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).

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 terrestrial ecological observations.

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.

**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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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 (χ² = 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 ($\chi^2 = 485.3, P < 0.0001$). 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 ($\chi^2 = 34.7, P < 0.0001$). 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%).

**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, we found that 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

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**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
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

![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.](image-url)
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 (e.g., 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 – i.e., 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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**References**


