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Community ecology

Effects of occupancy estimation on abundance–occupancy relationships

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Abundance–occupancy relationships predict that species that occupy more sites are also more locally abundant, where occupancy is usually estimated following the assumption that species can occupy all sampled sites. Here we use the National Ecological Observatory Network small-mammal data to assess whether this assumption affects abundance–occupancy relationships. We estimated occupancy considering all sampled sites (traditional occupancy) and only the sites found within the species geographic range (spatial occupancy) and realized environmental niche (environmental occupancy). We found that when occupancy was estimated considering only sites possible for the species to colonize (spatial and environmental occupancy) weaker abundance–occupancy relationships were observed. This shows that the assumption that the species can occupy all sampled sites directly affects the assessment of abundance–occupancy relationships. Estimating occupancy considering only sites that are possible for the species to colonize will consequently lead to a more robust assessment of abundance–occupancy relationships.

1. Introduction

Positive abundance–occupancy relationships—the observation that widely distributed species are also more locally abundant—is a general pattern in ecology [1] that has been described for vertebrates [2–4], invertebrates [5–7], plants [8–10] and bacteria [11]. Resource availability [12,13], species niche requirements and dispersal limitation [5,14] are among the mechanisms proposed to explain these positive relationships [12]. Although these mechanisms are usually evaluated individually, they can affect species occupancy and abundance simultaneously [15], with the relative importance of each mechanism being dependent on spatial scale [1]. Moreover, biotic and abiotic factors [16] as well as stochastic dynamics [17] also affect species abundance and occupancy patterns. This combined effect of different factors affecting species abundance and occupancy might explain why some taxa do not show positive abundance–occupancy relationships [18,19] as well as why these positive relationships are usually weak [1,4].

Abundance–occupancy relationships can be evaluated at small or large spatial scales [1], where occupancy is usually defined as the number or fraction of sites where a species occurs out of the full set of sampled sites [20,21]. Thus, the spatial scale sampled in a study can directly impact occupancy estimations. For example, although the major assumption that the species can occupy all sampled sites affects the occupancy estimation for all species, species with small geographic ranges are particularly affected by this assumption as they will inherently have exceptionally lower occupancy estimates when large spatial scales are sampled. However, a species occurrence at a site is affected by environmental conditions, dispersal limitation and biotic interactions [22,23]. The species environmental niche plays an important role on its ability to occupy sites [24], such that a species can only occupy sites that have environmental conditions that it can tolerate [25,26]. Consequently, species environmental niche breadth is positively related to geographic range size [27,28] and occupancy

[29]. Nevertheless, dispersal limitation [30–32] and biotic interactions [22,33] can still prevent a species from occupying environmentally suitable sites.

Knowledge on the species geographic range can be used to estimate occupancy given that in some cases environmentally suitable sites might be geographically inaccessible for the species occurrence because of dispersal barriers [34] such as mountains and rivers [35,36]. Similarly, information on the species realized environmental niche (i.e. the set of environmental conditions in which the species was found) can also be used to estimate occupancy as environmental conditions might be unsuitable in parts of the species geographic range [37]. For example, fragmentation processes occurring in parts of the species geographic range could lead to changes in environmental conditions in those locations and render them to be environmentally unsuitable for the species occurrence [38]. Thus, information on both the species realized environmental niche and geographic range can be used to estimate occupancy considering only sites that are possible for the species to colonize, a factor that is often ignored when abundance–occupancy relationships are assessed [10].

A challenging aspect of estimating species realized environmental niche and geographic range is obtaining enough occurrence points for the species such that its geographic range and realized environmental niche can be confidently estimated. The development of online databases, such as the Global Biodiversity Information Facility (GBIF), where species occurrence points are made publicly available, provide an opportunity to overcome this problem. Here, we use occurrence points obtained from GBIF to estimate the geographic range and realized environmental niche of 122 North American mammal species that have abundance and occurrence data available in the National Ecological Observatory Network dataset [39,40]. We use this information on species geographic range and realized environmental niche to estimate spatial occupancy, and explore how this influences the assessment of abundance–occupancy relationships. Occupancy was estimated as the fraction of all sampled occupied sites, as the fraction of environmentally suitable occupied sites, and as the fraction of occupied sampled sites within the species geographic range. The occurrence of interspecific abundance–occupancy relationships (i.e. the assessment of the scaling between species mean abundance and occupancy) was assessed using these three occupancy estimates. We found that the observed abundance–occupancy relationships became weaker when occupancy estimates were constrained by the species realized environmental niche or geographic range. This occurred because species with small geographic ranges have their occupancy underestimated when it is measured following the traditional approach.

2. Methods

(a) Species abundance and occupancy data

We used the National Ecological Observatory Network (NEON) small mammal data sampled between 2014 and 2019 [41]. NEON is a continental research platform where occurrence and density data is collected for small mammals in 46 terrestrial sites spread over 20 ecoclimatic domains across the USA [39,40]. Several 10 × 10 trap grids (plots) are used per site to sample mammals. Each of the 100 traps present in the plots are separated by 10 m. Although the number of traps is standardized for each plot, there can be six different types of trap status depending on the sampling outcome. Only traps that had captures or no captures (i.e. trap status 4–6) were used to calculate species abundance. Traps not set, disturbed or with trap door open or closed with faeces left behind or with bait missing (i.e. trap status 1–3) were not considered in our analyses. Moreover, individuals recaptured in the same month were not considered when calculating species abundance. Abundance and occurrence data were only obtained for individuals that were identified to the species level ($n = 122$).

(b) Estimating the species realized environmental niche and geographic range

Species geographic ranges were estimated with minimum convex polygons from occurrence points sampled in the USA obtained from the GBIF database [42]. To estimate the species realized environmental niche we used the 19 bioclimatic variables available in the BioClim database [43] at a resolution of 10 arc-min covering the Americas and performed a principal component analysis (PCA). The first two axes explained more than 80% of the variance in the data, and were selected to estimate the species realized environmental niche. We extracted the environmental values associated with the species occurrence points found in the Americas from the two PCA axes and used minimum convex polygons to estimate the species realized environmental niche (see electronic supplementary material for more details).

(c) Abundance and occupancy estimation

We estimated mean annual abundance as the mean abundance across sampling months and sites, standardizing monthly estimates of abundance based on the number of trapnights. Mean annual occupancy was calculated in three different ways. First, we estimated occupancy using the traditional approach, where occupancy was defined as the number of sites where a species was found divided by the number of total sampled sites, hereafter traditional occupancy. In this case, all sampled sites are used to calculate the species occupancy regardless of whether the sites are suitable for the species occurrence. An extreme example of a case like this would be estimating occupancy considering sites that do not have the required habitat for the species occurrence. For the second and third cases, we only considered sites found within the species realized environmental niche and known geographic range to estimate occupancy, hereafter environmental and spatial occupancy respectively. Abundance and occupancy estimates were weighted according to the annual number of sites sampled for each species.

(d) Evaluating abundance–occupancy relationships

We assessed the abundance–occupancy relationship using an interspecific approach that evaluates the generality of the scaling between species abundance and occupancy across species. Spearman's rank correlation was used to assess the correlation between the species $\log_{10}$ mean abundance and the three different occupancy metrics estimated.

3. Results

(a) How different are the estimated occupancies?

The mean fraction of occupied sites by the species was the lowest for traditional occupancy (mean ± s.d.; 0.07 ± 0.09) followed by environmental occupancy (0.17 ± 0.15) and it was the highest for spatial occupancy (0.32 ± 0.27; figure 1*a–c*). Traditional occupancy estimates were lower because it considered all sites when occupancy was estimated, whereas spatial occupancy was higher than environmental occupancy because it was generally

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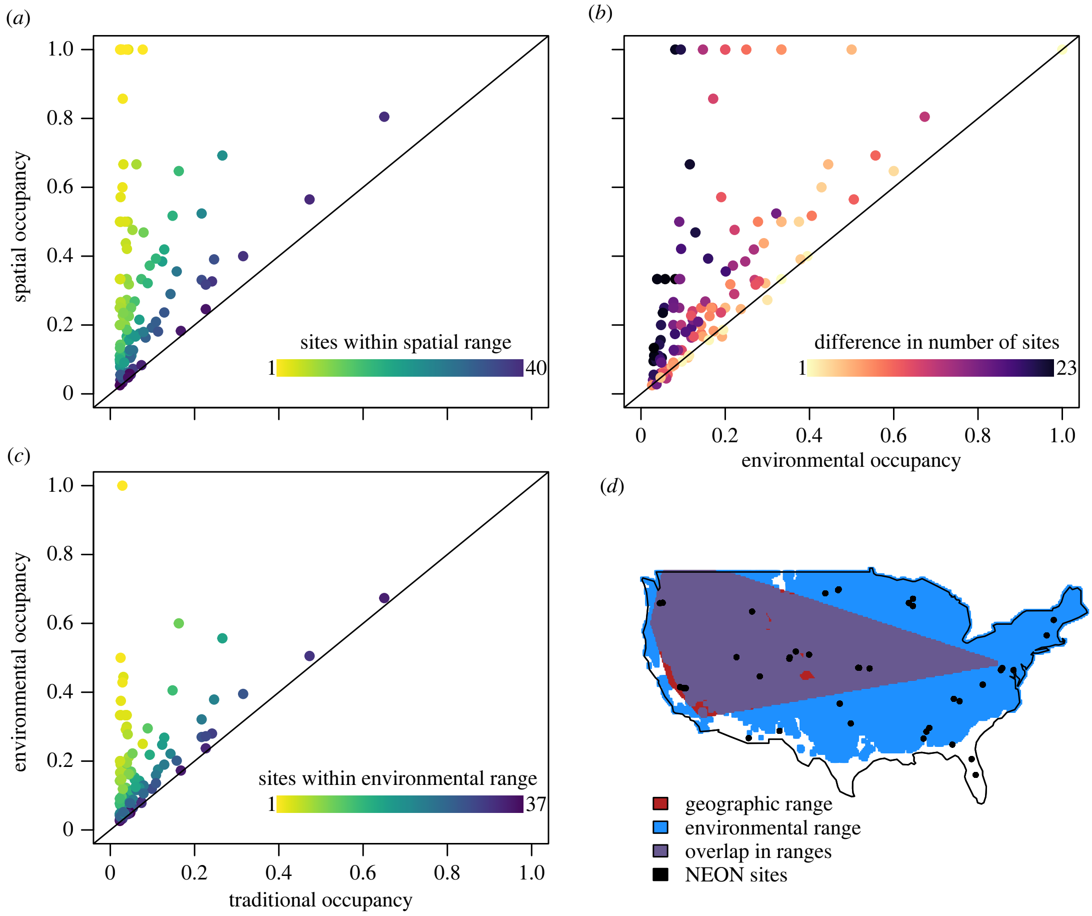

Figure 1. Comparison between traditional and spatial (*a*), environmental and spatial (*b*), and traditional and environmental (*c*) occupancy estimations. Points closer to the identity line represent species that have more similar occupancy estimates in the compared approaches. Legends represent the number of sites within species geographic range (*a*) and environmental niche (*c*), and the difference in the number of sites within the species geographic range and environmental niche (*b*). In panel (*d*), we show areas suitable for *Ochotona princeps* occurrence based on its geographic range (in red) and realized environmental niche (in blue). Areas in purple represent locations that are suitable for the species occurrence based on both the species geographic range and realized environmental niche and black points are the sampled NEON sites.

more restrictive in the number of sites a species could potentially occupy (figure 1*d*). Thus, occupancy estimates were higher when fewer sites were considered to estimate it.

(b) How do occupancy estimations affect abundance–occupancy relationships?

We found positive abundance–occupancy relationships using all three occupancy metrics, but, based on the observed Spearman's rank correlation coefficient (ρ), the relationship was stronger when using traditional occupancy ($\rho = 0.53$, $p < 0.01$) than when using environmental occupancy ($\rho = 0.39$, $p < 0.01$) or spatial occupancy ($\rho = 0.36$, $p < 0.01$). These differences in the strength of the observed relationship seem to occur because the association between species abundance and occupancy becomes more unclear when occupancy is not estimated traditionally (figure 2*a–c*). In general, species with small geographic ranges have their occupancies underestimated to a higher degree than species with large ranges (figure 2*d*), although this underestimation is not dependent on species abundance as there is no relationship between species range size and abundance ($\rho = 0.12$, $p = 0.18$).

4. Discussion

Occupancy estimation is a fundamental step for the evaluation of abundance–occupancy relationships, but the assumption that species can occupy all sampled sites is generally overlooked when occupancy is estimated. We show that this assumption directly affects abundance–occupancy relationships, and these relationships become weaker when occupancy is estimated based only on sites possible for the species to colonize. This result is driven mostly by species with small geographic ranges that have their occupancy highly underestimated when occupancy is estimated considering all sampled sites. Thus, removing the unrealistic assumption that species can occupy all sampled sites [10] has a clear and strong effect on the assessment of one of the most commonly reported macroecological relationships.

These effects of occupancy estimation will be more pronounced for smaller-ranged species, although these effects might be limited when smaller spatial scales are sampled as most of the species geographic range will be found within the sampled area [1]. On the other hand, abundance–occupancy relationships assessed over broad spatial scales typically consider species with different ecological characteristics. Considering these species differences, especially in terms of geographic ranges and environmental niche, when estimating occupancy is important as it can provide a more realistic depiction of abundance–occupancy relationships. For example, taking these species differences into account will improve our assessment of the effects of specialist and generalist species on abundance–occupancy relationships [5,44] given that specialist species generally have narrower environmental niches and smaller geographic ranges than generalist species [45,46].

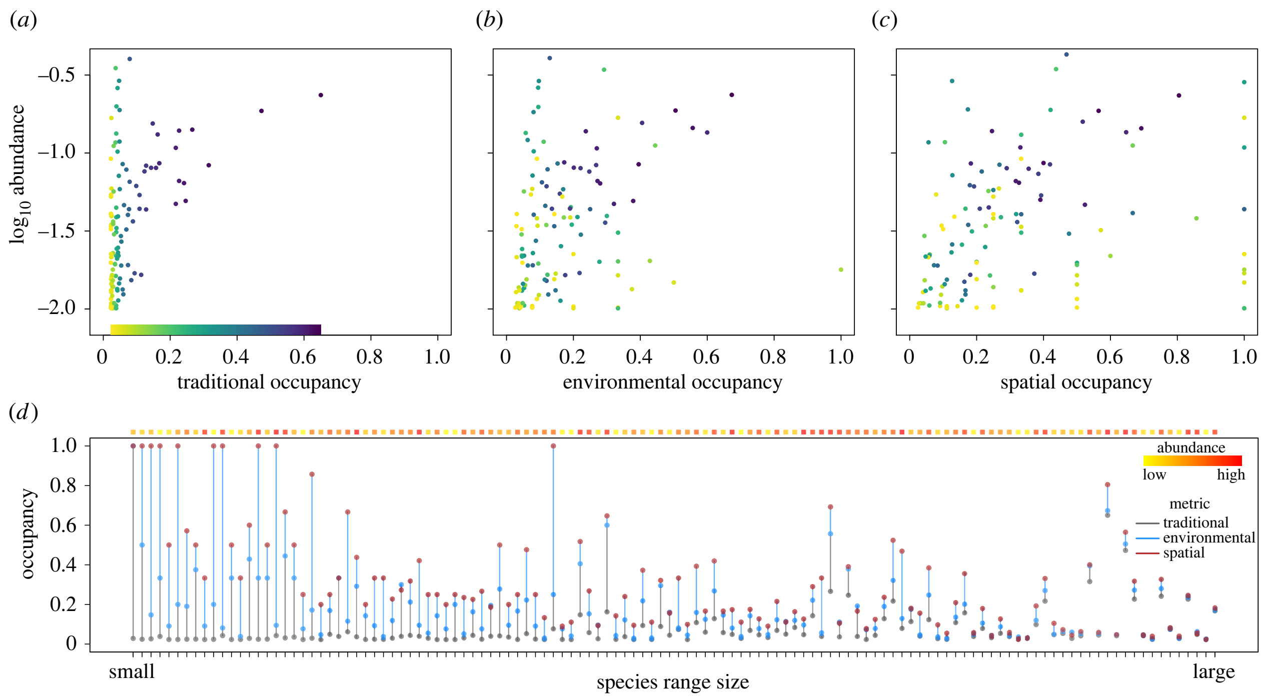

Figure 2. Relationships between $\log_{10}$ species abundance and traditional (*a*), environmental (*b*) and spatial (*c*) occupancies. Points are coloured based on the traditional occupancy estimation in the three panels. Panel (*d*) shows how species with small geographic ranges have their occupancies more strongly underestimated (i.e. traditional occupancy is substantially smaller than environmental or spatial occupancies) than species with larger geographic ranges. These differences in occupancy estimates were independent of abundance given the lack of a clear relationship between species abundance (shown in the squared symbols) and differences in the species occupancy estimates.

The positive relationship between species environmental niche and geographic range size [27,28] suggests that both factors are intrinsically related and are important to determine species occurrences. Thus, using knowledge on the species geographic range and realized environmental niche provide biological realistic ways to estimate occupancy given that environmental suitability and geographical accessibility are needed for a species to occur at a location [34,37]. In general, we show that species with small geographic ranges are the most affected when occupancy is estimated traditionally as several sites that are unsuitable for the species occurrence are considered to estimate their occupancy. This result suggests that attempts to predict species abundance from occupancy patterns [47] should be done carefully as some species occupancy might be underestimated when occupancy is estimated traditionally.

We show that estimating species occupancy considering all sampled sites directly affects the assessment of abundance–occupancy relationships. This assumption ignores the fact that species have different spatial and environmental constraints that can prevent them from occupying a given site. This can particularly affect the assessment of macroecological patterns at large spatial scales where species occurring in an assemblage might show high variation in terms of geographic ranges and environmental niches. This could explain differences in abundance–occupancy relationships observed for different taxa when these relationships are evaluated over broad spatial scales [4]. Thus, a more realistic description of species occupancy patterns will be obtained when species differences are considered during occupancy estimation, and this will also lead to a refined assessment of abundance–occupancy relationships.

Data accessibility. R code and data to reproduce the analyses are available on figshare at https://doi.org/10.6084/m9.figshare.19323644 [41].

Authors' contributions. C.T.C.: conceptualization, data curation, formal analysis, visualization, writing—original draft, writing—review and editing; L.A.H.: conceptualization, data curation, formal analysis, visualization, writing—original draft, writing—review and editing; T.D.: conceptualization, data curation, formal analysis, visualization, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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