

A multi-scale study of Orthoptera species richness and human population size controlling for sampling effort

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Abstract Recent large-scale studies have shown that biodiversity-rich regions also tend to be densely populated areas. The most obvious explanation is that biodiversity and human beings tend to match the distribution of energy availability, environmental stability and/or habitat heterogeneity. However, the species–people correlation can also be an artefact, as more populated regions could show more species because of a more thorough sampling. Few studies have tested this sampling bias hypothesis. Using a newly collated dataset, we studied whether Orthoptera species richness is related to human population size in Italy’s regions (average area 15,000 km²) and provinces (2,900 km²). As expected, the observed number of species increases significantly with

increasing human population size for both grain sizes, although the proportion of variance explained is minimal at the provincial level. However, variations in observed Orthoptera species richness are primarily associated with the available number of records, which is in turn well correlated with human population size (at least at the regional level). Estimated Orthoptera species richness (Chao2 and Jackknife) also increases with human population size both for regions and provinces. Both for regions and provinces, this increase is not significant when controlling for variation in area and number of records. Our study confirms the hypothesis that broad-scale human population–biodiversity correlations can in some cases be artefactual. More systematic sampling of less studied taxa such as invertebrates is necessary to ascertain whether biogeographical patterns persist when sampling effort is kept constant or included in models.

Keywords Biogeography · Crickets · Grasshoppers · Invertebrates · Macroecology · Scale dependence

Introduction

There is an increased interest of ecologists, conservation biologists and biogeographers in large-scale patterns of biodiversity (Hawkins and Porter 2003; Wolters et al. 2006; Qian and Ricklefs 2008). Species richness is the fundamental feature of biodiversity together with genetic and ecosystem diversity. Higher species richness is often associated with a higher number of habitat types. In turn, higher species richness enables higher ecosystem function, services and health (Naeem 2002; Symstad et al. 2003; Egoh et al. 2007). Some recent studies show that species richness can be positively correlated also with human

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population size (Luck 2007; Pautasso 2007; Knapp et al. 2008).

Typically, a positive correlation between species richness and human population emerges over large regions, both in terms of study extent (the overall region analysed) and grain (the subdivision of the region). Such pattern is now known for Africa (Balmford et al. 2001; Fjeldså and Burgess 2008), North (McKinney 2001; Vazquez and Gaston 2006) and South America (Diniz-Filho et al. 2006; Fjeldså and Irestedt 2009), Asia (Hunter and Yonzon 1993; Ding et al. 2006), Australia (Luck et al. 2004; Luck 2007) and Europe (Araújo 2003; Marini et al. 2008b; Moreno-Rueda and Pizarro 2009). Although most studies of the species–people correlation have dealt with plants and vertebrates, there is some evidence for analogous findings with invertebrates (Luck et al. 2004; Pautasso and Fontaneto 2008; Schlick-Steiner et al. 2008; Pautasso and Powell 2009). A broad-scale positive species–people correlation has implications for conservation, as the detrimental human local impacts on biodiversity will be even greater if species-rich regions tend to be more densely inhabited.

Several mechanisms have been tested as explanations for large-scale correlations of biodiversity with human population. First, these might be the consequence of both variables correlating with other environmental factors such as energy availability and habitat heterogeneity (Araújo 2003; Hope et al. 2003; Fjeldså 2007; Moreno-Rueda and Pizarro 2007). Second, it is possible that a more numerous human population could result in a more effective conservation of species and individuals, as suggested for ancient trees in Italy (Pautasso and Chiarucci 2008). Third, higher human population size has been often related to a higher number of species introductions (McKinney 2001; Loss et al. 2009; Walker et al. 2009), and this could explain a positive correlation of human population size with exotic species richness, although also in this case, the presence of exotic species can be affected by patterns in productivity and habitat diversity. Little attention has been paid to an additional mechanism, i.e. sampling bias. In this study, we test whether the number of species is higher in more populated regions simply because these have been sampled more thoroughly.

Using data for the order Orthoptera, we test whether or not there is a positive human population–species richness correlation in Italy's regions and provinces. We then repeat the same analysis controlling for the number of records available for each Orthoptera species in the database upon which the analysis is based. We also make use of Chao's bias-corrected species richness estimator. Orthoptera are a relatively well-known taxonomical order which is not restricted to a particular biogeographical region (Green 1998). As Orthoptera species are characterised by widespread distribution, functional importance

and sensitivity to disturbance, they are useful indicators for ecosystem management (Baur et al. 1996; Baldi and Kisbenedek 1997; Andersen et al. 2001; Fontana et al. 2002; Bock et al. 2006; Guo et al. 2006; Davidson and Lightfoot 2007).

For European countries, there is at first sight a positive correlation between grasshopper (Caelifera) species richness and human population size, but this correlation disappears when controlling for plant species richness (Steck and Pautasso 2008). This has been interpreted as evidence for both grasshopper species and people being positively related to habitat heterogeneity, but the data available for European countries do not allow testing for sampling bias, which is the main aim of the present study. A secondary aim is to test for any scale dependence in the species–people correlation of Orthoptera. There is evidence that species–people correlations change in form (from negative to positive) and increase in strength with increasing scale of the analysis (Hardy and Dennis 1999; Luck 2007; Pautasso 2007), but we are not aware of any test of this pattern for Orthoptera.

Material and methods

Observed species richness for the order Orthoptera of Italian regions (21) and provinces (103) were obtained from the checklist and distribution of the Italian fauna database (Ruffo and Stoch 2007). This is a recently compiled nation-wide collection of faunistic records. Data come from private faunistic collections, museum specimens and publications. The temporal span for the Orthoptera data is 1860–2003 (average and median record year=1967), but most (97%) of the data were collected after 1900 and the vast majority (88%) of records dates from after the Second World War. In this analysis, we present results obtained using the more recent half of the data (after 1967). This meant leaving out of the analysis at the provincial level six provinces for which there were no Orthoptera records after 1967 (Asti, Cremona, La Spezia, Prato, Ravenna and Terni).

Given the broad grain size of the analysis (average region size=15,000 km², average province size=2,900 km²) and the nature of the database (records collected by various authors and publications, rather than obtained from a systematic survey), it is impossible to prove that the regional or provincial extinction of a species has taken place. A certain species may not have been recorded after a certain year in a given region/province, but this does not necessarily imply that that species has disappeared from the region/province. In the database, there are only two exotic Orthoptera species (*Acheta gossipyii* and *Tachycines asynamorus*), both occurring rarely.

Estimated species richness was calculated by means of the software EstimateS using Chao's bias-corrected formula (Chao 1984, 2005),

$$\text{Chao2} = [F3] + ([F1]*([F1] - 1))/(2*([F2] + 1)),$$

where F3 is the total number of species observed, F1 is the number of singletons and F2 is the number of doubletons. Chao's estimated species richness is thus based on the number of singletons and doubletons (species recorded once and twice) and assumes that rare species carry the most information about the number of not recorded species. We repeated the same analyses using the Jackknife estimated number of species. Results using the Jackknife estimator (Hortal et al. 2006) were in agreement with those using the Chao's estimator; we thus only present those referring to Chao.

Italy is a country of approximately 300,000 km² and inhabited by roughly 60 million people, with climates ranging from alpine and sub-continental to sub-tropical and Mediterranean and a relatively long history of landscape and habitat modifications by human beings (Maiorano et al. 2006, 2008; Falcucci et al. 2007; Girardello et al. 2009; Chiari et al. 2010). Human population size (2001) and area of Italy's regions and provinces (which are completely nested levels) were obtained from the Italian National Institute of Statistics. As in Pautasso and Dinetti (2009), at the regional level, Trentino and Alto Adige were considered separately.

The correlation of observed and estimated Orthoptera species richness with human population size was analysed on its own and controlling for variations in number of records and area amongst regions and provinces using multivariate models (as e.g. in Pautasso and Fontaneto 2008). If sampling effort explains the species–people correlation, we expected a positive species–people correlation to disappear when including in the multivariate model the number of records. We then analysed whether the observed number of species was correlated with number of records and whether number of records was correlated with human population size. Both correlations were predicted to be positive by the hypothesis that sampling effort explains the species–people correlation.

We used full models rather than attempting model simplification in order to prove that a certain explanatory variable (e.g. human population size) was not significantly related to the response variable (Orthoptera species richness) when including in the model other factors such as the number of records. Moreover, model simplification was already achieved in advance, by only considering three key explanatory variables (human population size, area and number of records). Number of observed and estimated Orthoptera species, records, as well as human population size, were log-transformed to conform to the assumptions of statistical tests. We tested whether squared terms of the explanatory variables improved model fit and did not find that this was the case.

Analyses were carried out in SAS 9.1. Spatial autocorrelation was controlled for using mixed models with exponential co-variance structure (as in Pautasso and Zotti 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) 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).

Results

The database has 8,670 entries (occurrences) of 315 Orthoptera species (of 131 genera). The number of species in the database confirms that Italy is one of the most species-rich European countries for Orthoptera (Heller and Willemse 2007). No Orthoptera species was reported from all regions. *Glyptobothrus brunneus*, *Oedipoda caeruleascens*, *Phaneroptera nana* and *Tettigonia viridissima* were reported from 17 regions, whilst 128 species were reported from one region only. No species was reported from all the 97 provinces with presence of data and 67 species were reported from one province only. Twenty-one species had more than 100 entries in the database and 31 species had just one record in the database.

Observed Orthoptera species richness increased significantly with increasing human population size both for Italian regions (Fig. 1a) and provinces (Fig. 1b). Human population size explained more variation in species richness at the regional (40%) compared to the provincial (2%) level.

Observed Orthoptera species richness also increased significantly with increasing number of records, both for regions (Fig. 1c) and provinces (Fig. 1d). In this case, the proportion of variance in species richness explained by the number of records was comparable for provinces (93%) and regions (90%).

Observed Orthoptera species richness did not increase significantly with increasing human population size in a model controlling for variation in number of records and area both for regions and provinces (Table 1).

The number of records of Orthoptera species increased significantly with increasing human population size both for regions (Fig. 1e) and provinces (Fig. 1f). The proportion of variance in number of records explained by human population size was higher for regions (28%) than for provinces (2%).

These results were confirmed using estimated rather than observed Orthoptera species richness. Estimated species richness was in fact well correlated with observed Orthoptera species richness both for regions and for provinces. Estimated

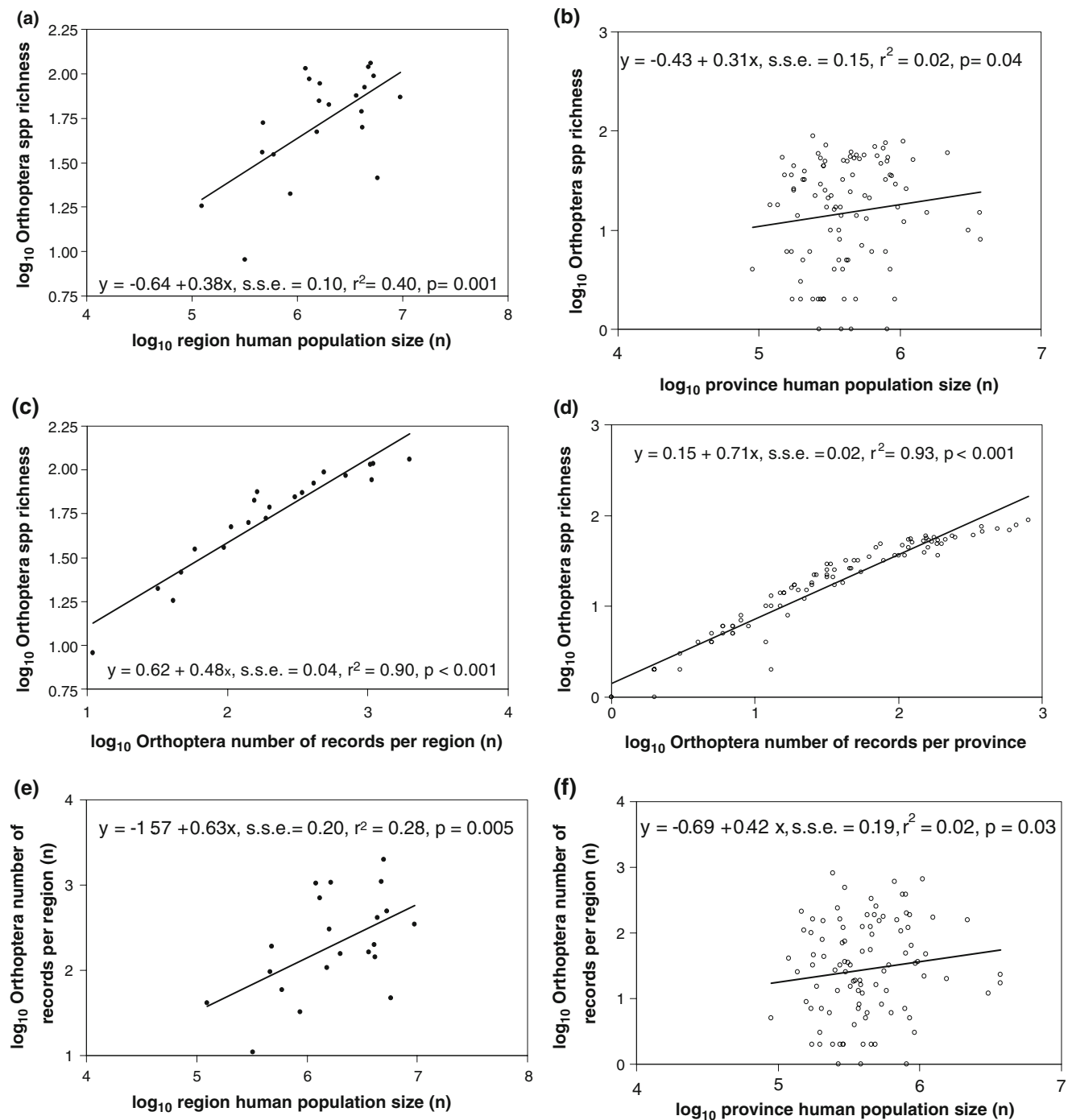


Fig. 1 The relationship between observed Orthoptera species richness and human population size (**a**, **b**); observed Orthoptera species richness and number of records (**c**, **d**); and Orthoptera number of records and human population size (**e**, **f**) in Italy's 21 regions (**a**, **c**, **e**)

and 97 provinces (6 provinces had no presence of Orthoptera in the database; **b**, **d**, **f**) on a log–log scale (s.s.e slope standard error). Human population size is from the 2001 census, Orthoptera species richness and number of records are from the period 1968–2003

Orthoptera species richness increased significantly with increasing human population size for regions, whilst there was no significant variation for provinces. Estimated Orthoptera species richness did not increase significantly with increasing human population size in a model controlling for variation in number of records and area for regions and for provinces.

Discussion

As reported for other taxa analysed in recent regional studies (see review by Luck 2007), the observed number of Orthoptera species in Italy's regions and provinces increases with increasing human population size. As expected, this

Table 1 Multivariate model of observed Orthoptera species richness (1968–2003) as a function of (a) human population size, (b) area and (c) number of records for Italy's regions ($n=21$) and provinces ($n=97$, six provinces had no presence of Orthoptera in the database)

	r^2	Intercept	a	b	c
Reg	0.92	0.03	0.10±0.08	0.02±0.15	0.42±0.04
<i>p</i>			0.25	0.87	0.001
Part. r^2			0.01	0.01	0.90
Prov	0.93	0.14	−0.00±0.05	0.01±0.06	0.71±0.02
<i>p</i>			0.96	0.88	0.001
Part. r^2			0.00	0.00	0.93

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

relationship is stronger at the coarser resolution (the proportion of variance explained at the provincial level is minimal). Nonetheless, when controlling for sampling effort and area, there is no longer a significant increase of observed and estimated Orthoptera species richness with increasing human population size. Reported variations in observed and estimated Orthoptera species richness amongst Italy's provinces and regions are mainly associated with variations in the number of records available. That this is the case not just for observed, but also for estimated species richness is an interesting result in its own right, because such species richness estimators are designed to overcome sampling effects. Therefore, species richness estimators have performed inadequately in this particular case, as they have insufficiently corrected for sampling effort.

The number of records of Orthoptera is positively correlated with human population size, so that sampling bias can contribute in explaining the scale dependence of the relationship between observed species richness and human population size. This is because there is a stronger relationship between the number of Orthoptera records and human population size for regions compared to provinces which translates into a stronger relationship between species and people at the coarser resolution. Sampling intensity was suggested to influence the degree of nestedness in Orthoptera species assemblages in the Netherlands (Schouten et al. 2007), and we confirm the importance of sampling bias in diversity analyses at different scales (e.g. Cantarello and Newton 2008).

Our analysis shows that variations in observed Orthoptera species richness amongst Italy's regions and provinces are only at first sight correlated with human population size and are mainly associated to a non-homogenous sampling effort. The conclusion, that the investigated species richness–human population relationship is artefactual, needs to be taken with caution, as this is based on estimated species richness values which are still not independent of sampling effort. However, also in the case of estimated species richness, there is at first sight a positive regional relationship between this species richness and human population size which then disappears when including number of records in the model. This

implies that at least some observed positive species–people relationships may be due to a more thorough knowledge of species occurrences in more populated areas (Stadler et al. 2000). For grasshoppers, this sampling issue has been raised for North America (Davidowitz and Rosenzweig 1998). Although there is some independent evidence that at least for birds and plants, such a sampling argument may not explain the observed positive species–people relationships in Britain and the USA, respectively (Evans et al. 2007; Pautasso and McKinney 2007), each dataset needs to be tested against the influences of sampling bias.

The species richness of Orthoptera is increasingly investigated locally and regionally for habitat conservation, monitoring and restoration (Illich and Haslett 1994; Nagy 1997; Gebeyehu and Samways 2006; Steck et al. 2007a; Knop et al. 2008). Local studies of the impact of human beings on Orthoptera communities clearly show that where anthropogenic disturbance is greater, the biodiversity of this group tends to decline (Bieringer and Zulka 2003; Fartmann et al. 2008), although in some landscape contexts some human activities may be beneficial for Orthoptera (e.g. the maintenance of grassland and open habitats; Theuerkauf and Rouys 2006). If people have settled preferentially and become more numerous in regions which also have more biodiversity, and if this correlation is not a sampling artefact, then there is a more pressing challenge for nature conservation than if people were more numerous in areas with relatively low biodiversity.

Nevertheless, the evidence available for Orthoptera in Italy's regions and provinces supports the hypothesis that positive regional species–people correlation can in some cases be artefactual. The strong correlation between number of records and species suggests that there is still the need for additional systematic sampling of countrywide Orthoptera biodiversity. Amongst the major impediments for the achievement of the goal of halting biodiversity loss in Europe by 2010 or a subsequent target year are not only the abandonment of traditional extensive agricultural activities and the intensification of land use (e.g. Batary et al. 2007; Steck et al. 2007b; Marini et al. 2008a; Öckinger and Smith 2008; Braschler et al. 2009; Pullin et al. 2009), but also the

bias in knowledge about large-scale patterns of species and assemblage distributions.

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