When human needs meet beetle preferences: Tenebrionid beetle richness covaries with human population on the Mediterranean islands

Short title: Men and beetles on Mediterranean islands

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Abstract. 1. Human presence can affect biodiversity in many ways. If anthropization is one of the major drivers of species extinctions, at the same time, human-induced increases environmental heterogeneity may also increase species richness.

2. In many cases, however, heterogeneity is not enough to explain the unexpectedly high biodiversity found in some densely populated areas.

3. A possible explanation to such situations is the partial overlap in resource requirements between man and other species, which promotes a tendency for humans to settle in sites characterized by environmental conditions that are particularly favourable also for many other organisms.

4. To test this hypothesis, we investigated the relationships between human population and species richness of native (non-synanthropic) tenebrionid beetles in Mediterranean islands, many of which have been inhabited by humans for millennia.

5. Using partial correlation analyses, we found that tenebrionid diversity increased not only with island area and maximum elevation (used herein as a measure of environmental heterogeneity), but also with human population.

6. This may suggest that islands that were (and are) more accessible and hospitable to humans are also those which can be more easily colonized by tenebrionids, owing to their larger areas and higher environmental heterogeneity.

Key words. Conservation, Habitat diversity, Human population, Island biogeography, Species-area relationship

Introduction

Most of the anthropogenic causes of species extinction are more or less strictly associated with increasing human population size; thus, all other things being equal, species richness is expected to decrease accordingly (McKee *et al.*, 2003; Davies *et al.*, 2006; Goudie, 2013). Nevertheless, some species are known to benefit from human presence (e.g., Adams, 1994; Vitousek *et al.*, 1996; Adler & Tanner, 2013), and increased environmental heterogeneity resulting from human activities may lead to high species diversity in areas subject to moderate disturbance (e.g., McKinney, 2002a; Roxburgh *et al.*, 2004; Johst & Huth, 2005). At the same time, studies conducted in urban areas, where human population reaches the highest densities, have demonstrated that species richness is usually low in heavily built up and densely populated sites (Wootton, 1998; McKinney, 2002b; Müller *et al.*, 2013). In this context, it is difficult to find general patterns in the relationships between human population and species richness. Some studies conducted on plants and vertebrates at large scales have reported a positive correlation (Gaston, 2005; Luck, 2007; Luck *et al.*, 2010), but, to the best of our knowledge, no effort has been focused on investigating the relationship between insect diversity and human population at a finer scale in non-urban contexts. We tried to partially fill this gap by focusing on the diversity of tenebrionid beetles inhabiting the Mediterranean islands. Island ecosystems are excellent natural laboratories for conservation studies (Ladle & Whittaker, 2011) and species extinctions that occurred on islands after human colonization are considered insightful examples of the threats posed by mankind to the biodiversity (Whittaker & Fernández-Palacios, 2007; Lomolino *et al.*, 2010). However, contrary to expectation, we found a positive relationship between human population and tenebrionid species richness on the Mediterranean islands. In this paper we report these counter-intuitive results and we offer possible explanations that could also apply to other biogeographical settings. We used the Mediterranean islands because they are numerous, and because human influence on their natural environment is well documented (Arnold, 2008). We focused on tenebrionid beetles because their species distribution among islands is well known. Moreover, thanks to their low dispersal ability, tenebrionids have been repeatedly used to investigate the biogeography of Mediterranean islands (Fattorini et al., 2015).

Materials and methods

We collected presence data on native tenebrionid species for 61 Italian islands (including the Maltese Islands) and the 32 Aegean Islands from literature sources (Appendix S1, Supplementary Material), with the addition of a few personal new records. Values of species richness per island, island area, elevation, human population and population density are given in Tables S1 and S2 (Appendix S2, Supplementary Material). All the islands included in this study have been subject to intensive sampling targeted towards tenebrionids, so that their tenebrionid fauna is considered virtually complete by authors that have performed the sampling or revised the data.

Because species number increases with area (a phenomenon known as the species-area relationship; see Triantis *et al.*, 2012 for a review) and environmental heterogeneity (see Fattorini *et al.*, 2015 for a review), the effect of inter-island differences in area size and environmental heterogeneity should be removed in order to assess the actual correlation between species richness and human population. Therefore, we included island area and elevation (which is considered a good proxy for environmental diversity; see Newmark, 1986 and Allouche *et al.*, 2012) as additional variables explaining variation in species richness among islands.

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, it is also related to island geological dynamics and evolution (Whittaker et al., 2010)

We extracted values of island area, elevation and human population from Arnold (2008). For uninhabited islands not included in Arnold (2008), we used values of area and elevation as given in the papers reported in Appendix 1. Values of area and elevation of all islands were also checked using Google Earth satellite maps.

We modelled the species-area relationship by using the ln-transformed power function $\ln(S) = \ln(c) + z \times \ln(A)$, where S is the number of species, A is the area, and c and z are constants (see Triantis *et al.*, 2012 for a discussion of this model). We also found that a ln-ln model best fitted both the species-human population relationship (expressed either as number of resident people or population density), and the species-elevation gradient relationship. We used a $\ln(x+1)$ transformation to cope with islands with no inhabitants or 0 m elevation. To identify the correlation between species richness and human population or human density after controlling for (i.e., partialling out) island size and island elevation, we used partial correlation analyses (Legendre & Legendre, 2012).

Results and Discussion

In the Italian islands, tenebrionid species number (S) increased with island area (A) according to the power function $\ln(S) = 2.202 + 0.253\ln(A)$ ($R^2 = 0.713$, $P < 0.000001$). A power function also modelled the relationships of species richness with maximum elevation (E) ($\ln(S) = -0.467 + 0.543\ln(E)$; $R^2 = 0.609$, $P < 0.000001$), human population (expressed as number of resident people, P) ($\ln(S) = 1.258 + 0.231\ln(P)$; $R^2 = 0.653$, $P < 0.000001$) and human population density (expressed as number of inhabitants per km^2, D) ($\ln(S) = 1.277 + 0.342\ln(D)$; $R^2 = 0.606$, $P < 0.000001$). In the Aegean islands, species number (S) increased with island area (A) according to the power function

$\ln(S) = 1.400 + 0.268\ln(A)$ ($R^2 = 0.407$, $P < 0.0001$). A power function also modelled the relationships of species richness with maximum elevation (E) ($\ln(S) = -1.233 + 0.614\ln(E)$; $R^2 = 0.314$, $P = 0.001$), human population (P) ($\ln(S) = 0.601 + 0.249\ln(P)$; $R^2 = 0.558$, $P < 0.000001$), and human population density (D) ($\ln(S) = 1.252 + 0.425\ln(D)$; $R^2 = 0.308$, $P = 0.001$).

Thus, area and elevation explain, individually, a proportion of variance in species richness similar to, or even larger than, the proportion explained by human population. However, when the contribution of each variable was assessed by partialling out that of the others, human population was clearly the most important one (Table 1). In the Italian islands, when human population (or population density) was considered together with area and elevation, all variables correlated significantly with species richness. In the Aegean islands, where area and elevation explained less variation in species number, population or population density was the only significant correlate, after the influence of area and elevation was controlled for. Thus, human population correlates positively with species richness and can even overwhelm the influence of both area and environmental diversity, which are typically strong predictors of tenebrionid species richness and composition of island biotas (Fattorini, 2002, 2010, 2011; Fattorini *et al.*, 2015). This unexpected result suggests that islands that can be more easily colonized by tenebrionids, because of their larger areas and higher environmental heterogeneity, were also more accessible and hospitable to humans. Actually, we found significant relationships of human population with area and elevation for both the Italian islands (Spearman rank correlation: $r_s = 0.875$ for area, $r_s = 0.803$ for elevation) and the Aegean islands ($r_s = 0.857$ for area, $r_s = 0.710$ for elevation; $P < 0.0001$ in both cases). Thus, there is indication that both human population and tenebrionid diversity are positively correlated with area and environmental diversity.

Positive relationships between biodiversity and human population have already been noted at large scales (Gaston, 2005; Luck, 2007; Luck *et al.*, 2010), but the underlying mechanisms remain elusive. The most generally accepted explanation is that species richness and numbers of people both respond positively to energy availability, because the higher the energy, the greater the biomass and the number of individuals to be sustained, which, in turn, allow more species to maintain viable populations within an area (Gaston, 2005; Evans & Gaston, 2005). Thus, it can be hypothesized that early human populations settled clumped and grew more readily in warm and productive areas where there is high abundance and diversity of plants and animals that can be used as food or for other purposes. In the case of the Mediterranean islands, environmentally more varied islands have a greater variability of resources, and hence a higher probability of including key resources for both human populations (such as drinking water) and other species. Higher diversification and abundance of resources can promote the maintenance of more species (including both tenebrionids and plants and animals used as food by people). Thus, larger and environmentally more varied islands may support both larger human populations and more tenebrionid species. Yet, people and tenebrionids have different needs, which explains the fact that there is some fraction of tenebrionid richness explained by environmental diversity even after the co-variation with human population is partialled out.

A further explanation of a positive relationship between biodiversity and human population is that plants and animals tend to be attracted or introduced by people (Gaston, 2005). However, this explanation cannot be advocated in our case because we have excluded all the tenebrionid species strictly associated with humans (synanthropic species).

While common dependence of numbers of people and numbers of species on other variables may explain positive species-humans relationships, it is difficult to understand how high species richness can persist in densely populated areas, because extinction rates should increase with human population density (Thompson & Jones, 1999). To explain this apparent contradiction, two main hypotheses can be proposed: (1) the negative effects of human density could lower the overall slope of the species richness-human density relationship, but might be not so strong to reverse it or make it humpshaped (Gaston, 2005); and (2) the negative effect of human population cannot be revealed at coarse spatial resolutions, because remnants of suitable biotopes can be found even where human density is high. In this regard, strong positive relationships between diversity and human populations were found when comparing entire cities urban areas (Sukopp, 1998; Luck *et al.*, 2010), while they were weak or absent when smaller and more homogeneous urban areas within cities were compared (McKinney, 2008; Faeth *et al.*, 2011). In our case study, most of the largest islands have been inhabited for millennia and people have exerted a profound influence on island biotas (Fattorini, 2008a). However, the human population in the Mediterranean islands is usually concentrated in small towns, so that the impact on most of the islands' surfaces is probably too small to obscure the species richness-human density relationship.

In conclusion, our results provide analytical support to the hypothesis that patterns of human colonization could overlap with those of other species as a common response to the same environmental drivers, namely island size and environmental heterogeneity. If human populations tend to colonize areas with high diversity, this inexorably increases the extinction risk on the islands, which are particularly fragile ecosystems (Whittaker & Fernández-Palacios, 2007) and are now important tourist destinations (for a discussion of the impact of tourism on biodiversity, see Hall, 2010). Many Mediterranean islands are under strong tourist pressures and also those having a relatively small permanent population may experience peaks in population density during the tourist seasons (for example, an island like San Domino, Italy, has a resident population of 236 people, but may host up to 1600 people if all visitor capacities are full; Arnold, 2008). In such a dramatic situation, our study of human population – animal diversity covariation may represent a useful benchmark to better understand of the potential effects of tourism on island biotas.

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Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: …......................................:

Appendix S1. Data source.

Appendix S2. Island characteristics, human population and tenebrionid richness

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Table 1. Results of partial correlations among tenebrionid richness, island characteristics and human populations.

	Italian islands		*Aegean islands*	
Variables	$r_{partial}$	*P*-level	$r_{partial}$	*P*-level
(a) area and elevation				
Island area	0.569	<0.00001	0.368	0.042
Elevation	0.306	0.017	0.008	0.966
(b) area and human population				
Island area	0.536	<0.00001	-0.144	0.439
Human population	0.372	0.003	0.520	0.002
(c) elevation and human population				
Elevation	0.416	<0.00001	0.033	0.862
Human population	0.554	<0.00001	0.597	0.0004
(d) area, elevation, human population				
Island area	0.368	0.004	-0.248	0.186
Maximum elevation	0.262	0.045	0.207	0.273
Human population	0.338	0.009	0.549	0.002
(e) area and human density				
Island area	0.610	<0.00001	0.613	0.0003
Human density	0.389	0.002	0.520	0.002
(f) elevation and human density				
Elevation	0.548	<0.00001	0.618	0.0002
Human population density	0.542	<0.00001	0.614	0.0002
(g) area, elevation, human density				
Island area	0.410	0.001	0.178	0.347
Maximum elevation	0.270	0.038	0.207	0.273
Human population density	0.364	0.005	0.549	0.002