

RESEARCH ARTICLE

Occupancy model reveals limited detectability of lichens in a standardised large-scale monitoring

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Abstract

Question: What are the extent and the possible causes of imperfect detection in lichens? Because lichens are sessile and lack seasonality, they should be easier to survey than animals that can move or plants and fungi with seasonal morphology, and one could therefore expect relatively high detection probabilities.

Location: 826 standardised sampling plots across Switzerland.

Methods: Using repeated detection/non-detection data from a national lichen survey conducted by professional lichenologists, we estimated the mean and variation in detectability for 373 tree-living species with a multi-species occupancy model. We also quantified the effect of species conspicuousness, identifiability and observer experience on detection probability.

Results: The average detection probability for a single survey was unexpectedly low with an average of 0.49 (range across species: 0.25–0.74). Conspicuous species showed higher average detectability (0.56) than inconspicuous species (0.41), and identifiability as well as previous experience with a species substantially increased the probability of a person detecting it. Accounting for experience, the mean detection probabilities of observers ranged from 0.32 to 0.69.

Conclusions: Our study confirms that detection probability per survey is often far below 1 also in sessile organisms, even when a standardised survey is conducted by experts. When species are seasonal (plants, fungi, etc.), survey areas are larger, or field personnel are less experienced, as is the case for many surveys and monitoring programs, detectabilities are likely to be substantially lower. We therefore argue that imperfect detection should systematically be considered in the survey design and data analysis also for sessile organisms.

KEYWORDS

detection probability, epiphytic lichens, imperfect detection, lichen, monitoring, observer error, occupancy model, repeated surveys, sampling error, sessile organism, Switzerland

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1 | INTRODUCTION

Standardised biodiversity surveys provide high-quality data for estimating species distributions, local species richness, or community changes over time. Unfortunately, biodiversity cannot always be assessed without error. Species can be missed at sites where they are present (representing imperfect detection) or erroneously recorded at sites from which they are absent (e.g. because of species misidentification). One way to account for such sampling errors is to adopt a repeated-measures design; i.e. to conduct multiple independent surveys for at least some of the sampling units (MacKenzie et al., 2002; Tyre et al., 2003). Repeated survey data of communities, which consist of the observed detection/non-detection state of several species (often inaccurately called “presence/absence” data), can then be analysed with multi-species occupancy models (Dorazio & Royle, 2005). When ignored, sampling errors can bias estimates of species distribution and abundance (MacKenzie et al., 2002; Royle, 2004; Kéry & Schmidt, 2008; Guillera-Aroita et al., 2014), biodiversity metrics (Broms et al., 2014; Iknayan et al., 2014; Jarzyna & Jetz, 2016; Guillera-Aroita et al., 2019), demographic rates like (local) colonisation and extinction (MacKenzie et al., 2003; Rossman et al., 2016; Manna et al., 2017), or the strength of habitat associations (Tyre et al., 2003; Gu & Swihart, 2004; Kéry, 2004; Lahoz-Monfort et al., 2014).

Animal ecologists have long been aware that the mobility of their subjects makes them particularly prone to imperfect detection. Many recent studies on birds, reptiles or amphibians therefore directly account for imperfect detection in the analysis (Mosher et al., 2018; Maphisa et al., 2019; Amburgey et al., 2021; Moor et al., 2022; Siffert et al., 2022). However, this is often not the case for sessile organisms (for exceptions, see Al-Chokhachy et al., 2013; Bonneau et al., 2019; Moor et al., 2020). Possibly, researchers of sessile study organisms think what John L. Harper wrote in the preface to his book *Population Biology of Plants*: “plants stand still to be counted and do not have to be [...] estimated” (Harper, 1977). It is true that plants (or other sessile organisms) cannot escape detection by movement, but it does not necessarily follow that they will always be detected. Many vascular plants, some bryophytes, and most fungi change morphology over the year, with some forms being entirely invisible, difficult to identify, or at least very inconspicuous. In addition, some species are smaller or less conspicuous than others, survey areas can be large, and observers can commit errors. Evidence for imperfect detection also in sessile organisms is indeed accumulating (Garrard et al., 2008, 2013; Chen et al., 2009, 2013; Perret et al., 2023). Some studies have reported observer differences in plant records (Nilsson & Nilsson, 1985; Klimeš et al., 2001; Vittoz et al., 2010; Burg et al., 2015), and species differed in their detectability depending on their morphological (Gregg & Kéry, 2006; Chen et al., 2009; Garrard et al., 2013) or seasonal reproductive state (Halme & Kotiaho, 2012; Abrego et al., 2016; Kapfer et al., 2016). Even large stationary structures of otherwise small and mobile species such as ant nests or caterpillar colonies are not always detected (Berberich et al., 2016; Brown et al., 2017). Despite this mounting

evidence for the prevalence of detection errors also in sessile study objects, many recent studies on sessile communities still assume perfect detection, perhaps (but not always) because of a lack of resources to gather the necessary data (Kolb et al., 2010; Zhang et al., 2014; Newman et al., 2015; Perring et al., 2018; Bjorkman et al., 2020; Jönsson et al., 2022; Staude et al., 2022).

Although detectability may vary greatly between species, observers or sampling schemes, and should thus be estimated on a case-by-case basis, some aspects of it can be inferred from other studies. Not surprisingly, earlier studies suggest that conspicuous and easy-to-identify species are more likely to be detected (Cáceres et al., 2008; Chen et al., 2009; Löhmus, 2009), or that an observer's previous experience with a species increases the chance that she/he will find it again (McCune et al., 1997; Brunialti et al., 2012; Erickson & Smith, 2021). It remains to be tested whether these factors (conspicuousness, identifiability and observer experience) can facilitate the estimation of detection probability in a large-scale standardised monitoring.

Lichens are among those terrestrial organisms that are not only sessile but also look the same all year round (other examples are different species of bryophytes, terrestrial algae, or cyanobacteria). Lichens are perennials (with very few exceptions), and reproductive structures, once produced, remain visible. They are therefore always available for detection and their occurrence should be easier to assess than that of fungi or plants. Nevertheless, imperfect detection was first mentioned for lichens long ago (McCune et al., 1997). Later researchers also reported that observed species richness increased with every additional person who visited a site, implying that many species remained undetected after a single or even several visits (Cáceres et al., 2008; Britton et al., 2014; Vondrák et al., 2016). However, none of these studies explicitly estimated detectability at the species level. Casanovas et al. (2014) were, to the best of our knowledge, the first to systematically collect data to estimate the detectability of individual lichen taxa using multiple independent observers. A second study by Outhwaite et al. (2020) also estimated the detectability of lichens, but the authors extracted multiple-visit type data from presence-only observations in a database, following an approach suggested by Kéry et al. (2010), rather than designing a systematic survey with multiple standardised visits. Casanovas et al. (2014) highlight the improvement in accuracy that an explicit estimation of detectability made to their estimates of species occurrence and suggest that future lichen surveys include repeated surveys to estimate detectability. Nonetheless, we are not aware of any published studies that followed their suggestion.

The purpose of the current study is to estimate the detectability of individual lichen species and study the effects of some potential factors affecting it. Does their sessile and non-seasonal nature make them easily detected or not? More precisely, the goal of this study is to: (a) estimate the average detectability of tree-living lichen species in a large-scale, standardised survey; (b) quantify the variation in detectability among species in relation to their conspicuousness or identifiability; and (3) quantify differences in detection probability among observers depending on their previous experience with each

species. We also illustrate the effect of ignoring imperfect detection in our data on estimates of species occupancy and discuss the requirements that must be fulfilled to be able to account for detectability in lichens.

2 | METHODS

2.1 | Lichen data

The lichen data set was collected between 1995 and 2000 for the national Red List of corticolous lichens (lichens growing on bark, called “tree lichens” in the following) in Switzerland (Scheidegger et al., 2002), using the design developed by Dietrich and Scheidegger (1997). The full sample comprises 826 sites, chosen in a stratified random manner among all 41,291 intersection points of the Swiss 1-km coordinate grid. Stratification was based on combinations of the biogeographic region (five strata), elevational belt (six), and vegetation type (forest/non-forest), making the sample representative of Switzerland with respect to these major variables. A site was defined as a circle with a radius of 12.62 m centred on an intersection point (area 500 m²). After inspecting the selected locations on a map, 185 were excluded as either being unsuitable for tree lichens (e.g. lakes, glaciers, intensive agricultural fields without trees or shrubs) or inaccessible. For our analysis, we further excluded sites without any tree substrate, resulting in a final data set of 416 sites (Figure 1). On these, all bark substrate below 2 m above ground was searched by one of six lichen experts (observers 1–6) with the

aim of detecting as many lichen species as possible on each species of substrate tree (one list for *Abies alba*, one for *Acer pseudoplatanus*, etc.). When a lichen specimen could not be identified with certainty in the field, a small part of it was collected for later identification with microscope and/or thin-layer chromatography. Survey duration was loosely restricted by the expectation that every person should survey two sites per day on average, which led to an average survey time of 93 min (range 5–540 min). More details on the sampling protocol are given in Scheidegger et al. (2002). Two years into the fieldwork, when the first data were available, 46 sites were chosen for a second survey, all of which were conducted by a single person (observer 7). To minimise the probability that the lichen flora had changed, repeat surveys were only conducted at sites where the first survey was <1 year ago and where at least ten lichen species had been recorded. Also, these sites were spread across all major biogeographic regions, elevational belts, and vegetation types. Time was not restricted in this second survey, and the surveyor typically spent considerably more time on the site than the first surveyor (on average 174 min).

2.2 | Species indices

We developed three indices to explain variation among species or observers in detectability: species conspicuousness and identifiability, and observer experience. These scores were created outside our main analysis; i.e. they are independent from our estimates of detectability.

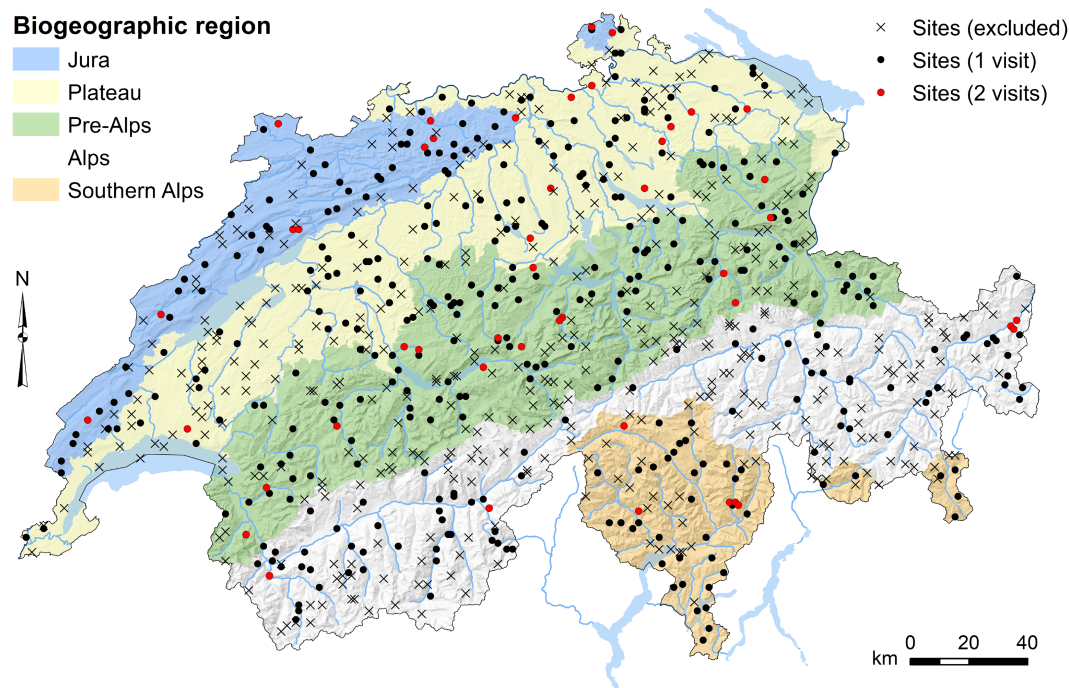


FIGURE 1 Map of Switzerland with the location of the sampling sites. Among all 826 sampling sites, 410 were excluded because they did not contain any substrate for tree lichens. Of the remaining 416 sites, 46 were surveyed twice. Background colours illustrate different biogeographic regions. The topographic map was provided by Swisstopo (Federal Office of Topography).



2.2.1 | Species conspicuousness

Our conspicuousness score (1/0) quantifies how easily a species can be spotted in the field. Species with large or protruding thalli and/or conspicuous colours (white, yellow, orange, bright green) were considered conspicuous (value 1) and were expected to have a higher detectability, whereas species with small and/or closely appressed thalli of dull colours (darker grey, brownish, dark green) were considered inconspicuous (value 0) and were expected to have a lower detectability (Cáceres et al., 2008). The assignment to either group was based on the majority judgement of five field-experienced lichenologists (GH, MD, CK, SE, CS) and can be found in Appendix S1.

2.2.2 | Species identifiability

The identifiability score quantifies how easy it is to identify a species based on its taxonomic delimitation and its morphological differences with other species (Appendix S1). Possible index values are 1 (species can be identified in the field with a hand lens), 0.5 (can be identified in the field using spot tests), -0.5 (requires simple microscopy for identification), and -1 (requires advanced microscopy or thin-layer chromatography for identification). Cáceres et al. (2008) used a similar index and called it “distinctiveness”. We treated this score as a continuous variable.

2.2.3 | Observer experience

We defined experience (1/0) as the presence or absence of a report of the same species by the same observer in any previous year. For example, if an observer first recorded species A to the national lichen database SwissLichens (Stofer et al., 2019) in the second year of the study, whether the record came from a sampling site or from an opportunistic record, then this observer's experience score for species A was considered 0 (no experience) for all surveys conducted in years one and two, and 1 (with experience) for all surveys conducted during years three and later. This permanent change in index value induced by a contact event is similar to capture-recapture studies, where animals may develop a “trap happiness” or “trap avoidance” response after having been caught the first time (Otis et al., 1978; Williams et al., 2002).

2.3 | Occupancy modelling

We fitted a single-season community occupancy model to the lichen survey data (Dorazio & Royle, 2005; chapter 11 in Kéry & Royle, 2016), using the “mixed” data from sites visited two times together with data from sites visited only once (Hirschheydt et al., 2023). This occupancy model estimates the occupancy probability of each species separately from its detectability; i.e. the probability of detecting a species given its presence, while

assuming that no species is detected by mistake. Under this “no-false-positives” assumption, the true occupancy state z of site i ($i = 1, 2, \dots, 416$) for species k ($k = 1, 2, \dots, 373$) is modelled as a function of occupancy probability Ψ , which is described by covariates in the form of a logistic regression:

$$z_{ik} \sim \text{Bernoulli}(\Psi_{ik})$$

$$\begin{aligned} \text{logit}(\Psi_{ik}) = & \alpha_{0,k} + \alpha_1 \times \text{substrate}_{ik} + \alpha_{2,k} \times \text{elevation}_i + \alpha_{3,k} \times \text{elevation}_i^2 \\ & + \alpha_{4,k} \times \text{precipitation}_i + \alpha_{5,k} \times \text{precipitation}_i^2 \\ & + \alpha_{6,k} \times \text{solar.radiation}_i + \alpha_{7,k} \times \text{solar.radiation}_i^2, \end{aligned}$$

$$\alpha_{x,k} \sim \text{Normal}(\mu_{\alpha_x}, \sigma_{\alpha_x}^2), \text{ for } x = 1, 2, \dots, 7.$$

where μ_{α_x} and $\sigma_{\alpha_x}^2$ are the hyperparameters that describe the random species effect. We considered variables that were thought to explain the largest variation in species occurrences based on the ecology of tree lichens, while trying to keep the number of covariates low enough for the model to converge. The categorical variable *substrate* (0/1) indicates whether a site contained a tree species that was suitable for species k based on the pH of the bark and the lichen's preference for that pH class (Barkman, 1958). This suitability of pH classes for lichen species was estimated from all available data in the SwissLichens database (Stofer et al., 2019) excluding data analysed in this study: If at least 10% of a species' records came from a given substrate, that substrate was judged suitable. The continuous variables *elevation* (provided by the National Forest Inventory LFI, 2020), mean yearly precipitation (variable RnormY8110 provided by MeteoSwiss, 2020) and mean yearly solar radiation (variable SnormY8110 provided by MeteoSwiss, 2020) were all standardised to mean = 0 and standard deviation (SD) = 1.

The true occupancy state is only partially observed because the observed data y is the result of the detection process, which depends on both the underlying true state z and detectability p . For site i , species k and survey j ($j = 1, 2$), detections are modelled as:

$$y_{ijk} \sim \text{Bernoulli}(z_{ik} \times p_{ijk})$$

$$\begin{aligned} \text{logit}(p_{ijk}) = & \beta_{1,o[ij]k} + \beta_2 \times \text{conspicuousness}_k + \beta_3 \\ & \times \text{identifiability}_k + \beta_4 \times \text{experience}_{o[ij]k} \end{aligned}$$

$$\beta_{1,o[ij]k} \sim \text{Normal}(\mu_{\beta_o}, \sigma_{\beta_o}^2)$$

Each observer o thus has their own mean detectability μ_{β_o} (fixed observer effect) and associated variance $\sigma_{\beta_o}^2$ over which the species can vary (random species effect). The other coefficients ($\beta_2, \beta_3, \beta_4$) are constants.

2.3.1 | Software, settings, model validation

We carried out all analyses in R (version 4.1.2; R Core Team, R Foundation for Statistical Computing, Vienna, AT). The occupancy



model was fitted in JAGS (Plummer, 2003) with Markov chain Monte Carlo (MCMC) simulations, using the R package *jagsUI* (Kellner, 2021) as an interface. We defined uniform(0,1) priors for the intercepts on the probability scale (Kéry & Royle, 2016), Cauchy priors with an SD of 2.5 for regression coefficients (Gelman et al., 2008), and half-Cauchy priors with an SD of 2.25 for the standard deviation in the normal distribution that governs the random species effects (Broms et al., 2016). We assessed sensitivity to priors by fitting the same model with much more vague priors and could not find any effect on parameter estimates (Appendix S2). We ran five MCMC chains of 50,000 iterations each, the first 30,000 were discarded as burn-in, which, together with a thinning rate of 1 in 20, resulted in a posterior sample size of 5,000. MCMC convergence was inferred when the scale-reduction factor $\hat{R}$ was <1.1 for all parameters (Gelman & Rubin, 1992; p. 285 in Gelman et al., 2013) and when trace plots showed good mixing of the MCMC chains. Goodness-of-fit of the model was assessed at species level using posterior predictive checks (Gelman et al., 1996) and was satisfactory, with the exception of a few species (Appendix S3).

3 | RESULTS

Mean occupancy probability across species at average elevation and without suitable substrate was estimated at the very low value of 0.017, with a 95% credible interval (CRI) of [0.013, 0.022], as given by the transformation of the intercept in Table 1. This estimate refers

to the probability of occupancy of a site without suitable substrate which must, by definition, be low. Not surprisingly, the presence of suitable substrate strongly increased the probability of occurrence more than fivefold on the probability scale to 0.092, 95% CRI [0.076, 0.110]. The strong effect of this covariate emphasises the importance of including this variable in the model. Our data set contained a list of tree species within each plot, but where such high-resolution data are not available, it may be possible (and desirable) to obtain a proxy for it at a coarser resolution from forestry data. Even with suitable substrate, however, average occupancy was still very low, which confirms previous observations that most lichen species tend to be very rare (Edwards et al., 2004). Elevation had, on average, a negative linear and a positive quadratic effect on occupancy but with considerable variation among species. The effects of precipitation and solar radiation also varied among species but were closer to zero.

Observer-specific detection intercepts (on the probability scale) varied between 0.289 [0.233, 0.352] for observer 4 and 0.696 [0.625, 0.760] for observer 7 (Figure 2a, from Table 1). Interestingly, observers also differed in the consistency with which they detected different species, after accounting for species attributes and observer experience, as measured by the species-specific random-effect variance σ^2 , which was estimated separately for each observer (Figure 2b). Observers 4 and 5 had considerably greater, and observer 6 considerably lower, among-species variation in detectability than the others. Modelling species random effects separately for each observer allowed species to have very different (or very similar) detectabilities

TABLE 1 Parameter estimates obtained as posterior means from the community occupancy analysis.

Parameter	Estimate [95% CRI]	σ of random species effect [95% CRI]
Occupancy process		
Intercept $\mu_{\text{intercept}}$	-4.05 [-4.30, -3.81]	1.78 [1.63, 1.94]
Substrate α_1	1.76 [1.61, 1.91]	-
Elevation μ_{elev}	-2.56 [-2.80, -2.34]	1.44 [1.24, 1.65]
Elevation ² μ_{elev^2}	0.15 [-0.15, 0.45]	2.65 [2.41, 2.93]
Precipitation μ_{precip}	-0.27 [-0.33, -0.20]	0.42 [0.36, 0.48]
Precipitation ² μ_{precip^2}	-0.01 [-0.05, 0.04]	0.20 [0.15, 0.25]
Solar radiation μ_{solar}	0.01 [-0.06, 0.08]	0.45 [0.39, 0.53]
Solar radiation ² μ_{solar^2}	-0.22 [-0.28, -0.17]	0.25 [0.19, 0.31]
Detection process		
Observer 1 $\mu_{\text{obs}1}$	-0.73 [-1.00, -0.45]	0.71 [0.52, 0.91]
Observer 2 $\mu_{\text{obs}2}$	-0.43 [-0.71, -0.16]	0.63 [0.46, 0.82]
Observer 3 $\mu_{\text{obs}3}$	-0.54 [-0.81, -0.27]	0.79 [0.61, 0.99]
Observer 4 $\mu_{\text{obs}4}$	-0.90 [-1.19, -0.61]	1.09 [0.88, 1.31]
Observer 5 $\mu_{\text{obs}5}$	-0.43 [-0.75, -0.11]	1.08 [0.70, 1.53]
Observer 6 $\mu_{\text{obs}6}$	0.26 [-0.04, 0.56]	0.54 [0.12, 0.86]
Observer 7 $\mu_{\text{obs}7}$	0.83 [0.51, 1.15]	0.93 [0.70, 1.18]
Conspicuousness β_2	0.25 [0.04, 0.45]	-
Identifiability β_3	0.56 [0.43, 0.70]	-
Experience β_4	0.56 [0.34, 0.78]	-

Note: All estimates, and associated Bayesian 95% credible intervals (CRI), are given on the logit scale.

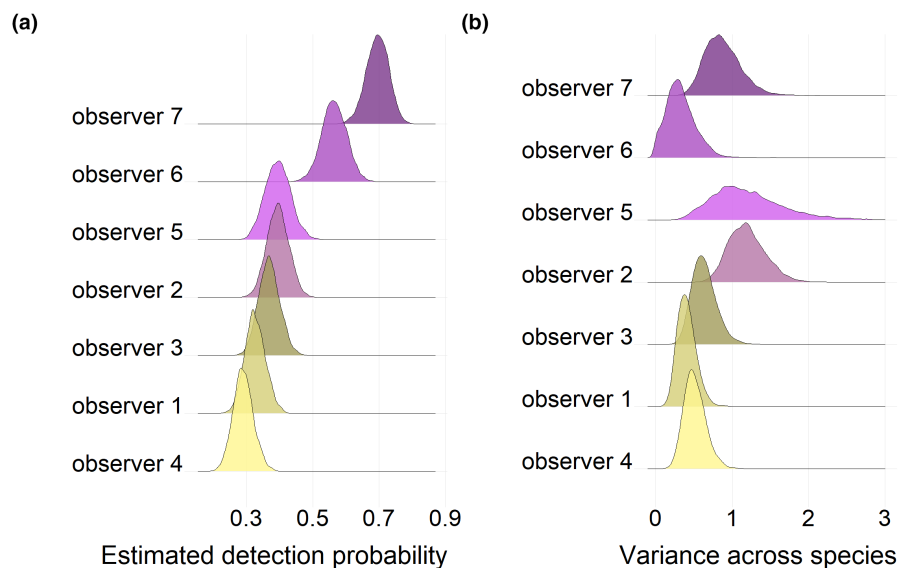


FIGURE 2 Posterior densities of observer-specific detection intercepts with a random species effect. (a) Estimated mean per observer, i.e. the expected probability that an observer finds a species that is inconspicuous and without prior experience. (b) Estimated variance across species, where a small variance means that species cluster closer around the observer's mean detection probability, and a large variance means that species vary greatly within that observer.

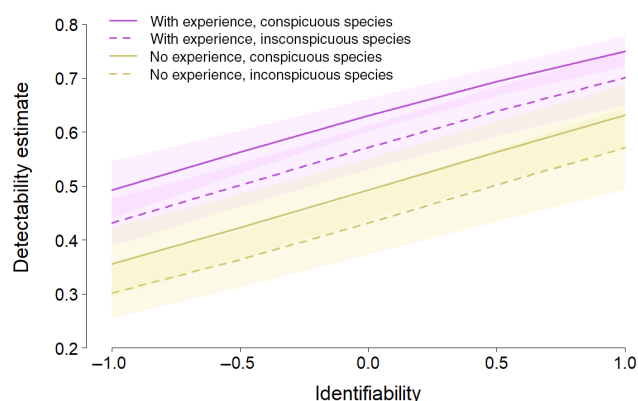


FIGURE 3 Posterior estimates of detection probability in relation to identifiability, observer experience and species conspicuousness. The shaded areas represent Bayesian 95% credible intervals (CRI).

for different observers. For instance, whereas *Pseudevernia furfuracea* (conspicuousness=1, identifiability=1) had estimated mean detectabilities between 0.639 and 0.744 for all observers, estimates for *Lecanora barkmaniana* (conspicuousness=1, identifiability=-1) ranged from 0.099 to 0.764 for different observers (Table S1). Identifiability and experience had equally strong positive effects on detectability with 95% CRI not overlapping zero (Table 1, Figure 3). The effect of conspicuousness was likewise positive, with the entire 95% CRI above zero, but it was slightly weaker (Table 1). Species with high occupancy probabilities tended to have high detectabilities but with considerable variation (Figure 4). Although not tested here, this positive relationship may be the result of variation in local abundance. The common species *Pseudevernia furfuracea*, for example, often occurs in great numbers when it is present at a site, leading to a high cumulative detectability. *Lecanora barkmaniana*, on the other hand, is not only less widespread but also rarely reaches high local densities, making it harder to detect. Taking conspicuousness, identifiability and the time-varying observer experience into account,

mean detectability across all species for a first survey was estimated at 0.482 [0.460, 0.504] at the beginning of the study period, when the average observer was acquainted with 60% of all species, and increased to 0.507 [0.487, 0.527] at the end of the study period, when an average observer had experience with 82% of species. The mean detectability across the entire period was thus estimated at 0.494 [0.474, 0.515]. Given this estimate, the model predicted considerably larger numbers of species occurrences than were actually observed in the field (Figure 5). The same was true for species richness, which was always estimated at a higher value than what was observed (Appendix S4). Although estimates of species occupancy and species richness seem reasonable when averaged across all sites, we would be cautious to draw inferences at the site level (Appendix S4). The environmental covariates in the occupancy model do not capture the full heterogeneity between sampling sites, making the model predictions more similar than the sites probably are. We thus suspect that there is a slight positive bias for species-poor sites and a slight negative bias for species-rich sites.

4 | DISCUSSION

Our study explicitly estimates the detectability of lichen species using data from a highly standardised sampling protocol. Averaged across all species and observers, we found that the per-survey detectability was surprisingly low at 0.49, which means that with a single survey, half of the species are likely to be missed. Experience slightly improved the detection probability of observers over the course of the study from 0.48 at the start to 0.51 at the end of the study period. Specifying experience as a time-dependent variable (which was updated for each observer-species pair after each field season) allowed the model to depict this learning effect. Detection probabilities varied considerably among species (Casanovas et al., 2014), and also among observers, which has been documented before in comparisons of the species numbers detected by different

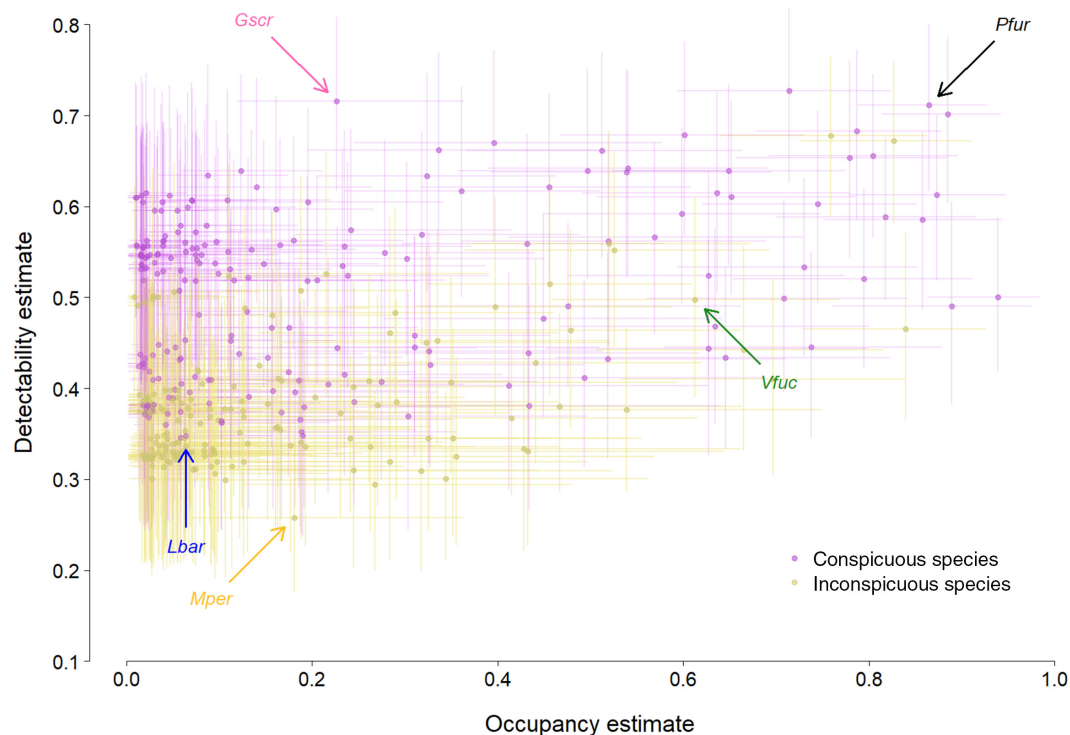


FIGURE 4 Species-specific estimates of detectability against estimates of occupancy probability obtained from the community occupancy model fit to survey data from 373 Swiss tree lichens. Points represent the posterior means and bars the Bayesian 95% credible intervals (CRI). Detectability estimates are averaged across all observers assuming no previous experience with the species (experience = 0). Occupancy estimates assume the availability of suitable substrate (substrate = 1). Five example species are indicated with an arrow and their abbreviated name: *Pseudovernia furfuracea* (Pfur), *Graphis scripta* (Gscr), *Violella fucata* (Vfuc), *Myriolecis persimilis* (Mper) and *Lecanora barkmaniana* (Lbar).

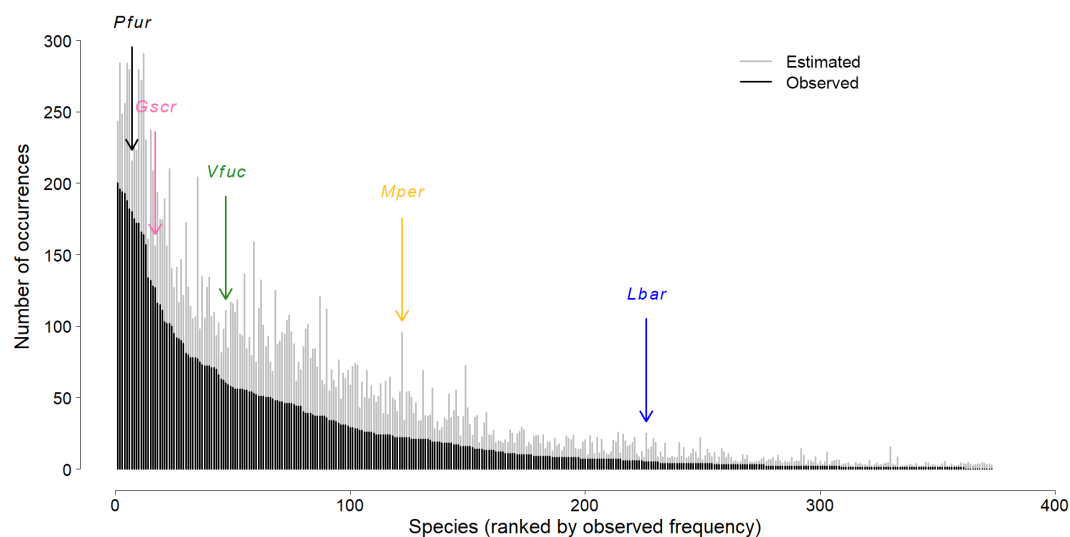


FIGURE 5 Number of occurrences per species that were observed (black bars) or estimated by the occupancy model (grey bars) for 373 tree lichen species at a total of 416 surveyed sites. No species was observed at more than 200 sites, but 17 species were estimated to occur at more than 200 sites. Five example species are indicated with an arrow and their abbreviated name: *Pseudovernia furfuracea* (Pfur), *Graphis scripta* (Gscr), *Violella fucata* (Vfuc), *Myriolecis persimilis* (Mper) and *Lecanora barkmaniana* (Lbar).

people at the same site (McCune et al., 1997; Vondrák et al., 2016). Not surprisingly, conspicuous species had a higher detectability than inconspicuous species (Cáceres et al., 2008; Vondrák et al., 2016). Taxonomic identifiability of the species also mattered: species that

can be identified in the field showed higher detectability than species that require microscopy for identification. This effect was surprisingly strong despite the generous amount of resources available for data collection in this project, which allowed the sampling and



subsequent microscopic analysis of most specimens that could not be identified in the field. In some way, our survey thus represents a seemingly ideal case and other lichen studies, with more limited resources, may arguably show even lower detectabilities for species that are difficult to identify (Cáceres et al., 2008; Löhmus, 2009).

Although we were aware of some detection errors in our data, we would a priori have expected a much higher average detection probability for several reasons: (a) lichens are sessile and (mostly) non-seasonal, which means that lichen inventories are free from many of the difficulties associated with those of mobile species (most animals) or flowering plants; (b) all surveyors in this study were experienced lichen specialists; and (c) the sampling protocol was intended to be exhaustive (survey time per site was not strictly limited and specimens collected in the field were all later identified in the laboratory). Although the sampled area per site was relatively large (500 m²), we had hoped that the generous allowance of survey time would have counter-balanced this less-favourable aspect. Instead, the estimated detection probabilities in this study lie very much within reported detection probabilities of mobile organisms like birds (0.26–0.83 in Tyre et al., 2003; 0.03–0.99 in Kéry & Schmidt, 2008; 0.48–0.60 in Bailey et al., 2009) or amphibians (0.34–0.51 in Tyre et al., 2003; 0.33–0.62 in Bailey et al., 2009) and sessile organisms like plants (0.26–0.57 in Al-Chokhachy et al., 2013; 0.44–0.74 in Perret et al., 2023), and they were lower than those reported for wood-dwelling fungi from sites of similar size (0.79–0.94 in Moor et al., 2020).

With an average detection probability of 0.49 across all 373 detected species, the estimated species frequencies were considerably larger than what was actually observed in the field. The number of occurrences (and thus the population size and the distribution range) of most species would have been severely underestimated if detection probability had been ignored (MacKenzie et al., 2002; Tyre et al., 2003). Although local species richness was not the focus of this study, estimated richness was also often considerably larger than observed richness (Dorazio & Royle, 2005; Dorazio et al., 2006; Appendix S4). Previous studies have found that imperfect detection of lichens can lead to species richness being underestimated when based on species lists from a single observer, but when combining lists from two, three and up to eight observers, richness estimates approached an asymptotic value (McCune et al., 1997; Cáceres et al., 2008; Britton et al., 2014; Vondrák et al., 2016). However, this is the first study to formally estimate species-specific detectability using standardised data from a nationwide survey. Our results provide strong evidence that lichens, despite their sessile and non-seasonal nature, are far from being easily detected in the field, even when observers are experts, the search area is limited and time is not limiting. It is likely that under less favourable conditions (larger search areas, tighter time restrictions or less experienced observers), detection probability would be even lower.

This study adds another piece to the growing body of evidence that also sessile organisms are far from being perfectly detected (Kéry & Gregg, 2003; Cáceres et al., 2008; Garrard et al., 2008, 2013; Chen et al., 2009, 2013; Vittoz et al., 2010; Casanovas et al., 2014; Berberich et al., 2016; Morrison, 2016; Vondrák et al., 2016; Brown et al., 2017;

Dennett et al., 2018; Dennett & Nielsen, 2019; Iles et al., 2019; Middleton & Vining, 2022; Perret et al., 2023). Yet, detection probability is not commonly accounted for in analyses of occurrence or abundance data from plants, lichens and other sessile organisms. Vegetation ecologists often use pseudo-turnover (Nilsson & Nilsson, 1985), i.e. the degree of mismatch between two species lists from the same location, to estimate inter- and intra-observer error (reviewed in Morrison, 2016). Although pseudo-turnover can give insight into some aspects of detection errors, it does not allow the model to actually account for the estimated error, and species-specific inferences are limited. Occupancy models, by contrast, do both, which is why they have become so popular (Guillera-Aroita, 2017). Like other authors (Chen et al., 2009, 2013; Casanovas et al., 2014; Middleton & Vining, 2022; Perret et al., 2023), we believe that we do not yet realise the full potential of occupancy models in studies of sessile species. We acknowledge that occupancy models require slightly more data than other species distribution models (at least two visits on at least a subset of the sites) and some experience in model fitting. Where detection probability is considerably below 1, however, the benefits of more accurate estimates of species occupancy will arguably outweigh the costs of such an undertaking. Generally, the larger the number of repeated visits and/or repeat-visit sites, the more precise and accurate the estimates will be (for optimal distribution of sampling effort in occupancy studies see MacKenzie & Royle, 2005). But if resources do not allow an extensive data collection or if the data have already been collected, a few repeated visits to a subset of the sampling sites is enough to allow the explicit modelling of detection errors (von Hirschheydt et al., 2023). Recall that in our study we had two replicated visits in only 46 of 416 sites and models converged to reasonable estimates.

There are a few limitations to our study. First, the sampling protocol targeted only lichens growing up to 2 m from the ground. Our occupancy estimate therefore describes only the probability that a species occurs within the physical reach of an observer without climbing equipment. This sampling strategy may give a representative picture of the occurrence of most species, but for lichen species that prefer the crown of trees, our estimates may thus still be biased low. Unfortunately, the list of species to which this applies and the magnitude of the bias seem to vary considerably between substrates and habitats (Boch et al., 2013; Marmor et al., 2013; Kiebach et al., 2016), and we could not infer the proportion of tree-crown occurrences found in these previous studies to the extent and heterogeneity of our data. The second limitation is that we included only a few environmental covariates in the occupancy part of our model because the sample size did not allow for greater model complexity. With more data, additional variables like measures of habitat complexity or slope exposure would be desirable to include in the model to improve accuracy in site-specific predictions. The third limitation is that we considered only false-negative detection errors (imperfect detection) and assumed the absence of false-positive errors (typically due to species misidentification). The way the sampling was standardised – difficult species were always collected and any remaining doubtful observations were excluded – convinced us that the false-positive errors would be negligible. However, we cannot exclude the possibility that some small



false-positive error may have affected our estimates. Future research can investigate which information lichen surveyors could collect to fulfil the requirements of models that account for both types of error simultaneously (Royle & Link, 2006; Miller et al., 2011).

5 | CONCLUSIONS

It is tempting to assume that sessile organisms are easy to detect because they cannot move. Lichens in particular should be easy to assess, because they do not show any seasonality in morphology, in contrast to plants or fungi. Here, however, we showed that detecting these sessile species can be very difficult indeed. Using data from a standardised, expert-based survey, the average lichen species was overlooked with a probability of 0.51 during a single survey. We believe that equally considerable imperfect detection is at work in other surveys of lichens, and also of other sessile organisms such as plants and fungi, even when data are collected with a standardised protocol. It is important that ecologists studying species distributions, conservation status, habitat associations or trends over time of such sessile organisms, take this issue into consideration. The quality and credibility of assessments would benefit from an explicit modelling of this ubiquitous sampling error.

AUTHOR CONTRIBUTIONS

GvH, MK, SE, SS and CS designed the study. GvH cleaned and analysed the data with help of MK and SE. SS, MD, CK and CS collected the lichen data. GvH took the lead in writing the manuscript. All authors provided feedback on the interpretation of the results and the manuscript.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All cleaned data from this study and all R code used to generate the presented results and figures are available on the EnviDat repository: <https://www.doi.org/10.16904/envi.dat.491>. In the published data, observers are anonymised, and sites are given without their geographic coordinates to preserve the local populations of protected and rare species.

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SUPPORTING INFORMATION

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

Appendix S1. Contains a table with species-specific indices, data summaries, and estimated detection probabilities.

Appendix S2. Reports the results of the prior sensitivity analysis.

Appendix S3. Reports the results of the posterior predictive checks.

Appendix S4. Illustrates and discusses the estimated species richness per site.

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