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Ecological effects of non-native species in marine ecosystems relate to co-occurring anthropogenic pressures

Running title: Anthropogenic pressures and invasion impact

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Abstract

Predictors for the ecological effects of non-native species are lacking, even though such knowledge is fundamental to manage non-native species and mitigate their impacts. Current theories suggest that the ecological effects of non-native species may be related to other concomitant anthropogenic stressors, but this has not been tested at a global scale. We combine an exhaustive meta-analysis of the ecological effects of marine non-native species with human footprint proxies to determine whether the ecological changes due to non-native species are modulated by co-occurring anthropogenic impacts. We found that non-native species had greater negative effects on native biodiversity where human population was high and caused reductions in individual performance where cumulative human impacts were large. On this basis we identified several marine ecoregions where non-native species may have the greatest ecological effects, including areas in the Mediterranean Sea and along the northwest coast of the USA. In conclusion, our global assessment suggests co-existing anthropogenic impacts can intensify the ecological effects of non-native species.

Keywords: invasive, exotic, alien, introduction, anthropogenic impacts, global change

INTRODUCTION

Non-native species are major drivers of losses in biodiversity (Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016) and ecosystem services (Pejchar & Mooney, 2009) at the global scale, as demonstrated for terrestrial invertebrates (Cameron, Vilà, & Cabeza, 2016), plants (Vilà et al., 2011), birds (Martin-Albarracin, Amico, Simberloff, & Nuñez, 2015) and marine species (Anton et al., 2019), among others. Humans are a main vector of non-native-species introductions and the total number of non-native species are associated with anthropogenic impacts (Dawson et al., 2017; McKinney, 2002; Pyšek et al., 2010). Studies have found positive associations between the abundance of non-native species and anthropogenic stressors using a variety of proxies, including gross domestic product, human population density, time since modern human settlement and cumulative human impacts (Dawson et al., 2017; Gallardo, Zieritz, & Aldridge, 2015; McKinney, 2001; Pyšek et al., 2010; Seabloom et al., 2006). The ecological impact of non-native species, and not just their abundance, could be magnified by anthropogenic disturbances (Byers, 2002). However, a global analysis of the relationship between the effects of non-native species and anthropogenic disturbances is lacking.

Anthropogenic disturbance can potentially affect the ecological effects of non-native species through multiple mechanisms, such as creating novel habitats that facilitate invasion (Byers, 2002), reducing native fauna (e.g., removing potential predators and competitors of non-native species) and introducing the propagules of non-native species, which may increase their chances of establishment (Simberloff, 2009) and associated impact (Ricciardi & Kipp, 2008). For example, hydrological management and the enhancement of non-native species propagule supply (associated with shipping activity) resulted in the dominance of non-native over native zooplankton in the San Francisco Bay (Winder, Jassby, & Mac Nally, 2011). Moreover, warming can facilitate non-native species in fouling communities because native species may be more sensitive to temperature changes (Sorte, Williams, & Zerebecki, 2010). Armoring the coast with artificial structures can also enhance the abundance of non-native macroalgae and alter local nutrient dynamics (Geraldi, Smyth, Piehler, & Peterson, 2014). However, a holistic global assessment to determine if the observed effects of non-native species on recipient communities are modulated by anthropogenic stressors remains to be explored.

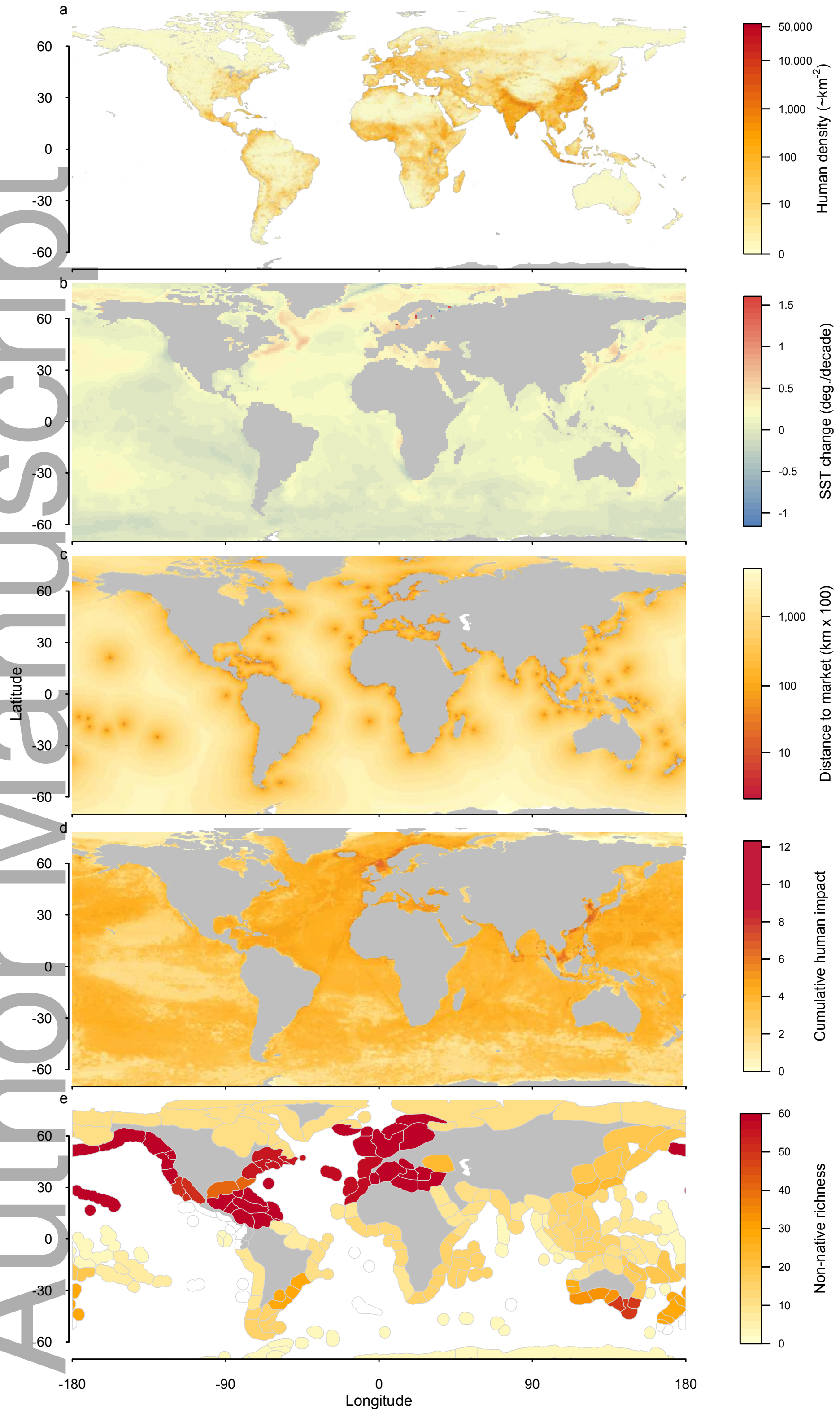
Here we combined an exhaustive database documenting the ecological effects of marine non-native species (Anton et al. 2019) with global data layers of relevant human footprint to determine whether the ecological impacts of non-native species are related to anthropogenic disturbances. Specifically, we *a priori* chose five predictor variables of human disturbance that are available at a global scale (Table 1; Fig. 1).

Table 1. Summary of drivers and hypotheses for why human footprint can enhance the effects of non-native species.

Category	**Hypotheses**	**Predictor variable as proxies**
Environmental degradation from human presence	Environmental degradation from human stressors will increase introductions and their impact (Gallardo et al., 2015; Halpern et al., 2012; Ogutu-Ohwayo, 1990; Pyšek et al., 2010)	Distance to market (Yeager, Marchand, Gill, Baum, & McPherson, 2017), human population within 100km (CIESIN, 2017), cumulative human impact (Halpern et al., 2008)

Invasion meltdown	Synergistic interactions among invaders will enhance impacts on native ecosystems, an invasion meltdown hypothesis (Simberloff, 2006; Simberloff & Von Holle, 1999)	Richness of non-native species (Molnar, Gamboa, Revenga, & Spalding, 2008)
Global warming	Warming will enhance the performance of non-natives and negatively affect the native species, resulting in greater ecological impacts of non-native species (Sorte et al., 2013, 2010)	Change in sea surface temperature (Rayner et al., 2003)

Figure 1. Global maps of the human footprint proxies including human density (a), sea surface temperature (SST) change (b), distance to market (c), cumulative human impact (d) and number of non-native species (e).



The variables and the rationale for inclusion are as follows. Human population density was included because of its strong association with environmental change and number of non-native species (Dawson et al., 2017; McKinney, 2002; Pyšek et al., 2010). The rate of sea surface temperature (SST) change was included given that global warming can enhance the effect of non-native species (Sorte et al., 2013, 2010). Distance to market (e.g., provincial capitals) was included because it is a measure of fishing pressure (Cinner, Graham, Huchery, & Macneil, 2013) and a proxy for isolation from human development given that increased number of non-native species may proceed or be at the front of human development (McKinney, 2001; Seabloom et al., 2006). Cumulative human impact, a component of the ocean health index (Halpern et al., 2012, 2008), was included because it is a global and inclusive estimate of many anthropogenic disturbances that are often cited for ecosystem degradation. Finally, a spatial layer of the number of non-native species within marine ecoregions (Molnar et al., 2008) was included because the effect of non-native species may be facilitated by the presence of other non-native species (Ricciardi & Kipp, 2008), which has been referred to as invasion meltdown (Simberloff, 2006; Simberloff & Von Holle, 1999). We then use the statistical models obtained to assess the potential ecological effect of non-native across worldwide ecoregions.

METHODS

A literature search was performed on the effect of marine non-native species and a quantitative meta-analysis was conducted as detailed in Anton et al. (2019). Briefly, the Web of Science was searched for papers that quantified the ecological effect of non-native species in the marine environment in June of 2016. The search resulted in 1,111 research articles, of which 316 articles included studies that quantitatively assessed the ecological effect of non-native species. Hedges *g* and the variance for Hedges *g* were calculated following Koricheva et al. (2013) and are the preferred metric for meta-analysis (Koricheva et al., 2013). Hedges *g* was used as the effect size for each of the entries to quantify increases or decreases in ecological variables. The effect sizes for each study were matched with their location and then overlaid with global databases of environmental and human impact variables. We focused on human footprint proxies because strong relationships did not exist between ecological effects and environmental or geographic factors (e.g. latitude (Anton et al., 2019), and human footprint proxies were more important than climatic or geographic variables in predicting the number of non-native species (Dawson et al., 2017; Pyšek et al., 2010).

Predictor variables were chosen because they represented the most direct measures of human caused environmental degradation in the marine environment and had global, fine-scale coverage. We avoided including predictor variables that could be redundant. For example, we chose not to include gross domestic product, which has been used as a combined proxy for propagule pressure, pathways of introduction, eutrophication, and intensity of anthropogenic disturbance (Pyšek et al., 2010). Instead we used cumulative human impact because it encompassed more direct measures of these human impacts including shipping traffic, nutrient pollution, and multiple metrics of fishing pressure (Halpern et al., 2008). Predictor variable were collected from 5 open sources. Distance to market as a measure of market access and the human impact through commerce and fishing (Cinner et al., 2013) were retrieved from the Marine Socio-Environmental Covariates database (Yeager et al., 2017). Cumulative human impact was used as an overall measure of anthropogenic effects and includes a compilation of 17 different variables including fishing, pollution, and commerce (Halpern et al., 2012, 2008). The human population within a 100 km radius of the study location was included as another measure of direct anthropogenic disturbance and was determined from UN WPP-Adjusted Population Count, v4.10 (CIESIN, 2017). The number of non-native species was extracted for each coastal province for each study (Molnar et al., 2008). The linear rate of temperature change was calculated from mean annual SST from 1980 to 2016, which was calculated from the HadISST data (Rayner et al., 2003) using the load_hadsst function from the hadsstr package (Byrnes, 2016).

Data from each layer was extracted for each study location with R using the *raster* package (Hijmans & van Etten, 2012). If data from multiple years was available, the mean of the data from 2000 to 2012 was used because this time frame included the majority of studies. If needed, the layers were re-projected in WGS84. The nearest layer value was extracted if the study location was not within the layer extent (i.e., some study locations were intertidal or estuarine, and were not included in marine data).

To determine the relationship between the human footprint proxies (predictor variables, fixed factors) and the effects of non-native species on recipient communities (response variables), we ran general linear models using the lmer function in the lme4 package (Bates, Mächler, Bolker, & Walker, 2015, p. 4), along with the lmerTest package to determine p-value (Kuznetsova, Brockhoff, & Christensen, 2017). Three separate models were used to test the relationship between predictor variables and the effect size (Hedges' *g*) of the following response variables: abundance (changes in the number or density of native individuals), biodiversity (changes in richness and diversity measures of native taxa), and effects on individual performance (changes in growth, survival, and fitness of native taxa). To account for effects of running multiple tests, a p-value of 0.0167 (0.05 p-value / 3 tests) was the cutoff for significance.

To reduce potential dependence among response data, the models also included two random variables that represented study nested in marine biome (1|biome/study ID) and non-native species nested in trophic level (1|exotic trophic level /species ID). The variance associated with Hedges *g* was included in the model as a weight (1/variance) in order to give less emphasis to effect sizes with greater variance (Koricheva et al., 2013). All two-way interactions were initially included in each model and models were subsequently re-run after the non-significant interaction having the highest p-value was removed; this procedure was repeated until only significant interaction terms remained ($p<0.05$). Predictor variables were converted to z-scores (i.e. subtracted the mean and divided by standard deviation) to reduce differences in scale and reduce multicollinearity among terms. In addition, human population density and distance to market were transformed (log(x+1)) to reduce the influence of outliers. There was no indication of multicollinearity among independent variables (variable inflation factor < 1.5, measured using vif function from the HH package; Heiberger, 2017). The response variable (effect size Hedges' *g*) was log transformed to reduce outliers (the absolute value of negative numbers was used for transformation, log(abs(x)+1)*-1). The model fit was deemed appropriate based on plotting the residuals vs fitted data (randomly distributed points), normal Q-Q plots (linear relationship) and fitted vs actual data (linear relationship). The explanatory power of models (r^2 values of each of the three overall models including the random variables as well as r^2 values of all predictor variables and significant interaction terms) was determined using the r.squaredGLMM function from the MuMIn package (Bartoń, 2018).

To predict which marine regions may be most susceptible to ecological effects of non-native species, we extrapolated our findings to coastlines around the globe. First, a marine bathymetry raster layer (minimum depth within cells of 0.5 arc minutes; Bio-oracle, (Assis et al., 2017) was limited to -60 to 70 latitude and 10 m above to -30 m below sea-level. These elevations included all but 16 of the 1111 data entries of the original meta-analysis database. Although this method in identifying coastal locations left some steep coasts out of the analysis, such as the northwest coast of South America, these regions had no studies and we deemed this the most appropriate way to only include areas that were consistent with input data. The filtered raster layer was converted to points (centroid of the raster cell) and the data for each predictor variable used in the linear models was extracted for these points. Only points that had data for all predictor variables were included, which resulted in 88,843 points worldwide. The effect size was then determined for each of these points using the models previously described with the predict function from the lme4 package (Bates et al., 2015). To identify coastal regions that may be most vulnerable to ecological effects of non-native species, we calculated the median predicted effect size per ecoregion (Spalding et al., 2007). Ecoregions with effect sizes different from 0 were determined by the 95% confidence interval of all points within the ecoregion not overlapping with 0 using the ci function from the gmodels package (Warnes, Bolker, Lumley, & Johnson, 2018). All analyses were conducted in R version 3.5.3, R code used is available at https://github.com/ngeraldi/marine-exotics-global-analysis.

RESULTS

Reductions in native biodiversity due to non-native species were greatest where human population density was largest, and this response variable was also related to three significant 2-way interactions between predictor variables (Table 2, Fig. 1, 2b, and 3a).

Table 2. Statistical model summary of the variance explained by predictor variables. Study nested within biome and species nested within trophic level were included as a random variables in the mixed effects linear model. Significant predictor variables with a p-value<0.0167 (accounts for multiple tests) are indicated with asterisks. The number of studies and number of entries for each model are indicated in parentheses under the response label, respectively. Sea surface temperature is abbreviated as SST

Response	Predictor	Estimate	Std. Error	df	t value	Pr(>|t|)
Effect size of non-native species on:						
Taxa	Distance to market	-0.093	0.045	89.6	-2.077	0.041

abundance						
(112, 632)	Human population within 100km	-0.086	0.043	66.3	-2.002	0.049
	Non-native species richness	0.041	0.040	71.7	1.023	0.310
	Cumulative human impact	0.002	0.034	74.4	0.064	0.949
	Rate of SST change	-0.023	0.040	75.1	-0.563	0.575
Native biodiversity	Distance to market	-0.039	0.079	29.5	-0.489	0.628
(54, 188)	Human population within 100km	-0.243	0.095	26.9	-2.555	0.017*
	Non-native species richness	-0.093	0.068	42.5	-1.358	0.182
	Cumulative human impact	0.101	0.060	18.2	1.693	0.108
	Rate of SST change	0.011	0.071	33.2	0.162	0.873
	Distance to market: Non-native species richness	0.162	0.059	38.2	2.751	0.009*
	Human population: Cumulative human impact	-0.164	0.059	15.3	-2.759	0.014*
	Human population: Rate of SST change	0.201	0.071	33.1	2.854	0.007*
Individual performance	Distance to market	-0.009	0.046	25.5	-0.192	0.850
(32, 112)	Human population within 100km	-0.049	0.055	14.8	-0.883	0.391
	Non-native species richness	0.036	0.050	15.8	0.720	0.482
	Cumulative human impact	-0.132	0.049	20.9	-2.688	0.014*
	Rate of SST change	-0.130	0.059	14.5	-2.190	0.045

Figure 2. Location and effect size of non-native species based on studies from the meta-analysis measuring changes in organism abundance (a), biodiversity (b) and individual performance (c) using Hedges *g*.

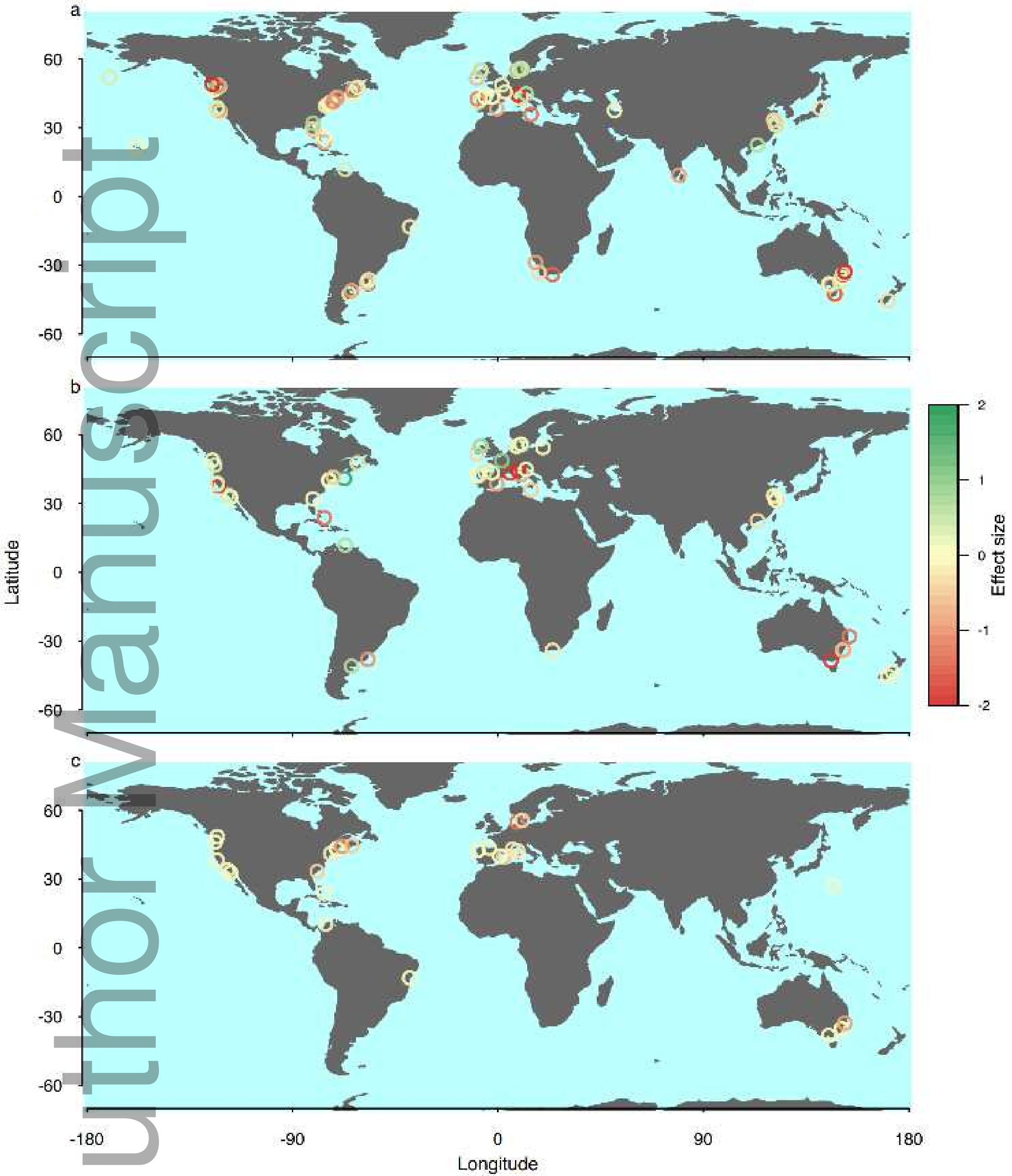
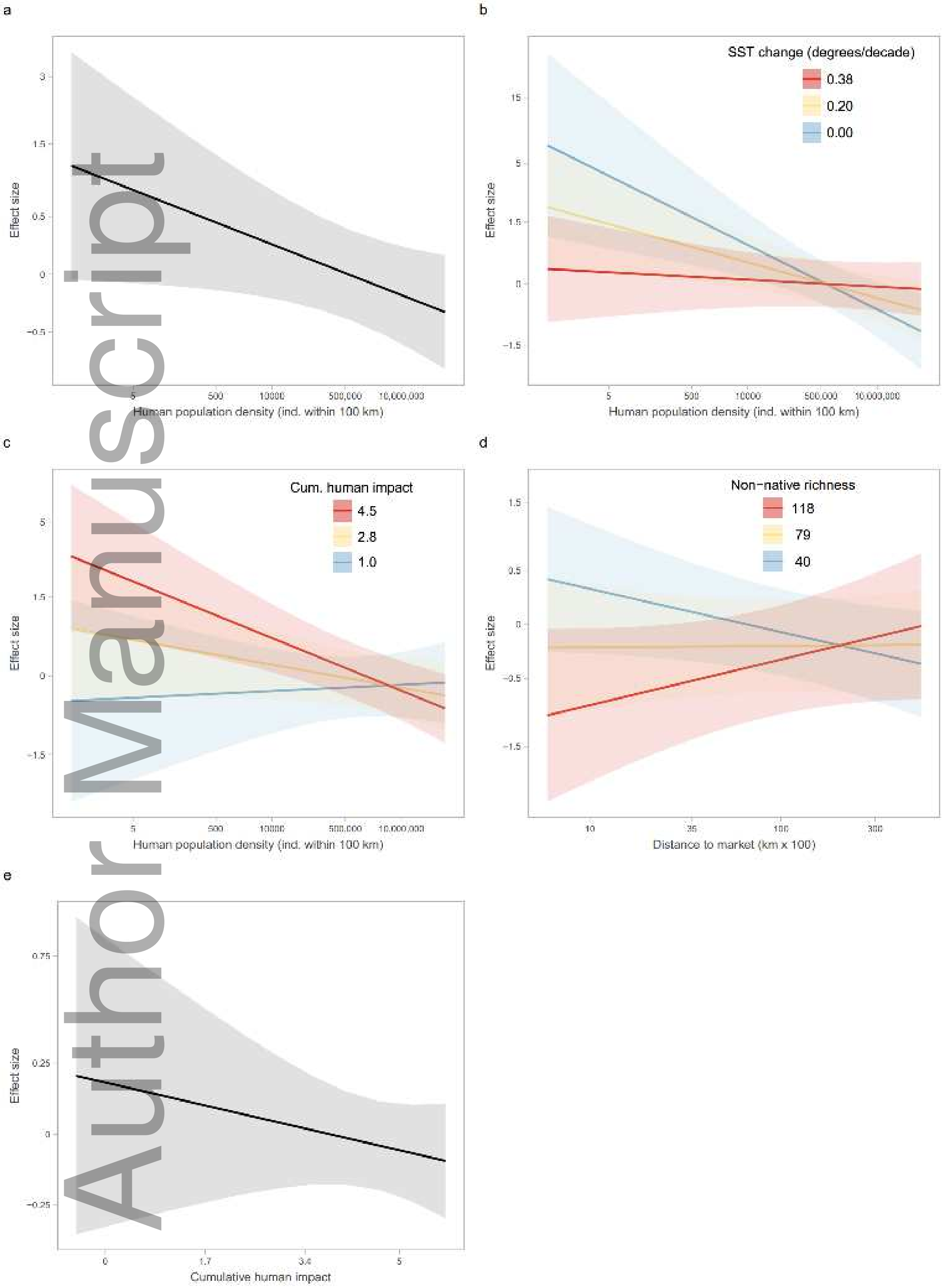


Figure 3. The model output relating human footprint proxies and the effect size of non-native species on biodiversity including the significant terms, human population density (a), and the interactions between human population density and sea surface temperature (SST) change (b), human population density and cumulative human impact (c), and distance to market and the

richness of non-native species (d), as well as how the effect size on individual performance was related with cumulative human impact (e). Human footprint increases from left to right on x-axes except for d. For interaction plots (b,c,d), one interaction term is shown on the x-axis, while the other is divided into 3 categories: Red indicates the data higher than 1 standard deviation from the mean; yellow shows the data within 1 standard deviation of the mean; and blue indicates the data lower than 1 standard deviation from the mean. Mean values of data within deviation categories (-, ~, +) are shown in legend. Shading indicates 95% confidence intervals. The data are plotted in the form they were modeled, but labels were back-transformed so findings were interpretable.


a
Effect size
3
1.5
0.5
0
−0.5
5
500
10000
500,000
10,000,000
Human population density (ind. within 100 km)
b
SST change (degrees/decade)
0.38
0.20
0.00
Effect size
15
5
1.5
0
−1.5
5
500
10000
500,000
10,000,000
Human population density (ind. within 100 km)
c
Cum. human impact
4.5
2.8
1.0
Effect size
5
1.5
0
−1.5
5
500
10000
500,000
10,000,000
Human population density (ind. within 100 km)
d
Non−native richness
118
79
40
Effect size
1.5
0.5
0
−0.5
−1.5
10
35
100
300
Distance to market (km x 100)
e
Effect size
0.75
0.25
0
−0.25
0
1.7
3.4
5
Cumulative human impact

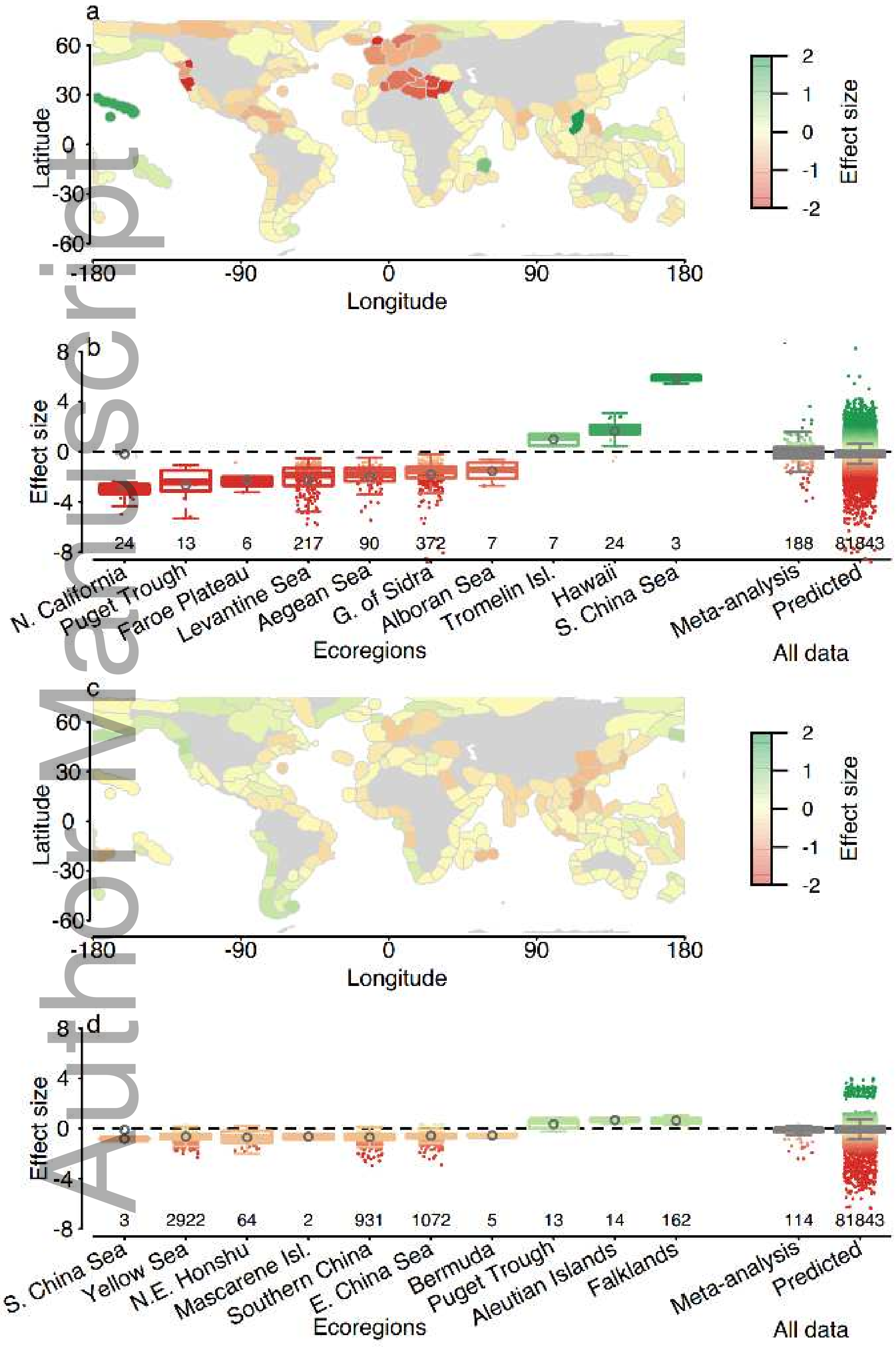
Hence, the negative effect of non-native species on biodiversity as human population increased was most pronounced when SST change was low and was amplified when the cumulative human impact was high (Fig. 3b and c). Moreover, when the non-native species richness was low, the effect of non-native species on native biodiversity shifted from positive to negative as the distance to market increased (Fig. 3d). The opposite trend occurred when the non-native species richness was high and the effect of the non-native species on biodiversity turned from negative to positive as the distance to market increased. This model relating the effect size of non-native species on biodiversity to predictor variables had an r^2 of 0.36 and the predictor variables together had an r^2 of 0.11. Results from the model and presented in Fig.3 for human population density are presented as number of humans within 100 km of the study location. To estimate human density per km^2 and compare this to Fig. 1a, human density around study location needs to be divided by 314,000. Using this calculation, when the modeled effect size becomes negative at ~700,000 humans within 100km radius equates to a mean of ~22 individuals per km^2.

The effects of non-native species on native species abundance were not significantly related with any of the predictor variables (p-values > 0.0167; Fig. 1 and 2a, Table 2). In addition, the model had a low overall r^2 of 0.13 and the fixed factors had an r^2 of 0.014. The effect size of non-native species on individual performance was significantly related to cumulative human impact, with non-native species having greater negative effects on individual performance as cumulative human impact increased (Fig. 1, 2c, and 3e; Table 2). This model had an overall r^2 of 0.28 and the predictor variables had an r^2 of 0.11.

The results of the two models predicting effects of non-native species on biodiversity and individual performance based on human pressures were extrapolated world-wide to characterize the vulnerability of coastal ecoregions to the ecological effects of non-native species. In general, non-native species were projected to have a greater effect on biodiversity than on individual species (Fig. 4).

Figure 4. The predicted effect size of non-native species on biodiversity (a-b) and individual performance (c-d) in coastal ecoregions. The effect size was calculated from 0.5 arc degree cells with minimum elevations of 10 to -30 m. Predicted values were based on the mixed effects general linear models with the 5 predictor variables for each coastal cell. The median effect size for each ecoregion across the globe was included for the effect on biodiversity (a) and individual

performance (c). Data for biodiversity (b) and individual performance (d) are shown as boxplots for the ecoregions with the lowest 7 and greatest 3 median effect sizes and all meta-analysis and predicted data (2 boxplots on right). Boxplots indicate upper and lower quartile with whiskers extending up to 1.5 times the respective quartile. Points within boxplots are predicted value for each coastal cell and total cells per ecoregions or dataset are indicated below box. Colors of boxplot and points indicate effect size (red to green represent low to high values).


a
Latitude
60
30
0
-30
-60
-180
-90
0
90
180
Longitude
Effect size
2
1
0
-1
-2
b
Effect size
8
4
0
-4
-8
24
13
6
217
90
372
7
7
24
3
188
81843
N. California
Puget Trough
Faroe Plateau
Levantine Sea
Aegean Sea
G. of Sidra
Alboran Sea
Tromelin Isl.
Hawaii
S. China Sea
Meta-analysis
Predicted
Ecoregions
All data
c
Latitude
60
30
0
-30
-60
-180
-90
0
90
180
Longitude
Effect size
2
1
0
-1
-2
d
Effect size
8
4
0
-4
-8
3
2922
64
2
931
1072
5
13
14
162
114
81843
S. China Sea
Yellow Sea
N.E. Honshu
Mascarene Isl.
Southern China
E. China Sea
Bermuda
Puget Trough
Aleutian Islands
Falklands
Meta-analysis
Predicted
Ecoregions
All data

In most (67%) of the ecoregions, non-native species were predicted to reduce biodiversity (118 of 175 ecoregions), while they were predicted to enhance biodiversity in only 18% of the ecoregions (31 of 175 ecoregions) and to have no effect on biodiversity in the remaining 15% (26 of 175; Fig. 4a and b) of ecoregions. The ecoregions that appear most vulnerable to reductions in biodiversity from non-native species include the Mediterranean Sea, areas around Northern Europe, and Northern California. These regions, particularly around Europe, were associated with areas of high human population density, high non-native species richness, and high warming (Fig. 1). Some regions, for example the Hawaiian Islands, had positive relationships between non-native marine species and biodiversity, which resulted from high richness of non-native species and far from markets, median levels of warming and cumulative human impact, but low human density (Fig. 1-4). Non-native species were predicted to reduce individual performance of native species (e.g., growth or survival) in 81 of 175 ecoregions (46%), while increasing individual performance in 58 of 175 ecoregions (33%), and have no effect in the remaining ecoregions (Fig. 4c and d). Ecoregions that were predicted to be most vulnerable to reductions in individual performance resulting from non-native species include the China and Baltic Seas (Fig. 4c and d), largely because of the high cumulative human impact in these areas (Fig. 1d, Table 1).

DISCUSSION

Our findings support existing theory that anthropogenic stressors can exacerbate the effects of non-native species (Byers, 2002), as the overall effect of non-native species on native biodiversity became negative as human population density decreased, which was most evident in areas with high cumulative human impact and minimal changes in SST. This hypothesis was further supported by the negative relationship between effects of non-native species on the performance of native individuals and cumulative human impacts. Next steps will be to elucidate the mechanisms that drive these patterns and determine if unaccounted variance can be attributed to other global or local factors or if it is stochastic.

In this study we performed a global assessment of concomitant effects of anthropogenic stressors and non-native species, which have been suggested to act synergistically (Byers, 2002). For instance, highly populated areas are associated with many impacts on the environment including the enhancement of habitat degradation, nutrient enrichment, harvest of natural resources, and transportation which can alter the environment that native species have adapted, removing the evolutionary advantage of the latter when compared to non-native species (Byers, 2002). Studies on the relationship between the richness of non-native species and human impacts in terrestrial and freshwater ecosystems have found that human population density and wealth were the best predictors of the richness of non-native species, even when models included climate and geographic predictors (Dawson et al., 2017; Pyšek et al., 2010). In addition, human population density has been correlated with the abundance of non-native fish and plant species (McKinney, 2001).

We found similar results for links between human footprint and the ecological effects of non-native species; with greater human footprint generally associated with enhanced negative effects of non-native species. The effect of non-native species on biodiversity also included interactions indicating that 1) stressors may act in synergy as was the case with human population density and cumulative human impact, 2) environmental degradation may reach a point beyond which increasing additional stressors no longer worsen the effect of non-native species, such as with SST change and human population density, and 3) a stressor can have opposing effects on biodiversity depending on the strength of another stressor, as was the pattern between distance from market and richness of non-native species. While examples of thresholds and synergies exist in ecological context of stressors, the third example is more complex, and resulted in non-native species reducing native biodiversity in areas with both high non-native richness and close to markets, as well as low non-native richness and long distances from markets (e.g. Arctic ecoregions of North America). This seemingly contradictory finding, i.e. that both isolated, less degraded areas and regions with a large human footprint, can be associated with the greater effects of non-native species agrees with two existing theories in invasion ecology: insular vulnerability (i.e., large impact of non-native species on islands; Doherty *et al.* 2016; McCreless *et al.* 2016) and invasion meltdown (i.e., introduced species facilitate one another's establishment, spread, and impacts; (Simberloff, 2006). Our findings suggest that biodiversity on both sides of the spectrum of habitat degradation (less degraded and heavily altered areas) may be the most vulnerable to the impacts of non-native species.

Our findings have a number of limitations, as they derive from statistical relationships where specific mechanisms are not explicit. However, the patterns uncovered and the associated predictions have value, as the context-dependent nature of introductions and ecological effects of non-native species (e.g., the successful establishment and effects of the exotic species may vary depending on location or environmental conditions; (Green & Crowe, 2014; South, Dick, McCard, Barrios-O'Neill, & Anton, 2017), imply that large-scale predictors for the effects of non-native species are almost non-existent. Context-dependency was likely a driving factor for why the effect of non-native species on abundance of natives was not related to any human footprint proxy. The statistical models reported here provide a first-order attempt at using human footprint proxies to predict the effects of marine non-native species at a global scale. Our models on the effects of non-native species on biodiversity and individual performance explained about 30% of the variation and human footprint proxies accounted for 10% (the other 20% was explained by random variables). Considering the myriad of factors that influence the effect of non-native species, including context dependencies as well as the current limited ability to predict the effect of non-native species on recipient communities, explaining 10% of the variability in effects of non-native species on biodiversity using a few human footprint proxies represents a significant step toward improving our understanding of the influence of non-native species on marine ecosystems. A limitation of broad-scale models, such as this one, are that while patterns are described, mechanisms cannot be ascertained and the quality of the output is dependent on the quality and breadth of the input data. In some ecoregions predicted values of both diversity and individual performance were outside the range of input values and therefore have high levels of uncertainty, which is evident for Hawaii and the South China Sea Islands (Fig. 4). Improvement of predictive models will occur as more quantitative data on the effects of non-native species can be included and as human footprint proxies measured at global scales become more accurate (i.e., global estimates of non-native richness exist only at marine providence scales) and inclusive. A final consideration is the use of negative and positive effect sizes as negative and positive ecological effects of non-native species, which relies on a human evaluation of damage (e.g., deleterious or beneficial effects). We make this inference because our response variables were limited to ones indicative of direct consequences for native species or communities (e.g., decreases on native species biodiversity, abundance or fitness indicate negative effects on the ecological properties of native communities). Thus, results were interpreted with the denotation and not the connotation associated with negative and positive ecological effects of non-native species.

Our global spatial analyses help delineate where non-native species could be exerting the greatest effects. Our results indicate that the northern and southern coasts of Europe and areas of the northwestern coast of the USA might be particularly vulnerable to losses of biodiversity as a consequence of non-native species. This is specifically important given the need to reverse the current trend of biodiversity loss in the Anthropocene (Ceballos et al., 2015; Ceballos, Ehrlich, & Dirzo, 2017). Although coastal regions of eastern Asia and northern Europe may experience the greatest effect of non-native species on individual performance of native species, this seems to be minor when compared to the effect sizes on biodiversity (predicted effect size for the ecoregions with the lowest effect sizes were -3 for biodiversity but greater than -1 for individual performance).

Simberloff (2006) summed up a primary concern of invasion ecology by stating that predicting the impacts of invasions "*is part of the larger search for the Holy Grail of invasion biology*". The goal of predicting the impacts of non-native species has remained elusive given context-dependency and the limited data availability for the ecological effects of non-native species, which is particularly evident for marine ecosystems (i.e., the effects of only 6% of marine non-native species have been quantified; (Anton et al., 2019). Knowing that terrestrial communities on islands are extremely vulnerable to non-native species has resulted in prioritizing management actions to minimize introductions and initiate eradication strategies (Jones et al., 2016; Simberloff, 2001). Our results suggest similar management priorities for non-native marine species introduced to isolated and less degraded areas, but should also target highly degraded areas to mitigate the global negative effects of non-native species on biodiversity.

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REFERENCES

Anton, A., Geraldi, N. R., Lovelock, C. E., Apostolaki, E. T., Bennett, S., Cebrian, J., … Duarte, C. M. (2019). Global ecological impacts of marine exotic species. *Nature Ecology & Evolution*, *3*, 787–800. https://doi.org/10.1038/s41559-019-0851-0

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E. A., & Clerck, O. D. (2017). Bio-ORACLE v2.0: Extending marine data layers for bioclimatic modelling. *Global Ecology and Biogeography*, *27*(3), 277–284. https://doi.org/10.1111/geb.12693

Bartoń, K. (2018). *MuMIn: Multi-Model Inference*. Retrieved from https://CRAN.R-project.org/package=MuMIn

Bates, D. M., Mächler, M., Bolker, B. M., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*, 1:48. https://doi.org/10.18637/jss.v067.i01

Byers, J. E. (2002). Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos*, *97*(3), 449–458. https://doi.org/10.1034/j.1600-0706.2002.970316.x

Byrnes, J. E. (2016). *hadsstr: Calculate the Velocity of Climate Change Using Hadley Centre SST*.

Cameron, E. K., Vilà, M., & Cabeza, M. (2016). Global meta-analysis of the impacts of terrestrial invertebrate invaders on species, communities and ecosystems. *Global Ecology and Biogeography*, *25*(5), 596–606. https://doi.org/10.1111/geb.12436

Ceballos, G., Ehrlich, P. R., Barnosky, A. D., García, A., Pringle, R. M., & Palmer, T. M. (2015). Accelerated modern human–induced species losses: Entering the sixth mass extinction. *Science Advances*, *1*(5), e1400253. https://doi.org/10.1126/sciadv.1400253

Ceballos, G., Ehrlich, P. R., & Dirzo, R. (2017). Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proceedings of the National Academy of Sciences*, *114*(30), E6089–E6096. https://doi.org/10.1073/pnas.1704949114

CIESIN. (2017). *Center for International Earth Science Information Network - CIESIN - Columbia University.* Gridded Population of the World, Version 4 (GPWv4): Population Count Adjusted to Match 2015 Revision of UN WPP Country Totals, Revision 10.

Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). https://doi.org/10.7927/H4JQ0XZW.

Cinner, J. E., Graham, N. a. J., Huchery, C., & Macneil, M. A. (2013). Global Effects of Local Human Population Density and Distance to Markets on the Condition of Coral Reef Fisheries. *Conservation Biology*, *27*(3), 453–458. https://doi.org/10.1111/j.1523-1739.2012.01933.x

Dawson, W., Moser, D., Kleunen, M. van, Kreft, H., Pergl, J., Pyšek, P., … Essl, F. (2017). Global hotspots and correlates of alien species richness across taxonomic groups. *Nature Ecology & Evolution*, *1*(7), s41559-017-0186–017. https://doi.org/10.1038/s41559-017-0186

Doherty, T. S., Glen, A. S., Nimmo, D. G., Ritchie, E. G., & Dickman, C. R. (2016). Invasive predators and global biodiversity loss. *Proceedings of the National Academy of Sciences*, 201602480. https://doi.org/10.1073/pnas.1602480113

Gallardo, B., Zieritz, A., & Aldridge, D. C. (2015). The Importance of the Human Footprint in Shaping the Global Distribution of Terrestrial, Freshwater and Marine Invaders. *PLOS ONE*, *10*(5), e0125801. https://doi.org/10.1371/journal.pone.0125801

Geraldi, N. R., Smyth, A. R., Piehler, M. F., & Peterson, C. H. (2014). Artificial substrates enhance non-native macroalga and N2 production. *Biological Invasions*, *16*(9), 1819–1831. https://doi.org/10.1007/s10530-013-0629-2

Green, D. S., & Crowe, T. P. (2014). Context- and density-dependent effects of introduced oysters on biodiversity. *Biological Invasions*, *16*(5), 1145–1163. https://doi.org/10.1007/s10530-013-0569-x

Halpern, B. S., Longo, C., Hardy, D., McLeod, K. L., Samhouri, J. F., Katona, S. K., … Zeller, D. (2012). An index to assess the health and benefits of the global ocean. *Nature*, *488*(7413), 615–620. https://doi.org/10.1038/nature11397

Halpern, B. S., Walbridge, S., Selkoe, K. A., Kappel, C. V., Micheli, F., D'Agrosa, C., … Watson, R. (2008). A global map of human impact on marine ecosystems. *Science*, *319*(5865), 948–952.

Heiberger, R. M. (2017). *HH: Statistical Analysis and Data Display: Heiberger and Holland. R package version 3.1-34. URL https://CRAN.R-project.org/package=HH.*

Hijmans, R. J., & van Etten, J. (2012). *raster: Geographic analysis and modeling with raster data. R package version 2.0-12. http://CRAN.R-project.org/package=raster*.

Jones, H. P., Holmes, N. D., Butchart, S. H. M., Tershy, B. R., Kappes, P. J., Corkery, I., … Croll, D. A. (2016). Invasive mammal eradication on islands results in substantial conservation gains. *Proceedings of the National Academy of Sciences*, *113*(15), 4033–4038. https://doi.org/10.1073/pnas.1521179113

Koricheva, J., Gurevitch, J., & Mengersen, K. (Eds.). (2013). *Handbook of Meta-analysis in Ecology and Evolution*. Retrieved from https://www.jstor.org/stable/j.ctt24hq6n

Kuznetsova, A., Brockhoff, P. B., & Christensen, R. H. B. (2017). lmerTest Package: Tests in Linear Mixed Effects Models. *Journal of Statistical Software*, *82*(13), 1–26. https://doi.org/10.18637/jss.v082.i13

Martin-Albarracin, V. L., Amico, G. C., Simberloff, D., & Nuñez, M. A. (2015). Impact of Non-Native Birds on Native Ecosystems: A Global Analysis. *PLOS ONE*, *10*(11), e0143070. https://doi.org/10.1371/journal.pone.0143070

McCreless, E. E., Huff, D. D., Croll, D. A., Tershy, B. R., Spatz, D. R., Holmes, N. D., … Wilcox, C. (2016). Past and estimated future impact of invasive alien mammals on insular threatened vertebrate populations. *Nature Communications*, *7*, 12488. https://doi.org/10.1038/ncomms12488

McKinney, M. L. (2001). Effects of human population, area, and time on non-native plant and fish diversity in the United States. *Biological Conservation*, *100*(2), 243–252. https://doi.org/10.1016/S0006-3207(01)00027-1

McKinney, M. L. (2002). Do human activities raise species richness? Contrasting patterns in United States plants and fishes. *Global Ecology and Biogeography*, *11*(4), 343–348. https://doi.org/10.1046/j.1466-822X.2002.00293.x

Molnar, J. L., Gamboa, R. L., Revenga, C., & Spalding, M. D. (2008). Assessing the global threat of invasive species to marine biodiversity. *Frontiers in Ecology and the Environment*, *6*(9), 485–492. https://doi.org/10.1890/070064

Ogutu-Ohwayo, R. (1990). The decline of the native fishes of lakes Victoria and Kyoga (East Africa) and the impact of introduced species, especially the Nile perch, Lates niloticus, and the Nile tilapia, Oreochromis niloticus. *Environmental Biology of Fishes*, *27*(2), 81–96. https://doi.org/10.1007/BF00001938

Pejchar, L., & Mooney, H. A. (2009). Invasive species, ecosystem services and human well-being. *Trends in Ecology & Evolution*, *24*(9), 497–504. https://doi.org/10.1016/j.tree.2009.03.016

Pyšek, P., Jarošík, V., Hulme, P. E., Kühn, I., Wild, J., Arianoutsou, M., … Winter, M. (2010). Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the National Academy of Sciences*, *107*(27), 12157–12162. https://doi.org/10.1073/pnas.1002314107

Rayner, N. A., Parker, D. E., Horton, E. B., Folland, C. K., Alexander, L. V., Rowell, D. P., … Kaplan, A. (2003). Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late Nineteenth Century. *Journal of Geophysical Research*, *108*, 4407-[37pp]. https://doi.org/Rayner, N.A., Parker, D.E., Horton, E.B., Folland, C.K., Alexander, L.V., Rowell, D.P., Kent, E.C. and Kaplan, A. (2003) Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late Nineteenth Century. Journal of Geophysical Research, 108 (D14), 4407-[37pp]. (doi:10.1029/2002JD002670 <http://dx.doi.org/10.1029/2002JD002670>).

Ricciardi, A., & Kipp, R. (2008). Predicting the number of ecologically harmful exotic species in an aquatic system. *Diversity and Distributions*, *14*(2), 374–380. https://doi.org/10.1111/j.1472-4642.2007.00451.x

Seabloom, E. W., Williams, J. W., Slayback, D., Stoms, D. M., Viers, J. H., & Dobson, A. P. (2006). Human Impacts, Plant Invasion, and Imperiled Plant Species in California. *Ecological Applications*, *16*(4), 1338–1350. https://doi.org/10.1890/1051-0761(2006)016[1338:HIPIAI]2.0.CO;2

Simberloff, D. (2001). Eradication of island invasives: practical actions and results achieved. *Trends in Ecology & Evolution*, *16*(6), 273–274. https://doi.org/10.1016/S0169-5347(01)02154-1

Simberloff, D. (2006). Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? *Ecology Letters*, *9*(8), 912–919. https://doi.org/10.1111/j.1461-0248.2006.00939.x

Simberloff, D. (2009). The Role of Propagule Pressure in Biological Invasions. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 81–102. https://doi.org/10.1146/annurev.ecolsys.110308.120304

Simberloff, D., & Von Holle, B. (1999). Positive Interactions of Nonindigenous Species: Invasional Meltdown? *Biological Invasions*, *1*(1), 21–32. https://doi.org/10.1023/A:1010086329619

Sorte, C. J. B., Ibáñez, I., Blumenthal, D. M., Molinari, N. A., Miller, L. P., Grosholz, E. D., … Dukes, J. S. (2013). Poised to prosper? A cross-system comparison of climate change effects on native and non-native species performance. *Ecology Letters*, *16*(2), 261–270. https://doi.org/10.1111/ele.12017

Sorte, C. J. B., Williams, S. L., & Zerebecki, R. A. (2010). Ocean warming increases threat of invasive species in a marine fouling community. *Ecology*, *91*(8), 2198–2204. https://doi.org/10.1890/10-0238.1

South, J., Dick, J. T. A., McCard, M., Barrios-O'Neill, D., & Anton, A. (2017). Predicting predatory impact of juvenile invasive lionfish (Pterois volitans) on a crustacean prey using functional response analysis: effects of temperature, habitat complexity and light regimes. *Environmental Biology of Fishes*, *100*(10), 1155–1165. https://doi.org/10.1007/s10641-017-0633-y

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., … Robertson, J. (2007). Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. *BioScience*, *57*(7), 573–583. https://doi.org/10.1641/B570707

Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., … Pyšek, P. (2011). Ecological impacts of invasive alien plants: a meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, *14*(7), 702–708. https://doi.org/10.1111/j.1461-0248.2011.01628.x

Warnes, G. R., Bolker, B., Lumley, T., & Johnson, R. C. (2018). *gmodels: Various R Programming Tools for Model Fitting*. Retrieved from https://CRAN.R-project.org/package=gmodels

Winder, M., Jassby, A. D., & Mac Nally, R. (2011). Synergies between climate anomalies and hydrological modifications facilitate estuarine biotic invasions. *Ecology Letters*, *14*(8), 749–757. https://doi.org/10.1111/j.1461-0248.2011.01635.x

Yeager, L. A., Marchand, P., Gill, D. A., Baum, J. K., & McPherson, J. M. (2017). Marine Socio-Environmental Covariates: queryable global layers of environmental and anthropogenic variables for marine ecosystem studies. *Ecology*, *98*(7), 1976–1976. https://doi.org/10.1002/ecy.1884