of a species), potentially explaining the weaker relationship.

4.2 | Geographical implications of impacts of exotic species

The prevailing trend for exotic species to become established when introduced into cooler thermal regimes suggests that subtropical and tropical species might be more likely to succeed in temperate ecosystems than the other way around, supporting contentions that introductions of exotic species contribute to a tropicalization of temperate marine ecosystems (Vergés, Steinberg, et al., 2014; Wernberg et al., 2016). Likewise, temperate species might be expected to be more successful when introduced to polar and subpolar ecosystems (Krause-Jensen & Duarte, 2014) than to subtropical and tropical ecosystems. In addition, maximum impacts by exotic species on the abundance of native taxa were offset toward slightly cooler conditions than the thermal midpoint of the range of origin of exotic species. This pattern implies that there could be geographical differences in the severity of impacts by exotic species that emerge owing to geometric constraints on the thermal distributions of species, which are bound between the freezing point of seawater (i.e., −2°C) and maximum equatorial temperatures (*c*. 30°C). This implies that recipient sites close to the poles are more likely to fall below the thermal midpoint of an average species thermal distribution and sites close to the equator are more likely to fall above the thermal midpoint (Connolly et al., 2003). Given that the observed peak in impacts was offset below the thermal midpoint, this would suggest that cool-temperate and polar sites, by virtue of their geography, are more likely to experience large impacts by exotic species than tropical locations. These geographical differences suggest a mechanism that could help explain the phenomenon of weaker ecological impacts by exotic species in tropical regions (Elton, 1958) that is consistent with, and might even be amplified by, latitudinal differences in exotic species richness (Freestone et al., 2013).

4.3 | Additional factors influencing the distribution and magnitude of impacts

The magnitude of impact by exotic marine species was related to temperature, whereas the global redistribution of exotic species occurs independently of climate and climate change, per se. Additional factors must, therefore, influence the redistribution trajectory of exotic species toward higher, cooler latitudes and/or their ability to establish a viable population in these areas upon arrival. Invasion vectors, such as global shipping traffic, have been suggested as a potential driver of the poleward trajectory of exotic species (Drake & Lodge, 2004). Recent global analyses highlight that shipping, in conjunction with a multitude of geopolitical and socioeconomic factors, underpins the volume of species introductions (Sardain et al., 2019) and the capacity of nations to prevent or respond to exotic species (Early et al., 2016). These factors influence tropical, temperate and polar regions alike (Miller & Ruiz, 2014; Sardain et al., 2019; Seebens et al., 2013) and, in the case of maritime traffic, are projected to increase by 240–1,200% globally by 2050 (Sardain et al., 2019), resulting in a globally pervasive risk of marine species introductions.

Once a new species has arrived, the environmental characteristics of the recipient site and the biological traits of the exotic and recipient species then determine the success of its establishment. Greater biotic resistance to invasion in regions of high species richness (Freestone et al., 2013; Kimbro et al., 2013) or greater susceptibility to invasion in regions that already have high numbers of exotic species (Simberloff & Von Holle, 1999) are two such processes that can influence patterns of establishment and ecological impact. From our database, there was no evidence that invasion meltdown influenced patterns of impact in our study, and biotic resistance could not be tested directly.

Another explanation contributing to the high frequency of impacts of exotic species in cooler climates might be that upper thermal limits present a harder barrier for the establishment of exotic species than lower thermal limits. An asymmetrical plasticity in upper and lower thermal limits, whereby lower thermal limits are labile but upper thermal limits are conserved, has been observed widely among phylogenetically related terrestrial species (Araujo et al., 2013). In the ocean, the realized thermal distributions of fish and invertebrate species also support this idea, insofar as the temperature range of cold distribution limits is broader than the range of warm distribution limits (Stuart-Smith et al., 2017). The mechanisms underlying this phenomenon remain unresolved in the ocean, where, unlike on land, the freezing point of seawater buffers marine organisms against the need to adapt to extreme cold (Bennett et al., 2019). Intertidal species offer an obvious exception to this, whereby exposure to air temperatures can create a strong selection pressure for cold hardening (Aarset, 1982). However, patterns of species redistribution in our study suggested the opposite depth response, whereby intertidal species most closely conformed to their thermal range of origin, and species in deeper habitats showed a greater propensity to occur outside their range of origin, consistent with expectations of thermal depth refugia (Jorda et al., 2020). Nevertheless, greater capacity for acclimatization and adaptation to cold conditions could help to explain why 28% of marine exotic species were able to establish in climates colder than those experienced in their range of origin, compared with only 14% in warmer climates.

Another potential explanation for the high frequency of impacts of exotic species recorded in cooler climates could be an artefact of unequal research effort between temperate and tropical regions (Richardson & Poloczanska, 2008). Although this cannot be discounted, in intensively studied tropical regions, such as the Great Barrier Reef, Australia, there are no reports of impacts of exotic species, despite intense research effort and greater investment than in the less-studied Great Southern Reef, in temperate Australia (Bennett et al., 2016), where multiple exotic species have been reported (Supporting Information Figure S2). Nevertheless, research effort inequities do exist, such as in the Mediterranean Sea, where the amount of research on the impact of exotic species in the western basin is far greater than in the eastern basin (Supporting Information Figure S2). Reported impacts of exotic species in the western Mediterranean are often of temperate origin, whereas impacts by exotic species in the east are generally of tropical origin, owing to its proximity to the Suez Canal (Galil, 2007). To date, ecological impacts by the majority of exotic species in the eastern Mediterranean Sea have either not been quantified or are documented in the literature as climate-mediated instead of human-mediated redistributions (Vergés, Tomas, et al., 2014). The combination of research inequality and ambiguity about the redistribution vector would be likely to result in the Mediterranean Sea having a far greater impact of exotic species than currently reported.

4.4 | Influence of warming on impacts of exotic species

Human-mediated redistribution of marine species overcomes the obstacles and constraints imposed by geographical barriers, such as land masses and oceanographic fronts, to species migration with climate change (Burrows et al., 2014). For instance, the opening of the Suez Canal in 1869 has allowed > 500 Red Sea tropical species to enter the Mediterranean Sea (Galil, 2007), underpinning the documented tropicalization of this rapidly warming ecosystem (Raitsos et al., 2010). Impacts of exotic species on the abundance of native taxa suggest that ocean warming might generate a “conveyor belt” effect, whereby exotics establishing in cooler environments could have an increasing impact on recipient communities as climatic conditions approach their thermal optima and decline once conditions move beyond their optima, toward the upper thermal limits of the exotic species. Marine exotic species originating from warmer regions, which have established but seem to cause no harm, therefore need to be monitored carefully because they are candidates to develop larger impacts with future warming. At the same time, multiple factors will be likely to contribute to future impacts of exotic species, both for the existing interactions examined here and for new interactions that emerge because of ongoing introductions of exotic species and changing distributions of native and exotic species attributable to climate change.

In terms of the existing interactions, the projected temperature-driven decline in impacts of exotic species could be offset by even greater declines in the performance of native species. Previous studies examining the comparative effects of warming on exotic and native marine species have found that warming negatively affects native species to a greater extent than exotics (Sorte et al., 2013). This finding suggests that peak impacts could potentially be sustained beyond optimal temperatures in the future, if the performance of native species declines more rapidly than that of exotic species under warming. Alternative scenarios, such as the climate-driven expansion of warm-affiliated native species into sites with established exotic species, might be expected to drive down the impacts of exotic species, once beyond their optimal temperatures, owing to greater relative thermal performance of the range-extending species. The emergence of other novel interactions attributable to unrecorded impacts of established exotic species and new human-induced introductions of exotic species would be expected to result in similar patterns of impacts to those observed in the present study. Finally, climate-driven redistribution of both native and exotic species in response to warming has the potential to shift the location of species interactions and impacts in the direction of migrating isotherms, potentially reducing the impact in the original recipient site but moving the impact to neighbouring locations, resulting in similar net impacts within the broader region.

Temporal variability in temperature could also cause the impacts of exotic species to fluctuate over short time-scales. Indeed, analogous examples of this have been observed in the context of climate-driven range expansions, where tropical species have had large ecological impacts on recipient, cool-affinity communities after a marine heatwave (Bennett et al., 2015), resulting in lasting changes to community composition (Wernberg et al., 2016). Temporal changes in the relative strength of impacts on native communities are also widely recognized (Strayer et al., 2006) and could influence how existing interactions evolve over decadal scales. In our study, the elapsed time between the arrival of exotic species at recipient sites and the year impacts were measured averaged over 27 years and showed no relationship with the magnitude of effect sizes. Although predicting the specific outcomes of the diverse future scenarios is beyond the scope of this paper, evolutionary and ecological processes can influence the trajectory of impacts within recipient sites in addition to changes in temperature, with important implications for impacts by exotic species on the abundance of native taxa.

In conclusion, human activity relocates species around the world, and our results suggest that climatic conditions can influence the magnitude of the ecological impact that exotic species have on native communities. Impacts by exotic species suggest that evolved thermal niches continue to influence the performance of exotic species in foreign environments. Thermal conditions experienced by species relative to their range of origin or physiological optima can help to uncover broad-scale patterns in species interactions, with important implications for marine communities in the context of exotic species, range-shifting species and climate change.

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CONFLICT OF INTEREST

All authors declare no competing financial and non-financial interests.

AUTHOR CONTRIBUTIONS

S.B., J.S.-G., N.M. and C.M.D. conceived and designed the study. A.A., N.R.G., C.E.L., E.T.A., J.C., D.K.-J., N.M., P.M., J.M.P. and J.S.-G. constructed the exotic species impacts data set. S.B. and J.S.-G. compiled the exotic species range of origin data set, and G.J. compiled and analysed the observed and projected ocean temperature data. S.B. and J.S.-G. performed the data analyses, with contributions from all co-authors. S.B., J.S.-G. and C.M.D. wrote the manuscript, with contributions from all authors. All authors approved the submission.

DATA AVAILABILITY STATEMENT

All data underlying the study have been deposited in Digital CSIC (Bennett et al., 2020; http://dx.doi.org/10.20350/digitalCSIC/10863) and will be made publicly available upon publication.

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BIOSKETCHES

This work is the collaboration of an international working group looking at the global ecological impacts of marine exotic species. This article is the third publication from the working group.

Scott Bennett is a marine ecologist with a strong focus on the effects of climate change and comparative ecology of marine plants and animals across broad spatial and environmental gradients.

Julia Santana-Garcon is a marine ecologist who specializes in pelagic and coastal fish communities. Her work examines the effects of climate change on species interactions, stereo-video monitoring of pelagic and coastal fish assemblages and fisheries.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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