Mapping where ecologists work: biases in the global distribution of terrestrial ecological observations

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Although the geographical context of ecological observations shapes ecological theory, the global distribution of ecological studies has never been analyzed. Here, we document the global distribution and context (protected status, biome, anthrome, and net primary productivity) of 2573 terrestrial study sites reported in recent publications (2004–2009) of 10 highly cited ecology journals. We find evidence of several geographical biases, including overrepresentation of protected areas, temperate deciduous woodlands, and wealthy countries. Even within densely settled or agricultural regions, ecologists tend to study "natural" fragments. Such biases in trendsetting journals may limit the scalability of ecological theory and hinder conservation efforts in the 75% of the terrestrial world where humans live and work.

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The geographical context of field study sites greatly influences the ecological patterns, processes, and dynamics observed in these locations. For this reason, the disciplines of ecology and conservation biology have been criticized for disproportionately conducting field studies in temperate zones (Schoener 1983; Platnick 1991; Collen *et al.* 2008), biodiversity hotspots (Metrick and Weitzman 1994; Kier *et al.* 2005), and unpopulated areas (Botkin 1992; Collins *et al.* 2000). And though ecologists increasingly recognize the importance of urban ecology and "novel ecosystems" (Botkin and Beveridge 1997; Hobbs *et al.* 2006), ecological studies of urban and suburban areas represent just 0.4–6.0% of the ecological literature (Collins *et al.* 2000; Miller and Hobbs 2002). In contrast, landscapes transformed by agriculture and human settlements cover roughly 75% of Earth's ice-free land and incorporate nearly 90% of terrestrial net primary productivity (NPP; Ellis and Ramankutty 2008).

In a nutshell:

- Reviewing >8000 publications in 10 leading ecology journals, we discover that ecologists' terrestrial field study site selections are geographically biased
- Protected areas, the temperate zone, and wealthy countries are dramatically overrepresented; studies conducted in settled areas or agricultural landscapes tend to focus on "less disturbed" protected fragments
- These systematic biases may limit the global relevance of ecological research; to address pressing issues of global change, including the conservation of biodiversity and ecosystem services, we need to better understand ecological processes in globally common but understudied areas

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Although past critiques of the geographical distribution of field sites have been based on detailed disciplinary knowledge, few have been supported by quantitative assessments. There are three reasons why such quantification matters. First, because ecological field studies are costly in time and resources, they will always be in limited supply. The geographical distribution of this relatively small set of studies can therefore substantially influence conclusions reached by ecological theorists. Quantifying that distribution would enable those working to synthesize ecological knowledge to account for uneven sampling across study sites. Second, ecological knowledge is often used to prioritize conservation projects; it is therefore critical to know which biomes, regions, and landscapes remain understudied and undervalued. For example, the indicator framework of the Convention on Biological Diversity was recently criticized for incorporating a disproportionate amount of data from Europe and North America (Butchart *et al.* 2010; Pereira *et al.* 2010). There is also a complex relationship between "conservation attention" and the accumulation of ecological knowledge; better funded or longer protected sites are often more intensively studied, leaving open the question of whether protection follows study or vice versa (Ahrends *et al.* 2011). Third, the geographical distribution of study sites says much about the disciplinary norms of ecology; ecologists' selections of field sites are influenced by a wide array of physical, financial, and institutional constraints, as well as by the discipline's philosophical underpinnings, values, and history (Evans and Foster 2011). With these three considerations in mind, we set out to analyze the global distribution and environmental context of ter-

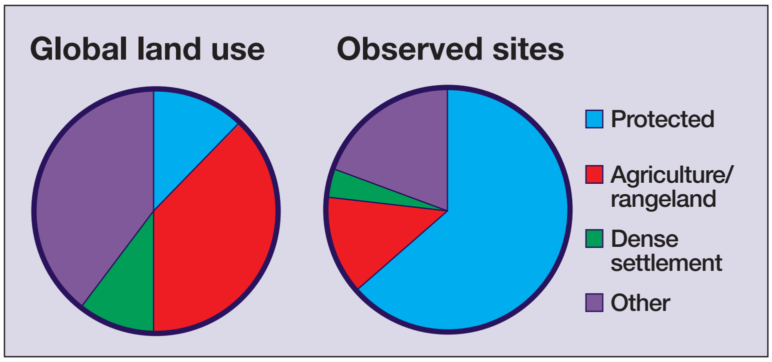

Figure 1. *The percentage of global ice-free terrestrial area in each anthrome category (left) as compared with the percentage of ecological sites (*n *= 2573) situated in each anthrome category (right). In the key, "other" refers to sites that were not densely settled or agriculture/rangeland but that did not contain adequate information to assign a protected status. Estimate of protected sites is therefore conservative. See WebTable 1 for exact values.*

restrial field studies published in 10 highly cited ecology journals over a consecutive 5-year period.

■ Methods

We reviewed the methods sections of all papers published between June 2004 and June 2009 in 10 journals with an ISI Web of Knowledge 2009 Journal Citation Reports 5-year impact factor ≥ 4.5 and in which > 30% of published articles are ecological field studies (n = 8040; the journals were: *American Naturalist*, *Conservation Biology*, *Ecological Applications*, *Ecological Monographs*, *Ecology*, *Ecology Letters*, *Global Change Biology*, *Journal of Animal Ecology*, *Journal of Applied Ecology*, and *Journal of Ecology*). By selecting frequently cited journals and by individually reviewing each article rather than relying on keyword searches, we were able to capture a comprehensive snapshot of the range of trendsetting research.

We analyzed the geographical distribution and environmental context of all terrestrial field sites reported in these journals (n = 2573 sites) using two meta-knowledge methods: content analysis and zonal statistics in Geographic Information System (GIS). We defined terrestrial field sites as experimental or observational studies located outdoors, exclusive of laboratory experiments, models, or studies of water bodies. To avoid double counting, we included synthetic studies of original data but not literature reviews or meta-analyses of previously published data.

We first performed a content analysis of the methods sections in which we used all information contained in authors' site descriptions to categorize the site as "protected", "densely settled", or "agriculture/rangeland". If a site description included a field station name or geographical coordinates, we then corroborated our categorization with Google Earth (Google Inc) and the World Database on Protected Areas (www.wdpa.org). We defined "protected" as a site under one of the six International Union for Conservation of Nature Protected Area Management Categories (Jenkins and Joppa 2009). We categorized sites described as urban, city, suburban, village, or exurban as "densely settled", and descriptions of active or fallow crop or rangelands as "agriculture/rangeland". We categorized a site as "unspecified" if we were unable to assign a protection status based on the descriptive or geographical information provided by authors and it was definitively not densely settled or agriculture/rangeland.

Our second analysis investigated the global geographic context of studies. We entered the locations of study sites for all 1330 articles that reported geographical coordinates or the names of georeferenced field stations into a GIS. When a publication referenced multiple sites, we treated each site as independent (n = 1476 sites). We determined the global environmental context of each site through zonal statistics in GIS, using spatially explicit global data on biomes (potential vegetation; Ramankutty and Foley 1999), anthromes (anthropogenic biomes; Ellis *et al.* 2010), NPP (potential NPP; Haberl *et al.* 2007), political borders, and gross national income (GNI, reported in binned deciles; http://siteresources.worldbank.org/DATASTATISTICS/Resources/GNI.pdf).

We then compared the site distributions generated from the first and second analyses (observed distributions) with the expected distributions given two hypothetical scenarios: (1) an even distribution of study sites across global ice-free terrestrial area, and (2) an equal number of study sites in each geographical category (eg the same number of studies are conducted in each biome). Although these hypothetical distributions are likely unachievable and perhaps undesirable, they are useful in describing the relative study effort in each geographical context. To test for significant differences between these observed and expected distributions, we calculated chi-square values in JMP 8.0 (SAS Institute Inc).

Finally, to visualize the global distribution of georeferenced field sites, we fitted a kernel density function to point locations, indicating the number of studies expected within a given 100-km × 100-km area (approximately 1 geographic degree), smoothed to a search radius of 500 km (approximately 10 geographic degrees) using a quadratic kernel function (Silverman 1986).

■ Results

Site distribution by protected status

Although less than 13% of Earth's ice-free land falls under some form of legal protection (Jenkins and Joppa 2009), over 63% of study sites were situated in a protected area – significantly more than expected by global extent (χ^2 = 5066.9, P < 0.0001; Figure 1; WebTable 1). Only 12.5% of study sites were described as agricultural/rangeland, though agricultural areas and rangelands account for approximately 40% of global terrestrial area (χ^2 = 485.3, $P < 0.0001$). Only 3.9% of study sites were described as densely settled, significantly fewer than the 6.9% expected by the global extent of this type (χ^2 = 34.7, $P < 0.0001$). There were 774 "unspecified" sites that, while definitively not agriculture/rangeland or densely settled sites, were not sufficiently described and did not include enough geographical information to allow us to determine their protected status. However, some of these sites – the majority of which were in forest settings – were likely also protected, suggesting that 63–84% of study sites were located in protected areas.

Ecological Monographs published the highest percentage of studies conducted in protected areas (87–93%), followed by *Ecology* (72–93%) and *Ecology Letters* (70–87%) (WebFigure 1; WebTable 2). *Journal of Applied Ecology* published the highest percentage of studies conducted in agriculture/rangeland (41%), followed by *Conservation Biology* (16%) and *Ecological Applications* (16%). *Ecological Applications* published the highest percentage of studies conducted in densely settled areas (10%), followed by *Conservation Biology* (9%) and *Journal of Applied Ecology* (7%).

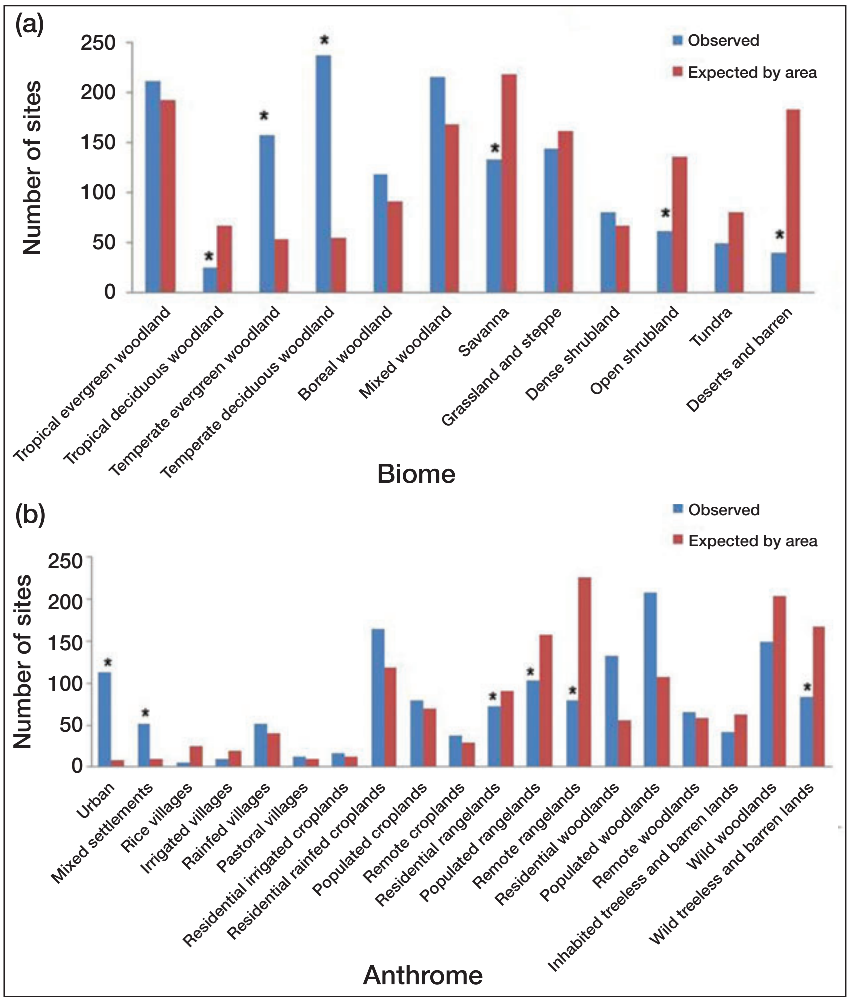

Figure 2. *Number of observed ecological field sites (blue) as compared with the number of expected field sites, given an even distribution across global area (red) by (a) biome and (b) anthrome (n = 1476). Significant differences between distributions are indicated by asterisks (chi-square test, P ≤ 0.05). See WebTables 3 and 4 for exact values.*

Site distribution by biome and NPP

Analysis of the georeferenced dataset revealed that field sites were situated in temperate deciduous woodlands over four times as frequently as expected by global extent of this biome (Figures 2 and 3; WebTable 3). Tropical deciduous woodland was the least frequently studied biome relative to global area (1.7% of sites), while the desert/barren biome was the most understudied (2.8% of sites, 12.4% of global area). Savanna, open shrubland, and deserts were also significantly understudied by area (Figures 2 and 3).

Comparing the observed study distribution to an expected distribution with an equal number of studies conducted in each biome, regardless of global extent, temperate deciduous woodlands, tropical evergreen woodlands, and mixed woodlands were studied approximately twice as frequently as would be expected, while tundra and deserts were among the most understudied biomes (Figures 2 and 3; WebTable 3). Furthermore, most studies were conducted in high-productivity sites; approximately 65% of sites fell within the top five deciles of NPP (WebFigure 2; WebTable 4).

Site distribution by anthrome

Anthromes represent global ecological patterns created by sustained direct human interactions with ecosystems (Ellis and Ramankutty 2008). By comparing site distributions with those expected by anthrome global extents, we found that the urban anthromes were sampled ~14 times more frequently than expected. Mixed settlements, populated rangelands, and remote rangelands were also overrepresented relative to their global area, whereas residential rangelands and wild treeless and barren lands were underrepresented (Figures 2 and 3; WebTable 5). Although these results may seem to contradict the results of the content analysis, when we integrate data from both analyses we find that only 19% of studies categorized as dense settlements by geographical coordinates were actually described by authors as dense settlements; 45% of these sites were described as protected, 16% were described as croplands or rangelands, and 20% were described as forest or open lands with unverifiable protected status (WebFigure 3; WebTable 6).

Site distribution by country

Studies with published geographical coordinates were conducted in 73 countries (WebTables 7 and 8), nine of which contributed significantly more sites than expected based on their ice-free land areas: Greenland (1085×), Costa Rica (49×), Switzerland (47×), Israel (43×), Panama (33×), the UK (20×), Sweden (12×), Germany (10×), and the US (5×). The Middle East was the most significantly understudied region based on land area, by a factor of 8.3, followed by Africa, Asia, and South America. Central America was the most overstudied by a factor of 8, followed by Europe and North America (WebTable 9). Unsurprisingly, countries with the lowest GNI were underrepresented, whereas countries with the highest GNI were overrepresented. Approximately 90% of studies were conducted in countries within the 70–100th percentiles of GNI; 41% were conducted in the five countries with the highest GNIs: US, China, Japan, Germany, and France (WebTable 5).

■ Discussion

Our results reveal multiple biases in the geographical distribution of terrestrial study sites. Most notably, ecologists overselected protected areas, temperate deciduous woodlands, and wealthy countries. Despite the indication of the geospatial analysis that many sites were located in urban areas, content analysis revealed that many of these were protected fragments situated in densely settled zones – in other words, many of these studies were not conducted for the explicit purpose of understanding the ecology of densely settled places. Taken together, these results lead us to several recommendations on how funding agencies, policy makers, publishers, and researchers could help advance ecological research in currently understudied areas (Panel 1).

Systematic regularities within a discipline can signal ghost theories: unspoken shared assumptions that shape research trajectories (Smail 2008). Within ecology, the overwhelming bias toward the study of certain sites constitutes one such pattern. In choosing study sites, ecologists are influenced by cultural precedents as well as institutional pressures. During the past 150 years, most ecologists have assumed that (seemingly) unpeopled environments better represent ecological and evolutionary processes and are therefore better objects of study (Worster 1977; Botkin 1992; Pickett and McDonnell 1993; Collins *et al.* 2000; Kohler 2002). It seems plausible that this position has shaped the global distribution of ecological study sites, given that scientific precedent is known to create "microparadigms" around established hubs of knowledge in other contexts (Rzhetsky *et al.* 2006; Evans and Forster 2011). It is also a well-documented phenomenon that scientific institutions, and therefore scientific outputs, tend to be concentrated in countries with high GNI and long histories of institutionalization (Hefler *et al.* 1999; Thompson 1999). Finally, many conservation institutions encourage ecological research on their lands, perpetuating the dominance of certain field sites (for example, 22% of the studies published in Central America were conducted at the Organization for Tropical Studies' La Selva Biological Station, Costa Rica). Meanwhile, it can be extremely time-consuming for an individual to gain permission to work on private property, and the risk that a study site will be "tampered with" is higher, or at least perceived as higher, on such parcels of land. These factors may lead ecologists to intentionally avoid sites perceivably used by humans – a trend that, as Metzger *et al.* (2010) concluded

Panel 1. Recommendations for promoting ecological research in understudied areas

Funding agencies and policy makers

- Direct funding and institutional support to long-term, multidisciplinary field studies in anthropogenic landscapes, including agricultural and settled ecosystems
- Support programs that aim to generalize globally from observations made locally, such as observational networks and multidisciplinary collaborations
- Support research that investigates "land sharing": the integration of biodiversity conservation and goods production within landscapes (eg Phalan *et al.* 2011)

Publishers

- Incentivize the publication of "applied" ecological research that explicitly includes a human context; overcome the current bias toward rewarding "basic" research conducted in "pristine" settings
- Require contributors to report the geospatial coordinates and landscape contexts of field studies (history of human use, including the status of surrounding ecosystems); only 52% of terrestrial field studies contained geographically explicit data

Researchers

- Consider human influence on the ecology of all field sites, including historical land uses and the influence of neighboring systems
- Encourage graduate students to pursue research in intensively used anthromes and "novel ecosystems" (Hobbs *et al.* 2006)
- Conduct spatially explicit studies beyond the plot scale; study functions, communities, and populations within "used" and "novel" ecosystems
- Embrace the wide range of possible future ecosystems that human agency enables

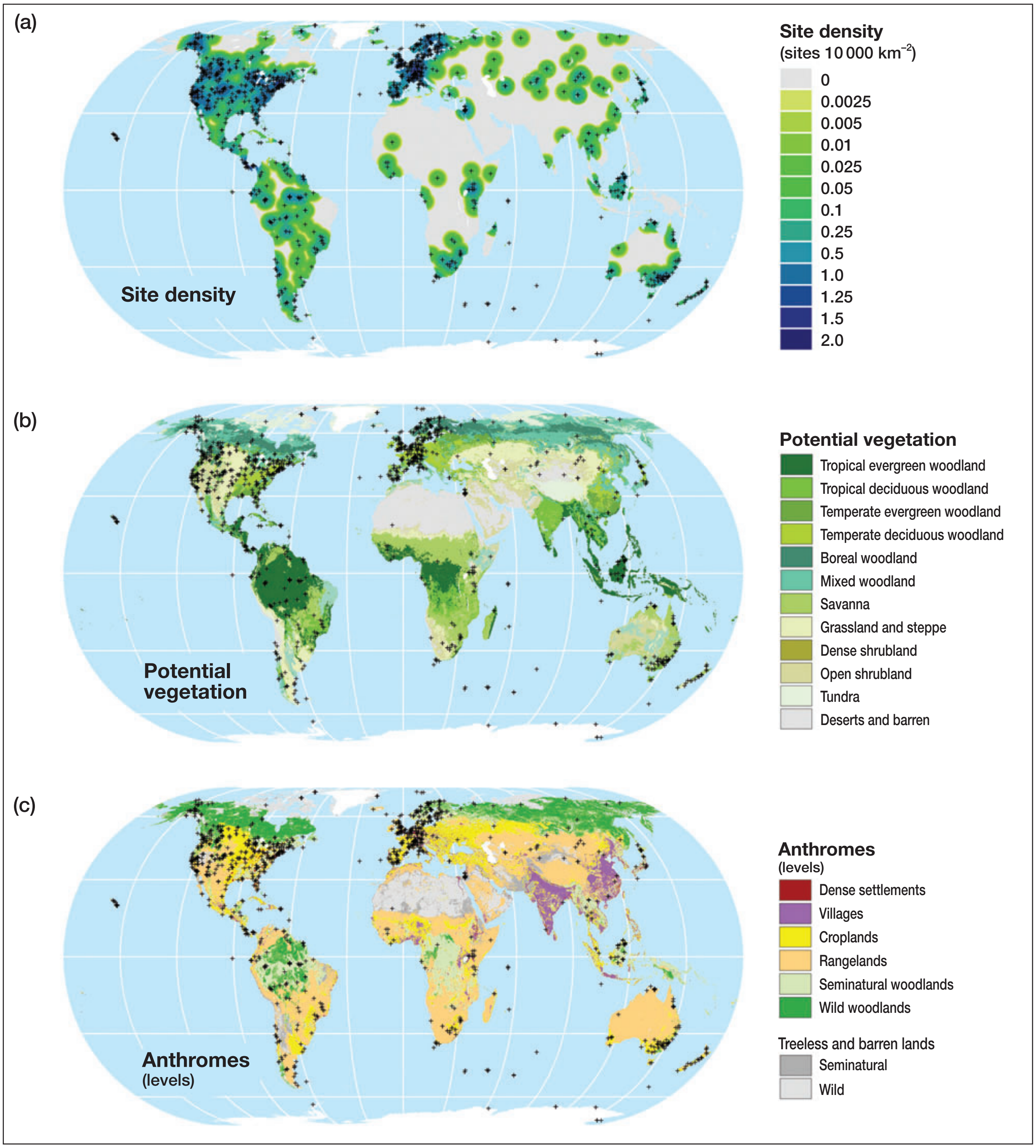

Figure 3. *Maps of (a) the global distribution of ecological field sites (kernel densities), (b) study site position (crosses) overlaid on the distribution of potential vegetation biomes (Ramankutty and Foley 1999), and (c) study site position (crosses) overlaid on the distribution of anthromes (Ellis* et al. *2010). All maps are expressed in Eckert IV Equal Area projection.*

in their analysis of European Long Term Ecological Research (LTER) site selection, illustrates "a bias for traditional ecological research away from human activity".

Although this review clearly does not sample the entire canon of ecological literature, it is an important first step toward applying meta-knowledge techniques to the discipline of ecology (Evans and Foster 2011). By basing our journal selection on citation rate, we were able to capture influential, interdisciplinary ecological studies. Such journals are sources of information and inspiration for scholars, journalists, textbook editors, and policy makers; it is therefore critically important to understand any underlying biases in "snapshots" of the ecological world. The number of journals included was constrained by the time required to review > 8000 articles, and it is worth noting that all journals were English-language journals and that our selection did not include publications with a particular geographic or taxonomic focus. This leaves open the question of how representative our results are of ecology writ large. On the basis of an informal review of other ecological journals, the very large differences between observed and expected site distributions, and the agreement of our results with past critiques, we would expect broadly similar results if this analysis were extended to other journals. Nevertheless, our results should be viewed as a snapshot of the most highly cited ecological research rather than a representation of the entirety or even the average of global ecological research.

In the analyses presented here, we have considered two null models: an even site distribution across terrestrial area and an equal distribution of sites across geographical categories (eg biomes, NPP). We chose these null models because they are based on robust global datasets. It is also reasonable to assume that an unbiased distribution would be spatially random. Of course, there are several alternative ways to describe distributional bias. For example, are studies evenly distributed by biodiversity level? By provisioning of ecosystem services? Are authors' addresses correlated with the distribution of study sites, or do ecologists tend to study farther away places? Analysis of these alternative null models would require higher quality global datasets that do not exist at present. Hopefully, an increasing enthusiasm for metadata research, along with collaborations between ecologists and computer programmers, will make such alternative ways of describing gaps in global observational processes accessible.

At present, we tend to privilege rare and "undisturbed" areas, but in a dynamic human-inhabited world, one of our most pressing questions is how to manage vast areas made up of novel biotic assemblages (Hobbs *et al.* 2006). Earth's most extensive anthropogenic landscapes are remote rangelands not fully transformed by intensive cultivation, in which many species are capable of sustaining populations. These are clearly worthy of ecological study and conservation, given that we know little about the impacts of agriculture on resident communities and ecosystem processes. Even where land use is intensive, anthropogenic landscapes are rarely homogeneous; instead, anthromes are mosaics of used and novel ecosystems (Ellis *et al.* 2010). Although humans have transformed three-quarters of Earth's ice-free land into anthromes, only about half of this area is actually in use directly for crops and pastures – the other half comprises remnant, recovering, and novel ecosystems embedded within used landscapes. Only by comparing the ecological effects of "land sharing" (integrating biodiversity conservation and goods production on the same land) and "land sparing" (separating land for conservation from human-use land – ie strict protection) can we decide how best to allocate limited conservation resources (Phalan *et al.* 2011). The 10 journals considered here tend to oversample the ecology of land sparing at the expense of land sharing. Large-scale corn or wheat fields, for example, are not all identical and should be of interest to ecologists. Notably, our study suggests that many ecologists actually are studying the ecology of intensively used anthropogenic landscapes, with the proviso that they are intentionally choosing the "least disturbed" or "most protected" areas within such geographic contexts for purposes other than understanding anthropogenic ecosystems.

The paucity of ecological field sites under explicit human use raises several concerns. First, it is an unresolved philosophical question whether we should discount human activity as external to ecosystems. If we recognize human activity as an integral force in the biosphere, then clearly it should fall within the purview of ecology. While ecologists are increasingly addressing this knowledge gap through experimental design (McDonnell and Pickett 1990; Fetridge *et al.* 2008; Pavao-Zuckerman and Byrne 2009), and while efforts such as urban LTER programs have made great strides in considering humans as integral organisms of ecosystems (Pickett *et al.* 1997; Grimm *et al.* 2000), our data suggest that human-use sites have yet to be fully incorporated into articles published by at least 10 highly cited ecology journals. It also remains unclear whether ecological theory developed from observations in protected areas is transferrable to other land-use categories or whether new theory must be developed for these areas (Collins *et al.* 2000; Pickett *et al.* 2008). Even if we maintain a distinction between natural and human activity, confining ecology to the non-human world sharply curtails its global relevance, because there are few, if any, places on Earth that have not been impacted by human activity (Redman 1999; Sanderson *et al.* 2002; Ellis and Ramankutty 2008).

Inferences about global ecology that are based on the current body of ecological literature are, by default, based on a small sampling of the actual spectrum of global ecosystems. A narrow geographical distribution of study sites has certainly shaped scientific consensus in other field-based disciplines; for example, while > 90% of geologists with Southern Hemisphere experience supported plate tectonic theory in the 1960s, only 48% of those with Northern Hemisphere experience did (Solomon 1992). Arguably, the geographical context of ecological study sites affects the content of ecology in similar ways.

But perhaps the most problematic aspect of the current site distribution is that the underrepresentation of lived-in landscapes in the mainstream ecological literature leaves us with little robust data about ecological relationships in our immediate habitat, the 75% of the terrestrial world most influenced by our actions. This lack of ecological work in human-use areas is untenable; although global protected area has increased substantially, biodiversity continues to decline (Rodrigues *et al.* 2004; Ceballos 2007; Wiersma and Nudds 2009; Butchart *et al.* 2010; CBD 2010). If we recognize humans as embedded within ecosystems, there is no reason to limit the scope of ecology and conservation to the 13% of the globe that is protected. To restrict ecological research to protected areas alone is to misrepresent our world.

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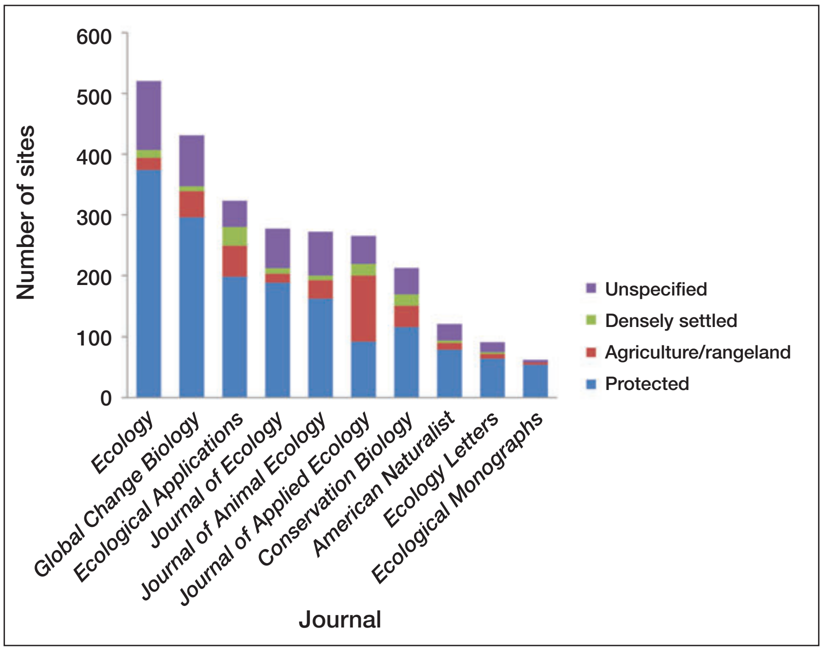
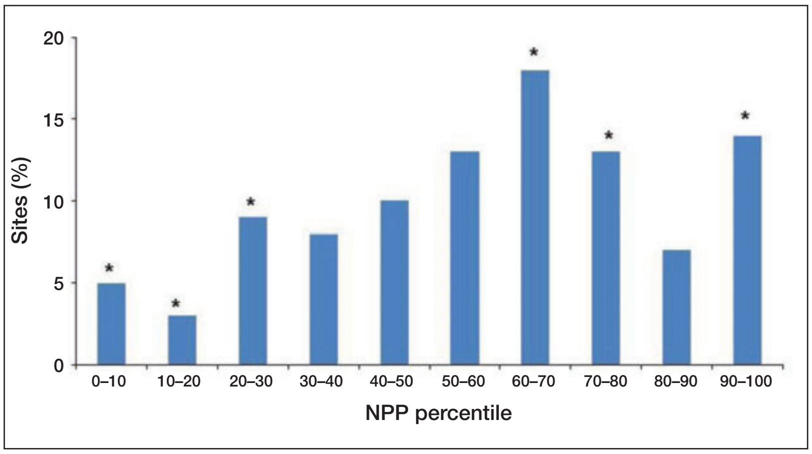
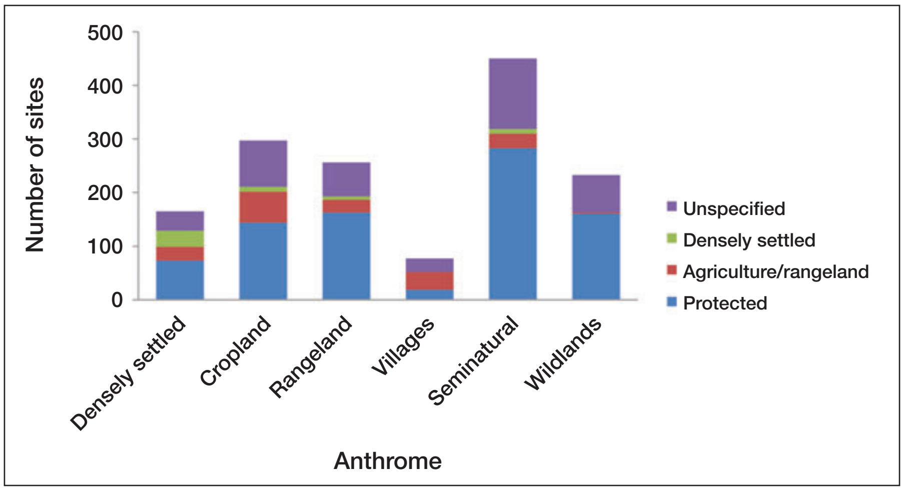


WebFigure 1. *Number of ecological field sites situated in four land-use categories by journal (n = 2573). "Unspecified" refers to sites that were definitively not densely settled or agriculture/rangeland but that did not contain enough information to allow us to assign a protected status. Estimate of protected sites is therefore conservative. See WebTable 2 for exact values.*



WebFigure 2. *Percentage of ecological field sites situated in each decile of net primary productivity (NPP; n = 1476). Higher deciles indicate higher NPP. Significant differences from the expected percentage of sites, given an even distribution across global area, are indicated by asterisks (chi-square test, $P \leq 0.05$). See WebTable 5 for exact values.*



WebFigure 3. *Number of sites per authors' site description category (generated by content analysis) by anthrome (generated from geospatial analysis; n = 1476). See WebTable 6 for exact values.*

WebTable 1. Number of observed (obs) ecological field sites and number of expected (exp) sites, given an even distribution of sites across global area by authors' descriptions of site land-use category (content analysis, $n = 2573$)

Land-use category	*Studies (exp)*	*Studies (obs)*	χ^2	P *value*
Protected	332	1629	5066.9	<0.001
Agriculture/rangeland	1030	323	485.3	<0.001
Dense settlement	180	101	34.7	<0.001
Other	1031	520	253.3	<0.001

Notes: Chi-square test indicates significant differences between distributions when $P < 0.05$.

WebTable 2. Number of ecological field sites by authors' descriptions of site land-use category (content analysis, $n = 2573$)

Journal	*Protected*	*Agriculture/rangeland*	*Densely settled*	*Unspecified*	*Total*
Ecology	374	20	13	113	520
Global Change Biology	296	43	8	84	431
Ecological Applications	198	51	31	43	323
Journal of Ecology	188	15	9	65	277
Journal of Animal Ecology	162	30	8	72	272
Journal of Applied Ecology	92	108	19	46	265
Conservation Biology	115	35	19	43	212
American Naturalist	79	11	4	26	120
Ecology Letters	64	8	3	16	91
Ecological Monographs	54	4	0	4	62

WebTable 3. Number of observed (obs) ecological field sites and number of expected (exp) sites, given an even distribution of sites across global area (left) or by an equal distribution among biomes (right) for each biome (geospatial analysis, $n = 1476$)

		By area				By equal distribution			
Biome	*Studies (obs)*	*Studies (exp)*	*obs/exp*	χ^2	*P value*	*Studies (exp)*	*obs/exp*	χ^2	*P value*
Tropical evergreen woodland	212	193	1.10	1.77	0.999	123	1.72	64.40	<0.001
Tropical deciduous woodland	25	67	0.37	26.29	0.006	123	0.20	78.08	<0.001
Temperate evergreen woodland	158	54	2.94	201.82	<0.001	123	1.28	9.96	0.535
Temperate deciduous woodland	237	55	4.29	597.41	<0.001	123	1.93	105.66	<0.001
Boreal woodland	119	92	1.30	8.17	0.698	123	0.97	0.13	1.000
Mixed woodland	216	169	1.28	13.30	0.247	123	1.76	70.32	<0.001
Savanna	133	218	0.61	33.15	<0.001	123	1.08	0.81	0.999
Grassland and steppe	144	162	0.89	2.06	0.998	123	1.17	3.59	0.980
Dense shrubland	81	68	1.19	2.37	0.996	123	0.66	14.34	0.215
Open shrubland	62	136	0.46	40.13	<0.001	123	0.50	30.25	0.001
Tundra	50	81	0.62	11.77	0.366	123	0.41	43.33	<0.001
Deserts and barren	41	183	0.22	110.30	<0.001	123	0.33	54.67	<0.001

Notes: Chi-square test indicates significant differences between distributions when $P < 0.05$.

WebTable 4. Number of observed (obs) ecological field sites and number of expected (exp) sites, given an even distribution of sites across global area (left) or by an equal distribution among anthromes (right) for each anthrome (geospatial analysis, $n = 1476$)

Anthome	*Subcategory*	*Studies (obs)*	*Studies (exp by area)*	*obs/exp*	χ^2	P *value*	*Studies (exp by area)*	*obs/exp*	χ^2	P *value*
Dense settlements	Urban	113	8	14.44	1414.1	<0.001	78	1.45	16.05	0.598
	Mixed settlements	52	10	4.96	164.5	<0.001	78	0.67	8.49	0.97
Villages	Rice villages	5	25	0.2	16.23	0.576	78	0.06	68.01	<0.001
	Irrigated villages	9	20	0.45	5.99	0.996	78	0.12	60.73	<0.001
	Rainfed villages	51	41	1.24	2.34	0.999	78	0.66	9.17	0.956
	Pastoral villages	12	9	1.27	0.69	1	78	0.15	55.54	<0.001
Croplands	Residential irrigated croplands	17	13	1.36	1.58	1	78	0.22	47.4	<0.001
	Residential rainfed croplands	164	119	1.38	17.31	0.502	78	2.11	95.91	<0.001
	Populated croplands	80	70	1.15	1.58	1	78	1.03	0.07	1
	Remote croplands	37	29	1.28	2.25	0.999	78	0.48	21.31	0.265
Rangelands	Residential rangelands	73	91	0.8	3.59	0.999	78	0.94	0.28	1
	Populated rangelands	103	158	0.65	19.36	0.37	78	1.33	8.25	0.975
	Remote rangelands	79	226	0.35	95.33	<0.001	78	1.02	0.02	1
Seminatural	Residential woodlands	132	56	2.34	101.41	<0.001	78	1.7	37.98	0.004
	Populated woodlands	208	107	1.94	94.9	<0.001	78	2.68	218.61	<0.001
	Remote woodlands	66	58	1.14	1.19	1	78	0.85	1.76	1
	Inhabited treeless and barren lands	42	63	0.67	6.93	0.991	78	0.54	16.39	0.565
Wildlands	Wild woodlands	149	204	0.73	15.03	0.66	78	1.92	65.47	<0.001
	Wild treeless and barren lands	84	168	0.5	42.31	0.001	78	1.08	0.51	1

Notes: Chi-square test indicates significant differences between distributions when $P < 0.05$.

WebTable 5. Number of observed (obs) ecological field sites and number of expected (exp) sites, given an even distribution of sites across deciles of gross national income (GNI by nation, left); number of observed ecological field sites and number of expected sites, given an even distribution of sites across global area by net primary productivity (NPP by land area, right); geospatial analysis, $n = 1476$

	GNI				*NPP*			
Decile	*Sites (obs)*	*Sites (exp)*	χ^2	P *value*	*Sites (obs)*	*Sites (exp)*	χ^2	P *value*
0–10	4	142.4	134.5	<0.001	61	147.6	50.8	<0.001
10–20	7	142.4	128.7	<0.001	43	147.6	74.1	<0.001
20–30	12	142.4	119.4	<0.001	63	147.6	48.5	<0.001
30–40	11	142.4	121.2	<0.001	106	147.6	11.7	0.231
40–50	25	142.4	96.8	<0.001	87	147.6	24.9	0.003
50–60	77	142.4	30.0	<0.001	144	147.6	0.1	1.000
60–70	14	142.4	115.8	<0.001	241	147.6	59.1	<0.001
70–80	86	142.4	22.3	0.008	315	147.6	189.9	<0.001
80–90	226	142.4	49.1	<0.001	200	147.6	18.6	0.029
90–100	962	142.4	4717.3	<0.001	216	147.6	31.7	<0.001

Notes: Chi-square test indicates significant differences between distributions when $P < 0.05$.

WebTable 6. Number of sites per authors' site description category (generated by content analysis) by anthrome (generated from geospatial analysis) ($n = 1476$)

Anthrome	*Protected*	*Agriculture/ rangeland*	*Densely settled*	*Unspecified*
Densely settled	73	26	30	36
Cropland	144	58	9	86
Rangeland	163	24	6	63
Villages	19	33	0	25
Seminatural	283	27	9	131
Wildlands	161	2	0	70

Notes: "Unspecified" refers to sites that were definitively not densely settled or agriculture/rangeland but that did not contain enough information to allow us to assign a protected status. Estimate of protected sites is therefore conservative.

WebTable 7. Number of observed (obs) study sites and number of sites expected (exp) by even distribution across global area by country or territory (geospatial analysis, $n = 1476$)

Country/territory	*Region*	*Land area (km^2)*	*Studies (obs)*	*Studies (exp)*	*obs/exp*	χ^2	P *value*
Afghanistan	Middle East	632697	0	7.15	0.00	7.15	1.000
Albania	Europe	28349	0	0.32	0.00	0.32	1.000
Algeria	Africa	2307271	0	26.09	0.00	26.09	1.000
American Samoa	Oceania	138	0	0.00	0.00	0.00	1.000
Andorra	Europe	315	0	0.00	0.00	0.00	1.000
Angola	Africa	1241496	0	14.04	0.00	14.04	1.000
Antigua & Barbuda	Caribbean	279	0	0.00	0.00	0.00	1.000
Argentina	South America	2735410	23	30.93	0.74	2.03	1.000
Armenia	Middle East	28634	0	0.32	0.00	0.32	1.000
Aruba	Caribbean	78	0	0.00	0.00	0.00	1.000
Australia	Oceania	7614927	65	86.10	0.75	5.17	1.000
Austria	Europe	81636	0	0.92	0.00	0.92	1.000
Azerbaijan	Asia	86251	0	0.98	0.00	0.98	1.000
Bahrain	Middle East	767	0	0.01	0.00	0.01	1.000
Bangladesh	Asia	136552	0	1.54	0.00	1.54	1.000
Barbados	Caribbean	430	0	0.00	0.00	0.00	1.000
Belarus	Europe	203264	0	2.30	0.00	2.30	1.000
Belgium	Europe	30283	3	0.34	8.76	20.63	1.000
Belize	Central America	21224	1	0.24	4.17	2.41	1.000
Benin	Africa	116918	0	1.32	0.00	1.32	1.000
Bhutan	Asia	38535	0	0.44	0.00	0.44	1.000
Bolivia	South America	1077842	11	12.19	0.90	0.12	1.000
Bosnia & Herzegovina	Europe	50733	0	0.57	0.00	0.57	1.000
Botswana	Africa	575345	0	6.51	0.00	6.51	1.000
Brazil	South America	8384088	46	94.80	0.49	25.12	1.000
Brunei	Oceania	5572	1	0.06	15.87	13.94	1.000
Bulgaria	Europe	109275	0	1.24	0.00	1.24	1.000
Burkina Faso	Africa	272547	0	3.08	0.00	3.08	1.000
Burundi	Africa	24458	0	0.28	0.00	0.28	1.000
Cambodia	Asia	176123	0	1.99	0.00	1.99	1.000
Cameroon	Africa	460389	0	5.21	0.00	5.21	1.000
Canada	North America	8638637	109	97.67	1.12	1.31	1.000
Central African Republic	Africa	616710	1	6.97	0.14	5.12	1.000
Chad	Africa	1261957	0	14.27	0.00	14.27	1.000
Chile	South America	694316	15	7.85	1.91	6.51	1.000
China	Asia	9256730	21	104.66	0.20	66.88	1.000
Colombia	South America	1131342	4	12.79	0.31	6.04	1.000
Comoros	Africa	1451	0	0.02	0.00	0.02	1.000
Congo	Africa	340437	1	3.85	0.26	2.11	1.000
Congo, DRC	Africa	2287188	0	25.86	0.00	25.86	1.000
Costa Rica	Central America	50646	28	0.57	48.90	1313.69	<0.0001
Cote d'Ivoire	Africa	318346	2	3.60	0.56	0.71	1.000

continued

WebTable 7. – *continued*

Country/territory	*Region*	*Land area (km^2)*	*Studies (obs)*	*Studies (exp)*	*obs/exp*	χ^2	*P value*
Croatia	Europe	54672	0	0.62	0.00	0.62	1.000
Cuba	Caribbean	105028	0	1.19	0.00	1.19	1.000
Cyprus	Europe	9560	0	0.11	0.00	0.11	1.000
Czech Republic	Europe	77736	3	0.88	3.41	5.12	1.000
Denmark	Europe	41183	5	0.47	10.74	44.16	1.000
Djibouti	Africa	20961	0	0.24	0.00	0.24	1.000
Dominica	Caribbean	748	0	0.01	0.00	0.01	1.000
Dominican Republic	Caribbean	47257	0	0.53	0.00	0.53	1.000
Ecuador	South America	250665	12	2.83	4.23	29.64	1.000
Egypt	Africa	990356	0	11.20	0.00	11.20	1.000
El Salvador	Central America	19053	0	0.22	0.00	0.22	1.000
Equatorial Guinea	Africa	26545	0	0.30	0.00	0.30	1.000
Eritrea	Africa	120218	0	1.36	0.00	1.36	1.000
Estonia	Europe	42364	5	0.48	10.44	42.67	1.000
Ethiopia	Africa	1121971	1	12.69	0.08	10.76	1.000
Falkland Islands	South America	1414	1	0.02	62.55	60.57	1.000
Fiji	Asia	16211	0	0.18	0.00	0.18	1.000
Finland	Europe	298327	29	3.37	8.60	194.70	0.612
France	Europe	542453	39	6.13	6.36	176.13	0.867
French Guiana	South America	81949	10	0.93	10.79	88.85	1.000
Gabon	Africa	258504	2	2.92	0.68	0.29	1.000
Georgia	Asia	68677	0	0.78	0.00	0.78	1.000
Germany	Europe	351526	41	3.97	10.32	344.92	<0.0001
Ghana	Africa	232365	0	2.63	0.00	2.63	1.000
Greece	Europe	126267	3	1.43	2.10	1.73	1.000
Greenland	North America	326	4	0.00	1085.21	4332.83	<0.0001
Grenada	Caribbean	314	0	0.00	0.00	0.00	1.000
Guadeloupe	Caribbean	1406	0	0.02	0.00	0.02	1.000
Guatemala	Central America	108246	0	1.22	0.00	1.22	1.000
Guinea	Africa	243330	2	2.75	0.73	0.21	1.000
Guinea-Bissau	Africa	31088	0	0.35	0.00	0.35	1.000
Guyana	South America	209198	1	2.37	0.42	0.79	1.000
Haiti	Caribbean	27094	0	0.31	0.00	0.31	1.000
Honduras	Central America	111996	1	1.27	0.79	0.06	1.000
Hungary	Europe	90853	0	1.03	0.00	1.03	1.000
Iceland	Europe	88930	1	1.01	0.99	0.00	1.000
India	Asia	3107699	2	35.14	0.06	31.25	1.000
Indonesia	Asia	1884648	12	21.31	0.56	4.07	1.000
Iran	Middle East	1608413	0	18.19	0.00	18.19	1.000
Iraq	Middle East	427601	0	4.83	0.00	4.83	1.000
Ireland	Europe	69595	1	0.79	1.27	0.06	1.000
Isle of Man	Europe	587	0	0.01	0.00	0.01	1.000
Israel	Middle East	26827	13	0.30	42.86	531.47	<0.0001
Italy	Europe	293992	18	3.32	5.42	64.80	1.000
Jamaica	Caribbean	10867	3	0.12	24.42	67.37	1.000
Japan	Asia	395405	18	4.47	4.03	40.94	1.000
Jersey	Europe	136	0	0.00	0.00	0.00	1.000
Jordan	Middle East	86597	0	0.98	0.00	0.98	1.000
Kazakhstan	Asia	2628778	4	29.72	0.13	22.26	1.000
Kenya	Africa	566637	15	6.41	2.34	11.53	1.000
Kuwait	Middle East	16719	0	0.19	0.00	0.19	1.000
Kyrgyzstan	Asia	192534	0	2.18	0.00	2.18	1.000
Laos	Asia	229666	0	2.60	0.00	2.60	1.000
Latvia	Europe	63091	0	0.71	0.00	0.71	1.000
Lebanon	Middle East	10445	0	0.12	0.00	0.12	1.000
Lesotho	Africa	30638	0	0.35	0.00	0.35	1.000

continued

WebTable 7. – *continued*

Country/territory	*Region*	*Land area (km²)*	*Studies (obs)*	*Studies (exp)*	*obs/exp*	χ^2	P *value*
Liberia	Africa	94510	0	1.07	0.00	1.07	1.000
Libya	Africa	1613988	0	18.25	0.00	18.25	1.000
Liechtenstein	Europe	116	0	0.00	0.00	0.00	1.000
Lithuania	Europe	63387	0	0.72	0.00	0.72	1.000
Luxembourg	Europe	2695	0	0.03	0.00	0.03	1.000
Macedonia	Europe	24610	0	0.28	0.00	0.28	1.000
Madagascar	Africa	589797	3	6.67	0.45	2.02	1.000
Malawi	Africa	96218	0	1.09	0.00	1.09	1.000
Malaysia	Asia	329312	18	3.72	4.83	54.74	1.000
Mali	Africa	1247707	1	14.11	0.07	12.18	1.000
Malta	Europe	268	0	0.00	0.00	0.00	1.000
Martinique	Caribbean	1108	0	0.01	0.00	0.01	1.000
Mauritania	Africa	1031380	1	11.66	0.09	9.75	1.000
Mauritius	Africa	408	1	0.00	216.78	214.78	0.242
Mayotte	Africa	395	0	0.00	0.00	0.00	1.000
Mexico	North America	1927471	27	21.79	1.24	1.24	1.000
Moldova	Europe	33220	0	0.38	0.00	0.38	1.000
Mongolia	Asia	1532099	9	17.32	0.52	4.00	1.000
Montenegro	Europe	13305	0	0.15	0.00	0.15	1.000
Montserrat	Caribbean	93	0	0.00	0.00	0.00	1.000
Morocco	Africa	399597	0	4.52	0.00	4.52	1.000
Mozambique	Africa	778112	0	8.80	0.00	8.80	1.000
Myanmar	Asia	661509	0	7.48	0.00	7.48	1.000
Namibia	Africa	817779	1	9.25	0.11	7.35	1.000
Nepal	Asia	144695	0	1.64	0.00	1.64	1.000
Netherlands	Europe	34963	10	0.40	25.30	233.36	0.058
Netherlands Antilles	Caribbean	442	0	0.00	0.00	0.00	1.000
New Caledonia	Oceania	18234	0	0.21	0.00	0.21	1.000
New Zealand	Oceania	264428	19	2.99	6.36	85.74	1.000
Nicaragua	Central America	117893	1	1.33	0.75	0.08	1.000
Niger	Africa	1175956	0	13.30	0.00	13.30	1.000
Nigeria	Africa	901763	0	10.20	0.00	10.20	1.000
North Korea	Asia	124158	0	1.40	0.00	1.40	1.000
Norway	Europe	300926	25	3.40	7.35	137.09	0.999
Oman	Middle East	308431	0	3.49	0.00	3.49	1.000
Pakistan	Asia	847997	0	9.59	0.00	9.59	1.000
Panama	Central America	72823	27	0.82	32.79	832.20	<0.0001
Papua New Guinea	Oceania	463046	0	5.24	0.00	5.24	1.000
Paraguay	South America	396539	0	4.48	0.00	4.48	1.000
Peru	South America	1278898	11	14.46	0.76	0.83	1.000
Philippines	Oceania	293204	0	3.32	0.00	3.32	1.000
Poland	Europe	307511	0	3.48	0.00	3.48	1.000
Portugal	Europe	88174	7	1.00	7.02	36.15	1.000
Puerto Rico	Caribbean	8442	12	0.10	125.72	1484.74	<0.0001
Qatar	Middle East	11007	0	0.12	0.00	0.12	1.000
Reunion	Oceania	2502	0	0.03	0.00	0.03	1.000
Romania	Europe	234040	0	2.65	0.00	2.65	1.000
Russia	Asia	16067496	15	181.67	0.08	152.91	0.995
Rwanda	Africa	23629	0	0.27	0.00	0.27	1.000
Samoa	Oceania	2632	0	0.03	0.00	0.03	1.000
San Marino	Europe	65	0	0.00	0.00	0.00	1.000
Sao Tome & Principe	Africa	884	0	0.01	0.00	0.01	1.000
Saudi Arabia	Middle East	1911094	0	21.61	0.00	21.61	1.000
Senegal	Africa	195924	0	2.22	0.00	2.22	1.000
Serbia	Europe	88228	0	1.00	0.00	1.00	1.000

continued

WebTable 7. – *continued*

Country/territory	*Region*	*Land area (km²)*	*Studies (obs)*	*Studies (exp)*	*obs/exp*	χ^2	P *value*
Sierra Leone	Africa	72370	0	0.82	0.00	0.82	1.000
Singapore	Asia	651	1	0.01	135.86	133.87	0.999
Slovakia	Europe	47566	1	0.54	1.86	0.40	1.000
Slovenia	Europe	20532	0	0.23	0.00	0.23	1.000
Solomon Islands	Oceania	26487	0	0.30	0.00	0.30	1.000
Somalia	Africa	634028	1	7.17	0.14	5.31	1.000
South Africa	Africa	1210545	28	13.69	2.05	14.97	1.000
South Korea	Asia	102585	0	1.16	0.00	1.16	1.000
Spain	Europe	500709	27	5.66	4.77	80.43	1.000
Sri Lanka	Asia	65068	0	0.74	0.00	0.74	1.000
St Kitts & Nevis	Caribbean	197	0	0.00	0.00	0.00	1.000
St Lucia	Caribbean	605	1	0.01	146.19	144.20	0.999
St Pierre & Miquelon	Caribbean	201	0	0.00	0.00	0.00	1.000
St Vincent	Caribbean	348	0	0.00	0.00	0.00	1.000
Sudan	Middle East	2478930	0	28.03	0.00	28.03	1.000
Suriname	South America	142926	0	1.62	0.00	1.62	1.000
Swaziland	Africa	16770	0	0.19	0.00	0.19	1.000
Sweden	Europe	408931	55	4.62	11.90	548.88	<0.0001
Switzerland	Europe	39409	21	0.45	47.13	948.17	<0.0001
Syria	Middle East	187856	0	2.12	0.00	2.12	1.000
Tajikistan	Asia	134625	0	1.52	0.00	1.52	1.000
Tanzania	Africa	878919	4	9.94	0.40	3.55	1.000
Thailand	Asia	511317	5	5.78	0.86	0.11	1.000
The Bahamas	Caribbean	6911	2	0.08	25.60	47.27	1.000
The Gambia	Africa	10371	0	0.12	0.00	0.12	1.000
Timor-Leste	Oceania	15091	0	0.17	0.00	0.17	1.000
Togo	Africa	55698	0	0.63	0.00	0.63	1.000
Tonga	Oceania	241	0	0.00	0.00	0.00	1.000
Trinidad & Tobago	Caribbean	4800	0	0.05	0.00	0.05	1.000
Tunisia	Africa	156127	0	1.77	0.00	1.77	1.000
Turkey	Middle East	767771	0	8.68	0.00	8.68	1.000
Turkmenistan	Asia	463983	0	5.25	0.00	5.25	1.000
Turks & Caicos Islands	Caribbean	221	0	0.00	0.00	0.00	1.000
Uganda	Africa	207006	0	2.34	0.00	2.34	1.000
Ukraine	Europe	580408	1	6.56	0.15	4.71	1.000
United Arab Emirates	Middle East	68537	0	0.77	0.00	0.77	1.000
United Kingdom	Europe	240132	54	2.72	19.89	968.72	<0.0001
United States	North America	8970280	470	101.42	4.63	1339.43	<0.0001
Uruguay	South America	175133	0	1.98	0.00	1.98	1.000
Uzbekistan	Asia	415819	4	4.70	0.85	0.10	1.000
Vanuatu	Oceania	10824	0	0.12	0.00	0.12	1.000
Venezuela	South America	904039	6	10.22	0.59	1.74	1.000
Vietnam	Asia	324751	1	3.67	0.27	1.94	1.000
Virgin Islands	Caribbean	213	0	0.00	0.00	0.00	1.000
Western Sahara	Africa	265433	0	3.00	0.00	3.00	1.000
Yemen	Middle East	452732	0	5.12	0.00	5.12	1.000
Zambia	Africa	737004	0	8.33	0.00	8.33	1.000
Zimbabwe	Africa	386491	2	4.37	0.46	1.29	1.000

Notes: Chi-square test indicates significant differences between distributions when $P < 0.05$.

WebTable 8. Countries overrepresented (top) and underrepresented (bottom) in the 10 reviewed journals

Overrepresented countries

Belgium	Finland	Japan	Singapore
Belize	France	Kenya	Slovakia
Brunei	French Guiana	Malaysia	South Africa
Canada	Germany*	Mauritius	Spain
Chile	Greece	Mexico	St Lucia
Costa Rica*	Greenland*	Netherlands	Sweden*
Czech Republic	Ireland	New Zealand	Switzerland*
Denmark	Israel*	Norway	The Bahamas
Ecuador	Italy	Panama*	United Kingdom*
Estonia	Jamaica	Portugal	United States*

Underrepresented countries

Argentina	Gabon	Mongolia	Venezuela
Australia	Guinea	Namibia	Vietnam
Bolivia	Guyana	Nicaragua	Zimbabwe
Brazil	Honduras	Peru	
Central AR	India	Russia	
China	Indonesia	Somalia	
Colombia	Kazakhstan	Tanzania	
Congo	Madagascar	Thailand	
Cote d'Ivoire	Mali	Ukraine	
Ethiopia	Mauritania	Uzbekistan	

Notes: Calculated as the difference between the observed number of ecological field sites and the number of expected field sites, given an even distribution across global area. Significant differences between distributions are indicated by asterisks (chi-square test, $P \leq 0.05$).

WebTable 9. Number of ecological study sites in the reviewed literature (obs) and number of sites expected (exp), given an even distribution of sites across global area per political region ($n = 1476$)

Region	*Studies (obs)*	*Studies (exp)*	*obs/exp*	χ^2	P
Africa	66	306	0.22	188.26	<0.001
Asia	130	455	0.29	231.69	<0.001
Australia	65	86	0.75	5.17	0.639
Central America	64	8	7.99	391.26	<0.001
Europe	349	64	5.43	1261.42	<0.001
Middle East	13	112	0.12	87.14	<0.001
North America	622	221	2.81	727.67	<0.001
South America	140	197	0.71	16.73	0.019

Notes: Chi-square test indicates significant differences between distributions ($P < 0.05$).