Web Ecol., 16, 63–65, 2016
www.web-ecol.net/16/63/2016/
doi:10.5194/we-16-63-2016

Human population density and tenebrionid richness covary in Mediterranean islands

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Received: 24 September 2015 – Revised: 25 November 2015 – Accepted: 2 February 2016 – Published: 17 February 2016

Abstract. Human population growth is expected to drive several species to local extinction. Yet, an unexpected high biodiversity can be found even in densely populated areas. Although a positive correlation between human density and biodiversity can be explained by the intermediate disturbance hypothesis, an alternative possible explanation may come from the tendency of human settlements to be located in sites whose environmental conditions are particularly favourable also for many other animal species. To investigate this hypothesis, we studied the relationships between human population density and species richness of native tenebrionid beetles in small Italian islands. We used partial regression analysis to assess the individual contribution of island area (to account for the species–area relationship), elevation (used as a proxy of environmental diversity), and human density to species richness. We found that tenebrionid diversity increased with human population density even after controlling for area and elevation. This may suggest that islands that were (and are) more hospitable to humans are also those which can be more favourable for tenebrionids.

1 Introduction

Species extinctions that occurred on islands after human colonization are considered paradigmatic of the threats posed by mankind to biodiversity (Lomolino et al., 2010). Since all of the anthropogenic causes of species extinction are more or less directly associated with increasing human population (McKee et al., 2003), human population density is frequently used as a proxy of human impacts on the environment (Goudie, 2013). In general, more people can produce more varied and more severe impacts, and, hence, promote higher extinction rates (McKee et al., 2013). As a result of increased extinction rates in densely populated areas, species richness is expected to decrease with human population, all other things being equal (McKee et al., 2003). If more people implies more species being lost, we expect that islands with higher human population density should have fewer species, after differences in island size and environmental diversity are accounted for. In this paper, we investigated the relationships between human population density and species richness in the tenebrionid beetles inhabiting Italian islands. Contrary to our expectation of a negative relationship, we found a positive one and we offer here an explanation for this unexpected result.

2 Methods

We collected presence data on tenebrionid species for 61 small islands from all Italian archipelagos, including the Maltese Islands. Data were obtained from Fattorini and Dapporto (2014) and Lillig et al. (2012). Cosmopolitan and strictly anthropophilic species, which are associated with stored food and with man-made biotopes, were not considered, since their presence on islands could be due to human introduction. All islands included in this study have been subject to intense insect sampling specifically targeted towards tenebrionids. Data included literature and museum records and were collected by a multitude of entomologists for ecological, faunistic, and taxonomic purposes. Records could not be assigned to specific locations and elevations within islands, but information on species distribution (presence/absence) among islands can be considered complete. Island area, elevation, and human population density were extracted from Arnold (2008). For uninhabited islands not included in Arnold (2008), we obtained values of area and elevation from Fattorini and Dapporto (2014). Because species number increases with area (a phenomenon known as the species–area relationship; Lomolino et al., 2010), it is important to remove the effect of differences in area size to assess the actual correlation between species richness and human density. Because a more varied landscape allows the co-existence of species with different ecological needs, it is also important to control for island environmental heterogeneity (Fattorini et al., 2015). We used island maximum elevation as a proxy for environmental diversity because elevation is correlated with variations in temperature, precipitation, humidity, wind speed, evaporation and insolation, and hence, according to the General Dynamic Model of island biogeography, with environmental heterogeneity (Whittaker et al., 2010; Fattorini et al., 2015). In the study systems, elevation is only moderately linearly correlated with area ($r = 0.428$, $p<0.001$). The species–area relationship is usually best modelled by a power function $S = CA^z$ approximated by the double logarithmic transformation: $\ln S = \ln C + z \ln A$, where S is the number of species, A is the area, and C and z are constants (Triantis et al., 2012). This also occurred in our study system. We also found that a ln-ln model best fitted the species–human-density relationship and the species–elevational-gradient relationship. To cope with islands with no inhabitants and/or with an elevation lower than 5 m elevation (and then recorded as 0 m), we used a $\ln(x+1)$ transformation. To identify the separate contribution of island area, elevation, and human density to species richness, we used partial correlation analysis, which makes it possible to assess the actual correlation between two variables while controlling for (i.e. partialling out) one or more other variables.

3 Results

Species number (S) increased with island area (A) according to the power function $\ln S = 2.202 + 0.253 \ln A$ ($R^2 = 0.713$, $F(1,59) = 146.84$, $p<0.000001$, $S_{yx} = 0.598$). A power function also adequately modelled the relationships between species richness and maximum elevation (E) ($\ln S = -0.467 + 0.543 \ln E$; $R^2 = 0.609$, $F(1,59) = 94.608$, $p<0.000001$, $S_{yx} = 0.569$) and between species number and human population density (D) ($\ln S = 1.277 + 0.342 \ln D$; $R^2 = 0.606$, $F(1,59) = 93.342$, $p<0.000001$, $S_{yx} = 0.6954$). Although the percentages of explained variance for the species–elevation and species–human-density relationships were lower than those of the species–area relationship, partial correlation analysis showed that there is a significantly positive correlation between species richness and human population density, even after island area and maximum elevation are partialled out (Table 1).

Table 1. Partial correlations between tenebrionid richness (dependent variable) and island area, maximum elevation, and human population density (independent variables) on the Italian islands. The partial coefficient indicates correlation between the respective variable and the dependent variable, after controlling for all other independent variables.

Variables	r_{partial}	p level
(a) area and elevation		
Island area	0.569	< 0.00001
Elevation	0.306	0.017
(b) area and human density		
Island area	0.610	< 0.00001
Human density	0.389	0.0021
(c) elevation and human density		
Elevation	0.548	< 0.00001
Human density	0.542	< 0.00001
(d) area, elevation, and human density		
Island area	0.410	0.0013
Maximum elevation	0.270	0.0383
Human density	0.364	0.0046

4 Discussion

Individually, area and elevation explained a larger proportion of variance in species richness than population density. However, when the contribution of each variable was assessed by partialling out that of the other ones, population density was more important than elevation and only slightly less important than area. This unexpected result suggests that islands that were (and are) more hospitable to humans are also those which can be more suitable for tenebrionids because of their larger areas and higher environmental heterogeneity.

A positive relationship between biodiversity and human population has already been noticed for a great variety of organisms worldwide (e.g. Gaston, 2005; Luck, 2007; Steiner et al., 2008). At the global level, the most generally accepted explanation for this pattern is that both species richness and numbers of people respond positively to levels of available energy (Gaston, 2005): more energy sustains more biomass and more individuals, hence permitting more species to maintain viable populations within an area. Moreover, human populations might tend to concentrate and grow where there is high abundance and diversity of plants and animals that can be used as food or for other purposes. In our case study, we can assume that environmentally more varied areas have a greater variability of resources (and hence a greater probability of including key resources for human populations, such as drinkable water), which, in turn, promote the establishment of a higher number of species (including tenebrionids). Of course, people and tenebrionids have very different needs, which explains the fact that a large fraction of tenebrionid richness is accounted for by environmental diversity even after the co-variation with human population is partialled out.

It has been also postulated that a positive humans–species richness relationship might be due to the fact that plants and animals tend to be attracted or introduced by people (Gaston, 2005). We have omitted from our analyses all tenebrionid species that are known to be strictly associated with humans (i.e. pests of stored products and species associated with man-made biotopes); thus, the introduction of species or creation of biotopes suitable for anthropophilic species can be hardly considered a major driver of tenebrionid diversity in this study. Although it can be postulated that cultural landscapes may have more tenebrionid species due to a higher diversity and/or complexity of habitats provided by regular human interventions, this does not seem to be the case because non-anthropophilic tenebrionids are negatively affected by land use changes (Fattorini, 2008). Our finding that tenebrionid richness is not negatively affected by human population suggests that the possible impacts of land use changes on tenebrionids of the study islands is not proportional to human population.

5 Conclusions

While common dependence of both human population and species diversity on other variables (such as energy and resource availability) may explain positive species–human relationships, it is difficult to understand how higher species richness can persist in densely populated areas, where extinction rates are typically high (Gaston, 2005). Most of the largest islands included in our study have been inhabited by people for millennia, and people have exerted a profound influence on island landscapes, especially through destruction of ancient forests, grazing, land conversion for agriculture, etc. This might have driven species associated with mature forests to extinction (Fattorini, 2008). However, there is a high correlation between human population density and tenebrionid species richness. This pattern of species–human covariation may be explained by assuming that (1) there were even more tenebrionid species before humans settled on the islands and (2) the number of tenebrionid beetles and population density vary in a similar way with variation in environmental parameters.

Acknowledgements. We are grateful to J. Röder and P. Borges for their comments on a first version of this paper.

Edited by: J. Stadler
Reviewed by: J. Röder and P. Borges

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