



Ants and people: a test of two mechanisms potentially responsible for the large-scale human population–biodiversity correlation for Formicidae in Europe

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ABSTRACT

Aim Recent coarse-scale studies have shown positive relationships between the biodiversity of plants/vertebrates and the human population. Little is known about the generality of the pattern for invertebrates. Moreover, biodiversity and human population might correlate because they both covary with other factors such as energy availability and habitat heterogeneity. Here we test these two non-mutually exclusive mechanisms with ant species–richness data from the Fauna Europaea.

Location Forty-three European countries/regions.

Methods We derived mixed models of total, native and exotic ant species richness as a function of human population size/density, controlling for country area, plant species richness (as a proxy for habitat heterogeneity), and mean annual temperature and precipitation (variables related to energy availability).

Results Ant species richness increased significantly with increasing human population. This result was confirmed when controlling for variations in country area. Both for human population size/density and for ant species richness, there were positive correlations with temperature but not with precipitation. This finding is in agreement with the energy-availability hypothesis. However, we observed a negative latitudinal gradient in ant and plant species richness, although not in human population size/density. Plant species richness was positively correlated with ant species richness but not with human population size/density. Thus, there is evidence that this type of habitat heterogeneity can play a role in the observed latitudinal gradient of ant species richness, but not in the positive correlation between ant species richness and human population. The results were confirmed for the 545 native and the 32 exotic ant species reported, and we observed a good correlation between exotic and native ant species richness.

Main conclusions Ant species richness in European countries conforms to six macroecological patterns: (1) a negative latitudinal gradient; and a positive (2) species–energy relationship, (3) species–area relationship, (4) correlation with plant species richness, (5) exotic–native species richness correlation, and (6) species–people correlation. There is some evidence for the energy-availability hypothesis, but little evidence for habitat heterogeneity as an explanation of the large-scale human population–ant biodiversity correlation. This correlation has implications for the conservation of ant diversity in Europe.

Keywords

Arthropods, biogeography, conservation priorities, entomology, environmental determinants, indicator taxa, Mediterranean hotspot, spatial autocorrelation, species density, Western Palearctic.

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INTRODUCTION

Many recent studies have documented a positive relationship between species diversity and human population size or density over coarse scales of analysis. This at first sight surprising pattern has been illustrated for plants (McKinney, 2001; Araújo, 2003; Keith & Warren, 2007) and vertebrates (Balmford *et al.*, 2001; Araújo, 2003; Diniz-Filho *et al.*, 2006) and thus seems to be a common biogeographical pattern (Gaston, 2005).

However, with the exception of some analyses on butterflies in North America and Australia (Luck *et al.*, 2004), little is known about the generality of the pattern for invertebrates (Luck, 2007). Invertebrates are notoriously species-rich yet understudied organisms (Oliver & Beattie, 1993). For the positive large-scale species–people correlation to be a general pattern, it needs to apply also to invertebrates, because these form the vast majority of the Earth's biodiversity (Colwell & Coddington, 1994). It is also important to investigate this issue for invertebrates, as they may be associated to the presence of human beings differently from plants and vertebrates, given their different body sizes, life histories and experienced spatial scales.

Moreover, the large-scale human–biodiversity correlation may disappear when controlling for confounding factors such as species introductions (McKinney, 2001, 2006a) and environmental productivity (Vazquez & Gaston, 2006; Fjeldså, 2007). In fact, in a previous analysis this correlation became negative when controlling for productivity (Ding *et al.*, 2006). There is thus a need for further studies of the species richness–people relationship controlling for potentially covarying factors.

We use data collated as part of the Fauna Europaea (2004) project to test for a human population–biodiversity correlation among European countries for ants (Hymenoptera: Formicidae). Ants are a ubiquitous and key component of ecosystems (Hölldobler & Wilson, 1990; Kaspari *et al.*, 2000a; Wilson & Hölldobler, 2005). They play a role in functions such as predation, herbivory, decomposition, soil turnover and seed dispersal. Moreover, ants have been often used as indicators of ecosystem health (Andersen & Majer, 2004; Stephens & Wagner, 2006; Underwood & Fisher, 2006).

Europe is a region with a relatively high human population and with a generally lower number of species relative to other continents, due to its distance from the tropics, and the barrier to species migration posed by mountain ranges parallel to the equator during the repeated glaciation events. For example, Costa Rica alone has more ant species (827; Longino, 2007) than the whole of Europe (577; Fauna Europaea, 2004). However, in Europe there are regions of high plant biodiversity (e.g. the Mediterranean hotspot; Vogiatzakis *et al.*, 2006), which can be reasonably expected to show a high ant species diversity as well. Moreover, the spatial distribution of species occurrences is relatively well known in Europe, given the high number of taxonomists and the long tradition of research on biodiversity. Nonetheless, with some exceptions, pan-Euro-

pean biogeographical studies have been rare, possibly because of the political and linguistic fragmentation of the different countries. This fragmentation provides an opportunity to test for two mechanisms that have been suggested to explain observed large-scale species–people relationships: habitat heterogeneity and energy availability. On the one hand, regions with higher human population size may also contain a higher variety of habitats, which in turn often correlates well with species richness (habitat heterogeneity hypothesis; Fjeldså, 2007; Luck, 2007; Moreno-Rueda & Pizarro, 2007). On the other hand, regions with higher human density may also have a more favourable climate, both for people and for (ant) species (energy-availability hypothesis; Araújo, 2003; Evans *et al.*, 2006; Luck, 2007).

In this study, we test whether there is a correlation between ant species richness and the human population size/density of European countries, and whether these two variables increase with (1) plant species richness, as plant species richness can be an indicator of habitat heterogeneity; and (2) mean annual temperature and precipitation, as predicted by the hypothesis that the presence of both species and people is positively correlated with energy availability. The two mechanisms are not mutually exclusive. Habitat heterogeneity is a strong broad-scale predictor of vascular plant species richness (Zhao & Fang, 2006; Barthlott *et al.*, 2007; Kreft & Jetz, 2007). Plant species, in turn, are an important component of the habitats of ants, and the structural heterogeneity of plant communities has been shown to be positively related to ant species richness (Rico-Gray *et al.*, 1998; Ribas *et al.*, 2003; Ribas & Schoederer, 2007). Mean annual temperature is related to the energy availability of individuals, species and ecosystems, and is hypothesized to drive metabolic and, ultimately, speciation rates (Brown *et al.*, 2004; Kaspari, 2004; Sanders *et al.*, 2007). Precipitation has been shown to be a limiting factor for ant species richness in studies of semi-arid regions (Gustavo *et al.*, 1994; Bestelmeyer & Wiens, 2001; Sanders *et al.*, 2003; but see Pfeiffer *et al.*, 2003).

MATERIALS AND METHODS

We based our analysis on the estimates of ant species richness for European countries provided by the Fauna Europaea (2004) project. This data base is the outcome of a project funded by the European Union and was coordinated by the Zoological Museum of Amsterdam (the Netherlands). The data base was generated by the Zoological Museum of Copenhagen (Denmark) and validated at the Muséum National d'Histoire Naturelle in Paris (France). The project involved more than 400 taxonomic experts. While there may be identification errors, differences in sampling effort among countries, new discoveries and advances in taxonomy (Ward, 2005; Schlick-Steiner *et al.*, 2006; Seifert, 2006), the various effects may well cancel each other out. For example, the current figure for ant species richness for Austria is the same as that in the data base, despite many recent updates in the checklist. There are some slight differences in the current

numbers for at least another 13 countries, but using these updated data instead of those from the Fauna Europaea did not lead to any qualitative changes in the results of the analyses, and quantitative changes did not alter any of the conclusions drawn. We thus avoided using partly updated data from some countries, and instead analysed the data of the Fauna Europaea for consistency's sake.

Native or exotic status of ant species was assessed on the basis of McGlynn (1999), Heinze *et al.* (2006), Bolton (2007), Bolton *et al.* (2007), Espadaler *et al.* (2007) and Seifert (2007). This resulted for the countries analysed, in 545 native and 32 exotic ant species (*Cardiocondyla emeryi*, *Cardiocondyla nuda*, *Hypoponera opaticeps*, *Lasius neglectus*, *Linepithema humile*, *Linepithema melleum*, *Monomorium monomorium*, *Monomorium pharaonis*, *Pachycondyla darwini*, *Paratrechina bourbonica*, *Paratrechina braueri*, *Paratrechina flavipes*, *Paratrechina longicornis*, *Paratrechina vividula*, *Pheidole anastasioi*, *Pheidole cellarum*, *Pheidole flavens*, *Pheidole kraepelini*, *Pheidole megacephala*, *Pheidole symbiotica*, *Plagiolepis allaudi*, *Solenopsis geminata*, *Strumigenys lewisi*, *Strumigenys rogeri*, *Tapinoma melanocephalum*, *Technomyrmex detorquens*, *Tetramorium bicarinatum*, *Tetramorium caldarium*, *Tetramorium insolens*, *Tetramorium lanuginosum*, *Tetramorium lucayanum*, and *Tetramorium simillimum*).

Human population size and density (referring to 2005), area and geographical coordinates of European countries/regions analysed were obtained from publicly accessible websites (EUROSTAT). We used both human population size and density in analyses, as both have been shown not to be independent of country area (Pautasso & Weisberg, 2008). Moreover, human population density may not be indicative of a number of environmental impacts that are better approximated by human population size. For example, for European countries there is a strong positive correlation between the total municipal waste produced and their human population size, but a weak one with their human population density (our unpublished observations). Mean annual temperature and precipitation were obtained from a global 10' latitude × 10' longitude data set of mean monthly climate variables for the period 1961–90 (New *et al.*, 2002). Estimates of vascular plant species richness were obtained from Gleich *et al.* (2000).

We followed the political entities used in the Fauna Europaea as closely as possible, but left out some countries in case of unreasonably low (zero or a few units) ant species richness estimates (Bosnia Herzegovina, Croatia, Faroe Islands, Franz Josef Land, Iceland, Novaya Zemlya, San Marino, Selvagens Islands, Svalbard Islands and Vatican City). We also omitted data for the Azores, Balearics, Canaries, Channel Islands, Cyclades, Dodecanese, Madeira and North Aegean Islands, as they may be affected by speciation events occurring in island groups. For a given area (and population size), island groups may tend to have disproportionately more species than the same area (and population size) of mainland because of speciation events due to the inherent fragmentation between different islands of island groups. However, repeating the analyses including data from Atlantic and Western Mediter-

Table 1 Maximum, minimum, mean, median, standard deviation and total ant and plant species richness, area (10^3 km²), human population (Pop, 10^3 individuals) and density (Dens, n km⁻²), mean annual temperature (Temp, °C) and precipitation (Prec, mm) in the 43 European countries analysed.

	Ants	Plants	Area	Pop	Dens	Temp	Prec
Max	285	5600	604	83,252	16,000	19.2	1387
Min	16	530	0.002	28	14	0.7	481
Mean	91	2500	130	13,150	627	9.7	777
Med	78	2100	48	5180	109	9.1	696
SD	58	1330	164	19,700	2519	4.6	235
Total	577	12,500	5600	565,000	101	–	–

anean groups of islands (we did not have reliable environmental data for the Eastern Mediterranean groups of islands) did not lead to any qualitative differences in results, and quantitative differences did not lead to any change in the conclusions. Given that an estimate of ant species richness was available for Corsica, Crete, Sardinia and Sicily, these islands were considered apart from mainland France, Greece and Italy. Given that a separate estimate was available for Northern Ireland and for the rest of the UK, these two regions were analysed separately. Russia was not included in analyses as there was an estimate for ant species richness in only four parts of Russia (for which area and human population size were not known). The data set analysed comprised 43 political geographical entities (Table 1; Appendix S1 in Supporting Information).

Analyses were run in SAS ver. 9.1. The correlation of ant species richness with human population size/density was analysed on its own and controlling for variations among countries in (1) area; (2) area and plant species richness; and (3) area, plant species richness, and mean annual temperature and precipitation. Additional models were run to test whether there were latitudinal gradients in human population size/density, and ant and plant species richness. We also analysed the relationship of ant species richness with plant species richness and the two climatic variables without including human population size/density in models. Numbers of ant [total, native and exotic (+1); for one country (Liechtenstein) no exotic ant species was reported] and plant species, human population size and density, area, and precipitation were log-transformed prior to analysis to conform to the requirement of a normal distribution. Mean annual temperature was Boltzmann-transformed as usually done in recent studies of the metabolic theory of ecology (e.g. Sanders *et al.*, 2007). A negative correlation of a variable with Boltzmann-transformed temperature implies a positive correlation of the same variable with untransformed temperature, as the Boltzmann-transformed temperature is obtained by calculating $1/kT$, where T is temperature in Kelvin. Spatial autocorrelation was controlled for using mixed models with exponential covariance structure (as in e.g. Pautasso & Weisberg, 2008). Results from non-spatial and spatial models are generally consistent, but we

present only the more robust results that take into account a potential spatial non-independence of data (Dormann, 2007). There may be spatial autocorrelation among countries in survey intensity, climate and species presence due to easier dispersal at closer distance. Model complexity and fit were assessed on the basis of the Akaike information criterion (AIC; Johnson & Omland, 2004).

RESULTS

Ant species richness significantly increased with increasing human population size (Fig. 1a) and with increasing area (Fig. 1b). This followed from the positive, although less than proportionate, relationship between human population size

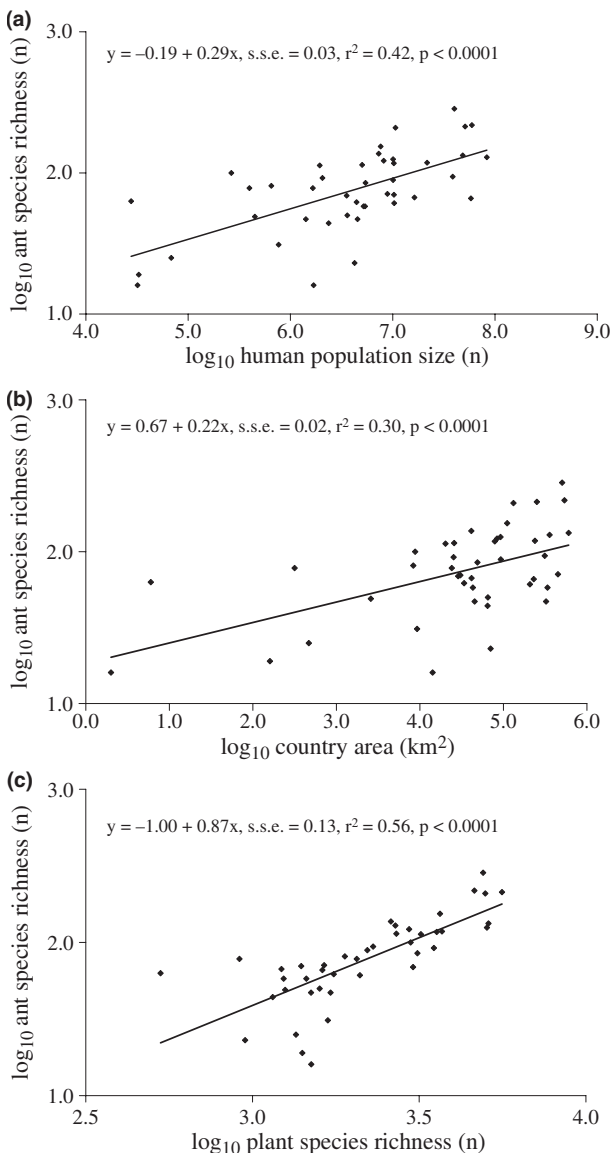


Figure 1 Relationship between total ant species richness and (a) human population size; (b) area; (c) plant species richness for the European countries analysed.

and area [$n = 43$, $r^2 = 0.82$, $\log_{10} \text{pop} = 3.60 + 0.66 \log_{10} \text{area}$, slope standard error (SSE) = 0.05, $P < 0.0001$]. However, ant species richness increased significantly with increasing human population size also when controlling for variations in area (Table 2).

This result was also confirmed when controlling for variations in plant species richness among countries (Table 2). In this model, country area dropped out as a significant explanatory variable, whereas ant species richness increased significantly with increasing plant species richness. This significant increase in ant species richness with plant species richness was also present when not controlling for the other factors (Fig. 1c).

The significant increase in ant species richness with increasing human population size and plant species richness was confirmed when controlling for temperature and precipitation (Table 2), which were not factors significantly associated with ant species richness, also when not controlling for the other factors (Fig. 2a,b).

The above results were confirmed when replacing human population size with density. The only difference was that, in the case of human population density, country area was still a significant factor in models of ant species richness as a function of area and plant species richness (Table 3).

When not including human population size or density in models (Table 4), ant species richness declined significantly with Boltzmann-transformed temperature. This was also the case when including plant species richness as an explanatory variable. Plant species richness was not a significant factor in these models without human population size or density. This was also the case when not including the climatic variables as an explanatory variable (Table 4).

We tested for the presence of simple nonlinear relationships by adding the square terms of all predictor variables in the models. Square terms of all predictor variables were non-significant in models of ant species richness as a function of human population size/density, country area, plant species richness, temperature and precipitation.

As for the interrelationships between the explanatory variables, human population size increased with country area, decreased with Boltzmann-transformed temperature, and did not vary significantly with variations in precipitation ($n = 43$, $r^2 = 0.85$, $\log_{10} \text{pop} = -8.04 + 0.73 \log_{10} \text{area} - 2.27 \text{boltz} + 0.47 \log_{10} \text{prec}$, SSE = 0.05, 0.87, 0.49, $P < 0.0001$, $P = 0.01$, 0.35). Plant species richness did not vary significantly with variations in human population size, increased with country area, decreased with Boltzmann-transformed temperature, and increased with precipitation ($n = 2$, $r^2 = 0.51$, $\log_{10} \text{plantspp} = -5.97 - 0.06 \log_{10} \text{pop} + 0.24 \log_{10} \text{area} - 1.60 \text{boltz} + 0.54 \log_{10} \text{prec}$, SSE = 0.09, 0.07, 0.48, 0.26, $P = 0.53$, 0.0003, 0.002, 0.04). These models gave consistent results when replacing human population size with human population density; the only difference was that human population density declined with area instead of increasing.

If, instead of using temperature and precipitation, latitude was included in models, this factor significantly explained

Table 2 Mixed models of total ant species richness (logsp) as a function of (a) human population size (logpop) and area (logarea); (b) human population size, area and plant species richness (logplant); and (c) human population size, area, plant species richness, Boltzmann-transformed mean annual temperature (boltz), and mean annual precipitation (logprec) in the European countries analysed.

	<i>n</i>	<i>r</i> ²	AIC	logsp	logpop	logarea	logplant	boltz	logprec
(a)	43	0.42	-17.2	$y = 0.21$ <i>P</i>	+0.15a (±0.06) 0.01	+0.12b (±0.04) 0.008			
(b)	42	0.68	-21.4	$y = -1.01$ <i>P</i>	+0.27a (±0.07) 0.001	-0.07b (±0.07) 0.32	+0.40c (±0.17) 0.02		
(c)	42	0.71	-24.1	$y = -5.06$ <i>P</i>	+0.22a (±0.08) 0.006	-0.03b (±0.07) 0.67	+0.39c (±0.16) 0.02	-0.95d (±0.67) 0.16	-0.02e (±0.26) 0.94

AIC, Akaike's information criterion.

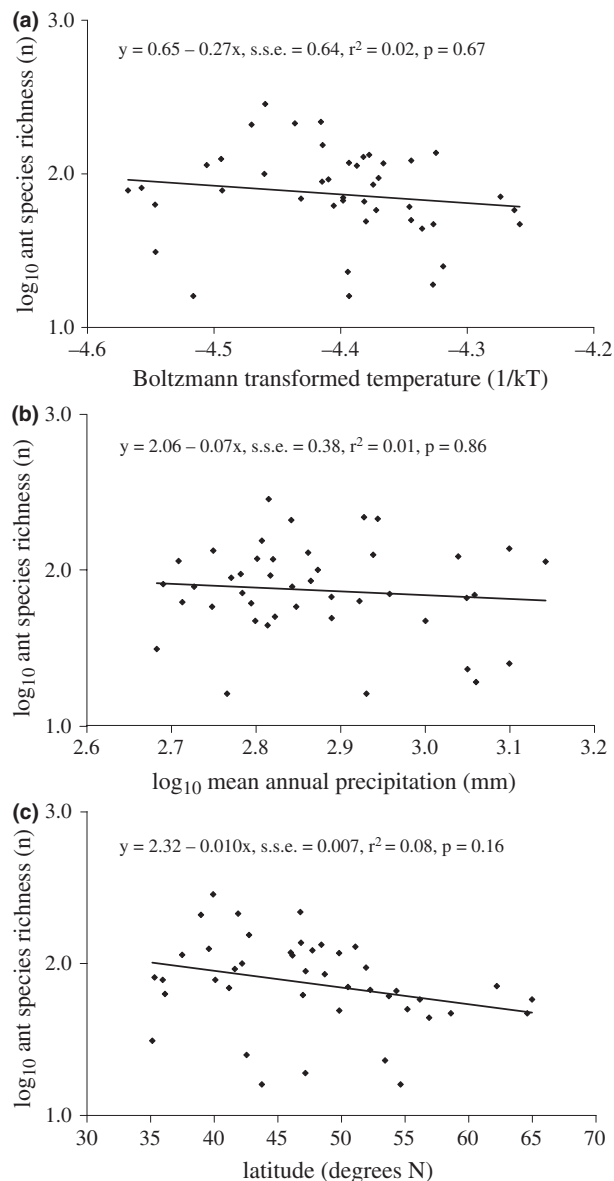


Figure 2 Relationship between total ant species richness and (a) Boltzmann-transformed temperature; (b) mean annual precipitation; (c) latitude for the European countries analysed.

variations in ant species richness, but not on its own (Fig. 2c) and only when not including plant species richness in models ($n = 43$, $r^2 = 0.67$, $\log\text{sp} = 1.42 + 0.15 \log\text{pop} + 0.11 \log\text{area} - 0.03 \text{ lat}$, SSE = 0.06, 0.04, 0.01, $P = 0.01$, 0.01, 0.03). This is because plant species richness was also negatively related to latitude ($n = 42$, $r^2 = 0.68$, $\log\text{plantspp} = 3.51 - 0.06 \log\text{pop} + 0.25 \log\text{area} - 0.02 \text{ lat}$, SSE = 0.06, 0.06, 0.01, $P = 0.33$, $P < 0.0001$, $P = 0.0009$). These models were entirely consistent when replacing human population size with human population density.

Unlike ant species richness, human population size did not vary significantly with latitude in a model controlling for variations in country area ($n = 43$, $r^2 = 0.83$, $\log\text{pop} = 3.93 + 0.68 \log\text{area} - 0.01 \text{ lat}$, SSE = 0.05, 0.01, $P < 0.0001$, $P = 0.37$). Human population density too, did not vary significantly with latitude in a model controlling for variations in country area, but instead of increasing with country area, it declined ($n = 43$, $r^2 = 0.56$, $\log\text{d} = 3.93 - 0.32 \log\text{area} - 0.01 \text{ lat}$, SSE = 0.05, 0.01, $P < 0.0001$, $P = 0.37$).

There was a good positive correlation between exotic and native ant species richness ($n = 43$, $r^2 = 0.33$, $\log\text{exotic} = -0.48 + 0.56 \log\text{native}$, SSE = 0.10, $P < 0.0001$) and between exotic and total ant species richness ($n = 43$, $r^2 = 0.36$, $\log\text{exotic} = -0.54 + 0.59 \log\text{sp}$, SSE = 0.10, $P < 0.0001$). There was a nearly perfect positive correlation between native and total ant species richness ($n = 43$, $r^2 = 0.997$, $\log\text{native} = -0.04 + 1.01 \log\text{sp}$, SSE = 0.01, $P < 0.0001$). When repeating all analyses carried out for total ant species richness by replacing it with native and with exotic ant species richness, the results for the two subsets were remarkably consistent with those already presented for total ant species richness. These additional analyses are provided in Appendix S2. In both cases (native and exotic ant species richness) we observed:

- (1) A significantly positive correlation with human population, which is robust to controlling for area, plant species richness, temperature and precipitation.
- (2) A significantly negative relationship with Boltzmann-transformed temperature (although not in models including human population), but none with precipitation.

Table 3 Mixed models of total ant species richness (logsp) as a function of (a) human population density (logd) and area (logarea); (b) human population density, area and plant species richness (logplant); and (c) human population density, area, plant species richness, Boltzmann-transformed mean annual temperature (boltz), and mean annual precipitation (logprec) in the European countries analysed.

	<i>n</i>	<i>r</i> ²	AIC	logsp	logd	logarea	logplant	boltz	logprec
(a)	43	0.43	-17.4	<i>y</i> = 0.20 <i>P</i>	+0.15a (±0.06) 0.01	+0.27b (±0.03) 0.0001			
(b)	42	0.68	-21.7	<i>y</i> = -1.02 <i>P</i>	+0.27a (±0.07) 0.0006	+0.19b (±0.04) 0.0001	+0.41c (±0.17) 0.02		
(c)	42	0.71	-24.3	<i>y</i> = -5.00 <i>P</i>	+0.23a (±0.08) 0.006	+0.19b (±0.04) 0.0001	+0.40c (±0.16) 0.02	-0.94d (±0.67) 0.17	-0.02e (±0.26) 0.93

AIC, Akaike's information criterion.

Table 4 Mixed models of total ant species richness (logsp) as a function of (a) area (logarea) and plant species richness (logplant); (b) area, Boltzmann-transformed mean annual temperature (boltz) and mean annual precipitation (logprec); and (c) area, plant species richness, Boltzmann-transformed mean annual temperature and mean annual precipitation in the European countries analysed.

	<i>n</i>	<i>r</i> ²	AIC	logsp	logarea	logplant	boltz	logprec
(a)	42	0.56	-13.3	<i>y</i> = 0.06 <i>P</i>	+0.18b (±0.04) 0.0001	+0.27c (±0.17) 0.13		
(b)	43	0.50	-21.1	<i>y</i> = -7.32 <i>P</i>	+0.24b (±0.02) 0.0001		-1.69d (±0.65) 0.01	+0.16e (±0.25) 0.52
(c)	42	0.61	-19.9	<i>y</i> = -4.85 <i>P</i>	+0.18b (±0.04) 0.0001	+0.28c (±0.17) 0.11	-1.70d (±0.68) 0.02	+0.14e (±0.27) 0.60

AIC, Akaike's information criterion.

(3) A negative latitudinal gradient (as for plant species richness, but unlike for human population size/density).

For exotic/native ant species richness too, using human population density instead of size did not lead to any differences in results. The only qualitative difference between native and exotic ant species richness was that plant species richness was a significant factor in models of native ant species richness as a function of human population size/density, plant species richness and climatic variables. On the contrary, plant species richness was a non-significant factor in the same model for exotic ant species richness. Exotic ant species richness thus appeared to be driven by human population size alone (for exotic ant species richness, adding plant species richness and climatic variables did not substantially improve the *r*² and AIC of models as it did for native and total ant species richness).

DISCUSSION

There is a positive correlation between ant species richness and human population density/size for European countries. Human population size explains more variance in ant species richness among European countries than country area, and the positive ant species–people correlation is robust to controlling for variations in country area, plant species richness, temperature and precipitation. These results are confirmed when replacing human population size with human population density in the models.

There is some evidence that this correlation can be explained by a correlation of both species richness and people with

energy availability (Herbers, 1989; Kaspari *et al.*, 2000b; Novotny *et al.*, 2006), as both for human population size and for ant species richness there are significant positive correlations with temperature when controlling for country area. When including human population size/density in this model, temperature drops out as a significant predictor of ant species richness, suggesting that variations in temperature are concurrent with variations in human population size and in ant species richness, and thus play a role in the observed species–people correlation.

In Europe there is a mismatch between temperature and latitude due to the milder climate in western countries made possible by the Gulf Stream (although latitude explains 85% of the variation in mean annual temperature among the countries analysed). Ant species richness decreases significantly with increasing latitude, but this is not the case for human population size/density. Ant species richness has been shown to increase with declining latitude for: (1) the New World from New Hampshire to Brazil (Jeanne, 1979; see also Kusnezov, 1957); (2) islands of East Asia (Terayama, 1992); and (3) Northern Europe (Cushman *et al.*, 1993). The same pattern has been confirmed for New England (Gotelli & Ellison, 2002), as well as Australia, Madagascar, and North and South America (Kaspari *et al.*, 2004). The available data provide evidence that the latitudinal gradient in ant species richness of European countries can be explained by variations in temperature, as ant species richness is significantly related to temperature when controlling for country area. However, there is no significant correlation between ant species richness and

latitude when controlling for variations in plant species richness. These findings suggest that the latitudinal gradient in ant species richness could be, at least in part, a consequence of the latitudinal gradient in plant species richness, as the latter variable is negatively correlated with latitude on its own. The latitudinal gradient is obviously a one-dimensional simplification of a two-dimensional pattern, but the ant species richness of the European countries analysed does not show any significant variation with varying longitude.

As for the hypothesis that habitat heterogeneity might explain the spatial correlation of ant species and human population size, we find that ant species richness is positively correlated with plant species richness, as predicted. However, plant species richness is not significantly correlated with human population size/density (contrary to the findings of Araújo, 2003, for Europe using a much narrower study grain, 50×50 -km grid cells). Hence, the increase of ant species richness with human population size/density in European countries is not explained by a positive correlation of both variables with plant species richness. This result is obtained controlling for the climatic variables in the models, so it is robust to any influence of energy availability on human population size/density, ant and plant species richness. However, plant species richness provides only a rough measure of habitat heterogeneity as perceived by ants (Englich *et al.*, 2005; Barrow *et al.*, 2006; Arnan *et al.*, 2007), and it is possible that habitat heterogeneity in terms of topographical relief and different types of land use could contribute to explaining the observed positive ant species–people correlation. Nonetheless, there is no evidence for a significant association of the range in temperature, precipitation and altitude with ant species richness (our unpublished observations). These ranges in temperature, precipitation and altitude are a good estimate of the topographical heterogeneity of a country and, unlike plant species richness, are not correlated with absolute temperature (our unpublished observations).

The positive correlation of ant species richness with plant species richness in European countries (which is robust to controlling for variation in country area, human population size/density, temperature and precipitation) is interesting in its own right. It makes biological sense, as the biodiversity of consumers can reasonably be expected to track variations in the diversity of producers. However, there are only a few studies documenting a correlation between plant and insect species over large extents and with a large study grain (e.g. Gaston, 1992; Wolters *et al.*, 2006; Rodrigues & Brooks, 2007; Qian & Ricklefs, 2008). Examples of regional correlations of plant species richness with the diversity of other taxa come from California (Hawkins & Porter, 2003), China (Zhao *et al.*, 2006; Qian, 2007), sub-Saharan Africa (Kissling *et al.*, 2007) and the Cape Floristic Region, South Africa (Wright & Samways, 1998). For ants, no correlation with plant species richness was reported in a north–south transect in Mongolia (Pfeiffer *et al.*, 2003). The positive cross-taxon correlation between ants and plants in Europe can be explained, at least in part, by both variables responding positively to energy

availability, as both ant and plant species richness increase with increasing temperature when controlling for country area. However, while ant species richness is not significantly associated with precipitation, plant species richness also increases with increasing precipitation, suggesting that in this bioregion the distribution of plant species is more water-limited and that of ants is more temperature-limited.

A positive species–area relationship has been reported for ants from many regions of the world (Goldstein, 1975; Boomsma *et al.*, 1987; Terayama, 1992; Woinarski *et al.*, 1998; Wetterer, 2002; Kaspari *et al.*, 2003; Schoederer *et al.*, 2004; Botes *et al.*, 2006). For European countries, with area spanning more than five orders of magnitude, the positive ant species–area relationship is robust to controlling in the model for variations in latitude and human population. However, there is no significant relationship between ant species richness and country area when controlling for variations in plant species richness and human population size. This finding confirms that area *per se* might not have a direct influence on species richness, but might often correlate with other factors positively associated with species richness (Douglas & Lake, 1994; Ricklefs & Lovette, 1999; Johnson *et al.*, 2003).

The positive correlation between exotic and native ant species richness is in agreement with other coarse-scale studies (Sax, 2001; Davies *et al.*, 2005; McKinney, 2006a). The consistency of the results for total, native and exotic ant species strengthens their generality, although this would need to be tested in other regions. For total, native and exotic ants: (1) we observe a significantly positive correlation between ant species richness and human population size/density, which is robust to controlling for area, plant species richness, temperature and precipitation; (2) we show that ant species richness is significantly related to temperature (although not in models including the human population parameters), but not to precipitation; (3) we confirm that ant species richness shows a negative latitudinal gradient (as for plant species richness, but unlike human population size/density); and (4) we find that using human population density instead of size does not lead to any differences in the results. The finding that plant species richness is a significant factor in models of native ant species richness as a function of human population size/density, plant species richness and climatic variables, whereas it is a non-significant factor for exotic ant species richness in the same models, suggests that exotic ant species richness is less determined by environmental variables and is mainly governed by species introductions, which occur more frequently in countries with higher human population size.

Estimated ant species richness in European countries conforms to six macroecological patterns commonly reported in the literature: (1) a negative latitudinal gradient (e.g. Rohde, 1992); (2) a positive species–energy relationship (e.g. Currie, 1991); (3) a positive species–area relationship (e.g. Lomolino, 2000); (4) a positive correlation with plant species richness (e.g. Morrison, 1998); (5) a positive correlation between exotic and native species richness (e.g. Gilbert & Lechowicz, 2005); and (6) a positive species richness–people

correlation (see Introduction). There is some evidence that the positive ant species richness–people relationship observed can be explained by both factors covarying with energy availability (Araújo, 2003; Koh *et al.*, 2006; Luck, 2007), as both ants and human population size are positively related to temperature. Although there is evidence for an important role of plant species richness in the variations of ant species richness among European countries, there is little evidence that the ant species–people correlation can be explained by a correlation of both variables with habitat heterogeneity. We do not make any causal inference from the positive ant species–people correlation observed, that is, we do not argue that higher numbers of human beings in European countries result in a higher number of ant species in the same countries. Both factors covary with temperature, and there might be other factors that covary with ant species richness and human population size that should be further explored. These include topographical and geological diversity. However, it is also possible that a more numerous presence of human beings may favour ant species richness through beneficial processes such as the creation of a more diverse habitat mosaic (e.g. Andren, 1994), the effect of which, however, may possibly be partly counterbalanced by decreases in landscape connectivity (Steffan-Dewenter & Tscharntke, 2002; Dauber & Wolters, 2004).

One important issue that we could not address with the available data is whether sampling effort might be positively related to human population size/density. Although recent studies suggest that sampling bias might not be an explanation for positive species–people relationships of British birds and American plants (Evans *et al.*, 2007; Pautasso & McKinney, 2007), the issue of sampling bias is specific to each data set, so that each data set needs to be tested against such an influence. Comparing the data from the Fauna Europaea data base and the currently available data, we notice that the change [both positive (due to species discovery) and negative (due to taxonomic reconsideration)] in ant species richness is not significantly related to human population size or density (our unpublished observations). Future work could also investigate whether other measures of energy availability are correlated with ant species richness, and could address the effect of factors such as the proportion of different habitat types, the altitudinal range, and the degree of urbanization on the reported findings (Glaser, 2006; Dunn *et al.*, 2007). There might be a positive ant species richness–human population size/density correlation at the country level, but we need to know whether this positive correlation persists using a narrower grain of analysis, as such a correlation has been reported to be scale-dependent, at least for butterflies, plants and vertebrates (Hardy & Dennis, 1999; Pautasso, 2007; Pautasso & Chiarucci, 2008). Unfortunately, at present it is not possible to inquire whether there is any scale-dependence in the observed ant species richness–people correlation in Europe, because only patchy data are available for European provinces.

From an educational point of view, the broad-scale correlation of ant biodiversity and human population size at the

level of European countries is a positive finding (Turner *et al.*, 2004; Balmford & Bond, 2005). However, the coexistence of high numbers of people and ant species is also a challenge from a conservation perspective, as urbanization and human disturbance often result in extinction and homogenization processes (Balmford, 1996; López-Moreno *et al.*, 2003; Lessard & Buddle, 2005; Yamaguchi, 2005; Holway & Suarez, 2006; McKinney, 2006b; Olden & Rooney, 2006). Given that anthropogenic influence on land use is one of the most important issues in biodiversity conservation, we need an increase in people's awareness of the diversity of ants, and better strategies to enable both humans and ant colonies to thrive in today's human-modified landscapes.

ACKNOWLEDGEMENTS

Many thanks to the many people involved in the compilation of the Fauna Europaea data base, to H. Kreft for help in retrieving climatic data, to M. Bertaglia, K. Evans, K. Gaston, T. Hirsch, O. Holdenrieder, S. Jackson, M. Jeger, M. McKinney, I. Parmentier, G. Powell, I. Procaccia, A. Rodrigues, N. Russell, C. Steck, L. Vazquez, P. Warren and P. Weisberg for insights and discussions, and to F. Gennaro, R.J. Whittaker and anonymous reviewers for helpful comments on a previous version of the draft.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article:

Appendix S1 Data used in the analyses.

Appendix S2 Additional models for native and exotic ant species richness.

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BIOSKETCHES

Birgit Schlick-Steiner and **Florian Steiner** are interested in the conservation, invasion biology, phylogeny, phylogeography, population genetics, social organization, systematics and taxonomy of ants.

Marco Pautasso is interested in network epidemiology, landscape pathology and conservation biogeography.

Editor: Kate Parr