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RESEARCH PAPER

Exotic species richness and native species endemism increase the impact of exotic species on islands

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ABSTRACT

Aim Exotic species pose one of the most significant threats to biodiversity, especially on islands. The impacts of exotic species vary in severity among islands, yet little is known about what makes some islands more susceptible than others. Here we determine which characteristics of an island influence how severely exotic species affect its native biota.

Location We studied 65 islands and archipelagos from around the world, ranging from latitude 65° N to 54° S.

Methods We compiled a global database of 10 island characteristics for 65 islands and determined the relative importance of each characteristic in predicting the impact of exotic species using multivariate modelling and hierarchical partitioning. We defined the impact of exotic species as the number of bird, amphibian and mammal (BAM) species listed by the International Union for Conservation of Nature (IUCN) as threatened by exotics, relative to the total number of BAM species on that island.

Results We found that the impact of exotic species is more severe on islands with more exotic species and a greater proportion of native species that are endemic. Unexpectedly, the level of anthropogenic disturbance did not influence an island's susceptibility to the impacts of exotic species.

Main conclusions By coupling our results with studies on the introduction and establishment of exotic species, we conclude that colonization pressure, or invasion opportunities, influences all stages of the invasion process. However, species endemism, the other important factor determining the impact of exotic species, is not known to contribute to introduction and establishment success on islands. This demonstrates that different factors correlate with the initial stages of the invasion process and the subsequent impacts of those invaders, highlighting the importance of studying the impacts of exotic species directly. Our study helps identify islands that are at risk of impact by exotics and where investment should focus on preventing further invasions.

Keywords

Anthropogenic disturbance, colonization pressure, endemism, exotic species, extinction probability, islands, isolation, IUCN Red List.

INTRODUCTION

Exotic species are a major threat to biodiversity and ecosystems globally, as a result of predation and competition (Mack *et al.*, 2000; Sax & Gaines, 2008), hybridization with native species (Mooney & Cleland, 2001) and the disruption of ecosystem processes and functions (Mack *et al.*, 2000). Directly or indirectly, these impacts often lead to the decline of populations of native species and can cause local or global extinctions (Clavero & García-Berthou, 2005; Butchart, 2008). In response to these

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Table 1 The island characteristics used as explanatory variables under six proposed hypotheses to explain an island's susceptibility to the impacts of exotic species. The hypothesized directions of the relationships between the impact and the island characteristics are shown in brackets. Island type, another island characteristic, was not classified under a specific hypothesis, but was used in the analyses as a covariate.

Model	Hypothesis	Island characteristic
Colonization pressure	Regions with higher colonization pressure are more susceptible to the impacts of exotic species.	No. of exotic species [+] No. of major airports and ports [+]
Anthropogenic disturbance	Regions with greater anthropogenic disturbance are more susceptible to the impacts of exotic species.	Human population density (people km^{-2}) [+] Date of European settlement [−]
Biotic acceptance	Regions with higher species richness are more susceptible to the impacts of exotic species.	No. of BAM species [+] Island area (km^2) [+] Island isolation index [−]
Biotic resistance	Regions with lower species richness are more susceptible to the impacts of exotic species.	No. of BAM species [−] Island area (km^2) [−] Island isolation index [+]
Habitat heterogeneity	Regions with greater habitat diversity are more susceptible to the impacts of exotic species.	Island maximum elevation (m) [+] Island area (km^2) [+]
Species endemism	Regions with a higher proportions of endemic species are more susceptible to the impacts of exotic species.	Proportion of endemic species [+] Island area (km^2) [−] Island isolation index [+]

BAM: bird, amphibian and mammal species.

impacts, the number of international agreements and pieces of national legislation on exotic species has increased over the past 40 years (McGeoch *et al*., 2010), and one of the updated targets of the Convention on Biological Diversity (CBD) for 2020 specifically aims to control and eradicate exotic species (UNEP, 2010a). Despite this heightened concern over the impacts of exotic species, the rate of biodiversity loss due to exotic species has not significantly decreased (Butchart *et al*., 2010; McGeoch *et al*., 2010).

It is important to know the distribution of the biodiversity impacts of exotic species and where they are greatest if we are to reduce subsequent species loss. It is preferable to measure impact directly rather than use extent of invasion as a proxy, because the direct impact of exotic species on native species is invariably hard to detect (Williamson, 1996) and the ability of an exotic species to invade does not correlate well with its eventual impact on native species in the invaded ecosystem (Ricciardi & Cohen, 2007). Numerous studies have investigated which regions are more susceptible to the establishment and invasion of exotic species (Case, 1996; Blackburn & Duncan, 2001; Cassey *et al*., 2005; Blackburn *et al*., 2008; Chiron *et al*., 2009), which species are better invaders (Kolar & Lodge, 2001) and which conditions make an introduction more likely to succeed (Cassey *et al*., 2004; Chiron *et al*., 2009). Yet no study has directly determined which anthropogenic, biotic and abiotic factors make an area susceptible to the impact of exotic species. Moreover, few studies have examined spatial variation in the magnitude of the impact of exotic species on native species (Venter *et al*., 2006; Evans *et al*., 2011), even though it is through these impacts that the global threat of exotic species is manifested.

Here, we examine global-scale variation in the susceptibility of islands to the impact of exotic species on native species. We propose that anthropogenic, biotic and abiotic factors similar to those important for the introduction of exotic species and their establishment success are important in driving the impacts of exotic species on islands. We formalize these factors by creating six specific hypotheses (Table 1). We focus on islands because they often suffer greater negative impacts of exotic species than mainland regions (Clavero *et al*., 2009). To quantify the impact of exotics, we use data for each island on the number of threatened birds, mammals and amphibians that are known to be threatened by exotics according to the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (hereafter 'IUCN Red List'), relative to the island's native species richness. We identified 10 island characteristics as explanatory variables to test which hypotheses best explain an island's susceptibility to the impacts of exotic species (Table 1).

The colonization pressure hypothesis suggests that a region will be more susceptible to the impacts of exotic species when there are more invasion opportunities for exotics, through higher colonization (Williamson, 1996) or propagule pressure (Cassey *et al*., 2004, 2005; Lockwood *et al*., 2009). If correct, this hypothesis would imply that impact is not an intrinsic function of a location but rather is a consequence of how the location intersects with vectors of dispersal of exotic species. Our second hypothesis proposes that habitat disturbance due to anthropogenic activity may enhance the impact of exotic species because they are often human commensals and may have competitive or other advantages over native species in disturbed habitats (Case, 1996; Cassey *et al*., 2005; Blackburn *et al*., 2008; Leprieur *et al*., 2008; Chiron *et al*., 2009). The biotic acceptance hypothesis suggests that whichever factors cause a region to have high native species richness will also favour exotic species, and hence increase their impacts on the native biota (Stohlgren *et al*., 2006). Conversely, the biotic resistance hypothesis suggests that regions with high species richness have fewer niches available for exotic species to invade, increasing community stability and resistance against invasion and the impacts of exotic species (Elton, 1958). The fifth hypothesis suggests that habitat heterogeneity increases the probability of an exotic species finding a suitable niche and/or environment to establish and thrive in, with concomitant deleterious effects on native species (Rosenzweig, 1995; Case, 1996). These five hypotheses have previously been proposed as explanations for the variation seen in the number of exotic species that invade and establish on islands, whereas here we are using them as hypotheses to predict the actual impact of exotic species on native biota.

In a sixth and final hypothesis, we propose that the level of endemism in the native biota influences the susceptibility of an island to the impacts of exotic species. Isolation on islands is frequently argued to cause species to lower their defences against natural enemies, as fewer such enemies exist on islands. If longer isolation leads to lower defences, and if endemic species are assumed to have been isolated for longer than non-endemic species, then islands with high levels of endemism should suffer greater impacts from the sudden arrival of potential natural enemies in the form of exotic species (Biber, 2002; Berglund *et al*., 2009).

We quantified the impact of exotic species as the number of threatened or extinct bird, amphibian and mammal (hereafter 'BAM') species on an island that are (or were, in the case of extinct species) negatively affected by exotic species (weighted by their extinction risk), relative to the number of BAM species on that island. Extinction risk is the probability that a species will go extinct within a specified time frame, depending on its conservation status (Butchart *et al*., 2004; Clavero *et al*., 2009). Using this measure of impact, we determined the relative importance of each island characteristic, and consequently each hypothesis, for the susceptibility of an island's biota to the impacts of exotic species for 65 islands (or island groups and archipelagos).

METHODS

A global dataset including the impact of exotic species (response variable) and 10 island characteristics was collated for 65 islands and archipelagos world-wide (see Appendix S1 in Supporting Information). Islands and archipelagos were included in the dataset based on the following criteria: they were listed in the IUCN Red List 2009 (version 9.2, http://www.iucnredlist.org) (necessary for data on the response variable); are not politically divided into two countries (e.g. Dominican Republic and Haiti); are further than 2 km from the mainland (Hong Kong and Singapore were excluded); and data were available for all 10 explanatory variables. The set of islands was highly heterogeneous, as it included both continental and oceanic islands and archipelagos. We included a categorical variable in the analyses to account for potential differences in the impacts of exotic species between continental islands ($n = 14$), continental archipelagos ($n = 18$), oceanic islands ($n = 9$) and oceanic archipelagos ($n = 24$). Archipelagos with one large main island and several smaller islands, such as Cuba, Madagascar and Taiwan, were classified as islands, assuming that the majority of data would be related to the large island. We also conducted the analyses using a stricter definition of an island (Appendix S2), though this had no qualitative effect on our conclusions (Appendix S3).

Impact of exotic species on islands

We collected data from the IUCN Red List on the number of native, terrestrial and freshwater BAM species that are threatened or extinct on each island as a result of exotic species. The Red List is widely viewed as the most authoritative source of information on the conservation status of species globally and their associated threats (Rodrigues *et al*., 2006). We defined threatened species as those classified by the IUCN Red List as critically endangered (CR), endangered (EN) or vulnerable (VU) (IUCN, 2001). Species classified as extinct in the wild (EW) were included in the extinct (EX) category. We also collated the total number of native terrestrial and freshwater BAM species on each island, including extinct species, which have been assessed by the IUCN Red List for threats (N_i).

We defined the impact of exotic species on an island as the number of native BAM species that are threatened or extinct due to exotic species, weighted by extinction risk according to their level of threat, and in proportion to the number of BAM species on each island, which have been assessed by the IUCN Red List for threats (N_i as described above):

$$\text{exotic species impact on island } i = \frac{0.02\times \mathrm{VU}_i + 0.2\times \mathrm{EN}_i + 0.75\times \mathrm{CR}_i + \mathrm{EX}_i}{\mathrm{N}_i}$$

where VU_i, EN_i, CR_i and EX_i are, respectively, the number of species in each category that are threatened by exotic species on island *i*. We based the extinction risks on the IUCN Red List Criterion E, which quantitatively estimates a species' probability of extinction, whereby CR species have a probability of extinction of 50% within 10 years, EN species 20% within 20 years and VU species 10% within 100 years (IUCN, 2001). We standardized these quantitative extinction probabilities to a 20-year time frame while assuming that the annual extinction risk is constant, following Clavero *et al*. (2009), resulting in the weightings in the equation above. We used these quantitative measures of extinction risk as a way to weight the severity of threat, rather than predict future extinctions (Mace *et al*., 2008). The impact of exotic species can range from 0 to 1, with 1 signifying that all BAM species on an island are extinct due to exotic species. We mapped the measure of impact and the number of exotic species for the 65 islands used in this study to demonstrate the variation observed at a global scale. We also used this measure of impact as the response variable in multivariate modelling and hierarchical partitioning analyses, as described below.

To ensure that the specific weighting assigned to each threatened category did not unduly influence the outcomes of this study, we conducted the analyses using three alternative weighting options, following Clavero *et al*. (2009). These were: (1) weighting each threatened category equally; (2) ranking the VU, EN, CR and EX categories from 1 to 4, using an equal step weighting method; and (3) weighting the threatened categories by the geometric mean of the extinction probabilities of the IUCN criteria, where VU, EN, CR and EX categories where weighted 0.005, 0.05, 0.5 and 1, respectively (Butchart *et al.*, 2004). The results using these three alternative weightings methods did not differ importantly from the original method (Appendix S4).

Island characteristics and dataset

Sources for island characteristics used as explanatory variables are given in Appendix S2. The number of terrestrial and freshwater exotic plants and animal species on an island and the number of major airports and ports were used to the measure colonization pressure of exotic species on an island. Human population density and the date of European settlement were used as surrogates for the anthropogenic disturbance hypothesis. The biotic acceptance and biotic resistance hypotheses were tested using the number of native BAM species on an island, island area and island isolation index following MacArthur & Wilson (1967). Island area and maximum elevation were used as surrogates for the fifth hypothesis, habitat heterogeneity, and we used the proportion of endemic species, island area and island isolation as measures for species endemism.

Analyses

To determine which island characteristics influence the impact of exotic species, we used stepwise multivariate linear regression and hierarchical partitioning analyses. To improve normality and homoscedasticity, we applied a square root transformation to our measure of the impact of exotic species, and log + 1 transformations to the following explanatory variables: number of exotic species, number of airports and ports, human population density, species richness and island area.

We modelled the impact of exotic species on islands using bivariate and multivariate linear regression. There was high collinearity between several island characteristics, with correlation coefficients ranging from –0.47 to 0.71, calculated using Spearman's rank correlations (Appendix S5). We also measured the severity of multicollinearity between the island characteristics using variance inflation factors to include the categorical variable island type (Appendix S2). Island area was highly correlated with three other island characteristics ($r_s > 0.5$) and we found that multicollinearity between variables was sufficiently reduced when this characteristic was removed from the multivariate analyses. Island type was also correlated with other variables, identified using variance inflation factors, and was removed from this analysis.

The global multivariate linear model consisted of 10 island characteristics as explanatory variables: island type, the number of exotic species, the number of major airports and ports, human population density, date of European settlement, the number of extant BAM species, proportion of endemic BAM species, island isolation, maximum island elevation and island area. A minimum adequate model (MAM) was constructed using stepwise backward deletion of non-significant terms from the global model, after removing the collinear variables of island type and island area. At each step of the process, the least significant variable was removed from the model, until the simplified model was significantly different to the previous model (determined by an ANOVA test, where $P > 0.05$). The MAM was the last simplified model that did not differ significantly from the previous model.

Multivariate regression does not distinguish between the independent contribution of an explanatory variable in explaining the deviance of a response variable and its joint contribution with other explanatory variables (Mac Nally, 2000; Murray & Conner, 2009). Therefore, we used hierarchical partitioning to assess the importance of each variable in explaining the variance observed in the response variable, while accounting for correlations among the explanatory variables (Chevan & Sutherland, 1991; Mac Nally, 2000). Although causality cannot be determined without experimentation, hierarchical partitioning provides a reliable method to identify the most likely variables, because all possible models are considered simultaneously, as opposed to other regression modelling techniques which focus on one or a few models at a time (Chevan & Sutherland, 1991; Mac Nally, 2000). Hierarchical partitioning calculates a variable's contribution to the fit of each model (i.e. the independent effect size) from a subset of models made from all possible combinations of predictor variables containing the variable of interest, but unlike multivariate regression, it does not measure the direction and slope of the regression coefficient. The independent component of a variable is estimated by averaging the differences between the fit of all possible models involving the variable and the fit of these models when the variable is excluded (Chevan & Sutherland, 1991). The average of these independent contributions provides a measure of the independent effect (I_j) of that variable on the response, relative to the effects of other variables analysed, while the joint component (J_j) is the proportion of the explanatory variable's fit that is also explained by other variables.

We conducted a hierarchical partitioning analysis to test the relative importance of the 10 island characteristics (including island area and island type) in explaining why some islands are more susceptible to the impacts of exotic species, following Leprieur *et al.* (2008) and Chiron *et al.* (2009). We used R^2 as the goodness-of-fit measure. We calculated each explanatory variable's independent effect (I_j), and the significance of each variable using a randomization test (Mac Nally, 2002) with 1000 iterations. The total explained variance was calculated using the sum of the independent contributions of all variables. The initial analysis involved 1024 linear models (2^{10}); however, the accuracy of a hierarchical partitioning analysis decreases if more than nine variables are included (Mac Nally & Walsh, 2004). To ensure that the results were accurate we removed the variable with the lowest independent effect (date of European settlement) and performed the hierarchical partitioning again with the remaining nine variables as recommended. We performed these analyses using the *hier.part* package (Mac Nally & Walsh, 2004) in the statistical program R version 2.4.1 (R Development Core Team, 2005).

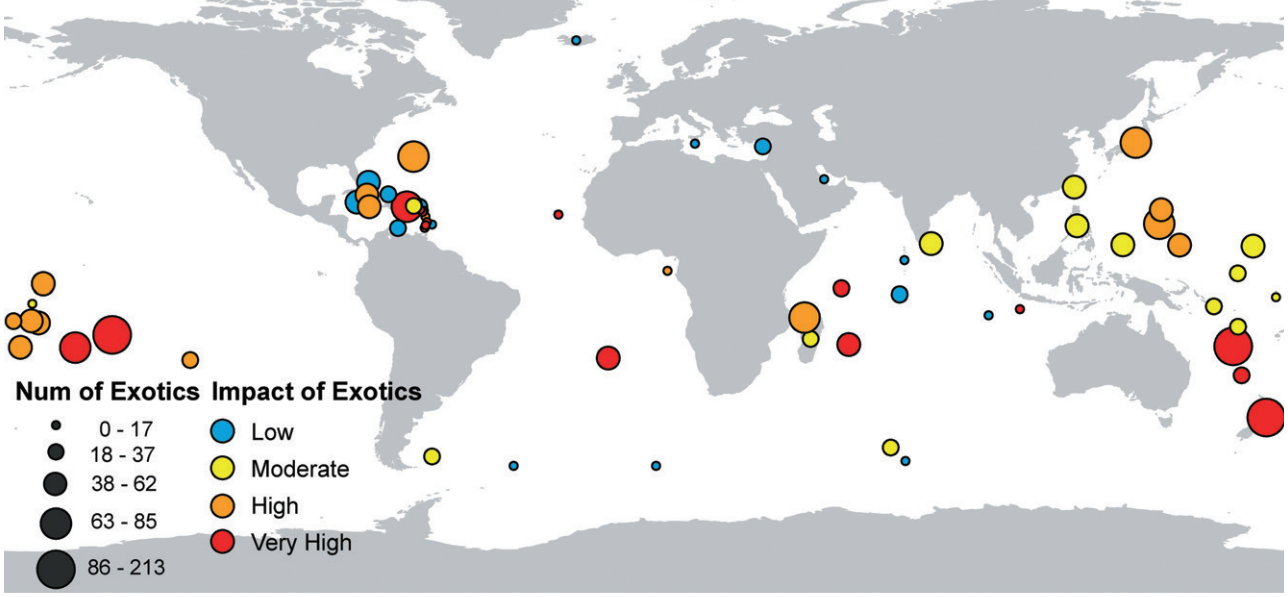

Figure 1 The variation in the level of biological impacts of exotic species across islands globally, shown by a different colour for each quartile. The number of exotic species on an island is represented by the size of the point. For the exact numbers of exotic species and the level of impact, refer to Appendix S1.

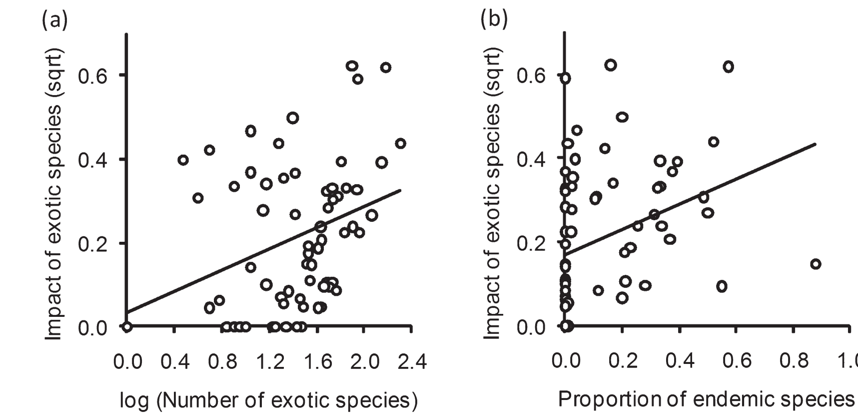

Figure 2 The relationship between the impact of exotic species and the island characteristics that were significant in influencing an island's susceptibility to the impacts of exotic species: (a) number of exotic species (β = 0.127, SE = 0.043, $t = 2.971$, $P = 0.004$, $R^2 = 0.123$) and (b) proportion of endemic species (β = 0.298, SE = 0.105, $t = 2.837$, $P = 0.006$, $R^2 = 0.113$).

RESULTS

The impact of exotic species varied markedly across islands (Fig. 1), with a mean impact measure of 0.11. Several islands in particular were heavily impacted by exotic species (e.g. Puerto Rico, impact measure = 0.39, and French Polynesia, impact measure = 0.38). Eleven of the 65 islands or archipelagos included in the dataset did not have any species threatened by exotics (impact measure = 0), even though all but two of these islands had exotic species present (maximum of 29 exotic species; Appendix S1). There were significant positive bivariate relationships between the number of exotic species on an island and the impact they have on the native species (Fig. 2a), and between the proportion of endemic species and the impact of exotic species (Fig. 2b).

Using a global multivariate linear model to account for the effects of all other island characteristics, we found that: (1) the number of exotic species, (2) the proportion of endemic species, and (3) maximum island elevation were significant predictors of the impact of exotic species (Table 2). Using backward stepwise removal of terms, elevation was not retained in the MAM, while BAM species richness remained significant (Table 3).

In both the global multivariate model and MAM, the impact of exotic species was greater on islands with more exotic species and higher proportions of endemic species (Fig. 2). Maximum island elevation was significant in the global model, but its low positive slope estimate (Table 2) and absence from the MAM suggests that differences in elevation between islands do not result in large differences in the impact of exotic species. BAM species richness was only significant in the MAM, where islands with low species richness were more vulnerable to the impacts of exotic species than species-rich islands (Table 3).

The importance of each island characteristic in explaining an island's vulnerability to the impacts of exotic species was further

Table 2 A global model predicting the impact of exotic species on islands using all island characteristics ($n = 65$, $R^2 = 0.383$). Parameter estimates (β) indicate the direction and slope of each predictor variable relationship.

Island characteristic	β	SE	*t*	*P*
Intercept	0.381	0.312	1.221	0.228
Island type: archipelago, oceanic	−0.030	0.068	−0.444	0.659
Island type: island, continental	0.039	0.060	0.656	0.515
Island type: island, oceanic	0.005	0.083	0.063	0.950
Log (no. of exotic species)	0.131	0.053	2.458	**0.017**
Log (no. of ports and airports)	−0.376	0.381	−0.988	0.328
Log (human population density)	0.051	0.035	1.452	0.153
Date of European settlement	0.000	0.000	−1.411	0.164
Log (BAM species richness)	−0.141	0.073	−1.920	0.060
Proportion of endemic species	0.338	0.136	2.489	**0.016**
Island isolation index	0.001	0.002	0.699	0.488
Island maximum elevation	0.000	0.000	2.540	**0.014**
Log (island area)	−0.028	0.046	−0.606	0.547

BAM, birds, amphibians and mammals.
Bold values indicate significant effects ($P < 0.05$).

Table 3 The significant island characteristics remaining in the minimum adequate model that best explain which islands are more susceptible to the impacts of exotic species ($n = 65$, $R^2 = 0.225$). The following variables were deleted from the global model due to non-significance: the number of major airports and ports, human population density, date of European settlement, island isolation index and maximum island elevation. Island area and island type were excluded prior to the analysis due to collinearity with other explanatory variables. Parameter estimates (β) indicate the direction and slope of each predictor variable relationship.

	β	SE	*t*	*P*
Intercept	0.168	0.085	1.969	0.053
Log (no. of exotic species)	0.116	0.045	2.567	**0.013**
Log (BAM species richness)	−0.101	0.050	−2.021	**0.048**
Proportion of endemic species	0.325	0.121	2.687	**0.009**

BAM: bird, amphibian and mammal species.
Bold values indicate significant variables ($P < 0.05$).

explored using hierarchical partitioning (Fig. 3). All nine variables (excluding date of European settlement) combined explained 35.9% of the total variance in the impacts of exotic species across islands, which is the sum of their independent contributions (I_j). The number of exotic species and the proportion of endemic species on an island had the strongest independent effects on the susceptibility of an island to the impacts of exotic species (Fig. 3), accounting for 24.0% and 22.9%, respectively, of the total explained variance. The maximum elevation of an island was also highly influential, independently contributing 15.9% of the total explained variance. These three island characteristics were significant in explaining the impact caused by exotic species, using a hierarchical partitioning randomization test (Mac Nally, 2002). The island isolation index was ranked fourth in its explanatory power, independently accounting for 10.1% of the explained variance. The remaining variables had low levels of importance (Fig. 3).

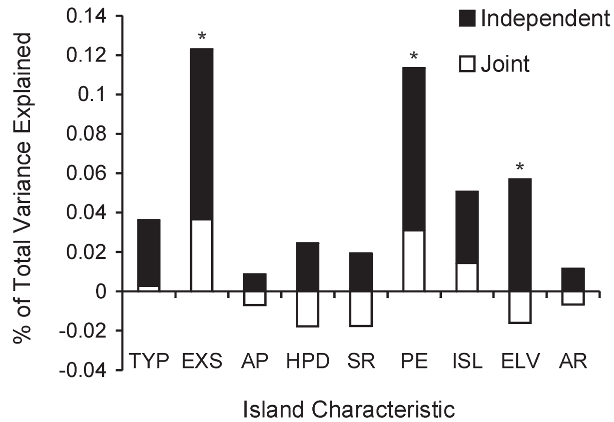

Figure 3 The percentage of total variance in the impact of exotic species across islands explained by the independent (I_j) and joint (J_j) effects of each explanatory variable *j*, determined using hierarchical partitioning. The sum of the independent effects from all variables explained 35.9% of the total variance, where three variables had significant independent contributions (shown by *). TYP, island type; EXS, number of exotic species; AP, number of airports and ports; HPD, human population density; SR, bird, amphibian and mammal species richness; PE, proportion of endemic species; ISL, island isolation index; ELV, maximum island elevation; AR, island area. Date of European settlement had the lowest explanatory power of any variable in a hierarchical partitioning analysis with all 10 variables, and was subsequently removed to allow for a more accurate analysis, keeping within the recommended limit of nine variables.

DISCUSSION

This study is the first to use a genuine measure of biological impact to assess factors that influence the impact of exotic species on islands at a global scale. Our results consistently support two of the six hypotheses (Table 1) proposed to explain the susceptibility of islands to the impacts of exotic species – those based on colonization pressure and species endemism. Our results provide some evidence in line with two other hypotheses – biotic resistance and habitat heterogeneity. The role (or lack thereof) of these mechanisms in determining the impact of exotic species suggests several consequences for theoretical invasion and biogeographical ecology, while providing practical information to conservation managers of exotic species on islands.

It is well known that during the initial stages of the invasion process, propagule and colonization pressures are important determinants of the probability of the introduction and establishment of exotic species (Cassey *et al.*, 2004, 2005; Chiron *et al.*, 2009; Lockwood *et al.*, 2009). However, evidence for an influence of such pressures on the impact of exotic species on the host environment has been lacking. Using the number of exotic species as a surrogate for colonization pressure, our results suggest that islands with high colonization pressure are more likely to experience greater impacts of exotic species. Other studies have found that the number of exotic species on an island positively correlates with the fraction of species that are threatened or extinct, but have not distinguished between different reasons for threat (Case, 1996; Blackburn *et al.*, 2004). We show that the impact of colonization pressure permeates beyond effects on introduction and establishment success through to exotic species impacts, and hence is important across the entire invasion process.

The number of endemic species on an island explains almost as much variation as colonization pressure with respect to the impact of exotic species on islands. The number of exotic species and the proportion of endemics were not significantly correlated (Appendix S5), highlighting the genuine importance of both variables in explaining which islands are more susceptible to exotic species. High levels of species endemism on islands are often a result of *in situ* evolution and low levels of exposure to immigrant species from continental mainlands (particularly predatory species) for long periods of time (Whittaker & Fernández-Palacios, 2007). This can consequently lead to a loss of costly defence mechanisms, making endemic species vulnerable to exotic species when they arrive, especially if large numbers of such species arrive concurrently. Endemism has previously been identified as an important driver of an island's vulnerability to the impacts of exotic species (Berglund *et al.*, 2009). However, it has not been found to be a good predictor of invasion success, indicating that the composition of the invaded community influences impacts independently of invasion pressure. This highlights the importance of directly studying the impacts of exotic species rather than predicting their likelihood of invasion.

It is common practice to link endemism with geographical isolation, based on the theory of island biogeography (MacArthur & Wilson, 1967; Keppel *et al.*, 2009). Berglund *et al.* (2009) concluded that isolation was the main factor influencing an island's vulnerability to the impacts of exotic species, by inferring its relationship with endemism. However, they did not test their measure of impact explicitly with isolation, nor other island characteristics that could be contributing to the observed species decline. Our results provide no evidence to suggest that the proportion of endemic species is correlated with island isolation (Appendix S5), nor that isolation influences the impacts of exotic species (Tables 2 and 3, Fig. 3). While this may be due to our particular sample of islands or because data on species extinctions before AD 1500 were not included in this study (see below), these findings suggest that the assumption that isolation and endemism are correlated may not be valid in all situations. It also suggests that our results may be relevant to insular but not isolated mainland ecological communities where exotic species are threatening biodiversity, for example inland lakes and freshwater systems, or fragmented habitat patches.

The biotic resistance hypothesis postulates that high species richness reduces the available niches for introduced species to establish and maintain viable populations (Elton, 1958; Leprieur *et al.*, 2008). We found a significant negative relationship between the impact of exotic species on islands and BAM species richness in the multivariate analysis, which is consistent with this hypothesis. Many studies find no relationship between species richness and exotic species invasion and establishment success (Case, 1996; Blackburn & Duncan, 2001; Cassey *et al.*, 2005), yet we found that islands with a higher BAM richness are less susceptible to the impacts of exotic species, as did Donlan & Wilcox (2008), emphasizing the need to look beyond invasion to the actual impacts. Nevertheless, BAM species richness had very little independent explanatory power in the hierarchical partitioning analysis (Fig. 3), contributing only 5.35% to the explained variance in the impacts observed across islands. The relationship between species richness and the impact of exotic species may be an artefact of the correlation between species richness and elevation (Appendix S5), as elevation is shown to be important in the full multivariate model (Table 2) and by hierarchical partitioning (Fig. 3). These latter results are consistent with the habitat heterogeneity hypothesis.

The level of anthropogenic disturbance is a strong determinant of the number of exotic species that establish in a region (Blackburn *et al.*, 2008; Leprieur *et al.*, 2008; Chiron *et al.*, 2009), but does not appear to have an effect on the severity of the impacts that the exotic species have on the native species once established. In heavily disturbed landscapes, it is possible that native species are threatened by processes directly related to habitat disturbance rather than by exotic species, especially if exotic species are largely confined to disturbed habitats and native species to undisturbed habitats. Even so, heavily disturbed regions tend to have higher numbers of exotic species (Leprieur *et al.*, 2008; Chiron *et al.*, 2009), which in turn ought to lead to greater impacts on native species (Figs 2 & 3). Therefore, our results do not discount anthropogenic disturbance as an important contributor when planning for management of exotic species and prevention strategies.

Our measure for the impact of exotic species provides conservation practitioners with information on which areas should be prioritized for management – either eradication or prevention. Islands that are heavily affected by only a few exotic species (shown by the small red points in Fig. 1) would be areas ideal for eradication, as the conservation outcome would be large (i.e. many native species would benefit) relative to the effort required to remove these few species. This is particularly true where the size of the current impact is not driven by actual extinctions, but more by threatened species that are extant. In contrast, islands that have experienced low levels of invasion and impact (small blue points in Fig. 1) should be considered for protection, with an emphasis on preventing further introductions of exotic species. To identify management priorities at a smaller scale, i.e. within the 'small red' or 'small blue' groups of islands, the proportion of endemic species on an island could be used, because this characteristic is also important in determining an island's susceptibility to the impacts of exotic species and is an appropriate surrogate for an island's biodiversity value. Large blue points would represent islands that are either resilient to the impacts of exotic species or have an 'impact debt' or latent extinction risk (Cardillo *et al*., 2006), where the expected impacts have not occurred yet, although no islands sampled in this study appeared in this category. In all cases the likely benefits of eradication and prevention need to be combined with information about cost and probability of success to prioritize actions (Joseph *et al*., 2009).

The IUCN Red List does not include extinctions that occurred before AD 1500. For example, early introductions of the Pacific rat (*Rattus exulans*), dogs (*Canis lupus familiaris*) and pigs (*Sus domestica*) (Milberg & Tyrberg, 1993; Anderson, 2009) resulted in many bird extinctions on Pacific islands (Steadman, 1995). This may especially affect estimates of the number of endemic species per island if these were more likely also to be driven extinct before AD 1500, and may explain the lack of correlation between endemism and island isolation in our data. Blackburn *et al*. (2004) showed that the impact of exotic mammalian predators as drivers of extinction in island birds was robust to whether or not prehistoric extinction data were included, which suggests that the same processes applied across both time periods. While we cannot prove the same is true of our analyses, it is not certain that prehistoric information would change our conclusions, and our results are nonetheless relevant to the current global situation, providing valuable predictions about the near future. Our study is further constrained by the availability of data on suitable surrogate measures, limiting our ability to test the importance of each proposed hypothesis. For example, it is certain that the numbers of exotic species documented in the Global Invasive Species Database are underestimated, and more so for less developed countries due to limited data availability (McGeoch *et al*., 2010).

Island biodiversity and exotic species are key issues identified by the Convention on Biological Diversity (UNEP, 2008, 2010b), and our results help prioritize among islands for the management of exotic species. We have shown that islands with more exotic species and higher proportions of endemic species are more susceptible to the impacts of exotic species and could be identified as 'at risk' from the impacts of exotic species. We have also demonstrated that the mechanisms driving the impacts of exotic species are somewhat independent of those influencing the introduction and establishment of exotics. This immediately suggests that we need more focus on impact, given that this is ultimately the most crucial stage in terms of conservation, but has been relatively neglected in the study of the invasion process (Blackburn *et al*., 2009). Our findings suggest that conservation efforts and resources should be focused on eradicating exotic species from islands that have a severe impact from only a few exotic species or preventing additional invasions on islands with few exotic species, low existing impacts and high species endemism.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Global island impact dataset.
Appendix S2 Supplementary methods.
Appendix S3 Results using an alternative subset of islands and archipelagos.
Appendix S4 Results using alternative measures of impact of exotic species.
Appendix S5 Collinearity between island characteristics.

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BIOSKETCH

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