



# Conservation implications of divergent global patterns of ant and vertebrate diversity

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## ABSTRACT

**Aim** Global conservation planning is often oriented around vertebrates and plants, yet most organisms are invertebrates. To explore the potential conservation implications of this bias, we assessed how well patterns of diversity for an influential group of invertebrates, the ants, correspond with those of three vertebrate groups (birds, mammals and amphibians).

**Location** Global.

**Methods** We compiled data on the number of genera of ants and the three vertebrate groups for 370 political regions across the world. We then compared their correlations both for overall diversity and between subsets of genera likely to be of conservation concern. We also developed generalized additive models (GAM) to identify regions where vertebrates and ants diverged in their diversity patterns.

**Results** While ant and vertebrate diversity do positively correlate, the correlations are substantially weaker for the ant lineages of the greatest conservation concern. Vertebrates also notably fail to predict ant diversity in specific geographic areas, including Australia and Southeast Asia, parts of Africa and Madagascar, and south-western China. These failures may be genuine differences in diversity patterns, or they may indicate important gaps in our knowledge of ant and vertebrate diversity.

**Main conclusions** We conclude that it is currently unwise to assume that global conservation priorities based on vertebrates will conserve ants as well. We suspect that this also applies to other invertebrates.

## Keywords

Ants, biodiversity patterns, conservation planning, genera, species richness, vertebrates.

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## INTRODUCTION

Planning for global biodiversity conservation is a balancing act between many possible options. Not the least of these is choosing the parts of biodiversity on which to focus and thus guide where to make conservation investments. Priorities have generally been oriented around plants and vertebrates, both for reasons of popular interest and the availability of data (Myers, 1988, 1990; Olson & Dinerstein, 1998; Stattersfield *et al.*, 1998; Myers *et al.*, 2000; Lamoreux *et al.*, 2006). However, most organisms are invertebrates, with more than a million species, mostly arthropods, described and perhaps several million more awaiting discovery (Erwin, 1982; Gaston, 1991;

Mora *et al.*, 2011; Zhang, 2011). While plants, vertebrates and invertebrates appear to have generally similar large-scale patterns of diversity (e.g. more diverse in the wet tropics than in cold tundra), it is still uncertain how well plants and vertebrates perform as global conservation proxies for invertebrates. This is a critical knowledge gap, for invertebrates are the majority of animal life on the planet.

Here, we use a novel dataset to compare global diversity patterns of one of the most influential invertebrate taxa, the ants, to those of three major vertebrate groups: birds, mammals and amphibians. Ecologically, ants are diverse (>14,000 species in >300 genera), among the most abundant of insects (Hölldobler & Wilson, 1990; Tobin, 1995), and ecologically

important (Way, 1963; Beattie, 1985; Stadler & Dixon, 2008; Rico-Gray & Oliveira, 2010). Ant species occupy essentially every trophic level and terrestrial habitat, from subterranean fungus farmers to predators in tree canopies. Studies of local diversity also find ants to be a potentially good surrogate for the diversity of other insects, although debate exists (Alonso, 2000; Leal *et al.*, 2010; Schuldt & Assmann, 2010). We know of no studies that have compared diversity patterns of insects with other taxa at the global scale, as has been carried out previously with vertebrates (Brooks *et al.*, 2004; Rodrigues *et al.*, 2004a,b; Grenyer *et al.*, 2006; Lamoreux *et al.*, 2006).

We expect ant diversity to correlate with vertebrate diversity, and even be predictable from vertebrate diversity, to a degree. This is likely the case for most terrestrial taxa, if for no other reason than that the tropics tend to be more diverse than higher latitudes for nearly everything. Such a broad view, however, is not useful for guiding conservation decisions other than to suggest more focus in the tropics than elsewhere. More informative would be to know the extent to which patterns for vertebrates predict and fail to predict the patterns for ants, especially for taxa of conservation concern. Failures could arise for at least two reasons. Our knowledge of the ants in an area might be poorer than our knowledge of vertebrates, such that the diversity of vertebrates predicts, in essence, ants we have yet to discover. Such areas should be of high priority for exploration. Alternatively, the differences could be real, and if so we would face the difficult reality that priority areas for vertebrates may not be priorities for invertebrates, and vice versa.

A common approach for a global comparative analysis of biodiversity is to use species range maps to infer global patterns. For ants, as for other large arthropod groups, we are years or probably decades away from completing such maps of all species (a relatively large proportion of ant species remains to be described, much less documented in detail). Considering the major threats to biodiversity and the urgency for protection, we cannot reasonably wait for this to happen before making decisions. However, our research group recently developed maps of the distribution of every ant genus in the world, at the spatial grain of political regions (Guénard *et al.*, 2010, 2012). Here, we consider those maps as a first step towards greater understanding of the global patterns of insect diversity.

We compared ants to vertebrates in three ways. First, we compared the total number of genera within regions. Second, we compared the diversity of range-restricted genera, our assumption being that range-restricted genera are more vulnerable to extinction, much as range-restricted species are known to be (Purvis *et al.*, 2000; IUCN, 2001). Third, we considered the diversity of monotypic genera, using them as a proxy for the extent to which low diversity but phylogenetically distinct genera concentrate in particular regions (Faith, 1992; Keane *et al.*, 2005). We then made predictions about ant diversity using generalized additive models (GAM) with vertebrate diversity metrics as predictors. By examining the

residuals from those model predictions, we were able to identify geographic areas of disagreement between ant and vertebrate diversity.

## METHODS

For ants, many individual species do not have enough localities to produce a range map. As well, many localities reference only a region, not specific geographic coordinates, limiting the ability to produce fine-scale maps. Our compromise was to use locality data for all species in a genus to produce a coarse-scale map based on 370 political regions (a shapefile and summary Table S1 are available online in Supporting Information). These regions are often countries, although for some larger countries we used lower political divisions (departments, provinces or states) or discrete geographic regions (*e.g.* islands). This was the case for Argentina, Australia, Brazil, Canada, Chile, China, Indonesia, Japan, Malaysia, Mexico, Russia and the United States of America. As much of conservation decision-making takes place within political defined regions (*e.g.* countries), not biologically defined ones, this division of the world is not entirely arbitrary. Others have explored the use of regional species lists in diversity studies, as opposed to traditional equal-area grids or range maps, and have found them suitable (Baselga, 2008; Keil & Hawkins, 2009). Nevertheless, we recognize that the unequal size of different regions could complicate interpretations, and we do include area as a covariate in models (described below). The authors compiled the data, and as of the date of analysis, there were 15,631 genus  $\times$  locality records in the database. A full description of the data and compilation process is in Guénard *et al.* (2012), and the latest version of the dataset is available at: [http://www.antmacroecology.org/ant\\_genera/index.html](http://www.antmacroecology.org/ant_genera/index.html).

To create a dataset for vertebrates that was comparable to that for ants, we combined the map of political regions with existing vertebrate range map data. We considered any vertebrate genera whose range overlapped a political region to be present in that region. To produce the maps for vertebrate genera, we merged the ranges of all constituent species in each genus. For amphibians and mammals, species range maps were from the IUCN Red List (IUCN, 2012). These are widely known as the Global Amphibian Assessment and Global Mammal Assessment maps. Bird data were from BirdLife International and NatureServe (BirdLife International & NatureServe, 2011; Ridgely *et al.*, 2011). We projected all maps to a cylindrical equal-area projection and analysed them in ArcGIS 10.

The concept of using a higher taxonomic level as a surrogate for species-level diversity is a long-standing one (Gaston & Williams, 1993; see Gaston, 2000 and Rodrigues & Brooks, 2007 for reviews). Indeed, recent estimates of the total species diversity likely to exist on the planet use the approach (Mora *et al.*, 2011). Empirical studies strongly support the idea, including studies on birds in the New World (Gaston & Blackburn, 1995), and on both plant and vertebrate taxa

in the Indo-Malay and Pacific Rim regions (Balmford *et al.*, 1996). There are caveats. The relationship between the number of genera and species appears to be nonlinear, and the predictions less certain in those places with the most species (Balmford *et al.*, 1996). While using genera for our analyses is not ideal, it is likely to be informative of what the results would be using species.

For each taxon, we analysed the genera in three groups: all genera, small-ranged genera and monotypic genera. We defined small-ranged as any genus with a range smaller than the median size for that taxon (amphibians = 219,297 km<sup>2</sup>; mammals = 1,305,376 km<sup>2</sup>; birds = 2,508,509 km<sup>2</sup>; ants = 10,101,581 km<sup>2</sup>). From extensive research on extinctions, we know that geographic range size is one of the strongest predictors of extinction risk (Purvis *et al.*, 2000). Applying this idea, one can use range size as a surrogate for extinction risk when formal assessments do not already exist (e.g. IUCN Red Lists), as they do not for most ants or other invertebrates. For vertebrates, we could apply the geographic range idea at the species level, but we restricted ourselves to genera there as well, for our primary purpose is the comparison to ants.

To calculate range sizes for ant genera, we summed the areas of all the political regions in which a genus occurs. This approach does create a potential upward bias in range size, for a genus must occur in only a portion of a region to have that region's entire area included. For larger ranged genera, their true ranges will be more likely to encompass entire political regions, and so the difference between actual and estimated range size should be less.

Monotypic genera were those with a single species according to the relevant taxonomy. For ants, we followed the taxonomy as defined in the Bolton World Catalog of Ants (Bolton, 2011). The systematics of ants is relatively well developed and is probably one of the best resolved among terrestrial insects (Bolton, 1994; Ward, 2007). For birds, we followed the latest taxonomy from BirdLife International, which was distributed with the range map data (BirdLife International & NatureServe, 2011; Ridgely *et al.*, 2011). For amphibians, the taxonomy follows that in the Amphibian Species of the World Database (Frost, 2011). Mammals generally follow Wilson & Reeder (2005), and full details of the taxonomy used in the Global Mammal Assessment are available through the IUCN website (IUCN, 2012).

To summarize the diversity of each region across all four taxa, we calculated an overall relative diversity. For each taxon, we rescaled the diversity of regions from 0 to 1 for each subset of genera to make them comparable. We then summed the values across the four taxa.

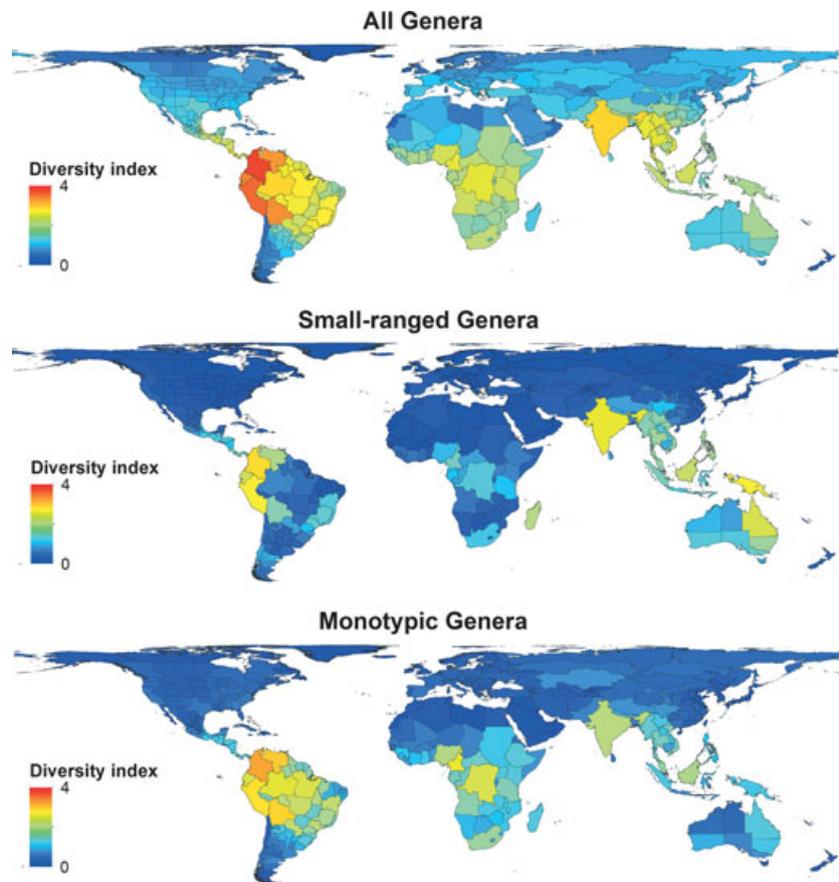
To compare global diversity patterns across taxa, we calculated Spearman's rank correlation coefficients in JMP (SAS Institute Inc., Cary, NC, USA). We did no adjustments for spatial autocorrelation, for it is a natural characteristic of biodiversity patterns. Were the goal to identify the causes of the biodiversity patterns, rather than describe them as we do here, spatial autocorrelation would need further attention.

To predict ant diversity using vertebrate diversity, we developed a series of GAMs for total, small-ranged and monotypic generic diversity (gam function from the mgcv package in R [Wood, 2011]; smooth terms were represented using penalized regression splines with smoothing parameters selected by generalized cross-validation). Because of high multicollinearity among the diversity of the three vertebrate taxa, we could not simultaneously include them in a model aiming to predict ant diversity. Instead, we used principal components analysis (PCA) to reduce the dimensionality of the vertebrate predictor pool. Distributions of vertebrate diversity were approximately normal, permitting the use of PCA. We centered and scaled the vertebrate diversity variables prior to PCA. We then entered the first principal component as a predictor into a GAM with ant generic diversity as the response. Correlations between PC1 and the diversity of each vertebrate taxon are in Table S2. The area of each political region was also included as a predictor, as it is widely known to correlate with diversity. Examining the residuals from the GAM enabled us to identify political regions where vertebrate diversity tended to over- or under-predict ant diversity. We also evaluated ordinary least-squares regressions, but the results were qualitatively similar and we report here only the results from the GAMs.

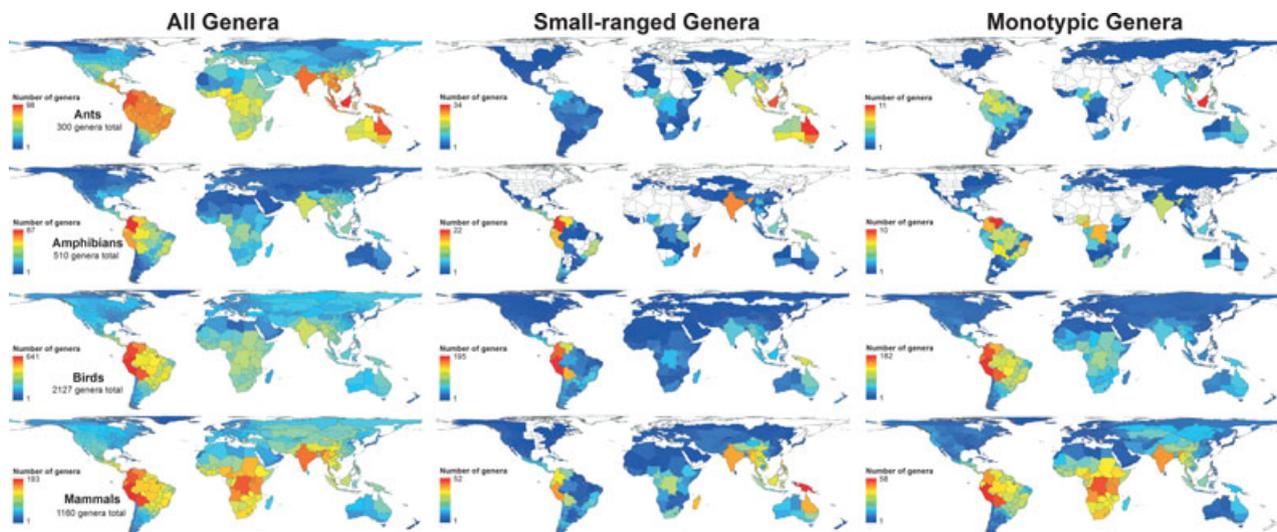
## RESULTS

Considering ants and vertebrates together, the tropical Andean countries (Venezuela, Colombia, Ecuador, Peru and Bolivia) rank higher than all other regions for total number of genera (Fig. 1). They are also generally diverse for small-ranged and monotypic genera. For small-ranged genera, the island of Madagascar, India, Borneo, New Guinea and north-east Australia also rank very high. For monotypic genera, much of the Neotropics ranks high as do the Democratic Republic of Congo and Cameroon in Africa. It is notable that South Africa, containing the fynbos and its extraordinary degree of plant endemism (Kreft & Jetz, 2007), is not exceptionally diverse for any of our measures of animal diversity.

For individual taxa (Fig. 2), tropical regions in general have the most genera, although patterns of diversity within the tropics differ markedly among taxa. Ants are more diverse in the Australasian and American tropics than in African regions, while amphibians and birds are most diverse in the tropical Americas, and mammal diversity is more even across the tropics. Most regions have few or no small-ranged genera of any taxa while a relatively small number of tropical regions rank highly for individual taxa. For vertebrates, these tend to be a similar set of tropical regions including the Andes, Madagascar, India, New Guinea, Queensland and parts of Southeast Asia. A distinct subset of these regions ranks highly for ants, mostly in Southeast Asia and Australia. Notably absent for ants are the tropical Andean countries, which appear to have few small-ranged ant genera. For amphibians and ants, monotypic genera are absent



**Figure 1** Overall relative diversity of the four taxa together. To calculate the index value, the number of genera in political regions was rescaled from 0 to 1 for each taxon and then the values summed across the four taxa.



**Figure 2** Diversity of genera for each taxon, showing total number of genera, small-ranged genera and monotypic genera. A small-ranged genus is one with a range smaller than the median size for that taxon. Maps use a linear colour scale where cooler colours (blues) represent fewer genera and warmer colours (orange to red) represent more genera. See Figs S4 to S6 in Supporting Information for alternative views of these results using heat maps.

(or unknown) from many regions. Patterns for birds and mammals broadly follow those for genera overall.

The total richness of regions for ant and vertebrate genera are strongly correlated (Spearman's rank correlation

coefficient  $r_s > 0.7$  in all comparisons,  $P < 0.001$ ,  $n = 370$  in all tests) but decline when considering small-ranged genera ( $0.57 < r_s < 0.69$ ,  $P < 0.001$ ) and are substantially lower when considering monotypic genera ( $r_s < 0.52$  in all

comparisons,  $P < 0.001$ ) (Fig. 3a). Correlations between birds and mammals for all diversity metrics were the highest among all taxonomic pairs, suggesting that conservation plans based on one or the other would be similar and thus least complementary (Fig. 3a). Amphibians differed more from the other vertebrates, particularly with regard to the diversity of monotypic genera. For scatterplots of the data, see Figs S1 to S3.

Within taxa, ants showed their highest correlation between the total number of genera and the number of small-ranged genera ( $r_s = 0.79$ ,  $P < 0.001$ ), with the other comparisons much lower ( $r_s < 0.56$ ,  $P < 0.001$ ) (Fig. 3b). Both birds and mammals had a very high correlation between the numbers of total genera and monotypic genera ( $r_s > 0.9$ ,  $P < 0.001$ ), but less so with the number of small-ranged genera ( $r_s < 0.76$  in all comparisons,  $P < 0.001$ ). Amphibians showed much lower correlations, regardless of the groups compared, with all correlations below 0.65 ( $P < 0.001$ ).

The vertebrate diversity-based GAM model severely underpredicted ant diversity in Australia, particularly for small-ranged genera and genera overall (reds in Fig. 4). Vertebrates also underpredicted ants in Borneo and many other Southeast Asian islands for all ant diversity measures. Select areas in Central Africa are underpredicted for small-ranged ant genera, mainly in the Congo and West African regions. Overpredictions are more widely scattered, with overall ant diversity overpredicted in parts of the southern Sahara and parts of central Asia (blues in Fig. 4). Overpredictions are also evident in some Andean regions, Madagascar and southwestern China for small-ranged genera and in much of Africa for monotypic genera. Summary statistics for all models are in Table S3.

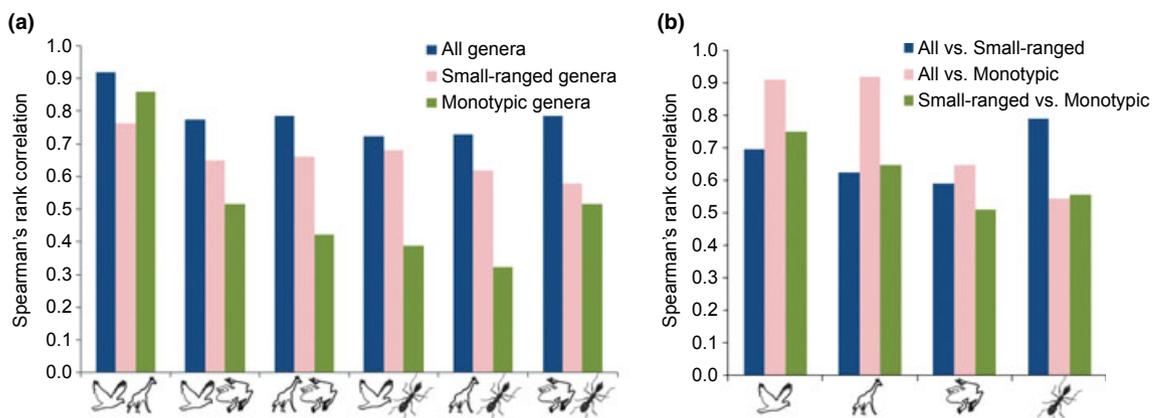
## DISCUSSION

That there is a correlation between global ant and vertebrate diversity is reassuring. It implies that global conservation plans based on vertebrates are not entirely random with respect to invertebrates. However, it is worrisome that the

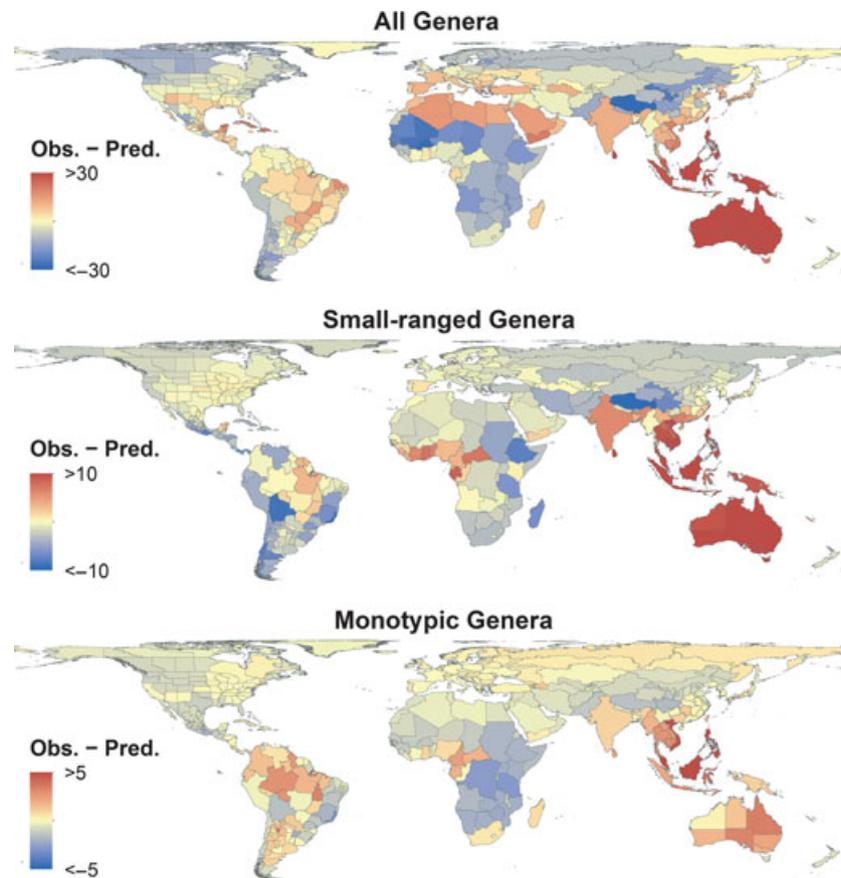
correlations for the higher priority groups, those genera with small geographic ranges and those that are phylogenetically distinct, are universally lower than for overall diversity. Magnifying this concern is that the spatial scale of our analysis is necessarily coarse, likely inflating the correlations and presenting an optimistic view. Previous work on vertebrates has shown that correlations decline as one refines the spatial scale (Grenyer *et al.*, 2006; Hurlbert & Jetz, 2007). The general cause is that a large region could appear diverse for both ants and vertebrates, but they may concentrate in different areas within the region. This is particularly notable as one approaches fine spatial scales, where studies on vertebrates and other taxa have found rather low levels of congruence (Prendergast *et al.*, 1993; Prendergast & Eversham, 1997; Howard *et al.*, 1998; Van Jaarsveld, 1998).

When trying to predict ant diversity patterns using vertebrates, we found some significant discrepancies between the model predictions and observed ant diversity, often showing a geographic pattern. We propose two possible explanations for those discrepancies, although there are likely others. One possible explanation is that the places predicted to have greater ant diversity than observed may be understudied for ants relative to other geographic regions. Many ants may still await discovery. As well, the taxonomy of known ants may need further resolution (e.g. species now in one genus might be divided into multiple genera). We previously explored some of these data gap issues in Guénard *et al.* (2012). If this explanation is correct, then the underpredicted locations should be priorities for new research on ants.

A second possible explanation for the discrepancies relates to the differing elevation preferences of ants and vertebrates. In the Andes, all three vertebrate groups have high rates of endemism on the eastern slopes, generally above 1500 m, and thus many small-ranged genera (Fig. 2). Ants, however, generally do not range to as high elevations in the tropics as do vertebrates (Janzen *et al.*, 1976; Samson *et al.*, 1997). It could be that the environments spawning such exceptional vertebrate diversity in the Andes may be the same ones that discourage ant diversity. The reverse could be true for places



**Figure 3** Spearman's rank correlations between taxa (a) and within taxa (b) for all genera, small-ranged genera and monotypic genera. All correlations were significant ( $P < 0.001$ ).



**Figure 4** Map of residuals from GAM model predicting ant diversity using vertebrate diversity. Red areas have higher ant diversity than predicted. Blue areas have lower ant diversity than predicted. Units are number of genera.

like Australia, where vast areas of warm drylands have tremendous ant diversity but are relatively poor for vertebrates (Fig. 2). A potentially interesting study would be to see if reptiles, which tend to be more diverse in dry areas, more closely mirror patterns of ant diversity. Unfortunately, adequate data on reptiles were not available for the present study.

Future work could improve upon our metric for phylogenetic distinctiveness, the number of monotypic genera. It is an admittedly crude metric and warrants further development. Indeed, a primary reason for comparing invertebrates to vertebrates is to capture more phylogenetic variety in global conservation planning. Ideally, we would use a continuous quantitative measure of how distinct organisms are from one another, such as distances in a phylogenetic tree (Faith, 1992; Keane *et al.*, 2005). By using such genetic distances, we could characterize regions more rigorously with respect to the amount of diversity they include for each taxon. This approach could also resolve a concern of whether a genus of ants is a reasonably equivalent entity to compare with a genus of vertebrates. Traditions differ within taxonomy as to how much variation corresponds to a given hierarchical level, and so the diversity recognized as an entire genus in ants may be very different from that in a genus of birds or amphibians. However, data limit what is currently practical. A consensus tree that covers all, or nearly all, ant genera does not yet exist. Although recent

studies do cover a large fraction of the genera (Brady *et al.*, 2006; Moreau *et al.*, 2006), they tend to miss many of the geographically rarest genera, which are of great interest with regard to conservation.

Given the apparent inadequacies of vertebrates as proxies for ant diversity, the question remains of how one might better include ants in conservation planning and in studies of biodiversity patterns. One approach would be to conserve those areas that are diverse for ants but not for vertebrates, in addition to those areas targeted for vertebrate conservation. This would tend to put more emphasis on conservation in dry regions than do current conservation plans, for example, parts of Australia and dry Africa. It is unclear, however, whether such an approach would capture the diversity of non-ant insects, particularly diverse taxa such as beetles and flies. For these taxa, plants might prove to be a more useful proxy than would vertebrates or ants. Some ant taxa, such as acacia ants (e.g. Janzen, 1966), are dependent on individual plant lineages, but most are not. In contrast, many beetle, Lepidoptera and fly lineages are dependent upon individual plant lineages. A useful next step in this regard would be to compare the extent to which plant diversity serves as a better proxy for invertebrate diversity. It might be that combining an invertebrate taxon that is relatively weakly connected to plant diversity and plant diversity itself would be a more useful framework for predicting the overall diversity of animal life than is the diversity of vertebrates.

If a goal is to conserve biodiversity in general, not just vertebrates, our results suggest we need new ways of identifying priority conservation areas. More work focused on the diversity of plants, perhaps complemented with data from well-studied taxa like ants, and maybe butterflies or some beetles, would be a useful step forward. Others have begun exploring this topic, although with a somewhat different approach than we used here (Qian & Ricklefs, 2008). The challenge is to test, rather than assuming, that the diversity of a group such as plants is a useful proxy. To our knowledge, country-level data on insects other than ants do not yet exist, but compiling such data would be possible for butterflies. Given their close relationship with host plants, understanding whether plant (or ant) diversity is predictive of their diversity seems disproportionately important.

Given our findings, we believe that it is currently unwise to assume that global conservation priorities focused on vertebrates will safely cover ants as well. This may also be true for other lesser-known invertebrates. To move towards a better inclusion of invertebrates in conservation, the scientific community needs to produce more finely resolved global spatial datasets for ants and other potentially feasible invertebrate groups (e.g. butterflies, bees, some beetles and spiders). Such data would enable a more thorough consideration of invertebrates in global conservation planning.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Table S1** Names of political regions, their area and measures of diversity of each taxon.

**Table S2** Spearman's rank correlation coefficient between PC1 for vertebrate diversity and the diversity of each of the component vertebrate taxa (amphibians, birds and mammals).

**Table S3** Summary statistics for the principal components analysis of vertebrate diversity, the relationship between vertebrate diversity PC1 and invertebrate diversity, and the generalized additive models to predict invertebrate diversity (accounting for differences in sampling area).

**Shapefile of political regions** – GIS data of the political regions.

**Figure S1** Scatterplots of each taxonomic pair comparing diversities of all genera by political region.

**Figure S2** Scatterplots of each taxonomic pair comparing diversities of small-ranged genera by political region.

**Figure S3** Scatterplots of each taxonomic pair comparing diversities of monotypic genera by political region.

**Figure S4** Heat maps as alternative views of results in Fig. 2.

**Figure S5** Heat maps as alternative views of results in Fig. 2.

**Figure S6** Heat maps as alternative views of results in Fig. 2.

## BIOSKETCH

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Author contributions: CJ, BG, SD, MW and RD wrote the article, interpreted results and prepared figures and tables; CJ, BG, SD and MW ran models and analysed results; SD and MW contributed actively to statistical techniques. All authors contributed to the design of the study and provided comments on the manuscript.

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