



# Temporal sampling and abundance measurement influences support for occupancy–abundance relationships

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## Abstract

**Aim:** Species occupying a greater fraction of habitat patches tend to also be more locally abundant. The relationship between the fraction of occupied habitat patches and mean abundance (i.e. occupancy–abundance relationships) are a common macroecological observation, though they are far from ubiquitous. The aim of this work was to examine occupancy–abundance relationships in a large set of Finnish moth species, and determine the sensitivity of the strength and sign of these relationships to abundance estimation approach and temporal sampling scale.

**Location:** Finland.

**Taxa:** Lepidoptera.

**Methods:** Using data on Finnish moth communities sampled over a period of 20 years, we examine species occupancy (fraction of sampled patches that were occupied) and mean abundance over time. We examine both intraspecific—the scaling of occupancy and local mean abundance for a single species—and interspecific—the scaling of occupancy and total mean abundance combining occupancy–abundance relationships for all species.

**Results:** We found evidence for both intraspecific and interspecific occupancy–abundance relationships, dependent on the temporal sampling scale and how species abundance was estimated. The effect of seasonality on moth population dynamics was evident in the occupancy–abundance relationships, where finer temporal scales lead to ‘stronger’ relationships.

**Main conclusions:** Together, we provide support for both intraspecific and interspecific occupancy–abundance relationships for a large set of Finnish moth species, but demonstrate sensitivity of support as a function of temporal sampling scale and abundance measurement.

## KEYWORDS

abundance, Finland, geographical range, moth populations, occupancy, species niche

## 1 | INTRODUCTION

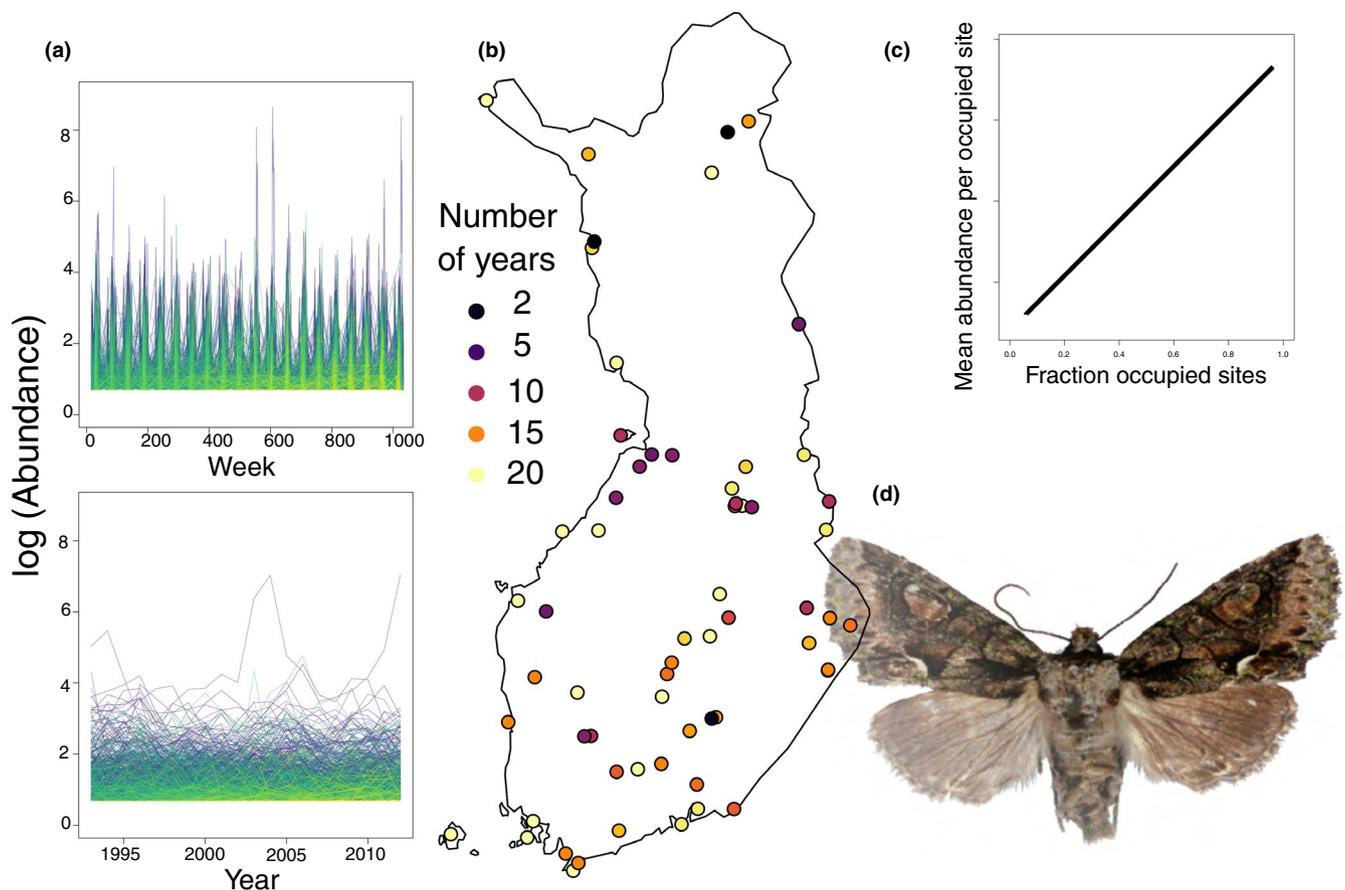
Species that occupy numerous sites are predicted to be more locally abundant on average (Brown, Mehlman, & Stevens, 1995). This prediction is at the centre of *occupancy–abundance* relationships (also

referred to as *abundance–occupancy* relationships), which posit that the fraction of sites occupied by a given species is positively related to average abundance (Blackburn, Cassey, & Gaston, 2006; Gaston et al., 2000; Gaston, Blackburn, & Lawton, 1998; Hanski, 1982; He & Gaston, 2003; Steenweg, Hebblewhite, Whittington, Lukacs, &

McKelvey, 2018). Positive occupancy–abundance relationships are well documented (Blackburn et al., 2006; Gaston et al., 2000, 1998; Webb, Freckleton, & Gaston, 2012), though numerous studies have failed to detect positive relationships between occupancy and abundance (Gaston & Curnutt, 1998; Symonds & Johnson, 2006; Webb, Noble, & Freckleton, 2007), with some even finding negative relationships (Donald & Fuller, 1998; Komonen, Päävinen, & Kotiaho, 2009). Several putative mechanisms exist to explain occupancy–abundance relationships, including synchronous range expansion and population growth, temporal variation in resource availability (Webb, Heinsohn, Sutherland, Stojanovic, & Terauds, 2019) and dispersal limitation (Gaston et al., 2000). Assuming a direct link between occupancy and abundance suggests that habitat fragmentation or loss could reduce species average abundance, creating what has been described as ‘double jeopardy’ (Lawton, 1993). This occurs because smaller populations are more prone to stochastic extinction, which serves to further reduce occupancy, suggesting that the causal relationship between species occupancy and abundance is through effects of changes in abundance on occupancy (Gaston et al., 2000). Regardless of directionality, understanding occupancy–abundance relationships has clear conservation implications (Gaston et al., 1998; Hui, Boonzaaier, & Boyero, 2012; MacKenzie & Nichols,

2004), as land use change may alter species occupancy, which may in turn influence species abundance in occupied patches.

Occupancy–abundance relationships may be examined either in terms of temporal (or occasionally spatial) dynamics within species (intraspecific) or across species (interspecific). Intraspecific occupancy–abundance relationships examine populations of a single species across a landscape, relating the fraction of sites the species occupied at a given time to species mean abundance over all occupied sites (Gaston, 1999). Meanwhile, interspecific occupancy–abundance relationships examine the scaling between species mean abundance and fraction of sites the species occupies (i.e. each species is a single point). Despite the differences between intraspecific and interspecific variants of the occupancy–abundance relationship, the overall goal is to relate aspects of species spatial distributions to species abundance, with the goal of documenting biogeographical and macroecological relationships and providing insight into the spatial distribution of species abundance. Furthermore, species life-history traits or niche requirements can provide insight into divergence from interspecific scaling relationships and the slope of intraspecific occupancy–abundance relationships (Verberk, Velde, & Esselink, 2010; Webb, Barry, & McClain, 2017; Webb, Tyler, & Somerfield, 2009). For instance Roney, Kuparinen, and Hutchings (2015) found



**FIGURE 1** Example time series data demonstrating seasonal fluctuations in abundance per species (each species is a different coloured line; a). The spatial distribution of sampling sites in Finland, where more yellow colours correspond to more well sampled sites (b). The hypothesized relationship between the fraction of sites a species is found and species mean abundance from sites where it was found (c). A representative Finnish moth species, *Allophyes oxyacanthae* (d; photo credit to Reima Leinonen)

variation in occupancy–abundance relationships as a function of taxonomic group when comparing distant groups. However, other efforts have failed to detect an influence of species traits on residual variation in occupancy–abundance relationships for British mammal and bird species (Holt & Gaston, 2003). These discrepancies may be a result of species temporal dynamics, data quality, and issues related to the estimation of species abundance (Holt, Gaston, & He, 2002; Steenweg et al., 2018; Wilson, 2008).

First, it is important to consider the influence of temporal and spatial sampling scales on resulting occupancy–abundance relationships. Recently, Steenweg et al. (2018) found that the curvature in occupancy–abundance relationships may depend on spatial grain and sampling design. In addition to these spatial sampling considerations, the dynamics of many species fluctuate as a result of changing seasonal conditions. Even if species have consistent year to year occupancy and abundance values, ignoring seasonal variation would likely generate a positive intraspecific occupancy–abundance relationship. This is a result of species life history resulting in relatively small populations during some parts of the season (often the beginning of spring), with pronounced seasonal dynamics (see Figure 1a). That is, occupancy–abundance relationships may be a natural outcome of species seasonal fluctuations, which is not of interest, as it is an artefact of the seasonal demography of the species, and not a true scaling relationship that can provide insight into the spatial distribution of abundance. This effect would be most pronounced given a lack of strong synchronous species emergence across habitat patches, and, in concert, create a situation where reduced species abundance and occupancy are a function of season and not a property of the species. Identifying the most appropriate sampling frequency for a species of interest is therefore important to gauge support for occupancy–abundance relationships at characteristic time-scales.

Second, the measure of abundance used to assess occupancy–abundance relationships varies among studies (discussed in Wilson[, 2008, 2011]). Strictly speaking, measures of abundance used are oftentimes measures of species density, as sampling is non-exhaustive and consist of the number of individuals in a specified area. Regardless, occupancy–abundance relationships may be assessed by quantifying abundance using abundance count data (e.g. Gaston et al., 1998) or using relative abundance measures (e.g. Zuckerberg, Porter, & Corwin[, 2009]). While the use of relative abundance is fairly rare, the difference between abundance and relative abundance may provide insight into the importance of site-level properties or community composition on species occupancy–abundance patterns. Specifically, the use of relative abundance integrates information on the existing community at each site, and could serve to highlight the effects of site-level variation in resource availability, the effects of interspecific competition, or the non-random spatial distribution of species. If evidence exists for occupancy relationships for abundance and relative abundance, it would suggest that more widespread species are both more locally abundant and more numerically dominant members of communities. Just as the use of local and global mean abundance—dealing with the issue of including

zero abundance values (Wilson, 2008)—the use of abundance or relative abundance is likely to strongly affect the resulting occupancy–abundance relationship.

Here, we utilize long-term survey data on moth communities in Finland to examine occupancy–abundance relationships. Apart from examining the existence of scaling between species occupancy and abundance, we use these data as a case study to explore the effect of abundance measure used and temporal scale considered on resulting support for occupancy–abundance relationships. These data are especially useful to address the issues of temporal sampling scale (i.e. frequency) and abundance estimation, as moth populations were extensively sampled, were strongly seasonal, and sampling was performed for entire communities of moths instead of single species. Moth communities were species-rich ( $n = 731$  species), providing extensive data with which to examine both intraspecific and interspecific occupancy–abundance relationships. Specifically, we examine, both within (intraspecific) and among (interspecific) species, (a) the scaling relationships between species occupancy and abundance, (b) the effect of temporal sampling scale on occupancy–abundance relationships and (c) the evidence for occupancy–abundance relationships when considering species relative abundance. We find general support for interspecific and intraspecific occupancy–abundance relationships, finding the strongest positive intraspecific occupancy–abundance relationships on average for the weekly time-scale. However, this temporal scale incorporates seasonal fluctuations, when species demographics are far from a steady state, violating core assumptions underlying common interpretations of occupancy–abundance patterns, while purporting to provide support. Furthermore, we find generally weak or opposite patterns for occupancy–relative abundance relationships. Overall, our findings suggest that temporal sampling scale (i.e. frequency) and the abundance measure used strongly influence occupancy–abundance relationships for seasonally fluctuating species.

## 2 | MATERIALS AND METHODS

### 2.1 | Moth data

Data on moth species abundances were gathered as part of the Finnish national moth monitoring scheme (Nocturna) (for an overview, see Leinonen, Pöyry, Söderman, & Tuominen-Roto[, 2016]). In the scheme, moths are observed by using light traps of the 'Jalas' model that are equipped with 160W mixed light or 125W Mercury (Hg) vapour bulbs (Jalas, 1960; Söderman, 1994). Traps were run every night from the early spring to late autumn, typically between April and October. Traps were usually emptied weekly and the moth specimens were identified and recorded by voluntary observers. Quality control of the data and cross-checking of moth identifications was carried out by the Finnish Environment Institute (SYKE). During the period 1993–2012, a total of 208 trap sites were included in the monitoring network. Of these sites, 65 traps with the least temporal gaps were selected for data extraction (Figure 1). While sampling sites tend to be aggregated in southern Finland, we found

no change in our results when northern sites were systematically removed from the analyses (see Figure S8). These data covered all species of Macroheterocera (i.e. macro-moths) and the families Hepialidae and Cossidae, and constitute observations of over 4.12 million individual moths belonging to 731 species.

Moth population dynamics are strongly seasonal (Figure 1), and these seasonal dynamics could lead to strong occupancy–abundance relationships that are simple artefacts of population dynamic processes. Moth species in Finland usually have one generation per season, and flight seasons vary between species. This creates a clear seasonal abundance peak between late June and late July in Finland. In order to demonstrate this effect, we examined the influence of seasonal fluctuations in moth demography on the slope of the relationship between mean local abundance and the fraction of occupied sites across a rolling window. To do this, we used a 12 sampling period window—at the weekly scale here, but some sites were not sampled every week—which moved forward one sampling period at each step, resulting in a time series of occupancy–abundance slopes that capture seasonal variation in demographic and phenological processes.

## 2.2 | Intraspecific occupancy–abundance relationships

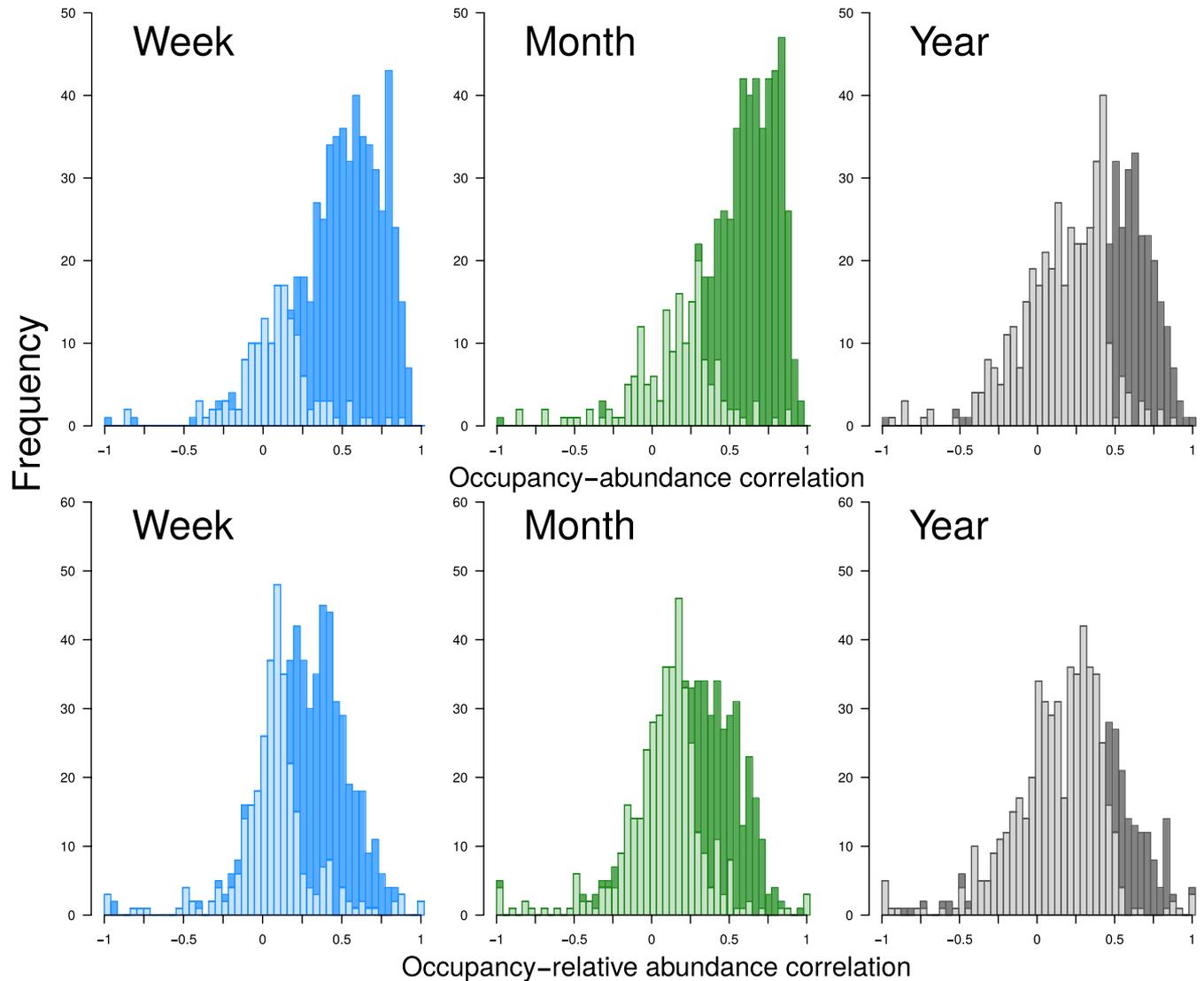
To address the potential confounding influence of temporal sampling scale and seasonally fluctuating population dynamics on intraspecific occupancy–abundance relationships, we examined three levels of temporal sampling scales; week, month and year. Occupancy was defined as the fraction of occupied sites given the number of unique sites that were surveyed at the temporal scale considered (i.e. week, month or year), whereas abundance was quantified as the number of individuals sampled during the standardized sampling duration (perhaps more akin to a measure of *density*). Following previous studies (Webb et al., 2012), we did not consider zero values of abundance in our calculation of mean abundance. Species that occurred in fewer than two sampling periods or with fewer than two unique values of occupancy or abundance were removed from the analysis. The number of moth species for which enough data were available to calculate correlation coefficients between abundance and occupancy differed slightly at the scales of week ( $n = 617$ ), month ( $n = 617$ ) and year ( $n = 616$ ). Sampling at week and month scales will still show seasonal fluctuations in population abundance with time (Figure 1), whereas using the entire year as a sampling period removes these abundance fluctuations entirely (Figure 1). We examined occupancy–abundance relationships at each of these temporal scales, and related the strength of resulting relationships to one another, providing evidence for the effect of temporal scale on distribution–abundance relationships.

Relationships between species occupancy and abundance address the link between distribution and abundance for a single species. However, observing different patterns for community-weighted abundance (e.g. relative abundance) could provide information on species dominance in communities as related to

occupancy. In fact, some researchers have previously used relative abundance to investigate occupancy–abundance relationships (e.g. Zuckerberg et al., 2009). Here, we calculate species relative abundance at a given site for each temporal sampling scale—week ( $n = 661$ ), month ( $n = 658$ ) and year ( $n = 655$ )—considered by dividing species abundance by the total abundance of the community observed at each site during each sampling period. The number of species examined for occupancy–relative abundance relationships was greater than those examined for occupancy–abundance relationships as a result of relative abundance calculation increasing the variance in abundance measures. That is correlation coefficients could not be calculated if no variation in abundance was present. Intraspecific occupancy–abundance relationships were quantified using the Spearman's rank correlation between estimated abundance (or relative abundance) and species occupancy, which was defined as the fraction of sites in which a given species was found out of the sampled sites. Spearman's  $\rho$  statistic is better suited for nonlinear correlations than Pearson's linear correlation. However, the formation of tied ranks could influence correlation estimates, which would be an issue when variance in occupancy values is small (e.g. if species occur in all sites during multiple sampling points).

## 2.3 | Interspecific occupancy–abundance relationships

We explored the influence of temporal dynamics on interspecific occupancy–abundance relationships by considering species abundance and distribution across the entire sampling period ( $n = 731$ ), and for each year separately ( $n = [526–613]$ ). This differs slightly from the goal of the intraspecific occupancy–abundance investigation, as fluctuating populations annually influence intraspecific relationships, whereas year to year variation could influence the strength of interspecific occupancy–abundance relationships. That is intraspecific relationships correlate the species occupancy in a given time period to mean abundance in that time window, whereas interspecific relationships look across species to examine the generality of scaling between annual species occupancy and abundance across species. This does not mean that temporal scale will not influence both intraspecific and interspecific occupancy–abundance relationships. To examine the effect of seasonality and temporal scale, we examine annual variation in interspecific occupancy–abundance slope, as previous studies have suggested that directional changes to biogeographical and macroecological relationships could indicate the effects of land use or climate change (Fisher, Frank, & Leggett, 2010). We further examine the influence of season on interspecific occupancy–abundance relationships in the Supplementary Materials. Lastly, we examined interspecific occupancy–abundance relationships when mean abundance was quantified as mean relative abundance for each species. Interspecific occupancy–abundance relationships were quantified using the Spearman's rank correlation, where each point represents the mean abundance and occupancy of an entire species.



**FIGURE 2** Frequency histograms of Spearman's rank correlation coefficients between moth species occupancy and abundance (top row) or relative abundance (bottom row) for each species. Intraspecific occupancy–abundance relationships were generally positive, but the temporal scale considered (week, month, year) influenced the strength of the relationship, with coarser—and more characteristic—temporal scales resulting in relationships closer to zero. When abundance was quantified as relative abundance, frequency distributions tended towards 0. Lighter colours indicate failure to detect a significant effect at  $\alpha = 0.05$

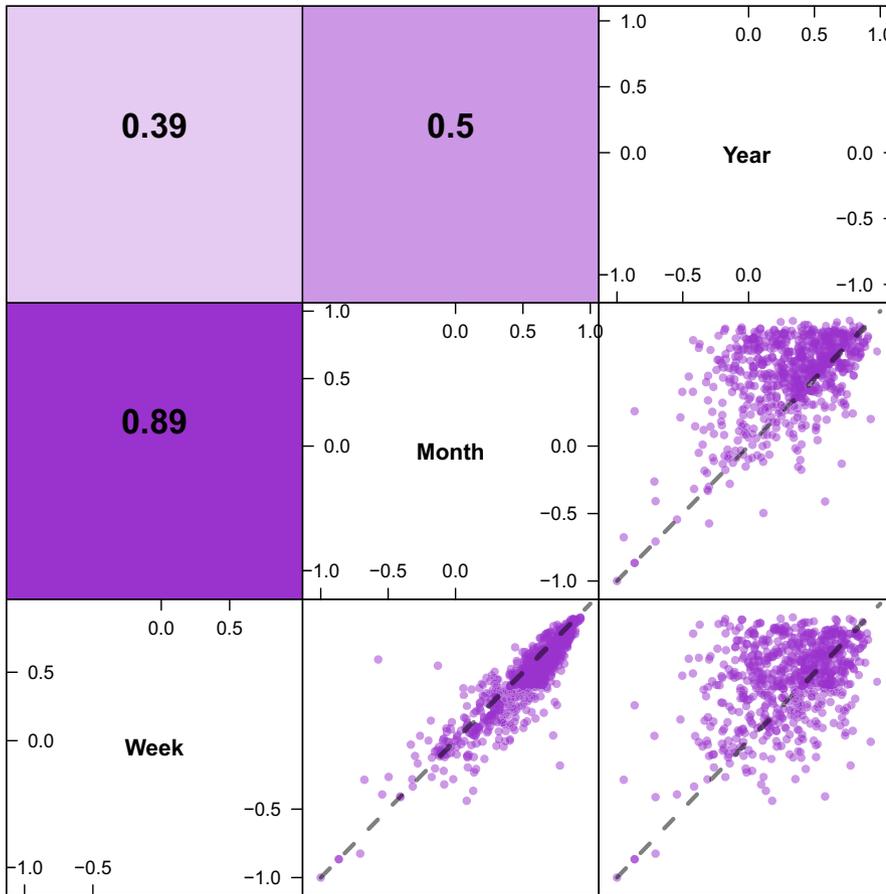
### 3 | RESULTS

#### 3.1 | Intraspecific occupancy–abundance relationships

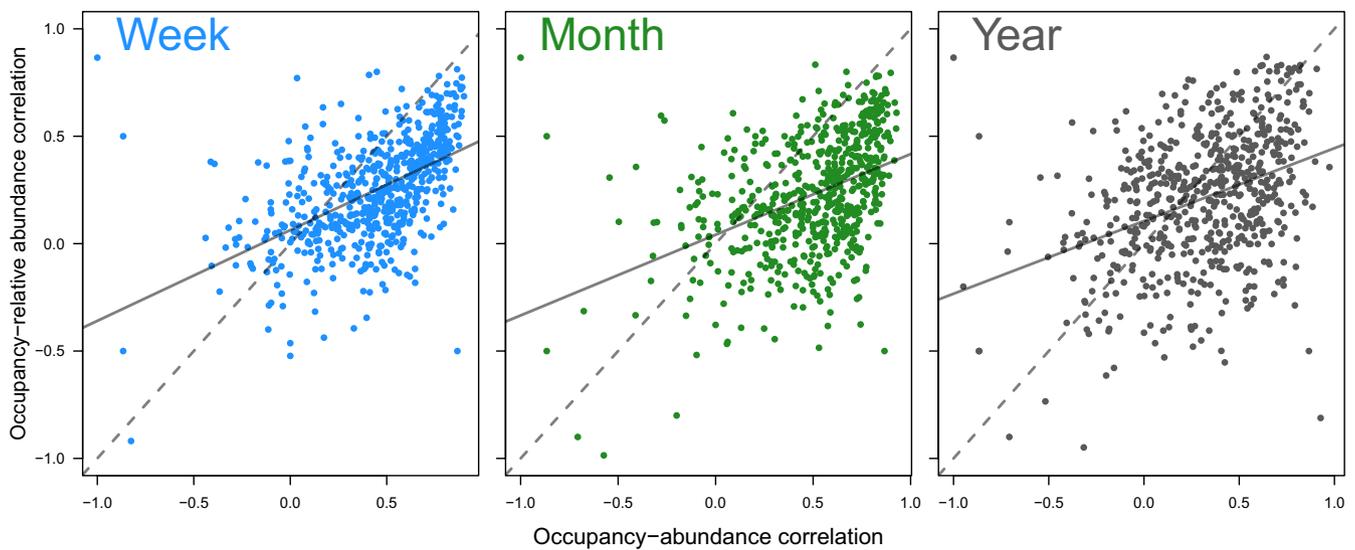
Positive intraspecific occupancy–abundance relationships, quantified using Spearman's rank correlation coefficient  $\rho$ , were detected at all three temporal scales considered; week ( $\bar{\rho} \pm SD = 0.42 \pm 0.33$ ), month ( $\bar{\rho} \pm SD = 0.49 \pm 0.33$ ) and year ( $\bar{\rho} \pm SD = 0.30 \pm 0.35$ ). However, the strength and the significance of correlation coefficients ( $\alpha = 0.05$ ) was influenced by sampling scale, where weekly and monthly time-scales resulted in 460 (out of 661) and 444 (out of 658) species with significantly positive occupancy–abundance relationships, whereas

the yearly time-scale resulted in 218 (out of 655) species with significant and positive relationships between species occupancy and abundance.

Interestingly, occupancy–abundance relationships were weakest at the annual time-scale, which is perhaps the most appropriate time-scale given the seasonality of moth population dynamics (Figure 2). The annual time-scale removes the influence of seasonality on moth population dynamics, which strongly influences occupancy and abundance patterns. This is clear when examining correlation strength between occupancy–abundance relationships measured at different temporal scales (Figure 3). While relationships measured at week and month temporal scales were fairly similar, both of these were quite different from the annual time-scale (Figure 3).



**FIGURE 3** Temporal scale influenced the strength of intraspecific occupancy–abundance relationships (plotted points are Spearman's rank correlation coefficients), resulting in quite different levels of occupancy–abundance relationship support for a given species at different time-scales (week, month or year). The dotted line provides the null expectation of equal values for species across temporal sampling scales



**FIGURE 4** Intraspecific occupancy–abundance relationship strength was generally positively related to the strength of intraspecific occupancy–relative abundance relationships, but the variation observed—especially at larger temporal sampling scales—suggests differences in abundance and relative abundance that could influence the level of support for intraspecific occupancy–abundance relationships more generally. Plotted lines correspond to the null expectation of equal correlation coefficients regardless of abundance estimation (dotted lines) and a fitted linear model (solid lines)

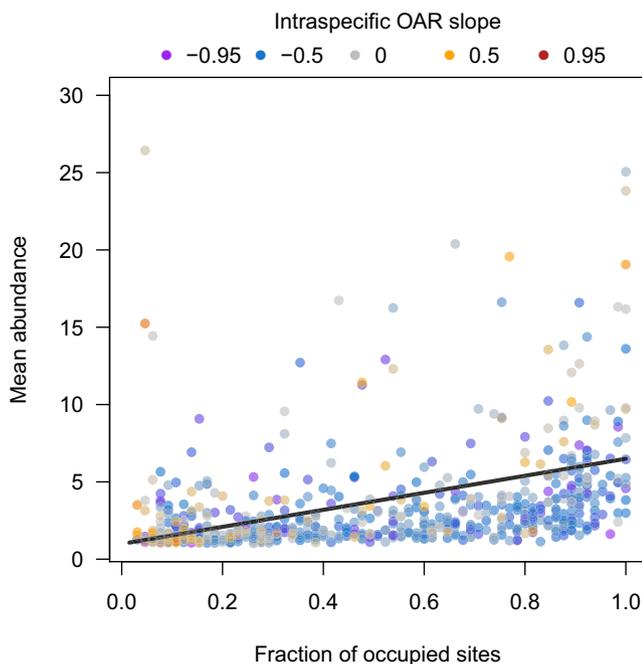
Occupancy–abundance relationships may be measured using species relative abundance. Here, we find that occupancy–relative abundance relationships tended to be closer to zero than

occupancy–abundance relationships, especially at the annual time-scale (Figure 2). At the weekly time-scale, occupancy–abundance and occupancy–relative abundance relationships were closely related

( $\rho = 0.58$ ). However, at coarser, and more representative, temporal sampling scales such as monthly ( $\rho = 0.46$ ) and yearly ( $\rho = 0.36$ ), this relationship was strongly weakened (Figure 4).

### 3.2 | Interspecific occupancy–abundance relationships

Aggregating data to where each moth species is represented by a single point, we found a significantly positive relationship ( $\rho = 0.66$ ,  $p < .0001$ ) between species occupancy and mean abundance (Figure 5). The fraction of occupied sites for each species was positively related to species intraspecific occupancy–abundance relationship slope ( $\rho = 0.25$ ,  $p < .0001$ ), suggesting that more geographically widespread species also tend to have more positive intraspecific occupancy–abundance relationships. This may be driven by a few site-specific species with very negative ( $< -0.8$ ) intraspecific occupancy–abundance relationships; *Bena bicolorana*, *Eucarta virgo*, *Eupithecia orphnata*, *Scopula caricaria* and *Xestia lorezi*. However, the removal of these species still results in a positive relationship between occupancy and intraspecific occupancy–abundance relationship ( $\rho = 0.21$ ,  $p < .0001$ ). This is opposite to the expected relationship, as it has been suggested that intraspecific occupancy–abundance relationships might be weaker when species occupancy is high (Webb et al., 2007).



**FIGURE 5** An interspecific occupancy–abundance relationship was observed for moth species, in which widespread moth species tended to also be more abundant. Points are coloured by the strength of the intraspecific occupancy–abundance relationship for each species. Those species with high abundance and a low fraction of occupied sites are likely habitat specialists, who reach locally high abundances but only under specific conditions or in certain habitats

### 3.3 | The effect of temporal scale on occupancy–abundance relationships

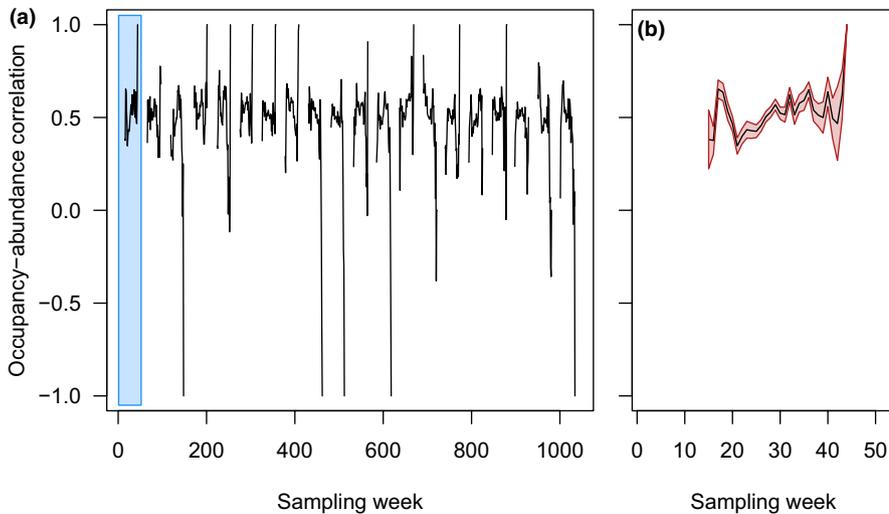
Temporal scale can strongly influence macroecological patterns (Fisher et al., 2010). We examined the effect of temporal sampling scale for both intraspecific and interspecific occupancy–abundance relationships. Examining intraspecific occupancy–abundance relationships across a moving window of 12 weeks, we find evidence that the sampling period can have pronounced effects on the resulting slope and sign of occupancy–abundance relationships (Figure 6). This result was insensitive to the size of the rolling window considered (see Supplementary Materials).

We further show that the interspecific occupancy–abundance relationship varies annually (Figure S3 and Figure 7), but fails to follow any consistent temporal pattern of change. Apart from annual variation, we examined each season (fall, winter, spring, summer) separately, finding qualitatively similar results when all data were analysed together (Figure S5).

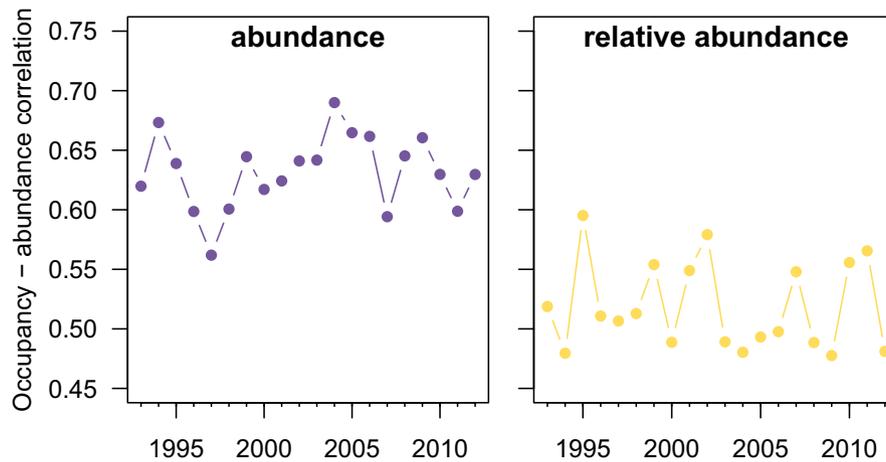
To explore the consistency of interspecific occupancy–abundance relationships, we divided the sampling period by year and examined relationships among species in each time period. Some species did not occur in every year, resulting in a range of species between 526 and 613 for any given year. Interspecific occupancy–abundance relationships remained strikingly constant when data were divided for each year of the sampling period ( $\bar{\rho} \pm SD = 0.632 \pm 0.03$ ; Figure S3). Furthermore, these relationships were slightly weaker when species mean abundance was quantified using relative abundance instead of raw abundance ( $\bar{\rho} \pm SD = 0.519 \pm 0.04$ ; Figure S4).

## 4 | DISCUSSION

Seasonally fluctuating populations may result in a pronounced effect of temporal sampling scale on macroecological relationships. In this instance, occupancy–abundance relationships in seasonally fluctuating moth populations were strongly influenced by temporal sampling scale. Under perhaps the most representative time-scale of a year, we still found evidence for intraspecific occupancy–abundance relationships generally, but for <30% of the moth species observed. However, occupancy–abundance relationships were weakened at this characteristic time-scale relative to occupancy–abundance relationships at the weekly or monthly scale. These relationships were weakened further when abundance was quantified as relative abundance. This suggests that site variation and differences in species distributions may drive differences in abundance for all species, and that species may respond independently to environmental gradients. The lack of support for occupancy–relative abundance relationships suggests that numerically dominant species in communities are not necessarily the most widespread. When considering the entire sampling period (1993–2012) and all species together, we found evidence for an interspecific occupancy–abundance relationship, though species were quite variable, suggesting the possibility for



**FIGURE 6** Temporal change in mean Spearman's rank correlations between species abundance and occupancy along a moving window of 12 weeks, demonstrating pronounced seasonal variation in occupancy–abundance relationships. Occupancy–abundance relationships varied considerably over the twenty year sampling period (panel a) and within each year (panel b corresponds to the blue box in panel a). The red polygon in panel b corresponds to standard error around estimates of occupancy–abundance relationships for each given sampling period



**FIGURE 7** Spearman's rank correlation coefficients between species occupancy and abundance (left panel) or relative abundance (right panel) as a function of year. While the strength of occupancy–abundance relationships changed over time, there was no clear trend in relationship strength as a function of sampling year. The strength of occupancy–abundance relationships were not related as a function of whether abundance was quantified as abundance (as in the left panel) or relative abundance (as in the right panel;  $r = -.31$ ,  $p = .18$ )

an underlying influence of geographical, phylogenetic, or trait variation. While we found evidence for occupancy–abundance relationships generally, these relationships tended to be weak, suggesting that forecasting species occupancy based on abundance may lead to variable and inaccurate predictions. Furthermore, caution is necessary when examining occupancy–abundance relationships, as well as other macroecological relationships, with respect to the estimation of key components (i.e. abundance) at different temporal and spatial extents. Taken together, we find general support for positive occupancy–abundance relationships at both within and between species scales, sensitive to the temporal sampling scale and estimation of abundance.

The support we observed for intraspecific occupancy–abundance relationships contributes to a large body of literature demonstrating a positive relationship between species occupancy and mean abundance (Blackburn et al., 2006; Gaston et al., 1998,

2000; Hanski, 1982; Steenweg et al., 2018). Macroecological relationships may receive mixed support due to underlying differences among species groups, or simply as a result of differences in measurement. That is, support for occupancy–abundance relationships differed when species abundance is quantified as species density (number of individuals per area) or relative abundance, and as a result of differences in temporal sampling frequency. Relative abundance may capture species dominance in a community, with the idea that species which are most dominant in the community should also be widespread (Zuckerberg et al., 2009). However, while our findings support the existence of intraspecific occupancy–abundance relationships in Finnish moth species, we failed to detect many significant occupancy–relative abundance relationships.

Temporal sampling frequency is especially important to consider, as seasonally fluctuating populations may strongly influence



resulting occupancy–abundance relationships. We found relatively weak correspondence in occupancy–abundance relationship estimates taken at the annual time-scale, which accounts for seasonal fluctuations in moth populations, and weekly or monthly time-scales. This supports previous findings suggesting that temporal sampling scale can influence the detectability and strength of occupancy–abundance relationships (Steenweg et al., 2018). This also suggests that strong occupancy–abundance relationships in fluctuating species could be a simple function of population phenology, and have no underlying basis. However, numerous studies have focused on this underlying basis, relating species niches (Heino & Tolonen, 2018), traits (Fournier, Mouquet, Leibold, & Gravel, 2017) and phylogenetic relationships traits (Fournier et al., 2017) to occupancy–abundance relationships. Using an appropriate time-scale to avoid the influence of seasonally fluctuating populations will help disentangle these ecological forces from phenological artefacts. Future work investigating how occupancy–abundance relationship strength changes as a function of climatic forcing at large spatial scales may provide insight into the dependence of macroecological patterns on short-term climatic variation (see Supplementary Materials for more detail on temporal variability in interspecific occupancy–abundance relationships).

The influence of temporal sampling scale may be especially important for seasonally fluctuating populations. While we found that finer temporal scales lead to stronger occupancy–abundance relationships, seasonal fluctuations and occasionally bi-weekly sampling during some periods in Northern Finland may have introduced temporal bias in abundance estimation. In order to remove seasonal fluctuations, we can consider the year as the characteristic time-scale (Steenweg et al., 2018). Examining numerous temporal sampling scales provided insight into the role of seasonality on the detection and strength of occupancy–abundance relationships. Changing levels of support as a function of temporal sampling scale are likely the result of fluctuating population abundance and occupancy, potentially suggesting that occupancy–abundance relationships at this temporal sampling scale are simply a result of demographical processes (Zuckerberg et al., 2009), and could easily emerge from neutral population models (Dolman & Blackburn, 2004). Furthermore, species with actively shifting geographical ranges as a function of climate change may have markedly different occupancy–abundance relationships from year to year. For instance previous work in this system found that species whose range shifted northward also occupied fewer patches (Pöyry, Heikkinen, Heliölä, Kuussaari, & Saarinen, 2018). Defining a characteristic time-scale at which to estimate occupancy–abundance relationships is critical, as seasonal population dynamics and generation times can strongly influence resulting occupancy–abundance relationships. A final concern relates to the geographical area of sampling relative to the geographical area of the studied species. Many of the moth species studied are not geographically confined to Finland. It is possible that southern Finland is at the Northern climatic limit of some moth species, which would result in a large number of sampled

sites where moth species cannot persist, despite locally high abundance within sites corresponding to climatic conditions within the species niche. This creates an interesting situation, where species overall geographical range—as well as the amount of overlap with competing species—may influence occupancy–abundance relationships. However, we find little consistent spatial variation in occupancy–abundance slope for each species (see Figure S7), as species largely occurring in southern Finland would be expected to have occupancy–abundance relationships closer to 0.

## 5 | CONCLUSION

Occupancy–abundance relationships are a commonly observed macroecological pattern (Blackburn et al., 2006; Gaston et al., 1998, 2000), though many exceptions exist (Gaston & Curnutt, 1998; Symonds & Johnson, 2006; Webb et al., 2007). Understanding the factors that contribute to generating occupancy–abundance relationships is crucial, as is the role of changing environmental conditions or land use on the relationship between species abundance and occupancy. This is especially true if occupancy–abundance relationships will be used to inform conservation or management efforts (Hui et al., 2009; Roney et al., 2015). For instance claims that reducing habitat availability will feedback to reduce species mean abundance based on occupancy–abundance relationships do not explicitly consider niche theory, in that the destruction of a habitat where the species could not have persisted will have no effect on species density in other patches. Also, the destruction of a patch corresponding to conditions within a species niche may still not influence species density in neighbouring patches. Beyond the conservation implications, the search for general patterns in ecological diversity is a large goal of ecological research, and disentangling how species life history, evolutionary history and species interactions influence such large-scale relationships is an interesting area for further research. The overall findings of this study demonstrate that experimental sampling design and abundance measurement are important considerations which strongly influence the level of support for occupancy–abundance relationships, and that a sizable degree of variation exists in occupancy–abundance relationships even at characteristic time-scales for a large set of well-studied moth species.

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## CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

## DATA AVAILABILITY STATEMENT

Data and R code to reproduce the analyses here are available on figshare at <https://doi.org/10.6084/m9.figshare.7406348.v1>.

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## BIOSKETCHES

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Author contributions: J.P. and R.L. contributed to experimental design and data collection. T.A.D. performed the analyses. All authors contributed to manuscript writing.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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