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Effects of human mediated disturbances on exotic forest insect diversity in a Chilean mediterranean ecosystem

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Abstract At the current rate of exchange of goods and people among geographic areas, the introduction of insect species into new habitats represents an increasing threat to insect diversity. The situation is especially acute in Mediterranean ecosystems where the high human population density incurs multiple sources of disturbance and high propagule pressure. In this study, we characterize the relationship between native and exotic forest insect richness and evaluate how human-mediated disturbances can influence this relationship in the Mediterranean central Chile. Exotic and native species richness were positively correlated across the study area, suggesting similar effect of environmental variables on both assemblages over large scales. When the effect of human-mediated disturbances was evaluated using generalized linear and additive models, we found that native richness, human population density and habitat diversity were the most important variables affecting exotic richness. Moreover, we detected strong nonlinearities in the effect of some variables. For instance, the influence of human population density on the exotic richness followed a threshold function, where below 1,000 hab/km^2, the proportion of exotics in the community grew rapidly with increasing human density, but above this threshold density, human population did not produce further increases in exotic richness. Two important conclusions arise from these results: first, there is a positive effect of human-mediated disturbances on the exotic richness in central Chile, and second, the key

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role that human population density has on the invasibility of insect communities in rural and semi-rural Mediterranean areas.

Introduction

The invasion of habitats by exotic species is probably the most challenging global phenomenon to ecologists due to its far reaching ecological, economic and social implications (Williamson 1999; Mack et al. 2002; Ruiz and Carlton 2003). Virtually, all countries have now hundreds to thousands of exotic species established in their ecosystems (Mack 2003) and it is expected that these numbers increase in the future as a result of the steady growth in international trade which produces human-aided long-distance dispersal of organisms (Pimentel 2002).

Insects, like other animals, live in a continually changing world, increasingly altered by the human footprint. Habitat fragmentation, landscape transformation and pollution have a strong influence on insect populations, forcing many species to survive in isolated pockets of suitable habitat (Hunter 2002; Samways 2005). Moreover, non-indigenous insects are frequently introduced accidentally as a byproduct of diverse human activities, and their establishment is strongly conditioned by competitors and predators in the new habitat (Mack et al. 2002). These phenomena probably are more severe in Mediterranean ecosystems than in any other partly due to their small size in comparison to the high concentration of the human population and the intensive agriculture that characterizes these regions of the world (Hannah et al. 1995; Samways 1998; D'Antonio et al. 2001; Armesto et al. 2007). Indeed, empirical evidence suggests that the loss of insect species and populations is coming about by the compound effects of direct habitat fragmentation (cities, road construction, forestry, agriculture) as well as other sources of disturbance (e.g. cattle grazing and mining; Samways 1998; Hendrickx et al. 2007; Schowalter 2012). These disturbed and fragmented landscapes induce some insect species to sharply increase in abundance, while others decrease or locally disappear (Schowalter 2012).

The central region of Chile represents one of the world's intensively exploited Mediterranean ecosystems. With a human population of nearly 6.5 million people, rapid economic growth, and increased centralization of human activities, this ecosystem has suffered significant changes in structure and disturbance regimes over the past last decades (Fuentes et al. 1993; Rundel 1998; Armesto et al. 2007; Schulz et al. 2010). Habitat fragmentation, changes in the land use and pollution are currently important processes in this region. At the same time, it is one of the most important passageways for international trade in and out of the country. Therefore, the propagule pressure for the introduction of exotic species is likely to be high. Actually, several exotic insect species have already been reported in the region (Grooves and Di Castri 1991; Rundel et al. 1998; Ruz 2002; Grez et al. 2010). However, the way in which these human-related habitat modifications are affecting the diversity of native and exotic insect species, and whether their establishment can be unequivocally associated to human-related activities are still unknown.

To evaluate the relative impact of human habitat modification on the richness of native and exotic species in central Chile, we analyzed an extensive database from the Chilean National Agriculture and Livestock Service (SAG). We attempted to answer three simple but yet very relevant questions for the application of potential conservation measures in

this system: (a) whether the number or the fraction of exotic species was negatively correlated to the number of native species across the region, (b) which are the main human-related disturbances affecting local insect diversity in this ecosystem, and (c) whether there are some nonlinear effects of human-mediated disturbances on the number or fraction of exotic species.

Materials and methods

Study site

The study area corresponds to the Metropolitan region of Chile, located in the middle of the Mediterranean region of Chile (33°–34° S Lat), and it is by far the region more affected by human-disturbances, with a population of more than 6.5 million people, in the Mediterranean ecosystem of Chile (30°–36° S Lat, Fuentes and Munoz 1995; Armesto et al. 2007). The Metropolitan region comprises the capital city Santiago, the biggest urban area of the country.

Topographically, this region is bounded by two parallel mountain ranges oriented from north to south, the Coastal Cordillera and the Andean range. They are separated by a narrow basin, which is an 80–100 km wide tectonic depression named Central depression. The climate is semiarid with hot and dry summers (average temperature in Santiago 20 °C) and cold and wet winters (average temperature around 10 °C) with most precipitation concentrated between April and September (338 mm, Luebert and Pliscoff 2006).

Biological and physical data

Data on forest insect species richness were obtained from the Agriculture and Livestock Service (SAG) of the Ministry of Agriculture of Chile. The data set was compiled as part of the program "Official Forestry Surveillance and Control", which operates along the entire country. In this study we used only the part of the database corresponding to Metropolitan region because this is inserted in the middle of the Mediterranean region of central Chile. This region includes both, large cities, towns, rural and semi-rural areas with sectors of native vegetation (OTAS 2002). Data were collected in 37 sample sites, distributed throughout the different habitats (HD) in the Metropolitan region (rural, semi-rural and urban environments, Fig. 1, Online Resource 1). The "Official Forestry Surveillance and Control" program is devoted to "protect, maintain and improve the condition of forest plantations, native forest and urban trees" (www.sag.cl). In this context, traps are located in several environments containing trees. Some of them are located in parks inside the city (urban habitats), others close to plantations (artificial habitats) and others in natural, semi-natural or rural areas (natural or semi natural habitats). The only restriction when defining trap locations was the availability of safe sites free from human damage or loss. To collect insects, Lindgren funnel traps with ethanol and α-pinene lures were used. They had a high performance catching several orders of insects during the operation of the project. Insects were collected from the traps every 15 days from September to May each year (spring, summer and fall). Traps were not deployed in winter months because they suffer great damage by rain and insect captures were almost null. Traps were located below trees. In this study, we used data collected during the 2002–2003 and 2003–2004 spring-fall seasons, allowing the determination of total richness of exotic and native insects per site. Trap samples were taken to the Lo Aguirre Quarantine Station (SAG laboratory) for
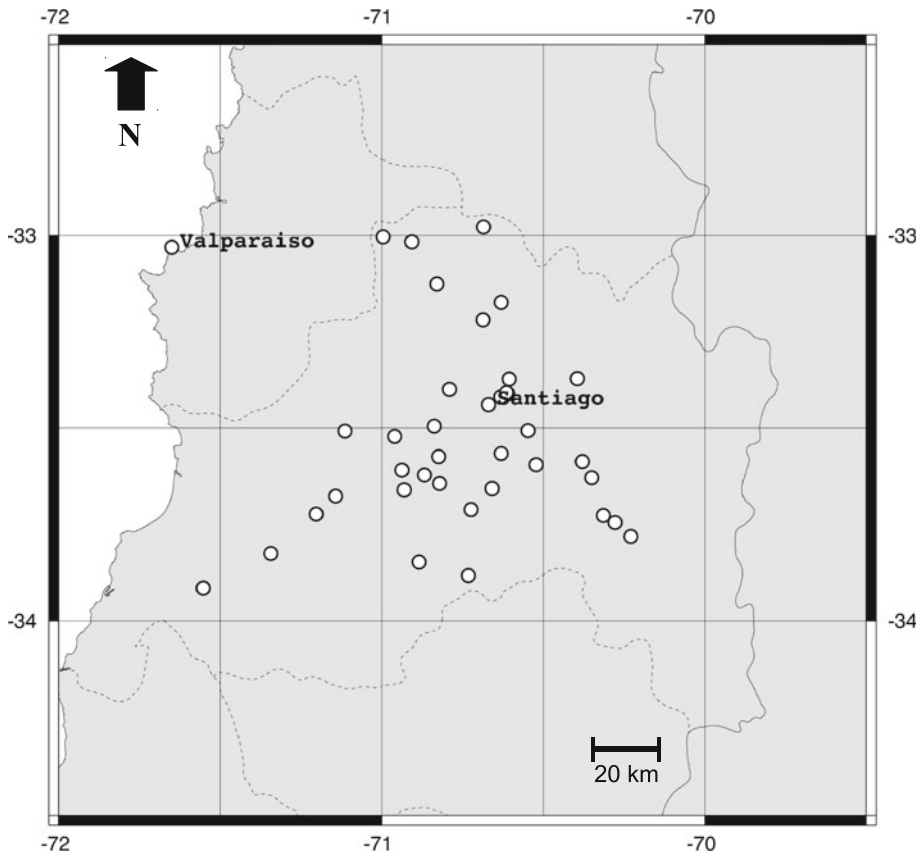
Fig. 1 Map of the Metropolitan region in central Chile. Points represent sample sites ($N = 37$)

identification of individuals, down to species or morphospecies, according to identification catalogs for each taxonomic group, and classified as native (N) or exotic (E). Data were previously checked for autocorrelation using Mantel test. E ($r = -0.03$, $p = 0.84$), N ($r = -0.01$, $p = 0.60$) and E/N ($r = -0.02$, $p = 0.71$) showed no signals of spatial autocorrelation. No information on numbers of individuals by species was collected.

Several variables were used to examine the influence of human activities on native and exotic species richness. Information on human population density (PD) was obtained from the National Institute of Statistics (INE), which registers the density of inhabitants in each of the 52 municipalities within the Metropolitan region (PD, hab/km^2). The rationale behind the use of this variable was that human density can increase the probability of finding exotic species because, for instance, humans usually cultivate exotic plants, which could be used as food or refuge by exotic (or native) insects.

The second type of information was related to the land use. It was obtained from the national vegetation inventory (INV) of the national forestry corporation (CONAF, Chile). The original data, containing several types of land use (>20), were simplified for the purpose of this study and reclassified into two categories: (a) percentage of soil covered by native vegetation (%NV) in a radius of 250 m around the trap (19.63 ha), and (b) the number of different habitats in the same radius around the trap, according to the habitats

classification of the INV. To accomplish this, 250 m buffers were created around each trap coordinates by using a geographic information system (QGIS 1.7). The intersection of the buffer and the vegetation map allowed us to calculate the percentage of NV and the number of different habitats per site. Each trap location was revisited to check the HD estimation. These variables were used in the models as estimates of human intervention of the vegetation around the insect traps. In the absence of information on actual dispersal, the selected scale (250 m radius) was chosen to encompass dispersal distances of most or all insect species in the community that was attracted by the trap. See the Online Resource 1 for the complete dataset used in this study.

Statistical analyses

To evaluate the relationship between native and exotic species across the region, we used Pearson correlation coefficients. Then, we evaluated the effects of human-disturbance variables on the diversity (number) of exotic species (E) and the ratio exotic/native (E/N), using generalized lineal models (GLM) and generalized additive models (GAM), in order to account for nonlinear relationship between variables (Wood 2006).

As a first step for the analysis, we fitted a GLM to evaluate the relative importance of native diversity (N), human (PD), NV coverage and HD on the diversity of exotic species (E) as well as the ratio exotic/native species (E/N). For this last variable we did not include N as an explanatory variable to avoid collinearity. In both cases we applied a stepwise variable selection based on the Akaike information criteria (AIC; Hastie and Pregibon 1992). Through this procedure we were able to discard variables that were not relevant to the model. In the second step, we fitted the same models using GAM. The procedure to fit GAM models is similar to the GLM procedure. GAM models are able to detect nonlinear relationships because these functions are piecewise-defined. The form of the partial functions related to each variable was determined by fitting cubic regression splines to the data, and the complexity of the curve (the number of degrees of freedom) and the smoothing terms were determined by penalized regression splines and generalized cross-validation (GCV) to avoid overfitting (Wood 2006). To allow variable selection (equivalent to the stepwise procedure in the GLM), we used cubic regression splines with shrinkage (Wood 2006). This technique allows for extra penalty to be added in the model, and if the penalty is high enough, it will shrink all smoothing coefficients to zero. In this case, the effective degrees of freedom of the variable(s) are so small that it (they) can be removed and the model is fitted again without these variables (Wood 2006). Moreover, effective degrees of freedom give an idea of the degree of nonlinear relationships. Values close to 1 represent linear relationships between variables, values higher than 1 (2 or higher) suggest a strong nonlinear relationship.

In GLM and GAM modelling we used Gaussian and Poisson error distribution for the dependent variables E/N and E, respectively. The link function was natural logarithm in both cases. Models were fitted in the R environment (R Development Core Team 2008; available at www.r-project.org) using the libraries stats and mgcv (Wood 2006).

Results

A total of 260 insect species were registered during the two seasons, 179 of them were identified as native and 81 (31 %) as exotic species. A slight variation was observed between years, with 192 species (139 natives and 53 (28 %) exotics) in the 2002–2003

Table 1 Total number of native and exotic species collected in each seasons and total in the sampling area

2002–2003				2003–2004		
Order	Natives	Exotics	Total	Natives	Exotics	Total
Coleoptera	71	28	99	52	23	75
Diptera	9	1	10	6	0	6
Hemiptera	24	12	37	29	11	40
Hymenoptera	10	9	19	3	12	15
Lepidoptera	25	3	28	15	7	22

The five main orders are shown

season and 157 species (104 natives and 53 (34 %) exotics) in the 2003–2004 season (Table 1 and Online Resource 2). At the order level, the exotics/natives ratio varied from a very low value in Diptera (0.08) up to a high ratio of 1.6 in Hymenoptera, with Coleoptera, Hemiptera and Lepidoptera at intermediate levels (0.39, 0.53 and 0.28, respectively).

The numbers of native and exotic species (raw data) were significantly and positively correlated at the scale of traps over the entire study region (Fig. 2, $r = 0.45$ [0.14–0.67], $p = 0.006$). Thus, richness of both assemblages responded in the same direction over the study region.

The best GLM according to the stepwise variable selection (Table 2) for exotic richness (E) showed that the variables with the highest influence were native species richness (N), human PD and HD. The influence was positive and in similar proportions, explaining a high proportion of the null deviance (50 %). Native vegetation coverage (NV) was discarded from the best model (Table 2). On the other hand, the ratio exotic/native (E/N) species was mainly positively influenced by PD and HD, but the explained deviance was poor (21 %). NV was also discarded in the best model for E/N.

The best GAM for exotic richness (E) (Table 3) showed the same structure than in GLM (Table 3). The selected variables were native species richness (N), human PD and HD. The best model explained a higher proportion of the null deviance (60 %) than the GLM which suggested strong nonlinearities between the variables (see below). NV was again discarded (Table 3). The best GAM for E/N ratio was influenced by PD and HD (Table 3), and again the explained deviance was low (29 %). NV was also discarded in the best model for E/N. One important point of these results is the clear non-linear relationship of E with PD (see estimated degrees of freedom for each model and variable in Table 3), but an almost linear relationship with N and HD. In the case of E/N we observed a strong non-linear relationship with PD, but an almost linear one with HD (see degrees of freedom in Table 3).

Discussion

Urbanization is a major force affecting insect community structure and the rates and probability of a successful invasion by exotic species (Samways 2005). Our results showed that across the heavily intervened landscape of the Metropolitan region of Chile, there is a positive correlation between native and exotic forest insect species richness (Fig. 2a). Multiple hypotheses have been advanced to explain this type of relationship, including random processes (Fridley et al. 2004), spatial heterogeneity (Davies et al. 2005) or resource availability (Byers and Noonburg 2003), especially when the interaction is examined over landscape scales (e. g. Byers and Noonburg 2003). In the first hypothesis,

Fig. 2 Scatterplot of the relationship between the raw numbers of native and exotic species
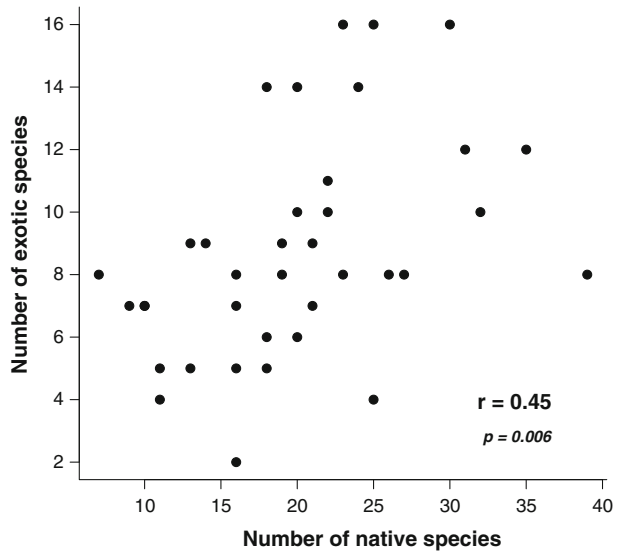
Table 2 Results of the GLM fitting for the exotic diversity (E) and the ratio exotic/diversity (E/N)

GLM	Model	AIC	D^2
Exotic diversity			
Full model	Ln(E) = 0.045N + 0.049PD + 0.004NV + 0.038HD	181.700	50.11
Best model (stepwise)	Ln(E) = 0.044N + 0.049PD + 0.040HD	179.700	50.05
Ratio exotic/native			
Full model	Ln(E/N) = 0.504PD + 0.189NV + 0.760HD	−12.060	21.96
Best model (stepwise)	Ln(E/N) = 0.536PD + 0.883HD	−13.750	21.37

Both full model (including all predictors) and the best model according to stepwise procedure are shown. All variables were measured in a 250 m radius buffer around each trap. AIC is the Akaike information criteria for the model and D^2 is the percentage of explained deviance. Coefficients are standardized to evaluate the relative importance of each variable in the model

N native diversity, *PD* human population density, *NV* residual native vegetation coverage, *HD* habitat diversity

Fridley et al. (2004) showed that the relationship between native and exotic species richness was negative at small spatial scales and positive at large scales for simulated communities where the use of space is passively determined by abundances in the regional pool of species (neutral sensu Hubbell 2001). According to the second hypothesis, because spatial heterogeneity in the environment increases as we increase the spatial scale, it is expected that richness of exotic and native species increase at larger spatial scales (Davies et al. 2005). Byers and Noonburg (2003) offered a different explanation to scale-dependent native-exotic richness correlations. They proposed that competitive interactions over local spatial scales generate negative correlations between native and exotic species richness (akin of Elton's biotic resistance hypothesis, Elton 1958), but increasing spatial scale changes the number of available resources, positively influencing both native and exotic species richness. The latter two hypotheses predict native and exotic richness to be positively correlated at large spatial scales due to the forcing of a third environmental variable,

Table 3 Results of the GAM fitting for the exotic diversity (E) and the ratio exotic/diversity (E/N)

GLM	Model	AIC	D^2
Exotic diversity			
Full model	$Ln(E) = 2.137 + s_1(N, df = 1.13) + s_2(PD, df = 1.61) + s_3(NV, df \approx 0) + s_4(HD, df = 1.23)$	178.078	57.00
Best model (shrinkage)	$Ln(E) = 2.133 + s_1(N, df = 1.06) + s_2(PD, df = 2.52) + s_3(HD, df = 1.05)$	177.762	60.10
Ratio exotic/native			
Full model	$Ln(E/N) = -0.750 + s_1(PD, df = 0.77) + s_2(NV, df \approx 0) + s_3(HD, df = 1.17)$	−13.750	21.10
Best model (shrinkage)	$Ln(E/N) = -0.758 + s_2(PD, df = 3.42) + s_3(HD, df = 1.11)$	−12.515	29.10

Both full model (including all predictors) and the best model according to shrinkage procedure are shown. All variables were measured in a 250 m radius buffer around each trap. s_i represents the cubic regression spline for this variables and *df* are the effective degrees of freedom for each term. AIC is the Akaike information criteria for the model and D^2 is the percentage of explained deviance

N native diversity, *PD* human population density, *NV* residual native vegetation coverage, *HD* habitat diversity

but differ in terms of mechanisms and the importance of competition over local scales. Our data showed that at the scale of individual traps and in both seasons, richness of natives and exotics were generally negatively correlated (results not shown here), but correlations were weak and non-significant. Thus, without information on individual abundances, evidence for the effect of local competition between natives and exotics is, at best, ambiguous. On the other hand, our analyzes suggest that the positive relationship between native and exotic insect richness observed across the region is the byproduct of the effect on both groups of human-mediated environmental variables, such as human PD and habitat diversity. Evidence in the same direction is provided by Etchegaray and Fuentes (1980) and Fuentes et al. (1981), who found, working in small scale experiments, that five native defoliating insects morphospecies associated to seven native shrub species were not equally associated to each plant, showing some degree of preference, but all morphospecies were found in each of analyzed shrubs. This could means that native insects show a generalist behavior in the use of the space and resources. If this result may be expanded to our current data, it would mean that at some degree native insects could change between different resources (food and refuges) with an expected effect in the average abundances, but no necessarily in the presence/absence patterns in the landscape.

The explained deviance was nearly twice higher in models of E than E/N (Tables 2, 3). Despite this, we will discuss the results in terms of the relative importance of each variable and the coincidences and differences between the E and E/N models. The results of GLM and GAM showed that E and E/N are positively influenced by human PD and habitat diversity (HD). The reasons underlying these relationships can be diverse. Humans are largely responsible for the transport of propagules from source areas to new habitats (McNeely 2005), and they can facilitate the establishment of new species, usually by creating disturbances (Mack et al. 2002; McNeely 2005). This positive influence of human PD on species richness has been amply described for many other ecological systems (Pautasso 2007; Pautasso and Fontaneto 2008). Such effect emerges because people prefer to settle in areas of high biodiversity and/or because of the high diversity of small-scale habitats typically associated to human settlements (Mack et al. 2002; Davies et al. 2005;

Pautasso 2007). Actually, in urban areas, gardens, parks and other human-made plantations create a mosaic of refugees and alternative sources of food for insects and other small sized organisms, an this fact, may enhance the coexistence within and between native and exotic species assemblages and may explain the positive influence of HD on E and E/N.

Another interesting point that emerges from the analysis is the null influence of the NV on E or E/N. This might seem contradictory at a first sight. The influence that native vegetation cover can have on the native insect diversity (and the reduction of the E/N ratio), by providing food and refugees, has been highlighted in several studies (Samways 2005 and references therein). The effect of native vegetation is especially critical in the case of specialized trophic relationship, like plant–insect pollinator or host-parasite. In these cases, the decrease or extinction of some native plants could trigger the extinction of the associated specialized native insects, or vice versa in the case of pollinators (Kearns and Inouye 1997; Allen-Wardell et al. 1998; Memmott et al. 2004). However, it seems that in Central Chile this variable is not a good predictor of the invasibility of the community. Following the results of Etchegaray and Fuentes (1980) and Fuentes et al. (1981) previously explained, the effect of the reduction of native vegetation cover could impact in averages abundances of native insects, but not the pattern of richness. In this way the expected increase of the E/N ratio due to the local extinction of native insects could not be observed. Another possible explanation for this situation could be that our measure of NV is not related to native vegetation richness. Most insects in our sampling are herbivorous, therefore, plant richness should have a positive effect on insect diversity due to the expected increase in food items. However, if NV is not related to native richness, for example if one or few species are dominating the vegetation coverage, then the effect of NV on E or E/N would be diminished. Unfortunately, we do not have the information needed to further evaluate the effects of native vegetation richness on insect richness.

The analysis using GAM showed that some relationships are strongly non-linear, although most of them are monotonic decreasing or increasing functions. The relationship between E and PD is particularly interesting. As shown in Fig. 3b, this relationship seems to have a threshold around 1,000 hab/km^2, below which the proportion of exotic species in the community grows rapidly as PD increases. Above this threshold, exotic richness seems to be largely unaffected by further increase in human population density. This population density threshold separates small towns from large densified cities. Thus, at least in Central Chile, the positive influence of human PD on the proportion of exotic insect species might be largely restricted to rural or semi rural areas, and be largely 'saturated' in big cities.

In another vein, the information and results showed in this study could be useful for developing or improving management tools for invasive species prevention. The list of exotic species already established is an excellent piece of information to determine which species are potentially invasive in this or other Mediterranean-type ecosystems (Samways 1999). This list also allows researchers to analyze the more common characteristics or traits in the current exotic fauna. The list containing these traits could be used to evaluate the risk associated to other potential invasive insects (Worner and Gevrey 2006; Peacock and Worner 2008). It has been suggested that assemblages of exotic insects are non-random, and the information provided by common traits and current distribution will improve pest risk assessments (Worner and Gevrey 2006; Stohlgren and Jarnevich 2009). Finally, when evaluating which human-related disturbances are correlated with a higher richness of exotic species, we may incorporate this variables into the programs of early detection of invasive species (Holcombe and Stohlgren 2009). For example, if sites with high population density or high HD show a high richness of exotic insects, then monitoring activities could be focalized or intensified in sites with these characteristics.
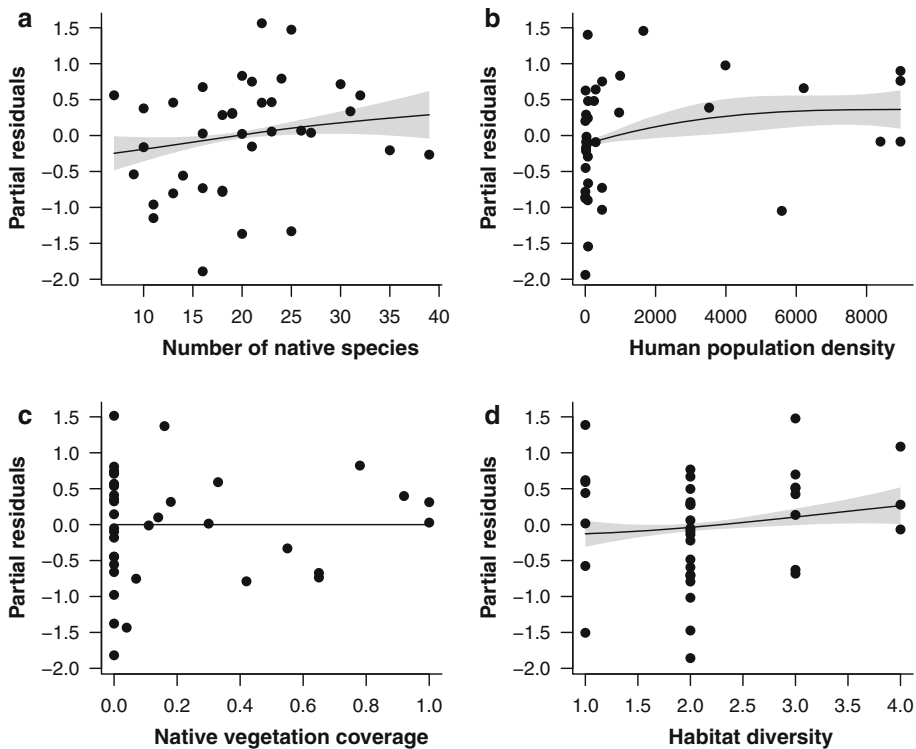
Fig. 3 Partial residuals of exotic richness using the full GAM for each variable. Points are partial residuals, *solid lines* are the predicted values of the model and shaded areas are confidence limits of 2 standard errors above and below the predicted value. **a** Native species richness, **b** Human population density, **c** Native vegetation coverage, **d** Habitat diversity

It is important to emphasize that we do not have information about the responses of insects in terms of population abundances, which is the major limitation of this study and our ability to understand the ecological relationship between native and exotic species in this system. For this reason, a logical next step would be the analysis of how abundances of native insects have been affected by the introduction and establishment of exotic insects. In order to fulfill this objective it would be required an exhaustive sampling in both time and space. This effort could be focalized in some key groups like Coleoptera or Lepidoptera, which have been described as good indicators of ecosystem health (Fleishman and Murphy 2009; Koivula 2011; Morrison III et al. 2012). Yet, we believe that our results represent an important first step in the understanding this type of processes and they constitute and potential explanatory hypothesis about insect diversity in the Chilean Mediterranean ecosystem.

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