

# Weak but consistent abundance–occupancy relationships across taxa, space and time

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## Abstract

**Aim:** Abundance–occupancy relationships posit that more locally abundant species occupy more sites than less abundant species. Although widely supported, the occurrence and detection of abundance–occupancy relationships is sensitive to sampling and detection processes. Data from large-scale standardized sampling efforts are key to address abundance–occupancy relationships. We aimed to use such a dataset to evaluate the occurrence of abundance–occupancy relationships across different spatial grains and over time for aquatic and terrestrial taxa.

**Location:** USA.

**Time period:** 2014–2019.

**Major taxa studied:** Birds, mammals, beetles, ticks, fishes, macroinvertebrates and zooplankton.

**Methods:** Species abundance and occupancy data were obtained from the National Ecological Observatory Network (NEON). Species mean abundance and occupancy (fraction of sampled locations that were occupied) were estimated for three different spatial grains (i.e., plot, site and domain) for all years sampled. Linear models were used to explore the consistency of interspecific abundance–occupancy relationships. The slope coefficients of these models were related to temporal and spatial variables and to species richness while controlling for taxa in a linear mixed-effects model (LMM) framework. **Results:** We found evidence for positive abundance–occupancy relationships across the three spatial grains and over time for all taxa we studied. However, our linear models had low explanatory power, suggesting that relationships, although general, were weak. Abundance–occupancy relationships were slightly stronger at the smallest spatial grain than at the largest spatial grain, but showed no detectable change over time for any taxa. Finally, species richness was not associated with the strength of these relationships.

**Main conclusions:** Together, our results suggest that positive interspecific abundance–occupancy relationships are fairly general but are not capable of explaining substantial variation in spatial patterns of abundance, and that other factors, such as species traits and niche, are also likely to influence these relationships.

## KEYWORDS

abundance–occupancy, aquatic, macroecology, range size, terrestrial

## 1 | INTRODUCTION

Abundance–occupancy relationships, which posit that more locally abundant species are also more widespread, are a widely studied phenomenon in ecology (Gaston, 1999; Gaston et al., 2000). Positive abundance–occupancy relationships can arise from biological mechanisms or sampling artefacts. For example, the resource availability hypothesis predicts that if a resource is widespread and is also more locally abundant, the species that use this resource will achieve higher occupancy and abundance (Borregaard & Rahbek, 2010; Gaston et al., 1997). Additionally, if species with broader niches are able to tolerate more different environmental conditions and use variable resources, they will also achieve higher abundance and occupancy (Brown et al., 1995; Gaston et al., 1997). The continued dispersal of individuals between occupied patches could also prevent species abundances and occupancies from decreasing and lead to a positive correlation between them (Gaston et al., 2000; Gonzalez et al., 1998). In addition to explaining how species attain high abundance and occupancy, these biological mechanisms also explain why species have low abundance and occupancy, which also contribute to positive abundance–occupancy relationships. On the contrary, if species with low abundance are less likely to be sampled, then their occupancy would be underestimated, contributing to a positive relationship (Bock & Ricklefs, 1983; Borregaard & Rahbek, 2010). In this case, a sampling artefact, and not a biological mechanism, would be leading to a positive abundance–occupancy relationship. Although positive abundance–occupancy relationships are widely documented (Gaston et al., 1998; Miranda & Killgore, 2019; Verberk et al., 2010), null (Harcourt et al., 2005; Webb et al., 2007) or even negative patterns (Ferenc et al., 2016; Komonen et al., 2009; Päivinen et al., 2005) have also been reported. Thus, although abundance–occupancy relationships are thought to be one of the most general patterns in ecology (Gaston, 1996), these relationships probably vary across taxa and environments (Holt et al., 2002). Understanding how and why the correlation between species' spatial distribution and abundance varies could provide insights into how species traits influence large-scale patterns (Webb et al., 2009), inform species distribution models (Koshkina et al., 2017) and allow the estimation of species abundance from presence–absence data (Tovo et al., 2019). In addition, it could also be used to forecast changes in species abundance with changes in occupancy (Hanski, 1982), which has direct implications for species conservation efforts.

An important issue when analysing abundance–occupancy relationships is the potential sensitivity to sampling protocols (McGeoch & Gaston, 2002; Steenweg et al., 2018). Abundance–occupancy relationships are sensitive not only to sample number and sampling intensity (McGeoch & Gaston, 2002), but also to the duration of the survey being carried (Dallas et al., 2019; Steenweg et al., 2018) and to the spatial grain size of the analyses (He & Gaston, 2000; Hui & McGeoch, 2007; Steenweg et al., 2018). All these factors can affect the detectability and the strength of these relationships. For example, sample number and sampling intensity affect the number of rare species observed in a study (McGeoch & Gaston, 2002), and it has been suggested that positive abundance–occupancy relationships

are more easily found when rare species are not sampled in a community (Komonen et al., 2009). This suggests a link between the occurrence of abundance–occupancy relationships and species richness, whereby positive abundance–occupancy relationships would be more likely to be found when fewer species are sampled in a community. In contrast, the effect of spatial grain on abundance–occupancy relationships is inconsistent. Some studies have found that abundance–occupancy relationships tend to be consistent across different spatial grains (Gaston & Lawton, 1990b; Steenweg et al., 2018), whereas others have shown that larger spatial grains could lead to more curved relationships (He & Gaston, 2000) or to the weakening, and even reversal, of positive abundance–occupancy patterns (Cowley et al., 2001). As the spatial grain increases, species occupancy estimations tend to be higher (McGeoch & Gaston, 2002), which leads to a mismatch between species abundance and occupancy that affects the form of these relationships.

Species abundances and distributions change over time (Fuller et al., 1995; Holt, 2003; Lloret et al., 2015; Taper et al., 1995), which could lead to variation in abundance–occupancy relationships for a given taxon dependent only on the timing of sampling. This temporal aspect of abundance–occupancy relationships is less understood, and there is a lack of consensus regarding whether abundance–occupancy relationships are temporally stable or not (Manne & Veit, 2020). Some studies found consistent positive abundance–occupancy relationships across time (Blackburn et al., 1998; Dallas et al., 2019; Suhonen & Jokimäki, 2019; Zuckerberg et al., 2009), whereas others showed a decrease in the strength of abundance–occupancy relationships over time (Fisher & Frank, 2004; Frisk et al., 2011; Webb et al., 2007). Such changes in abundance–occupancy relationships have been linked to human impacts on habitat (Manne & Veit, 2020) that would affect resource availability. Moreover, the temporal sampling scale (i.e., weeks, months or years) used in a study can also affect the detectability and strength of temporal abundance–occupancy relationships (Dallas et al., 2019; Steenweg et al., 2018). One potential cause of this variation is seasonally fluctuating populations. In this case, abundance–occupancy relationships tend to be stronger at finer temporal sampling scales (Dallas et al., 2019). Furthermore, stronger positive abundance–occupancy relationships are found in surveys that last longer because species occupancy is more precisely estimated (Steenweg et al., 2018).

Given that spatial and temporal sampling processes and decisions can influence abundance–occupancy relationships fundamentally, data from standardized and temporally resolved sampling are essential to gauging support for this macroecological relationship. The National Ecological Observatory Network (NEON) dataset is ideal for assessing the occurrence of abundance–occupancy relationships across taxa because standardized occurrence and abundance data are collected continually for several taxonomic groups.

In the present study, we evaluated the occurrence of interspecific abundance–occupancy relationships across seven different taxa. Among the seven taxa we studied, consistent findings of a positive relationship have been described for birds, mammals (Blackburn et al., 1997; Gaston et al., 1998; Roney et al., 2015; Suhonen &

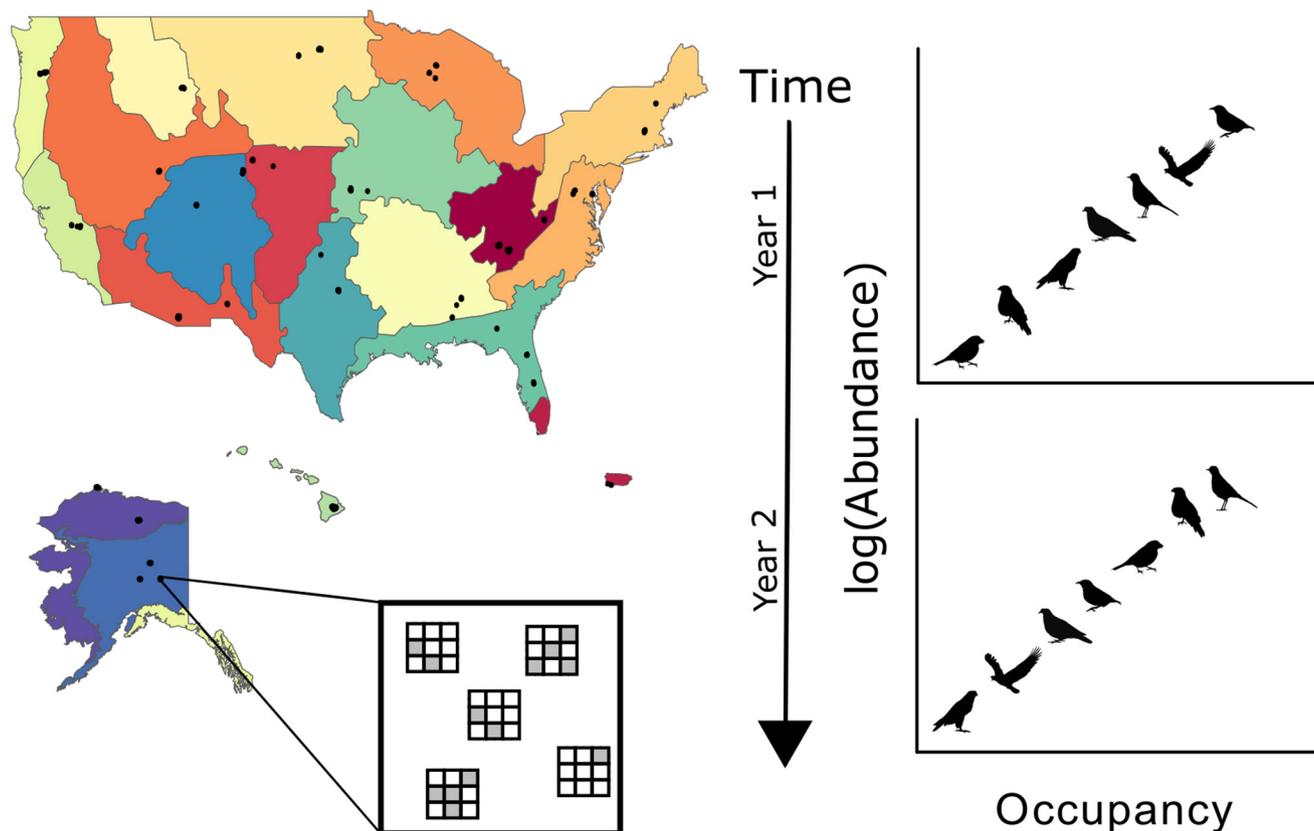
Jokimäki, 2019) and beetles (Gutiérrez & Menéndez, 1997; Kotze et al., 2003; Niemelä & Spence, 1994), suggesting that this positive pattern is prevalent within these groups. However, positive relationships were also found for macroinvertebrates (Foggo et al., 2003; Verberk et al., 2010), zooplankton (O'Brien et al., 2004) and parasites (Barger & Esch, 2002; Jenkins & Owens, 2011; Thielges et al., 2013), but the literature is more limited for these groups and we cannot make claims regarding the generality or consistency of these relationships. Furthermore, fishes show inconsistent patterns, whereby positive (Faulks et al., 2015; Miranda & Killgore, 2019), negative (Roney et al., 2015) and even no relationship (Gaston & Lawton, 1990a; Pyron, 1999) between abundance and occupancy have been described for them. We also evaluated whether these abundance–occupancy relationships were constant across three different spatial grains and over time. We found that the abundance of species was positively correlated with occupancy at the interspecific level for birds, mammals, macroinvertebrates, zooplankton, beetles and fishes. In contrast, ticks showed a less consistent positive relationship between abundance and occupancy. Additionally, our results suggest that spatial grain might affect the strength of abundance–occupancy relationships, although we only showed that plots (i.e., the finest spatial grain) had the strongest relationships, but no difference was found between sites and domains. Abundance–occupancy relationships

tended to be consistent across time, and species richness in a year was not associated with the strength of the relationships. Together, this demonstrates that interspecific abundance–occupancy relationships might be common, but are generally weak, suggesting that other processes (e.g., competition, dispersal limitation and parasitism) might constrain species abundance and occupancy.

## 2 | METHODS

### 2.1 | Species abundance and occupancy data

We used the NEON dataset spanning 2014–2019, which was obtained using the `NEONUTILITIES` R package (Lunch et al., 2021). The NEON was designed to collect and report standardized data on species occurrence and density across 47 terrestrial (Kao et al., 2012; Thorpe et al., 2016) and 34 aquatic (Goodman et al., 2015; Metzger et al., 2019) sites spread over 20 ecoclimatic domains across the USA (Figure 1). Terrestrial sites size varies from 5 to 215 km<sup>2</sup>, where data are collected for seven taxa (Kao et al., 2012; Thorpe et al., 2016), whereas aquatic sites are generally sampled in 1-km-long transects for five taxa (McDowell, 2015). Sampling (i.e., plot placement) is done in NEON sites with the goal of covering most of the habitat types



**FIGURE 1** Species were sampled at 81 aquatic and terrestrial sites (black points on map) across 20 ecoclimatic domains (coloured polygons on map), where each site several sampled plots (grids in the zoomed plot in Alaska). With sites being sampled every year, we obtained annual estimations of species (bird icons in the graph) abundance and occupancy, allowing assessment of the interspecific abundance–occupancy relationship for a given year and over time

present in the sites. Plot sizes are variable between taxa (for details for each taxon, see Supporting Information Methods), but are usually larger for terrestrial species (e.g.,  $3 \times 3$  grids, where each point in the grid is separated by  $\geq 250$  m for birds) than for aquatic species (e.g., up to ten non-overlapping plots of 80–120 m reaches for fishes). Thus, although individuals probably disperse between plots in a site, migration between sites, and especially domains, is likely to be limited given the long distance between most sites (i.e., mean pairwise distance of 2,119 km between sites). Among the terrestrial taxa, we obtained data for breeding landbirds (defined as smaller birds that are mostly non-aquatic), small mammals (mammals that are non-volant, nocturnal, forage mostly above ground and weigh between 5 and 500 g), ground beetles (comprising the Carabidae family) and ticks. Among the aquatic taxa, we obtained data for fishes, macroinvertebrates and zooplankton. For all taxa, we used data only for individuals identified to the species level. Overall, rarefaction curves show that the vast majority of sites were fairly well sampled (i.e., saturating rarefaction curves) for all taxa used in our analysis (Supporting Information Figures S1–S7). The Supporting Information (Table S1) shows lowest-highest abundance, occupancy and the number of plots, sites and domains sampled over the years for each taxon. Additionally, the Supporting Information (Figure S8) shows how species richness varied for each taxon across all sampled years.

## 2.2 | Estimation of abundance and occupancy

Species abundance and occupancy were estimated at the annual time-scale. Occupancy was defined as the fraction of plots/sites/domains where a species was found divided by the number of unique plots/sites/domains that were sampled in a specific year for that taxon. Species mean abundance was calculated according to the following steps. Initially, we estimated species abundance at the month temporal scale, whereby we counted all individuals that were sampled for a species in a specific plot for that specific month. Then, if the species was sampled more than once a year at a plot, we estimated the species mean abundance considering only the months in which it was sampled. Finally, we estimated the annual mean abundance of the species considering only the plots where the species occurred. The same approach was used to estimate species abundance for sites and domains, whereby species individuals were added up across plots at a site and across sites at a domain to obtain each respective abundance estimation. Although data collection is standardized across NEON sites, the number of plots in each site varies, as does the duration of time in a year when sampling is feasible, resulting in variation in sampling effort for the same taxon across different sites. We accounted for this by standardizing abundance measures by sampling effort (see Methods section in Supporting Information). Abundance data were  $\log_{10}$ -transformed, and both the  $\log_{10}$ -transformed abundance and the occupancy estimations were scaled (by subtracting the mean and dividing by the *SD*) for all taxa in order that the results for the different taxa could be compared more easily.

## 2.3 | How common are abundance–occupancy relationships?

The goal of the interspecific analysis was to evaluate the generality of the scaling between species occupancy and abundance across species. Abundance–occupancy relationships were quantified for each taxon and each year using linear models of mean species abundance as a function of occupancy, allowing us to estimate the slope of the interspecific abundance–occupancy relationship and estimate goodness-of-fit using measures, such as  $R^2$ . We were not able to evaluate the occurrence of abundance–occupancy relationships at the domain spatial grain for zooplankton for the year of 2014 because all species had the same occupancy estimation in that year.

## 2.4 | What affects abundance–occupancy relationships?

Given that evidence suggests that the strength of abundance–occupancy relationships might be affected by spatial grain (Cowley et al., 2001; He & Gaston, 2000) and that these strengths might change over time (Fisher & Frank, 2004; Webb et al., 2007), we also investigated the consistency of abundance–occupancy relationships at different spatial grains (plot/site/domain) and across sampling years (2014–2019). In addition, the number of species sampled in a community might also affect the strength of abundance–occupancy relationships (Komonen et al., 2009). To evaluate how spatial grain, time and species richness can affect the strength of abundance–occupancy relationships, we used a linear mixed-effect model, in which we used slope as the response variable and year (2014–2019), spatial grain (plot, site and domain) and taxa species richness at each year as fixed effects. We used taxa as a random effect to account for variation in these parameters across the taxa we studied.

## 3 | RESULTS

### 3.1 | How common are abundance–occupancy relationships?

Abundance and occupancy relationships were generally positive at the site spatial grain across years (mean  $\pm$  *SD*) for birds ( $0.29 \pm 0.07$ ), mammals ( $0.42 \pm 0.13$ ), fishes ( $0.45 \pm 0.07$ ), beetles ( $0.20 \pm 0.05$ ), macroinvertebrates ( $0.36 \pm 0.09$ ), ticks ( $0.63 \pm 0.16$ ) and zooplankton ( $0.33 \pm 0.09$ ). Both terrestrial and aquatic taxa showed similar patterns of abundance–occupancy relationships. Considering the site spatial grain, birds, macroinvertebrates, fishes, mammals and beetles followed the positive abundance–occupancy expectation in 100% of cases. Zooplankton and ticks also showed general positive abundance–occupancy relationships, although in some cases these relationships were not significant (Table 1; Supporting Information Figure S9). Similar results were also found for the plot and the domain spatial grains (Figure 2; Supporting Information Tables S2 and

S3), revealing that abundance–occupancy relationships were robust regarding spatial grain and sampling years.

### 3.2 | What affects abundance–occupancy relationships?

Although the occurrence of abundance–occupancy relationships tended to be robust across spatial grains, we found the strongest abundance–occupancy relationships for plot when compared with domain, but there was no differences between domain and site (Table 2; Supporting Information Figure S10). Likewise,  $R^2$  values show that the best fit of the data for abundance–occupancy relationships was found for plot. As spatial grain increased from plot to site and from site to domain,  $R^2$  values tended to be lower and less variable (Figure 3). The only clear exception to these patterns were for ticks, for which stronger relationships and a better fit of the data were found at the domain spatial grain. On the other hand, species richness did not affect the strength of the abundance–occupancy relationships. In addition, the strength of abundance–occupancy relationships was found to be fairly constant over time (Figure 2h; Table 2), suggesting that interannual variation did not appreciably influence the strength of abundance–occupancy relationships.

## 4 | DISCUSSION

Interspecific abundance–occupancy relationships were observed consistently across nearly all taxa and sampling years. In addition, spatial grain might have a potential effect on the strength of abundance–occupancy relationships, in that we found stronger relationships for plot (i.e., the finest spatial grain) when compared with site or domain grains, but we did not see a difference in the strength of these relationships between site and domain. Moreover, species richness did not affect the strength of these relationships. The low amount of explanatory power linking abundance and occupancy suggests that spatial patterns of abundance and occupancy might be subject to community processes (e.g., competition and predation), environmental drivers (e.g., temperature and precipitation

seasonality) or geographical barriers (e.g., dispersal limitation). Together, our results suggest that abundance–occupancy relationships are strikingly general, but that considering other spatial and ecological processes during the assessment of these relationships might also be important and will be likely to improve the explanatory power of the models and provide a more comprehensive understanding of the drivers of abundance–occupancy relationships.

The support we found for positive interspecific abundance–occupancy relationships across several taxa contributes to a growing body of evidence for similar positive relationships (Gaston, 1996; Gaston, Blackburn, & Lawton, 1998; Roney et al., 2015). The occurrence of positive abundance–occupancy relationships has been linked to incomplete sampling (Komonen et al., 2009), whereby geographically restricted but locally abundant species that could contribute to negative relationships would not be detected (Päivinen et al., 2005). Furthermore, it has been argued that positive abundance–occupancy relationships would be found when there is low sampling effort. In this case, positive relationships would be found only when a small proportion of the species found in a community are sampled (Komonen et al., 2009). The NEON data used here consisted of 81 total sites distributed across 20 different ecoclimatic domains in the USA, which were sampled multiple times each year, providing information on community dynamics across a wide geographical, environmental and temporal range. This standardized and geographically widespread sampling protocol present in the NEON data (Kao et al., 2012) addresses most sampling-related artefacts mentioned that might influence abundance–occupancy relationships. The representative sampling present in the NEON data coupled with the fact that positive abundance–occupancy relationships were found consistently for different taxa with varying levels of species richness and over time suggests that our results are not arising from sampling artefacts.

The finding of positive abundance–occupancy relationships across different spatial grains is consistent with previous studies that considered the role of space (Cowley et al., 2001; Gaston & Lawton, 1990b; Steenweg et al., 2018). However, previous studies have observed increased variability in abundance–occupancy relationships as a function of spatial grain (Steenweg et al., 2018), whereas we observed a difference in abundance–occupancy slope only between our two most extreme spatial grains (i.e., the plot and domain grains). It has been shown

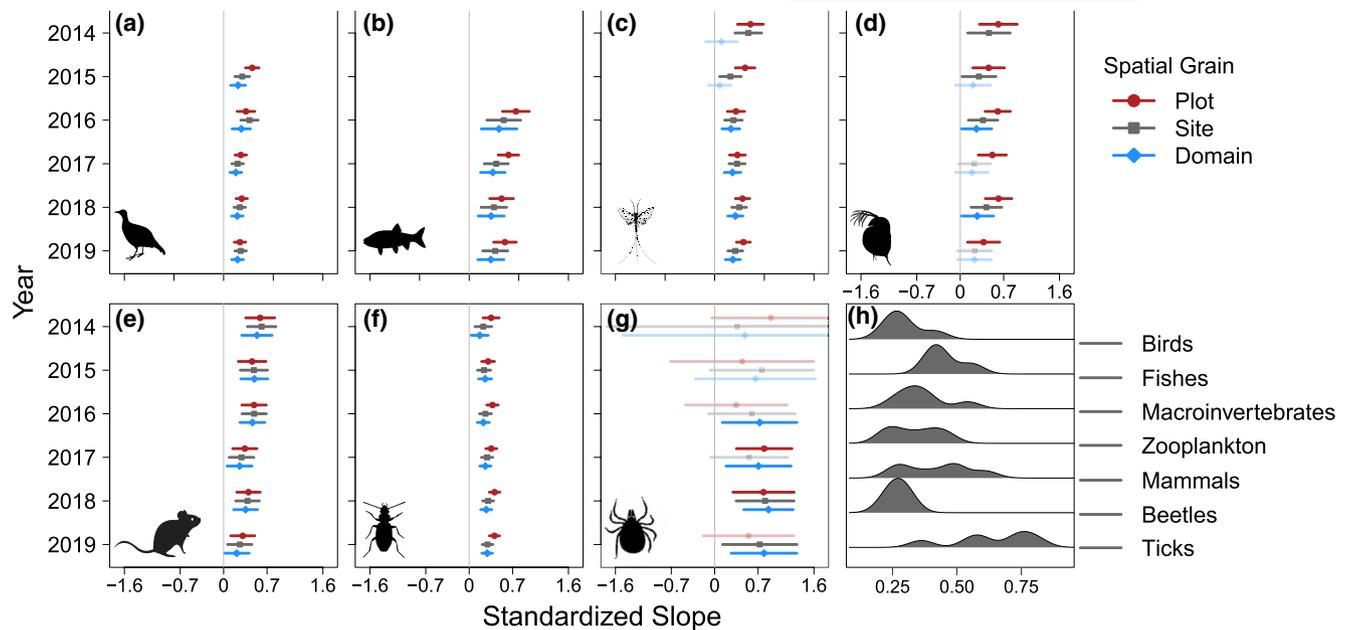
Taxa	2014	2015	2016	2017	2018	2019
Birds	–	.299***	.416***	.224***	.259***	.273***
Fishes	–	–	.557***	.436***	.399***	.420***
Macroinvertebrates	.542***	.253**	.302***	.360***	.394***	.331***
Zooplankton	.462*	.300*	.367**	.229	.421**	.232
Mammals	.611***	.487***	.491***	.287**	.384***	.260**
Beetles	.227**	.239***	.262***	.288***	.305***	.295***
Ticks	.361	.760	.599	.556	.812**	.725*

TABLE 1 Abundance–occupancy relationships (defined as slopes from linear models) and associated with each of the taxa and years, considering the site as the spatial grain

[Correction added on 18 March 2022, after first online publication: Table 1 has been corrected.]

Note: We find consistent positive relationships between abundance and occupancy over time for the majority of taxa.

\* $p < .05$ ; \*\* $p < .01$ ; \*\*\* $p < .001$ .



**FIGURE 2** Standardized slope of abundance–occupancy relationships for (a) birds, (b) fishes, (c) macroinvertebrates, (d) zooplankton, (e) mammals, (f) beetles and (g) ticks. Point shape delineates spatial grains. (h) Distribution of slopes for each taxon is shown for the site spatial grain [Correction added on 12 March 2022, after first online publication: Figure 2 has been updated.]

**TABLE 2** Fitted linear mixed-effects models exploring the influence of space, time and species richness on abundance–occupancy relationships

Fixed effects	Estimate	SE	d.f.	t	p-value
Plot	0.1288	0.0259	104	4.9653	<.001
Site	0.0471	0.0259	104	1.8174	.072
Year	−0.0012	0.0078	96.52	−0.1611	.872
Species richness	−0.0003	0.0001	26.77	−1.7044	.099

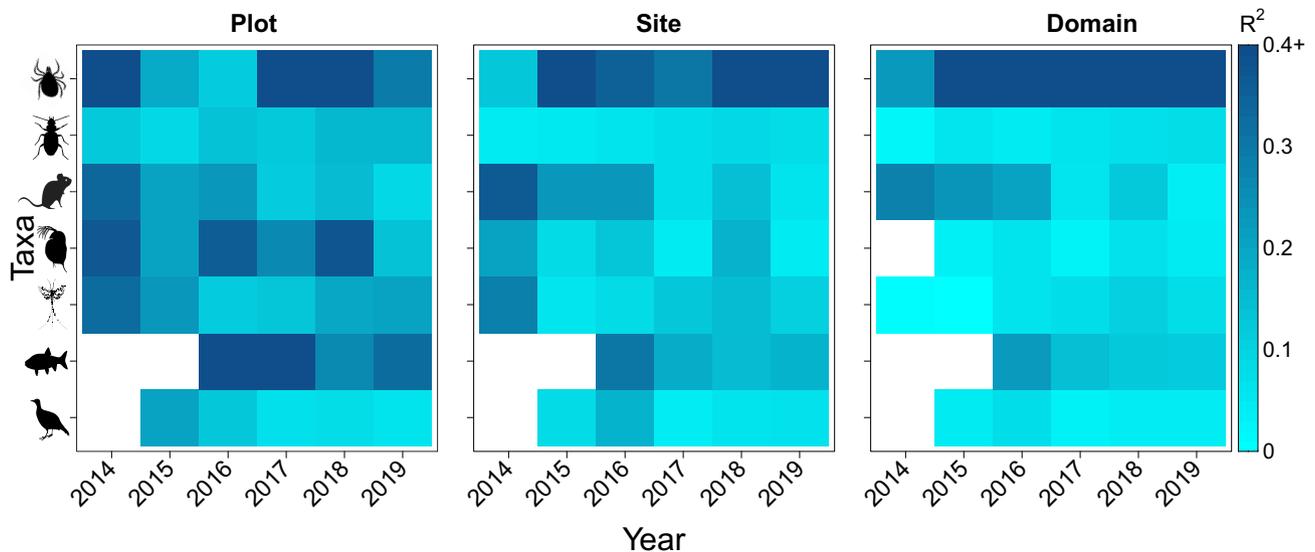
[Correction added on 18 March 2022, after first online publication: Table 2 has been corrected.]

Note: The first two rows show the negative effects of larger spatial grain on the strength of abundance–occupancy relationships. In this case, the domain spatial grain was used to compare with the plot and site grains. The third and fourth rows show the lack of effect of sampling year and species richness on the strength of abundance–occupancy relationships, respectively.

previously that random point processes could lead to the occurrence of positive abundance–occupancy relationships at small spatial grains (Wright, 1991), whereas others have failed to find a link between mean abundance and global range size (Sporbert et al., 2020). Here, we find that although these relationships become slightly weaker when comparing the most extreme spatial grains, they are still robust. This suggests that the drivers of abundance and occupancy are affecting these taxa in a similar manner across the different spatial grains we used. For example, environmental factors are important in affecting species occupancy at both large (Brändle & Brandl, 2001) and small (Frey et al., 2016) spatial grains. In contrast, species local mean abundance is influenced by resource availability (Curtis et al., 2015; Yamamoto et al., 2007) and biotic interactions (Schoener, 1983). Our results suggest that these factors are having similar effects on species abundances and occupancies at the different spatial grains at which we assessed these relationships, considering the spatial extent of our study.

Declines in the strength of abundance–occupancy relationships over time have been related to anthropogenic exploitation for fishes (Fisher & Frank, 2004) and to reduction in habitat

quality for birds (Webb et al., 2007), which would negatively affect species occupancy and abundance patterns. On the contrary, increases in resource availability have been suggested to be responsible for maintaining strong positive abundance–occupancy relationships over time (Zuckerberg et al., 2009). The stable positive abundance–occupancy relationships that we found over time for the taxa we studied could be because NEON sites are primarily located in non-disturbed areas, where anthropogenic impacts would be limited and habitat quality would probably be constant. In such case, species would be able to maintain relatively constant abundance and occupancy patterns over time across the sampled sites. Positive abundance–occupancy relationships could also be expected to arise from metapopulation dynamics (Hanski et al., 1993). In such cases, dispersal plays an important role in keeping species abundance high at different sites (Hanski, 1985, 1991). However, metapopulation dynamics play an important role at finer spatial scales, whereas at large spatial scales they have limited effects on abundance–occupancy relationships (Gaston et al., 2000; Lawton, 1993). Hence, although individuals could be



**FIGURE 3** Heatmaps showing  $R^2$  variation across years for ticks, beetles, mammals, zooplankton, macroinvertebrates, fishes and birds at plot, site and domain spatial grain. The  $R^2$  values are absent (i.e., white colour) for birds in 2014, fishes in 2014 and 2015 and for the domain spatial grain for zooplankton in 2014. Light blue colours represent small  $R^2$  values, whereas dark blue colours represent large  $R^2$  values [Correction added on 18 March 2022, after first online publication: Figure 3 has been updated.]

migrating between plots within a site, migration between sites or domains seems to be less plausible in our study. For example, the Western meadowlark (*Sturnella neglecta*) has an average home range of c. 0.13 km<sup>2</sup> (Bent, 1958), suggesting that migration between sites is unlikely even for birds in our study.

Studies that evaluated the occurrence of abundance–occupancy relationships over larger time spans have found contrasting results as to whether these relationships are consistent over time (Fisher & Frank, 2004; Manne & Veit, 2020; Webb et al., 2007; Zuckerberg et al., 2009). Although the NEON data we used are limited to a 6-year time span, the fact that these data were sampled consistently at such a large scale during these years provides strong evidence that species abundance and occupancy patterns are not changing over this relatively short period of time. Additional data that will be collected in the NEON sites during the forthcoming years will be valuable to assess whether abundance–occupancy relationships will remain constant or if long-term changes in abundance and occupancy patterns will affect these relationships. In addition to the time span, the temporal sampling scale (e.g., weekly, monthly or annual) used in a study could also affect the detection of temporal abundance–occupancy relationships (Dallas et al., 2019; Steenweg et al., 2018). Here, we binned our data annually so that we could compare results across taxa, because certain taxa are sampled less frequently (e.g., birds are sampled at most twice a year), and this would be difficult for comparing monthly estimations. In addition, abundance–occupancy relationships are usually weaker at the annual scale (Dallas et al., 2019), which suggests that the occurrence of this pattern at this temporal sampling scale is indicative that this relationship is not spurious for these taxa.

Overall, our findings show that positive abundance–occupancy relationships are common across different taxa and spatial grains and over time. However, like previous studies, much of the

variance in our models remains unexplained (Cowley et al., 2001; Gaston, 1996; Verberk et al., 2010). This unexplained variation is likely to be associated with species traits and niche characteristics (Verberk et al., 2010; Webb et al., 2017) and with community and spatial processes that affect species abundance and occupancy patterns that were not considered in our analyses. Nonetheless, we show that the strength of abundance–occupancy relationships might depend on the spatial grain used in the analysis, although this effect was seen only when comparing the results between plot and domain, but not when comparing the results between site and domain. Moreover, the temporal stability of abundance–occupancy relationships suggests that species are not going through short-term changes in their patterns of abundance and occupancy. Data that will be collected in the future will enable us to assess whether these patterns will remain stable or if changes in one of them (e.g., abundance) will also lead to changes in the other (e.g., occupancy).

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#### CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

#### DATA AVAILABILITY STATEMENT

R code and data used in this study are available on figshare at: <https://doi.org/10.6084/m9.figshare.18786161>. NEON data can also be accessed at: <https://data.neonscience.org>. Citation for each taxonomic group dataset can be found in the Supporting Information.

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## BIOSKETCHES

We are a group of ecologists who are interested in large-scale patterns of species diversity and disease dynamics.

## SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

[Correction added on 18 March 2022, after first online publication: Supporting information figures S6, S8, S9 and S10 and values in Tables S1, S2 and S3 have been updated.]

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