Is the human population a large-scale indicator of the species richness of ground beetles?

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Abstract

Empirical evidence has often shown a large-scale positive co-occurrence of biodiversity-rich and densely populated regions. This biogeographical pattern has important implications for conservation biology. Previous studies have supported two of the potential mechanisms behind this pattern: the distributions of biodiversity and of human beings tend to match climatic patterns, and human beings have settled in regions of higher habitat heterogeneity or they may have increased it. There has been little testing and evidence for an artefactual explanation: more populated regions may show more species only because of a more thorough sampling. Using a new country-wide dataset, we tested whether the human population density correlates with the species richness of ground beetles in Italy's regions, provinces and $10 \times 10\,\mathrm{km}$ (UTM) grid cells. As expected, the observed and estimated (Chao index) number of species increases significantly with increasing human population density for regions, while there is no significant variation for provinces. But this is not the case when controlling for sampling effort. Variations in observed and estimated species richness are primarily associated with the available number of records, which is in turn well correlated with human population size. These results were confirmed for endemic and widespread species richness. At the UTM level, when controlling for sampling effort and area, there was a significant positive correlation between the total/widespread species richness and variation in the human population size, while the correlation was negative for endemic species. We found no significant role of habitat heterogeneity in the above relationships. The available distributional data of Carabidae in Italy suggest (1) that the species richness of bio-indicators may not be a reliable measure for regional biological assessment; (2) that some broad-scale human population–biodiversity correlations can be artefactual.

Introduction

One of the approaches commonly used to simplify the study of biodiversity in biological assessment is the identification of biodiversity indicators (Davis & Simon, 1995; Halme et al., 2009; Lawler & White, 2008). Bio-indicators are taxa that are more easily sampled than other more cryptic and/or less well-known groups and whose variations in for example species richness are relatively well positively correlated with the variations in the species richness of other taxonomic groups (Rodrigues & Brooks, 2007). While bio-indicators are commonly used in conservation biology, there is still a need to assess how reliable they are over a range of scales and sampling intensities.

Surprisingly, many recent large-scale studies have shown that the species richness of certain taxa in a given region tends to be correlated with the size of the human population living in that region (Luck, 2007). This is counterintuitive, as densely populated areas have typically lost species due to the many environmental impacts associated with high human population densities (e.g. urbanization, landscape fragmentation and habitat degradation and loss). The direct negative effect of human high densities may be present at a local scale of analysis (Chiari et al., 2010; Magura, Lövei & Tóthmérész, 2009; McKinney, 2008; Savard, Clergeau & Mennechez, 2000); nevertheless, a positive regional correlation between species richness and human population size/density has now been documented at regional scales for different geographical areas. These include sub-saharan Africa (Fjeldså & Burgess, 2008), the USA (Luck et al., 2004), Mexico (Vazquez & Gaston, 2006), the Andes (Fjeldså, 2007), Argentina (Real et al., 2003), Nepal (Hunter & Yonzon, 1993), south-east Asia (Ding et al., 2006), Australia (Luck et al., 2004) and Europe (Araújo, 2003).

For reasons of data availability, the majority of the studies of the regional species–people correlation have dealt with plants and vertebrates (Luck, 2007). However, there is recent evidence for analogous findings with some invertebrate groups such as ants, butterflies, grasshoppers and stream macro-invertebrates (Luck et al., 2004; Pautasso & Fontaneto, 2008; Schlick-Steiner, Steiner & Pautasso, 2008; Steck & Pautasso, 2008). Given that most species on the planet are invertebrates, for the regional positive species–people correlation to be a general biodiversity pattern, it also needs to apply to invertebrates. If a positive species–people correlation is a general biodiversity pattern, then there is an important implication for conservation biology. The negative local human influences on biodiversity will tend to be even more detrimental than if species-rich regions were less densely inhabited.

The positive relationship between human population size and species richness of biodiversity indicators is thus an important pattern to consider, as it may drive political decisions for conservation strategies and priorities. If large-scale positive correlations of biodiversity and human population are the consequence of both variables responding in the same way to other environmental factors such as energy availability and habitat heterogeneity (Fjeldså, 2007; Hunter & Yonzon, 1993; Moreno-Rueda & Pizarro, 2007), then there is the potential for a conservation conflict. On the other hand, the large-scale positive biodiversity–human population correlation may be artefactual. If more populated regions have more recorded species simply because they have been sampled more thoroughly, then there is no point in basing conservation decisions on such a correlation. Surprisingly, little attention has been paid so far to the influence of sampling effort on this issue (Cantarello et al., 2010; Pautasso & McKinney, 2007).

In this study, we test the presence of a positive species richness–human population correlation in Italy's regions, provinces and 10×10 km grid cells for the insect family Carabidae (ground beetles, order Coleoptera). We choose carabids as they are a common, species-rich and well-studied family of ground-dwelling arthropods whose distribution is better known than that of other beetle families (Niemelä et al., 2002). Their ease of sampling and identification has made ground beetles a frequently used group in environmental and conservation assessments (Rainio & Niemelä, 2003). They have thus been widely used to document land-use change and the effect of urbanization in many countries (e.g. Japan: Ishitani, Kotze & Niemelä, 2003; Hungary: Magura, Tóthmérész & Molnár, 2004; Germany: Weller & Ganzhorn, 2004; Britain: Sadler et al., 2006). Given that at a local scale ground beetles are sensitive to human disturbances (Fujita et al., 2008; Hartley et al., 2007; Niemelä & Kotze, 2009), they are an intriguing taxon from the point of view of the analysis of the shape of the species–people correlation at different scales. The main aim of the present study is to test whether there is a positive regional species–people correlation for ground beetles in Italy, and whether this correlation is robust to controlling for sampling effort. Secondly, we wish to test for any scale dependence in the species–people correlation. Given that the species richness–human population correlation has been reported to be scale dependent, that is to increase its strength with increasing grain size, we would expect the correlation to be weaker for UTM cells and stronger at the regional level. Thirdly, we aim to investigate the role of habitat heterogeneity in any species–people correlation. Habitat heterogeneity has been tested less frequently as an explanation for regional species–people correlations than environmental productivity, but may be an important factor. Fourthly, we test whether the species–people correlation for Carabidae in Italy changes in form for endemic versus widespread species.

Italy is a suitable region for the study of the regional correlation between biodiversity and the human population. Italy is a Palaearctic hotspot of Carabidae biodiversity (Schuldt et al., 2009) and has a heterogeneous distribution of human population and habitats. A positive regional correlation of species and people has been documented in Italy for veteran trees, birds and macrofungi (Pautasso & Chiarucci, 2008; Pautasso & Dinetti, 2009; Pautasso & Zotti, 2009), although the latter correlation disappears when controlling for variations in area among regions. Italy is located in the Mediterranean hotspot of biodiversity (Mittermeier et al., 2004; Myers et al., 2000) and has climates ranging from alpine and sub-continental to sub-tropical and Mediterranean. At the same time, it is a country of approximately $300\,000$ km^2, which is inhabited by roughly 60 million people, with an average density of 200 inhabitants per km^2. Italy not only has a high current human population density but also a relatively long history of landscape and habitat modifications by human beings (Falcucci, Maiorano & Boitani, 2007; Maiorano, Falcucci & Boitani, 2006).

Methods

The correlation of ground beetle species richness with human population density was analysed at three geographically nested levels, regions, provinces and 10×10 km UTM grid cells, both on its own and controlling for variations in area, number of records and habitat heterogeneity using multivariate models (as in Pautasso & Fontaneto, 2008). When including area in the models, human population size (and not human population density) was used to avoid having area two times as an explanatory variable. We also analysed whether the observed number of species was correlated with the number of records (including repeated records for the same species), and whether the number of records was correlated with human population size. While there are many ways to gauge sampling effort, the number of records is a straightforward, quantitative indicator of sampling intensity, which is commonly used in biodiversity science (e.g. Ferrer et al., 2006). We repeated the same analyses using Chao's estimated number of species. The numbers of observed and estimated carabid species, records, human population size and area were log-transformed to conform to the assumptions of statistical tests.

Observed species richness for the family Carabidae of Italian regions, provinces and 10×10 km UTM grid cells

was obtained from CKmap, the checklist and distribution of the Italian fauna database (Ruffo & Stoch, 2007). This is a recently compiled country-wide collection of faunistic records. Not all Italian Carabidae are included in this database, but only the subfamilies with a well-known distribution and taxonomy [Carabinae (with both tribes Carabini and Cychrini), Pterostichinae (with all three tribes Abacetini, Pterostichini, Stomini) and Trechinae (with only the tribe Trechini)]. Endemic (216 species) or widespread (196 species) status was reported in the database studied (Ruffo & Stoch, 2007) or obtained from the Fauna Europaea (2004) for species described after 1993. There were no introduced Carabidae species in the data analysed. Estimated species richness was calculated using Chao's bias-corrected formula (Chao, 2005). Chao's estimated species richness is driven by the number of singletons and doubletons (species recorded once and twice). The assumption behind Chao's formula is that the presence of rare species provides the most information about the number of unrecorded species.

Human population size (2001) and the area of Italy's regions and provinces were obtained from the Italian National Institute of Statistics. The human population size of the UTM squares in 2001 was obtained from the Corine database of the European Union (data resolution 100×100 m). Habitat heterogeneity was quantified, at the three spatial scales, using the Corine land-cover classes at the third hierarchical level. From the land-cover map, we computed the Shannon index (Magurran, 2004) using FRAGSTATS (McGarigal *et al.*, 2002).

Province and 10×10 km UTM maps of Europe were imported from the EDIT Geoplatform (Sastre *et al.*, 2009) into GRASS (GRASS Development Team, 2009) through the QUANTUM GIS (Quantum GIS Development Team, 2009) interface. Italian provinces were extracted and grouped into Italy's regions. The UTM sheets covering Italy were joined together and then clipped with the country limits. The area of the UTM grid cells, which varies at national borders, the coastline and the unions between UTM zones, was calculated from the resulting map. Tables linked to the maps were populated with our data and estimates for geographic display.

Analyses were carried out in SAS 9.1. Spatial autocorrelation was controlled for using mixed models with an exponential covariance structure (as in Pautasso & Powell, 2009). Results from spatial and non-spatial models are qualitatively consistent, but (apart from the proportion of variance explained, which refers throughout to non-spatial models, and apart from results at the UTM level, where spatial models did not converge) we present only the results of the spatial models. Spatial models are more robust because they take into account a potential spatial non-independence of data in terms of species presence, survey effort and environmental parameters, which can lead to misleading parameter estimates (Dormann, 2007). We found significant Moran's I at short distances for all models. Significant Moran's I at short distances justify the use of models that take into account spatial autocorrelation.

Results

The database had 16 150 records (occurrences) of 408 species (of 45 genera). Only one species, *Poecilus cupreus*, was reported from all regions and 210 species were reported from one region only. Regional species richness varied between 16 and 136 (average: 65, median: 49, SD: 40). No species was reported from all 103 provinces, and 152 species were reported from one province only. The number of species per province ranged from 2 to 105 (average: 30, median: 24, SD: 21). The species with the most occurrences in UTM grid cells was *Steropus melas*, with 386 occurrences. Eighty-one species were reported from only one UTM grid cell. In the 1783 UTM grid cells (area ∼60% of Italy) with reported occurrences, species richness varied between 1 and 41 (average: 6, median: 3, SD: 6). Fifty species had >100 records in the database, while 47 species had only one record.

Observed total species richness (Fig. 1) increased significantly with increasing human population density for Italian regions (Fig. 2a). There was no significant variation for provinces (Fig. 3a). Species richness decreased significantly with increasing human population density for UTM grid cells (Fig. 4a).

Observed total species richness increased significantly with increasing number of records, for regions (Fig. 2b), provinces (Fig. 3b) and UTM cells (Fig. 4b). A squared number of records term was significant in the relationship of observed number of species as a function of number of records for provinces and UTM grid cells, but increased the proportion of variance explained only marginally.

Observed total species richness did not increase significantly with increasing human population size in a model controlling for variations in the number of records and area (which was also not significant), either for regions or for provinces (Table 1). For the UTM cells, there was a significant positive association of total species richness with human population size when controlling for the number of records and area, the latter also not being significant here (Table 1).

The number of records increased significantly with increasing human population size for both regions and provinces, but only in the latter case was this increase still significant after controlling for variations in area ($n = 103$, $r^2 = 0.15$, logrec $= -2.67 + 0.27$logpop $+ 0.90$logarea, SSE $= 0.11$, 0.14, $P = 0.02$, $P < 0.001$). For UTM grid cells, there was a significant decrease in the number of records with increasing human population size, although the proportion of variance explained was negligible ($n = 1873$, $r^2 = 0.00$, logrec $= 0.79$–0.04logpop, SSE $= 0.02$, $P = 0.01$). The decrease was more significant when including area, which had a significant positive relationship with the number of records ($n = 1873$, $r^2 = 0.04$, logrec $= 0.26$–0.08logpop $+ 0.36$logarea, SSE $= 0.02$, 0.04, $P < 0.001$ in both cases).

Estimated species richness (Chao) was well correlated with observed species richness for regions ($r^2 = 0.85$), provinces (0.91) and UTM grid cells (0.93). Estimated species richness qualitatively matched the results presented above
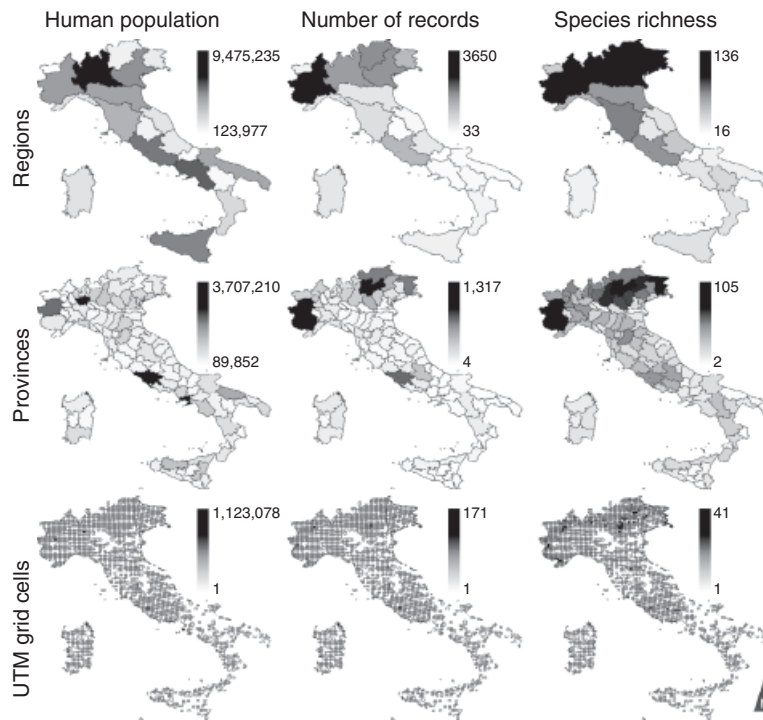
Figure 1 Human population size, number of records and species richness of ground beetles in Italian regions, provinces and UTM 10 × 10 km grid cells. Values are displayed in a grey scale, ranging from white (minimum) to black (maximum). Maps are in Lambert equal area projection (ETRS-LAEA). Grid cells without records are left white and without a contour line.

for observed species richness for regions, provinces and UTM cells, and quantitative differences did not alter any of the conclusions.

When the analysis was subdivided for endemic and widespread species, the same results as with total species richness were obtained for regions and provinces. For regions, both endemic and widespread species richness increased with increasing human population, but did not vary significantly when including the number of records in the model (Table 2). For provinces, there was no significant variation of endemic and widespread richness both in models including human population density only and in models including the number of records (Table 3). At the UTM level, endemic species richness decreased with increasing human population density (both on its own and when including the number of records in the model; Table 3), while widespread species richness increased with human population density when including number of records in the model (Table 3; there was no significant variation in the model without number of records).

Adding latitude and/or habitat heterogeneity (Shannon's index) to the above models did not affect any of the results. Habitat heterogeneity was not a significant factor in models of species richness as a function of human population density, area and number of records at the regional, provincial and UTM levels. At the UTM level, there was a positive correlation between human population density and habitat heterogeneity (Fig. 5).

Discussion

A spatial co-occurrence of human beings and ground beetle species richness over regional scales would be a challenge for conservation, as human pressure can lead to biodiversity loss and homogenization (Kühn & Klotz, 2006; Strayer, 2006). Italy is part of the Mediterranean biodiversity hotspot (Myers *et al.*, 2000; Mittermeier *et al.*, 2004) and is a relatively densely populated country, which has long been undergoing modifications from human activities (Cantarello *et al.*, 2010; Girardello *et al.*, 2009; Underwood *et al.*, 2009). Given the high threat currently experienced by Mediterranean ecosystems, a co-existence of carabid biodiversity and human population across Italy would be a particularly problematic result from a conservation biology perspective. This applies not just to endemic species but also to common ones, given that their often declining populations have become a concern in conservation biology (Conrad *et al.*, 2006; Thomas & Abery, 1995; Van Dyck *et al.*, 2009).

At first glance, the positive species–people correlation appears to be significant for ground beetles in Italy's regions. But when applying more realistic models controlling for number of records and habitat heterogeneity, the reverse situation occurs: the regional relationship between human population density and species richness disappears. Thus, human population does not appear to be a reliable large-scale indicator of the biodiversity of carabids in Italy. More populated Italian regions show more carabid species,
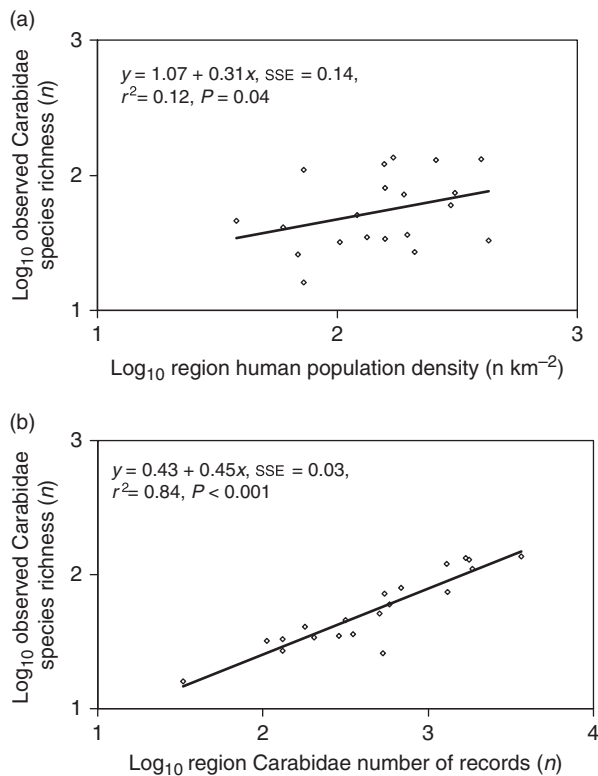
(a)

$y = 1.07 + 0.31x$, SSE $= 0.14$, $r^2 = 0.12$, $P = 0.04$

Log$_{10}$ observed Carabidae species richness (n)

Log$_{10}$ region human population density (n km^{-2})

(b)

$y = 0.43 + 0.45x$, SSE $= 0.03$, $r^2 = 0.84$, $P < 0.001$

Log$_{10}$ observed Carabidae species richness (n)

Log$_{10}$ region Carabidae number of records (n)

Figure 2 The relationship between observed ground beetle species richness and (a) human population density (2001) and (b) ground beetle number of records in Italy's 20 regions on a log–log scale. SSE, slope standard error.
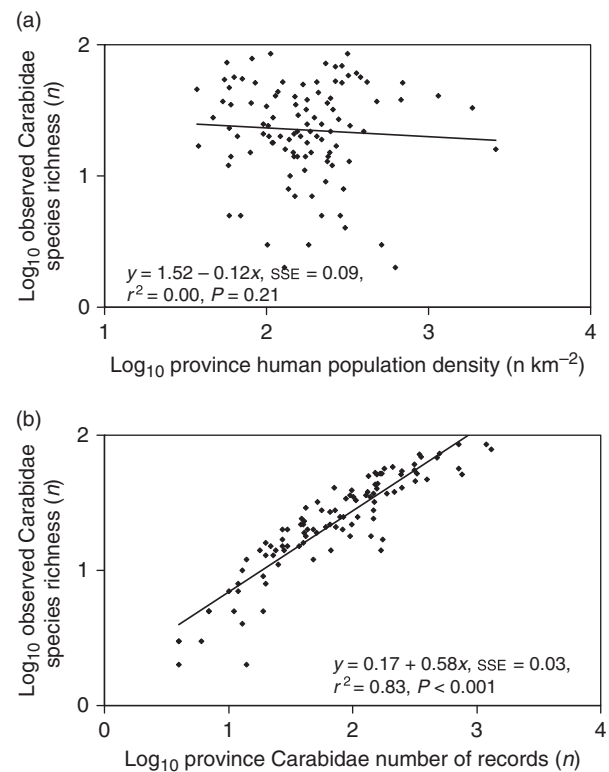

(a)

$y = 1.52 - 0.12x$, SSE $= 0.09$, $r^2 = 0.00$, $P = 0.21$

Log$_{10}$ observed Carabidae species richness (n)

Log$_{10}$ province human population density (n km^{-2})

(b)

$y = 0.17 + 0.58x$, SSE $= 0.03$, $r^2 = 0.83$, $P < 0.001$

Log$_{10}$ observed Carabidae species richness (n)

Log$_{10}$ province Carabidae number of records (n)

Figure 3 The relationship between observed ground beetle species richness and (a) human population density (2001) and (b) ground beetle number of records in Italy's 103 provinces on a log–log scale. SSE, slope standard error.

but only because these areas have been investigated more thoroughly. For provinces, we do not observe significant variation of species richness as a function of human population density, regardless of whether sampling effort is controlled for. At the UTM level, the negative correlation of total species richness with human population density becomes positive when including sampling intensity in the model. A negative correlation is instead present for endemic species richness at this grain of analysis.

These findings are not in agreement with similar studies on other taxonomic groups, showing that there is a regional positive species–people correlation that tends to disappear at more local scales of analysis (e.g. Hardy & Dennis, 1996; Pautasso & Chiarucci, 2008). They do, instead, support the suggestion that species–people correlations need to be studied over different scales for a wide range of taxa before their generality can be assessed (Luck, 2007; Pautasso, 2007). Moreover, the evidence available suggests that survey effort is not just a key factor in biodiversity research generally (Barbosa *et al.*, 2005; Ribas *et al.*, 2007; Sapia, Lovei & Elek, 2006) but can play an important role in the species–people correlation. Entomologists may focus on some areas of particular interest and neglect other areas where they do not expect to find a high diversity of species. Thus, survey effort needs to be considered when analysing

the congruence of biodiversity patterns with the distribution of the human population.

A similar point can of course be made for other biogeographical patterns not involving the human population. For example, for the data studied here, latitude is not a significant factor at the provincial level, is marginally significant for regions (with a reversed gradient, i.e. species richness decreases towards the equator) and significant for UTM cells (again with a reversed gradient). However, the number of records shows the same reversed latitudinal gradient, so that a similar conclusion can be drawn for latitude as for the human population: the pattern in species richness observed as a function of latitude (and human population) can be explained by the underlying variation in number of records as a function of latitude (and human population). Despite the importance of sampling effort in driving the species richness patterns in the database studied, there is an interesting pattern that is robust to including the number of records in the model: while widespread (and total) species richness increases with increasing human population at the UTM level, endemic species richness decreases. This difference may suggest that endemic species are more studied away from human settlements, or it could also imply that endemic Carabidae tend to be species-poorer in densely inhabited

10×10 km areas, because the result is obtained controlling for sampling effort.

Congruence between the broad-scale diversity of ground beetles and human population density can be expected if both variables tend to follow the same regional distribution, as shown for other taxa and regions (e.g. Ding et al., 2006; Schlick-Steiner et al., 2008). However, for ground beetles in Italy, this relationship is not robust to controlling for

Figure 4 The relationship between observed ground beetle species richness and (a) human population density (2001) and (b) ground beetle number of records in Italy's 1873 UTM grid cells with their presence on a log–log scale. SSE = slope standard error.

variations in sampling intensity among regions. Moreover, this result is confirmed when including habitat heterogeneity in models, although there is evidence that habitat heterogeneity increases with increasing human population size at the UTM level. The importance of habitat heterogeneity for carabid species richness has often been documented in local studies (e.g. Negro et al., 2007; Weibull, Ostman & Granqvist, 2003), but the countrywide data of the present analysis suggest that sampling effort is a more important variable than habitat heterogeneity in explaining the apparent correlation of number of carabid species and human population size. Moreover, it is likely that higher habitat heterogeneity is associated with higher habitat fragmentation, which has been shown to have a negative impact on carabid biodiversity (Niemelä, 2001).

After controlling for the potential confounding effects of number of records and area, a positive significant relationship between total/widespread carabid species richness and human population is present only at the most local scale of the 10×10 km grid cells. This does not necessarily mean that human activities have a positive impact on the species richness of a bio-indicator at this grain of analysis. It may be that carabid species richness is higher in spite of the higher human population size. Moreover, endemic species richness declines with increasing human population. Nevertheless, the species richness of ground beetles has been shown in some cases to be higher in human-modified habitats such as the agricultural landscapes than in pristine woodland habitats (Gobbi & Fontaneto, 2008; da Silva et al., 2008). This could be a reason for the positive people–species correlation at the most local scale of analysis. If this is true, the main message from this analysis is that the total species richness of bio-indicators may, on its own, be a misleading parameter for conservation purposes. The biological and ecological characteristics of the single species in the assemblages may be more useful than species richness as an indicator for biological assessment. Some of these characteristics have already been suggested for ground beetles, such as body size, ability to fly and diet (Kotze & O'Hara, 2003; Fujita et al., 2008; Gobbi & Fontaneto, 2008; Niemelä & Kotze, 2009). Our results confirm that the number of endemic species can be a more appropriate bio-
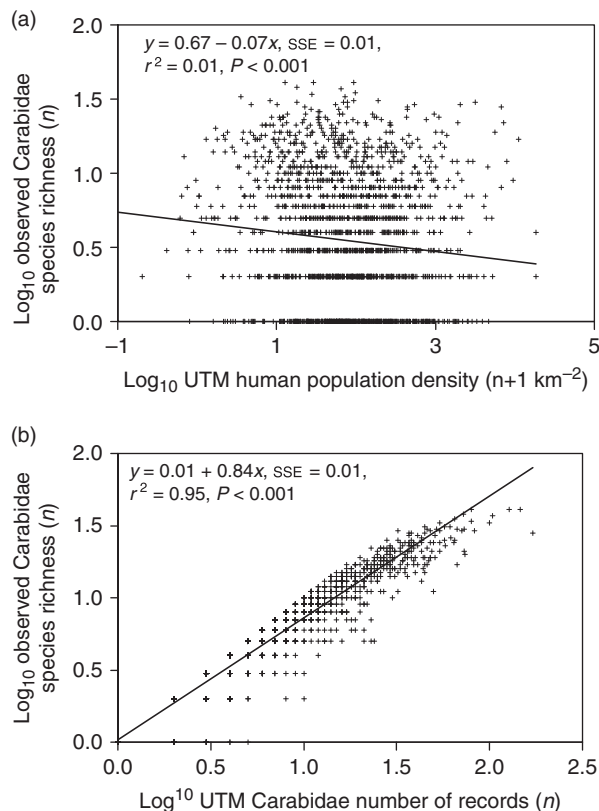
Table 1 Multivariate model of the total species richness of Carabidae as a function of (a) human population size, (b) area and (c) number of records for Italy's regions ($n = 20$), provinces ($n = 103$) and UTM cells with the presence of data ($n = 1873$)

	r^2	Intercept	a	b	c
Regions	0.87	0.47	0.05 ± 0.06	-0.08 ± 0.14	0.45 ± 0.01
		P	0.49	0.58	0.001
		Partial r^2	0.00	0.00	0.87
Provinces	0.84	0.28	-0.03 ± 0.05	0.02 ± 0.06	0.58 ± 0.04
		P	0.49	0.74	0.001
		Partial r^2	0.00	0.00	0.84
UTM	0.95	-0.06	0.016 ± 0.004	0.006 ± 0.008	0.85 ± 0.01
		P	0.001	0.44	0.001
		Partial r^2	0.01	0.00	0.94

All variables were logarithmically transformed. Parameter estimates are given together with their standard error, P values and partial r^2.

Table 2 Multivariate model of the observed species richness of endemic Carabidae as a function of (*a*) human population size, (*b*) area, (*c*) number of records and (*d*) habitat heterogeneity for Italy's regions (*n* = 20), provinces (*n* = 103) and UTM cells with the presence of data (*n* = 794)

	r^2	Intercept	*a*	*b*	*c*	*d*
Regions	0.84	−1.21	−0.02 ± 0.10	0.22 ± 0.22	0.52 ± 0.01	0.26 ± 0.25
		P	0.81	0.31	0.001	0.30
		Partial r^2	0.00	0.00	0.84	0.00
Provinces	0.84	−0.07	−0.07 ± 0.05	0.14 ± 0.06	0.54 ± 0.03	0.17 ± 0.07
		P	0.14	0.02	0.001	0.01
		Partial r^2	0.00	0.00	0.83	0.01
UTM	0.69	−0.05	−0.03 ± 0.01	0.06 ± 0.03	0.56 ± 0.01	0.02 ± 0.02
		P	0.001	0.03	0.001	0.39
		Partial r^2	0.02	0.00	0.67	0.00

All variables were logarithmically transformed. Parameter estimates are given together with their standard error, *P* values and partial r^2.

Table 3 Multivariate model of observed species richness of widespread Carabidae as a function of (*a*) human population size, (*b*) area, (*c*) number of records and (*d*) habitat heterogeneity for Italy's regions (*n* = 20), provinces (*n* = 103) and UTM cells with the presence of data (*n* = 1758)

	r^2	Intercept	*a*	*b*	*c*	*d*
Regions	0.85	0.84	0.03 ± 0.07	−0.20 ± 0.16	0.41 ± 0.05	0.18 ± 0.17
		P	0.71	0.23	0.001	0.30
		Partial r^2	0.00	0.00	0.85	0.00
Provinces	0.87	0.61	−0.06 ± 0.04	−0.05 ± 0.05	0.59 ± 0.03	0.04 ± 0.05
		P	0.11	0.37	0.001	0.37
		Partial r^2	0.00	0.00	0.87	0.00
UTM	0.96	−0.05	0.02 ± 0.00	0.01 ± 0.01	0.85 ± 0.01	−0.02 ± 0.01
		P	0.001	0.47	0.001	0.01
		Partial r^2	0.01	0.00	0.95	0.00

All variables were logarithmically transformed. Parameter estimates are given together with their standard error, *P* values and partial r^2.
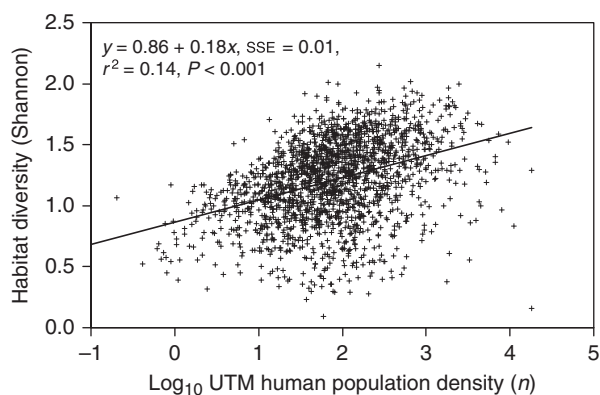
Figure 5 The relationship between habitat heterogeneity (Shannon index) and human population density (2001) for the 1873 UTM grid cells with the presence of ground beetle records, log scale for human population size. SSE = slope standard error.

Pautasso & Chiarucci, 2008) may not be a general trend for invertebrates, as for the total species richness of Italian ground beetles, the opposite seems to occur. More systematic country-wide surveys of less investigated groups such as invertebrates are needed to assess the generality of biodiversity patterns established on the basis of data on plants and vertebrates.

Acknowledgements

indicator than the total number of species (Prendergast *et al.*, 1993).

Our findings highlight the importance of accounting for sampling effort and resolution scale in ecological studies when drawing conclusions for environmental policy (Allan, Erickson & Fay, 1997; Boyero, 2003; Mykrä, Heino & Muotka, 2007). The weakening of the species–people correlation with decreasing grain (Hardy & Dennis, 1996;

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