Occupancy vs. detection:
Estimating changes in epiphytic lichen communities over 20 years

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To my siblings, Fenna, Philine, and Hauke.

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SUMMARY

The growing global human population is exerting increasing pressure on the natural environment. Habitat destruction and anthropogenic climate change are causing species to decline or to shift their distribution ranges, but some species cannot keep up with the unprecedented speed of these changes and go extinct. As a result, we are losing biodiversity at the pace of a mass extinction. Already now, this loss has entailed unwanted effects on human well-being by negatively affecting ecosystem services like food provisioning, climate regulation, or pest control. Increased political pressure has urged governments to take action towards the conservation of diversity of life on Earth. To be effective, however, actions aimed at the protection of species require the evaluation of the current status of the species and how the populations change over time. Like many others, the government of Switzerland uses national Red Lists to identify the most threatened species and to set priorities for conservation actions at the national scale. The data for these Red List assessments come from large-scale surveys or monitoring programs that were established for the purpose of observing and inferring changes over time. However, ecological surveys are subject to detection errors, i.e., failing to detect species where they occur. These errors can lead to biases in the estimation of species distributions, habitat associations, or population changes, potentially resulting in an inappropriate threat category and a misassignment of resources for conservation measures. It is the purpose of this thesis to obtain estimates of population change for epiphytic lichen species in Switzerland that are less affected by detection errors, using data collected within the scope of the national Red List assessment. To estimate detection errors, it was first necessary to test the applicability of the available statistical methods to the lichen data (**Chapter 1**). Given the scarcity of published literature on the subject of detection errors in lichens, it also made sense to investigate the extent and the causes of such errors in greater detail (**Chapter 2**). The insights from these investigations then allowed me to analyse the ecological patterns behind population changes of epiphytic lichens in Switzerland over the last 20 years (**Chapter 3**).

In **Chapter 1**, I tested whether the structure of the lichen data was generally suitable for the type of statistical models that are most often used to account for detection errors. They are called occupancy models and they require data from sites that were surveyed multiple times over a short period. The model uses the differences and similarities between the observations of the repeated visits to estimate the detection probability. In the standardised lichen data from the national Red List survey, only a small subset of all sites was surveyed a second time, while the others were surveyed only once. To find out whether these single-visit sites could contribute information to parameter estimation in an occupancy model, I simulated data under different designs but with the same mixed structure as the lichen data, i.e., with some repeated-visit sites (with two or four visits) and many single-visit sites. I first fitted an

occupancy model to only the repeated-visit portion of the data and extracted the precision of the parameter estimates. I then successively added more single-visit sites, reran the analysis, and checked whether the precision of the parameter estimates improved. Precision did improve with additional single-visit sites, both for the parameter occupancy and the parameter detection probability. This shows that single-visit sites contribute to parameter estimation, when they are combined with repeated-visit data, and that it is beneficial to include single-visit data in an occupancy analysis. When the number of repeated visits was raised from two to four, precision was not only generally better, but also the contribution of single-visit sites improved. This finding is of limited relevance for the analysis of the currently available lichen data, but it could be useful to make adjustments to the design in the future.

In **Chapter 2**, I explored the magnitude of and variation in detection probability in the lichen data that were collected during the first Red List assessment (1995–2000). I included the conspicuousness and the taxonomic identifiability of the species as covariates to detection probability, supposing that conspicuous and easy-to-identify species may have a higher detectability. The experience of observers with individual species was also likely to affect detectability in a positive way. Average detection probability across all observers was estimated at 49%, with substantial differences between observers and species, some of which were due to people’s experience or to the conspicuousness or identifiability of the species. As observer experience changed over time, detectability was slightly higher towards the end of the sampling period than at the beginning. The result that detection success was estimated to be almost a fifty-fifty chance was rather surprising. The standardised circumstances would have suggested a higher detectability: the size of the sampled area was limited, survey time almost unlimited, and all observers had prior experience with lichen surveys. In contrast to animals, lichens cannot run away or hide, and while most plants and fungi exhibit seasonality in their morphology, lichens do not. It is therefore likely that such low detection probabilities — in other words, such high detection errors — occur in most datasets of sessile organisms. Ignoring them would lead to a severe understimation of frequencies of occurrence and area of occupancy. The variation between species and differences between observers in combination with a potential spatial clustering of observers is expected to result in a stronger bias for some species than for others, an effect that is difficult to assess without the explicit estimation of detection probability.

In **Chapter 3**, I estimated how occupancy changed for 329 epiphytic lichen species in Switzerland between the first and the second national Red List assessment conducted over the periods 1995–2000 and 2018–2022. Although the model estimates occupancy at the species level, I took a more community-based approach in this chapter and grouped species into 18 ecological guilds. Three guilds described a preference for *free-standing trees*, *humid forests*, or *old trees*, two guilds represented

specialized photobionts (*trentepohlioid* and *cyano*), and twelve guilds were derived from high and low ecological indicator values for *temperature*, *precipitation*, *continentality*, *eutrophication*, *pH*, and *light availability*. With this guild-based approach, I was able to find potentially meaningful correlations with environmental change in Switzerland over the same time scale. An ongoing decline in species associated with *old trees* suggests that the low abundance of such trees, though increasing, has not yet allowed specialist lichens to recover from the severe loss they experienced due to unsustainable forestry practices in the last century. A strong increase in species indicative of high pH and tolerant to eutrophication in combination with a decline in eutrophication-sensitive and acidophytic species suggests a continuing effect of environmental pollutants on lichen communities. While acid deposition decreased to a very low level over the last decades, critical levels for nitrogen deposition are still exceeded in two thirds of the country. Some guild changes could also potentially be attributed to climate change. Species of high temperatures and low precipitation tended to increase, whereas species with a preference for low temperatures or high precipitation tended to decline. If these simultaneous environmental changes were indeed the driving force behind the observed changes, they are likely to continue in the near future.

In the three chapters, I have consequently shown that it was possible to use the mixed structure of the lichen data to obtain detection-corrected estimates of frequency of occurrence and population changes. I showed how large the detection error was despite many favourable circumstances, and how it can be accounted for in an ecological study. Limitations of this thesis include model assumptions that may not be entirely fulfilled, and the restrictions imposed by data scarcity on the number of covariates that could be included in the model. In the future, I see potential in combining the standardised data with the countless individual observations recorded by volunteers or in other projects. Including multiple sources in one integrated model could improve both accuracy and precision of estimates of population changes. At a larger scale, e.g., for standardised species distribution modelling for global Red List assessments, it would be valuable to find a set of readily available and reliable predictor variables to model lichen occurrences. It is important to keep in mind, however, that estimates of species frequency or population changes will not reduce the risk of extinction a species may be facing, however precise these estimates may be. Ultimately, conservation actions will be necessary to ensure the persistence of many species. Nevertheless, this thesis lays the foundation for a more accurate, data-based Red List assessment. As such, I hope it can direct conservation efforts to where they are most needed.

ZUSAMMENFASSUNG

Die wachsende menschliche Bevölkerung übt einen zunehmenden Druck auf ihre natürliche Umwelt aus. Arten werden aus ihren zerstörten Lebensräumen verdrängt und der menschengemachte Klimawandel zwingt sie, ihre Ausbreitungsgebiete zu verschieben. Einige Arten können mit der Geschwindigkeit der globalen Veränderungen nicht Schritt halten und sterben aus. Die Folge ist, dass wir gegenwärtig in einem solchen Tempo Artenvielfalt verlieren, wie es sonst nur während Massenaussterben geschehen ist. Bereits jetzt hat der Verlust an Vielfalt unerwünschte Folgen für uns Menschen nach sich gezogen, unter anderem durch verminderte Ökosystem-Dienstleistungen wie der Nahrungsversorgung, Klimaregulierung oder Schädlingsbekämpfung. Der steigende Druck durch die Bevölkerung und Nichtregierungsorganisationen hat Regierungen dazu veranlasst, sich vermehrt des Schutzes der biologischen Vielfalt auf der Erde anzunehmen. Damit Schutzmassnahmen effektiv greifen können, bedarf es einer Evaluation des gegenwärtigen Zustands der Artenvielfalt und die Möglichkeit, die Veränderung des Zustands über die Zeit zu verfolgen. Wie viele andere Länder verwendet die Schweizer Regierung nationale Rote Listen, um die Arten zu ermitteln, die am stärksten bedroht sind, und Prioritäten dort zu setzen, wo der grösste Handlungsbedarf besteht. Die Datengrundlage für die Rote-Liste-Einschätzungen stammt aus gross angelegten Erhebungen und Monitoringprogrammen, welche zu diesem Zweck eingerichtet wurden. Während solcher Erhebungen kann es jedoch vorkommen, dass Fehler gemacht werden, z.B. dass man eine Art nicht entdeckt, obwohl sie an einem Ort vorkommt. Viele einzelne Entdeckungsfehler führen zu einem systematischen Fehler bei der Schätzung des Verbreitungsgebiets, der Lebensraumpräferenzen oder der Populationsveränderungen von Arten. Dies kann zur Einteilung der Art in eine falsche Rote-Liste-Kategorie führen, was wiederum suboptimal angewandte Fördergelder nach sich ziehen kann. Um einen systematischen Fehler (eine Verfälschung oder Verzerrung) in den ökologischen Schätzwerten zu vermeiden, muss der Entdeckungsfehler geschätzt und entsprechend dafür korrigiert werden. Es ist das Ziel dieser Arbeit, unverfälschte Schätzungen für die Bestandsentwicklungen der borkenbewohnenden Flechten der Schweiz über die letzten 20 Jahre zu erhalten. Als Grundlage dienen Daten der Erhebungen, die im Rahmen der zwei nationalen Rote-Liste-Projekte durchgeführt wurden. Die Einschätzung der Entdeckungswahrscheinlichkeit verlangt den Einsatz besonderer statistischer Modelle, die bisher nur selten für Flechtendaten verwendet wurden. Daher habe ich in **Kapitel 1** dieser Arbeit untersucht, ob diese statistischen Modelle sich für die vorliegenden Flechtendaten eignen. Weil es zum Thema Entdeckungswahrscheinlichkeit von Flechten bisher nur begrenzt Literatur gibt, war es ausserdem sinnvoll, das Ausmass der Entdeckungsfehler sowie mögliche Gründe dafür in einem eigenen **Kapitel 2** zu diskutieren. Gewappnet mit den Erkenntnissen dieser ersten Untersuchungen, habe ich mich dann in **Kapitel 3** auf die Veränderungen konzentriert,

die in der Artzusammensetzung von borkenbewohnenden Flechtengesellschaften in der Schweiz über die letzten 20 Jahre geschehen sind.

In **Kapitel 1** habe ich untersucht, ob sich die Struktur der Flechtendaten für die Verwendung jener statistischen Modelle eignet, mit denen Entdeckungsfehler geschätzt werden können. Diese Modelle heissen auf Englisch *Occupancy models*, zu Deutsch etwa «Belegmodelle», weil sie die Wahrscheinlichkeit berechnen, dass eine Erhebungsfläche von der Art «belegt» ist, d.h. ob die Art dort vorkommt. Belegmodelle benötigen Daten von Erhebungsflächen («Plots»), die innerhalb einer kurzen Zeit wiederholt unabhängig erhoben worden sind. Das Modell schätzt dann die Entdeckungswahrscheinlichkeit aufgrund von Unterschieden und Gemeinsamkeiten zwischen den Wiederholungen. In den standardisierten Flechtendaten der Rote-Liste-Erhebungen sind nur ein kleiner Teil aller Plots wiederholt (genauer gesagt zweimal) erhoben worden. Alle anderen wurden nur ein einziges Mal erfasst. Um herauszufinden, ob diese einmalig bearbeiteten Flächen dennoch Information für die Parameterschätzung des Modells beisteuern, habe ich Daten simuliert, die in ihrer Struktur den Flechtendaten ähnlich sind. Die Simulation von Daten erlaubt es, die Leistung eines Modells zu evaluieren, da die richtigen Werte selbst gesetzt werden und darum bekannt sind. In einem ersten Schritt habe ich ein Belegmodell an den Teil der simulierten Daten angepasst, der von wiederholten Aufnahmen stammt, und die Präzision der Schätzwerte gespeichert. Dann habe ich sukzessive mehr und mehr Daten von einmalig bearbeiteten Flächen hinzugefügt, das Modell erneut angepasst und wiederum die Präzision der Schätzwerte extrahiert. Ich konnte feststellen, dass die Präzision mit steigender Anzahl an einmalig bearbeiteten Flächen zunimmt; sowohl die Präzision des Schätzwerts für die Belegwahrscheinlichkeit als auch des Schätzwerts für die Entdeckungswahrscheinlichkeit. Daraus lässt sich schliessen, dass auch einmalig besuchte Flächen zur Parameterschätzung beitragen, sofern sie mit Daten aus wiederholten Aufnahmen kombiniert werden. Bei einer Erhöhung der Anzahl Wiederholungen von zwei auf vier war nicht nur die Präzision im Allgemeinen höher, sondern auch der Beitrag der einmalig bearbeiteten Flächen. Dieses Resultat ist wenig relevant für die Analyse der vorhandenen Flechtendaten, aber es liefert wertvolle Hinweise, wie die Methode für zukünftige Flechtenerhebungen verbessert werden könnte.

In **Kapitel 2** habe ich die Grössenordnung und Variation der Entdeckungswahrscheinlichkeit in den Flechtendaten der ersten Rote-Liste-Einschätzung (1995–2000) unter die Lupe genommen. Als Einflussvariable habe ich die Auffälligkeit und die Bestimmbarkeit der Flechtenarten verwendet, weil ich davon ausgegangen bin, dass auffällige und leicht bestimmbare Arten eine höhere Entdeckungswahrscheinlichkeit haben. Auch die vorherige Erfahrung der Beobachter:innen mit einzelnen Arten habe ich als Variable einfliessen lassen. Die durchschnittliche Entdeckungswahrscheinlichkeit lag bei 49%, doch es gab grosse Variabilität zwischen Leuten und Arten, was sich teilweise durch unterschiedliche Erfahrung, Auffälligkeit oder Bestimmbarkeit der

Arten erklären liess. Da die Erfahrung der Beobachter:innen über den Erhebungszeitraum zugenommen hat, war die Entdeckungswahrscheinlichkeit zu Beginn kleiner als gegen Ende der Aufnahmen. Die Tatsache, dass der Entdeckungserfolg knapp einer 50:50 Chance gleichkommt, war etwas überraschend. Aufgrund des standardisierten Erhebungsverwahrens wäre eine höhere Entdeckungswahrscheinlichkeit zu erwarten gewesen: Die Grösse der Aufnahmeflächen war begrenzt, die Zeit für die Erhebung so gut wie uneingeschränkt und sämtliche Beobachter:innen waren erfahren im Erheben von Flechtendaten. Im Gegensatz zu Tieren können Flechten sich auch nicht vor einer Entdeckung verstecken. Und während die meisten Pflanzen und Pilze jahreszeitliche Unterschiede in ihrem Aussehen aufweisen, sehen Flechten das ganze Jahr über gleich aus. Man könnte also davon ausgehen, dass ähnlich tiefe Entdeckungswahrscheinlichkeiten, mit anderen Worten ähnlich grosse Entdeckungsfehler, in den meisten Erhebungen von sesshaften Organismen auftreten. Diese Fehler zu ignorieren, führt unweigerlich zu einer drastischen Unterschätzung der Häufigkeit dieser Arten. Aufgrund der grossen Variation zwischen Arten und Beobachter:innen in Kombination mit einer ungleichmässigen Verteilung der Leute, ist es ausserdem wahrscheinlich, dass die Verfälschung der Schätzwerte bei einigen Arten stärker ausfallen wird als bei anderen. Diese Unterschiede können nur dann verstanden werden, wenn die Entdeckungswahrscheinlichkeit der Arten explizit geschätzt wird.

In **Kapitel 3** habe ich geschätzt, wie sich die Häufigkeit von 329 borkenbewohnenden Flechten in der Schweiz zwischen den Jahren 1995–2000 respektive 2018–2022 verändert hat. Die Feldaufnahmen dafür fanden im Rahmen der ersten und zweiten Rote-Liste-Erhebung statt. Auch wenn das Belegmodell Veränderungen auf Artniveau berechnet, habe ich die Arten für dieses Kapitel in 18 ökologische Gilden eingeteilt, um die Veränderungen auf der Ebene der Flechtengemeinschaften zu beschreiben. Drei Gilden beschrieben eine Vorliebe für *freistehende Bäume*, *luftfeuchte Wälder* und *alte Bäume*, zwei Gilden waren definiert durch spezielle Photobionten (*trentepohlioid* und *cyano*), und zwölf Gilden waren von hohen und tiefen ökologischen Zeigerwerten hergeleitet für *Temperatur*, *Niederschlag*, *Kontinentalität*, *Eutrophierung*, *pH* und *Lichtverhältnisse*. Dank dieser gildenbasierten Herangehensweise konnte ich Verbindungen herstellen zwischen der Artzusammensetzung und Umweltveränderungen in der Schweiz über den gleichen Zeitraum. Ein kontinuierlicher Rückgang der Gilde *alte Bäume* lässt vermuten, dass sich diese spezialisierten Flechten noch nicht vom starken Rückgang erholen konnten, den sie im letzten Jahrhundert aufgrund von nicht nachhaltiger Waldwirtschaft erlitten haben. Die Anstrengungen der heutigen Waldwirtschaft, die Dichte alter Bäume zu fördern, konnten daran offenbar noch nichts ändern. Eine starke Zunahme eutrophierungstoleranter (*hohe Eutrophierung*) und basenliebender (*hoher pH*) Arten und eine gleichzeitige Abnahme eutrophierungssensibler (*geringe Eutrophierung*) und säureliebender (*tiefer pH*) Arten weist darauf hin, dass Flechtengemeinschaften nach wie vor stark von Schadstoffen in der

Luft und im Niederschlag betroffen sind. Während nämlich die Säureeinträge in den letzten Jahrzehnten kontinuierlich gesunken sind, werden die kritischen Werte für Stickstoffeinträge noch in zwei Drittel der Schweizer Landesfläche überschritten. Die Resultate lassen auch Vermutungen über den Effekt des Klimawandels zu. So haben wärmeliebende (*hohe Temperaturen*) und trockenheitsresistente (*wenig Niederschlag*) Arten zugenommen, während kälteliebende (*tiefe Temperaturen*) und feuchtigkeitsbedürftige (*viel Niederschlag*) Arten abgenommen haben. Sollten die genannten Faktoren tatsächlich die Gründe für die beobachteten Veränderungen sein, dann werden sich die Flechtengemeinschaften auch in den kommenden Jahrzehnten noch weiter in eine ähnliche Richtung entwickeln.

Ich habe in diesen drei Kapiteln gezeigt, dass es möglich ist, mit einem Datensatz aus teilweise wiederholten, teilweise einmalig durchgeführten Aufnahmen, Schätzwerte für die Häufigkeit von Arten zu erhalten, die für Erhebungsfehler korrigieren. Ich konnte zeigen, dass der Entdeckungsfehler trotz günstiger Voraussetzungen sehr gross sein kann in einer ökologischen Studie. Schwachstellen meiner Arbeit sind unter anderem gewisse Voraussetzungen der statistischen Modelle, die möglicherweise nur begrenzt erfüllt waren, und die Einschränkung der Modellkomplexität, die aufgrund der geringen Stichprobengrösse zustande gekommen ist. Für die Schweiz sehe ich zukünftig eine grosse Chance darin, die standardisierten Daten der Rote-Liste-Erhebungen mit den zahllosen Einzelbeobachtungen von Freiwilligen (oder aus anderen Projekten) zu kombinieren. Wenn Beobachtungen aus verschiedenen Quellen in einem einzigen Modell vereint würden, liessen sich Ausbreitung und Bestandsveränderungen in der Schweiz besser schätzen. Auf nationaler und internationaler Ebene, z.B. für globale Rote-Liste-Einschätzungen, wäre es ausserdem wünschenswert, eine Liste mit zuverlässigen und leicht zugänglichen Umweltvariablen zusammenzustellen, die die Modellierung von Flechtenvorkommen vereinfachen und standardisieren würde. Allerdings werden Schätzungen von Ausbreitungsgebieten oder Bestandsveränderungen allein die Aussterbewahrscheinlichkeit von Arten nicht reduzieren können, unabhängig von ihrer Genauigkeit. Schlussendlich müssen Massnahmen ergriffen werden, um das Fortbestehen der Arten zu sichern. Aber indem diese Arbeit dazu beigetragen hat, Rote-Liste-Einschätzungen zuverlässiger und genauer zu machen, hoffe ich, dass Naturschutzprioritäten gezielter dort gesetzt werden können, wo sie am meisten gebraucht werden.

INTRODUCTION

Importance of conservation assessments

We are in the middle of a biodiversity crisis. Animals and plants are becoming extinct at a pace observed only during the five major mass-extinction events found in the paleontological record (Barnosky et al., 2011; Ceballos et al., 2015; Cowie et al., 2022). Scientists largely agree that humans are the main cause of this accelerated species loss, through a combination of direct exploitation, human-induced land-use change (and associated habitat destruction), climate change, environmental pollution, and introduction of invasive species (Caro et al., 2022; De Schrijver et al., 2011; IPBES, 2019; Newbold et al., 2015; Sánchez-Bayo & Wyckhuys, 2019). Most scientists also agree that the extinction of many species in such a short time will entail a substantial reduction in the quality of human life on Earth, because an impoverished environment can no longer provide the ecosystem services on which we rely (Balvanera et al., 2014; Cardinale et al., 2012; Daily et al., 2000; Dobson et al., 2006; Gamfeldt et al., 2013; e.g., Naeem et al., 1994, 1997). Not least because of our dependence on ecosystems for our own survival and well-being, political leaders have come to understand the importance of biodiversity, at least in theory. In 1992, the Convention on Biological Diversity (CBD) took place in Rio de Janeiro, producing an agreement of the same name which has so far been signed by 168 states (https://www.cbd.int/information/parties.shtml, accessed 13 July 2023). Other international treaties and agreements followed, like the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), the Ramsar Convention on Wetlands of International Importance, and the International Plant Protection Convention (IPPC). Unfortunately, the CBD Secretariat (2020) announced in their regular report that not a single one of the 20 biodiversity targets for the period 2011–2020 (named “Aichi-targets” after the place of the conference) have been achieved. At the COP15 in 2022, the signatory parties of the CBD adopted the Kunming Montreal Global Biodiversity Framework, the most recent refinement of the global biodiversity targets for 2030 and 2050. Among others, the targets include 1) halting the human-induced extinction of threatened species, 2) reducing the rate of extinction of all species, and 3) using and managing biodiversity sustainably to ensure continued ecosystem services to people. In addition to global agreements, there are also regional agreements that make individual countries accountable for their conservation actions (or lack thereof). In Europe, the first agreement to ensure the conservation of biodiversity at the continental scale was the Bern Convention on the Conservation of European Wildlife and Natural Habitats from 1979. The governments of the individual countries are thus responsible for creating laws and ordinances that should halt the loss of biodiversity on their territory.

Halting the loss of biodiversity requires identifying the species most at risk and the factors that threaten them. This is a challenging task, because organisms differ strongly in their ecology, life-history traits, habitat requirements, and distribution patterns, making it difficult to measure the status of their populations with the same yardstick. Nevertheless, the International Union for the Conservation of Nature (IUCN) has developed a set of criteria that attempt just that. First suggested in 1994 (IUCN, 1994), adjusted a few times (latest in IUCN, 2012), and with guidelines most recently refined (IUCN, 2022), the IUCN criteria for a Global Red List are applicable to most groups of macro-organisms and to various data types, amounts, and qualities. Evaluating a species' global population against these criteria will result in a threat category that reflects the probability of extinction of the species at the global scale. There are eight major categories (Fig. 1): Extinct (EX), Extinct in the Wild (EW), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), and Data Deficient (DD). The status EX is given to species with no living individual on Earth, while EW means that the *natural* populations have disappeared or are no longer able to reproduce, but the species may still exist in captive populations. Species in either of the three categories CR, EN, and VU are considered *threatened*, with decreasing probability of extinction. NT indicates some probability of decline, but too low to qualify for any of the three threatened categories, and LC indicates that there is currently no indication that the species may disappear or decline in the near future. DD is assigned to a species only if data are so scarce or contradictory that no criterion can be applied in a satisfactory way. At the time of writing, 150 388 species have been assessed according to these criteria for the compilation of a Global Red List of Threatened Species (IUCN, 2023), including vertebrates, invertebrates, corals, plants, fungi, and species from several other organism groups.

National Red Lists (but also continental Red Lists, see e.g., EEA, 2018) are a regional version of the Global Red List, where the assessment is restricted to the part of a species' population that occurs within the national (or continental) borders. Most criteria are applied in the same way, but there are two additional categories: Regionally Extinct (RE) for species whose last individual within the defined area has disappeared, and Not Applicable (NA) for taxa whose population within the area is below a certain proportion (e.g., 2 %) of the global population (Fig. 1). Although national assessments can only be used for inference about a portion of the entire population, they also have advantages. First and foremost, most biodiversity-related legislation acts at the country level. A national assessment can thus be an instrument for national governments to quantify and improve the status of biodiversity within their political boundaries. Several countries use national Red List categories, directly or indirectly, to either prioritize species for conservation, designate conservation areas (e.g., based on a certain number of red listed species), or to choose actions that mitigate the most common threats. Second, within the same country, environmental data are often available at homogeneous resolution and in similar quality, because they are more likely to be monitored by the same authority than studies across borders.

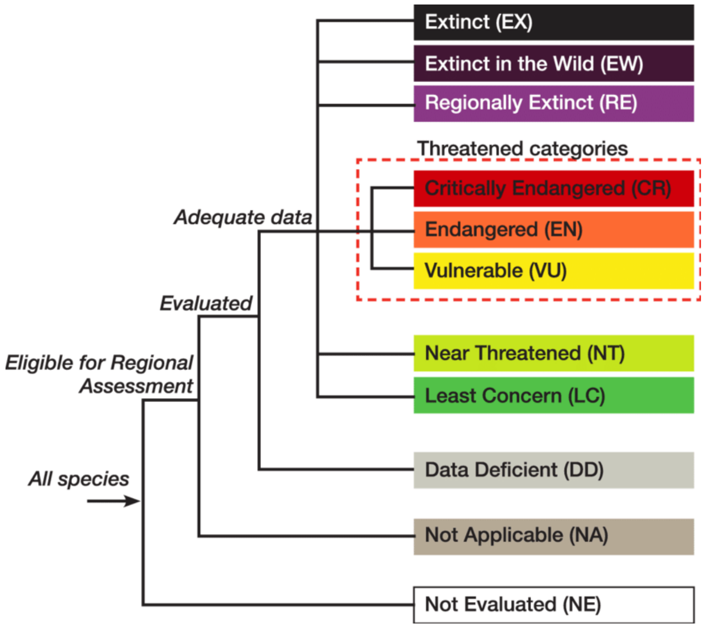

Fig. 1 Red List categories as defined by the IUCN (2012). The two categories Regionally Extinct (RE) and Not Applicable (NA) only apply to regional assessments. When a species is endemic to a country or region, the categories RE and Extinct (EX) are equivalents.

In Switzerland, the Federal Council is obliged by the 1991 Nature Protection Ordinance to commission national Red List assessments at regular intervals (Article 14 Paragraph 3 in Natur- und Heimatschutzverordnung NHV, SR 451.1, www.admin.ch/ch/d/sr/45.html). Although species listed as threatened on the national Red List are not *per se* protected, the Red List nevertheless serves as a legal document. On the one hand, the cantons (political subunits within Switzerland) are responsible for maintaining biodiversity on their land, and the persistence and/or support of threatened species is one criterion by which their performance can be evaluated. On the other hand, threatened species and their categories are used to select priority species for conservation (‘national prioritäre Arten’; BAFU, 2019) and to identify habitat types in need of protection due to their populations of threatened species.

In summary, national Red Lists are a government’s tool to assess the current status of the national biodiversity and to set conservation priorities as a way to fulfill their duty towards achieving the goals set up by the international community.

Switzerland over the last decades

In the last 20 to 30 years, different species groups have been assessed for the national Red List in Switzerland. At the same time, the Swiss landscape has continued to undergo land-use and other changes, and several political initiatives and programs have been started to enhance biodiversity conservation. The following sections give a short overview over these changes and how they apply to epiphytic lichens.

National Red Lists

At the time of writing, national Red List assessments exist for 20 different species groups in Switzerland (FOEN & InfoSpecies, 2023). There are still many species, however, that have either not been evaluated or for which the evaluation did not yield any conclusion due to data deficiency. While 10 844 species currently have a valid Red List status, we know little about the remaining 80% of all 56 009 species that are known to exist in Switzerland. Roughly half of the 10 844 evaluated species (53%) are considered LC, 12% are NT, 33% are threatened (16% VU, 11% EN, 6% CR), and 2% are considered RE (Fig. 2). Geographically, the concentration of threatened species is highest in the intensively managed Plateau and lowest in the more pristine Alps of eastern Switzerland. The main threats to species are the destruction or deterioration of habitat and, more generally, restricted extents of occurrence.

Comparisons between recent and historic Red Lists are only possible for six species groups that were consistently evaluated with the same methods (p. 23, FOEN & InfoSpecies, 2023). Amphibians and dragonflies have improved somewhat in Red List status, vascular plants and birds show a slight negative trend, and reptiles and fishes a clear negative trend. Despite some improvements in the conservation status of individual species, the report concludes that the conservation status of species in Switzerland has not generally improved and that Switzerland, just like other countries (CBD Secretariat, 2020), failed to achieve the Aichi-targets set at the COP10 in Japan.

Since 2016, Switzerland also has a Red List of threatened habitat types that complement the species-specific assessments (Delarze et al., 2016). Of 167 evaluated habitat types, 48% were categorized as threatened. Aquatic and wetland habitats are generally the most threatened while unproductive land and forest habitats are currently the least threatened (Fig. 3). The threat status of habitat types correlates with the number of threatened species in that habitat type, e.g., species bound to aquatic or wetland habitats are particularly threatened, but the assessment of threatened habitat types was made independently of the threatened species. Nevertheless, it is likely that species bound to highly threatened habitat types, but for which no species-specific Red List assessment was made, may be equally threatened.

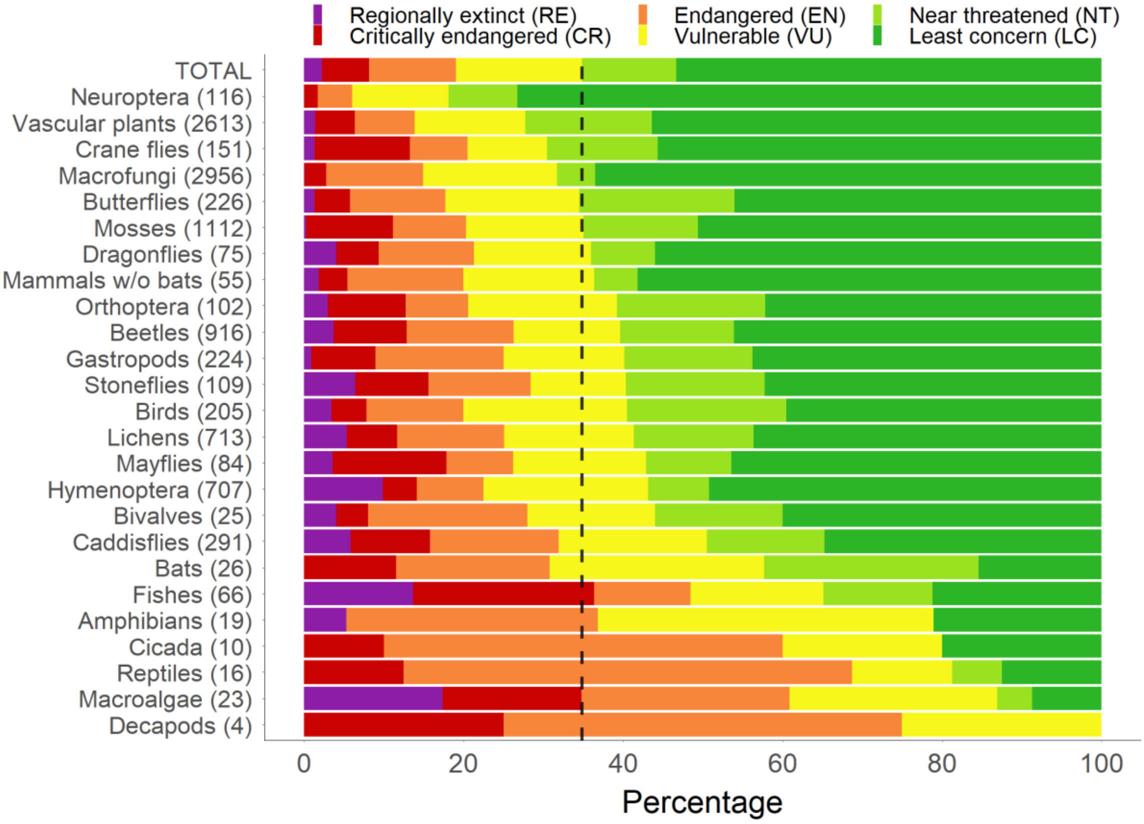

Fig. 2 Distribution of Red List categories of all currently evaluated species in Switzerland. The dashed black line marks the average percentage of threatened species. Source: FOEN and InfoSpecies (2023). Species evaluated as Data Deficient (DD) were omitted from this figure.

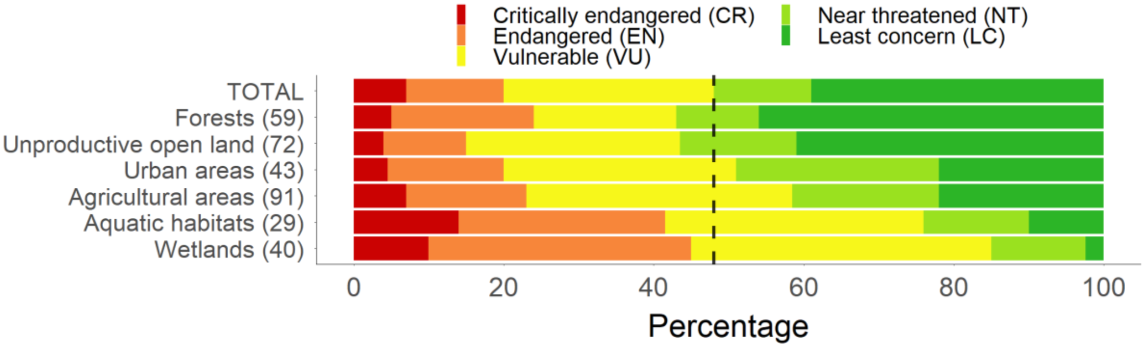

Fig. 3 Distribution of Red List categories of evaluated habitat types in Switzerland across major land-use types. The dashed black line marks the average percentage of threatened habitat types. Note that several habitat types occur in multiple land-use types, e.g., riverbanks may belong both to wetlands and to agricultural areas. Source: Delarze et al. (2016).

Land use

With a longitudinal width of 348 km and a latitudinal width of 220 km, Switzerland covers 41 285 km^2 reaching from its lowest point at 193 m a.s.l. to its highest point at 4636 m a.s.l. (The Federal Council, 2023). There are five major biogeographic regions: the calcareous Jura mountains in the Northwest, the densely populated and agricultural lowland Plateau, the Pre-Alps with a mix of forests and montane pastures, the scarcely populated higher-elevation Alps, and the forested and rather steep Southern Alps. According to the Federal Statistical Office (2021), 25.1% of Switzerland is considered unproductive land, 31.8% are covered by forests and wooded land, 35.2% are used for agriculture, and 7.9% are currently occupied by urban areas (Fig. 4).

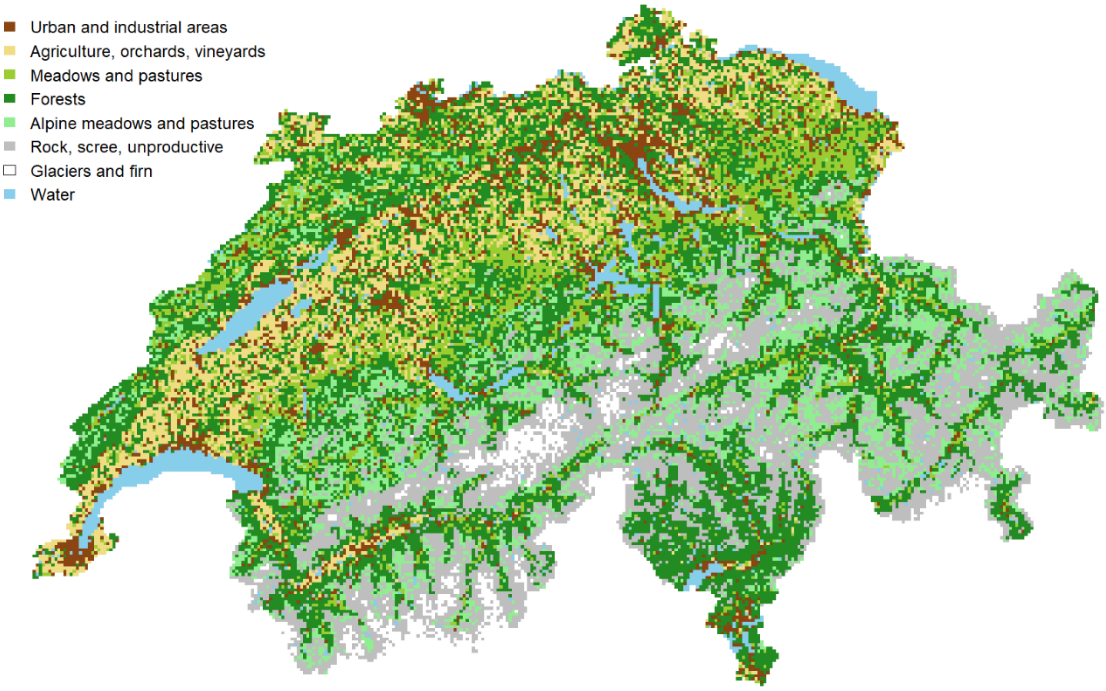

Fig. 4 Dominant land use in Switzerland 2013–2018 at a 1x1 km grid. The Jura mountains in the Northwest consist mostly of forest and meadows and pastures. The Plateau is dominated by agricultural land and urban areas, and the Pre-Alps, Alps, and Southern Alps are a mosaic of forests, meadows and pastures, and unproductive land in the form of glaciers and firm, bare rock, scree, or unproductive vegetation. The data for this map were downloaded from the Federal Statistical Office (2023).

The most striking change in land use over the last decades has been a substantial increase in the urban area from 6.8% in the 1992–1997 assessment to 7.9% in the 2013–2018 assessment (Federal Statistical Office, 2021). This expansion by 16% occurred largely at the expense of agricultural land (36.7% in 1992–1997 vs. 35.2% in 2013–2018), and it correlates with an increase of similar magnitude in human population from 6.8 million in 1992 to 8.0 million in 2013 (Federal Statistical Office, 2022).

From 1900 to 1990, the agricultural land had experienced a constant intensification (reviewed in Walter et al., 2010). The intensification involved heavier machinery, greater number of livestock animals, increased field size in conjunction with a decline in structural heterogeneity, heavily raised application of fertilizer and pesticides, and the widespread sowing of homogeneous and species-poor seed mixes. The result of the intensification was such a marking loss of species diversity, especially at lower elevations, that the Federal Constitution (Art. 104) was changed: the new Law on Agriculture (Landwirtschaftsgesetz 910.1) ties the payment of governmental subsidies to farmers to a proof of ecological standards ("ökologischer Leistungsnachweis"). In addition, the application of fertilizer and the number of livestock animals are restricted by the Swiss Ordinance on Air Pollution Control (SR 814.318.142.1). Since 2000, more conditions were added to the catalogue of requirements for subsidies, such as the obligation to designate a certain percentage of the land as ecological compensation area. Furthermore, several monetary incentives were created to encourage more sustainable agricultural practices (FOEN & FOAG, 2008, 2016).

These new regulations of agricultural practices have led to some improvement for biodiversity on agricultural land. For example, the abundance and diversity of vascular plants, grasshoppers, and wild bees was shown to be greater in meadows designated as ecological compensation areas than in conventionally managed hay meadows (Knop et al., 2006). Likewise, vascular plant and snail richness increased over a period of five years at sites that included ecological compensation areas and not in others (Roth et al., 2008). Nitrogen emissions, largely of agricultural origin, have also started to decline in Switzerland (Rihm & Künzle, 2023). After decades of world-wide increases, Europe is so far the only continent that has succeeded in bending that curve (Liu et al., 2022; Seitler et al., 2021; Vivanco et al., 2018). Despite the reduced emissions, however, nitrogen deposition still exceeds ecologically critical levels in more than half the country (Rihm & Künzle, 2023).

The forest management in Switzerland has undergone several important changes over the last decades. After a long period of profit-oriented forestry, the Swiss forests of the 2000s were young, evenly aged, and rather dark (Brassel & Brändli, 1999) and had lost much of their diversity (Bollmann et al., 2009; Scheidegger et al., 2010; Walther & Grundmann, 2001; Watt et al., 2007). The implementation of a new Forest Policy (FOEN, 2013) and a Swiss Biodiversity Strategy (FOEN, 2012) introduced more sustainable forestry practices with more structural and tree species heterogeneity, and a slowly increasing number of old trees (Brändli et al., 2020). It is, however, too early to draw conclusions about the effectiveness of the Biodiversity Strategy, as the first period for the implementation of the Biodiversity Action Plan will end only in December 2024 (FOEN, 2017, 2023).

Climate

The climate in Switzerland is generally temperate with warm summers and cool winters, some precipitation throughout the whole year but with the maximum over the summer months. Due to Switzerland's topography, however, there is great spatial variation in temperature and precipitation. The ongoing climate change has led to temperature increases that lie above the international average increase, longer periods of extreme heat and drought in summer, more intense solar radiation, melting of glaciers and permafrost, and fewer precipitation days with heaver downpours (Köllner et al., 2017; NCCS, 2018; Scherrer et al., 2016). Fig. 5 illustrates how average temperature, solar radiation, and number of precipitation days have changed from the period 1986–2000 to the period 2008–2022.

Situation for epiphytic lichens

Lichens are symbiotic organisms that consist of at least two symbiont partners, a fungus and a green alga or cyanobacterium. Nearly 2000 species of lichens have been reported from Switzerland (Stofer et al., 2019a), of which 500–600 are primarily epiphytic, which means that they grow on bark of trees or shrubs. Among the epiphytic lichens, 520 species were evaluated for the national Red List with 208 species (40%) being considered threatened (categories VU, EN, CR) and 199 species (38%) being considered LC (Scheidegger et al., 2002). Habitats with a particularly high number of threatened species were light forests with long ecological continuity and a copious supply of dead wood, open forests with old oaks, wooded meadows and pastures, and free-standing deciduous trees, such as ash or sycamore maple, but also fruit trees in areas without application of fertilizer or pesticides.

Epiphytic lichens must naturally be affected by forest management and by regulations that relate to the management of trees in the agricultural landscape. While the profit-oriented forestry practices of the last century led to a decline in epiphytic lichens in more heavily managed forests (Scheidegger et al., 2010), there is hope that the current trend towards lighter, more heterogeneous forests with increasing amount of dead wood and old trees will have a positive effect on their suitability for lichens. The ongoing change in the open landscape, however, may be less favourable for epiphytic lichens. Since 2008, the invasive fungus *Hymenoscyphus fraxineus* has infected thousands of European ashes *Fraxinus excelsior* (Klesse et al., 2021), killing many free-standing or road-side trees that would have been suitable substrate for several specialist lichens. More free-standing trees have disappeared through the ongoing abandonment of traditional wooded pastures in the Alps, especially those dominated by sycamore maple *Acer pseudoplatanus* (Kiebacher et al., 2018). Like other extensively used alpine pastures, many of these biodiverse habitats had to give way to more intensively grazed pastures, or they were overgrown by forest when no longer grazed (Tappeiner et al., 2003).

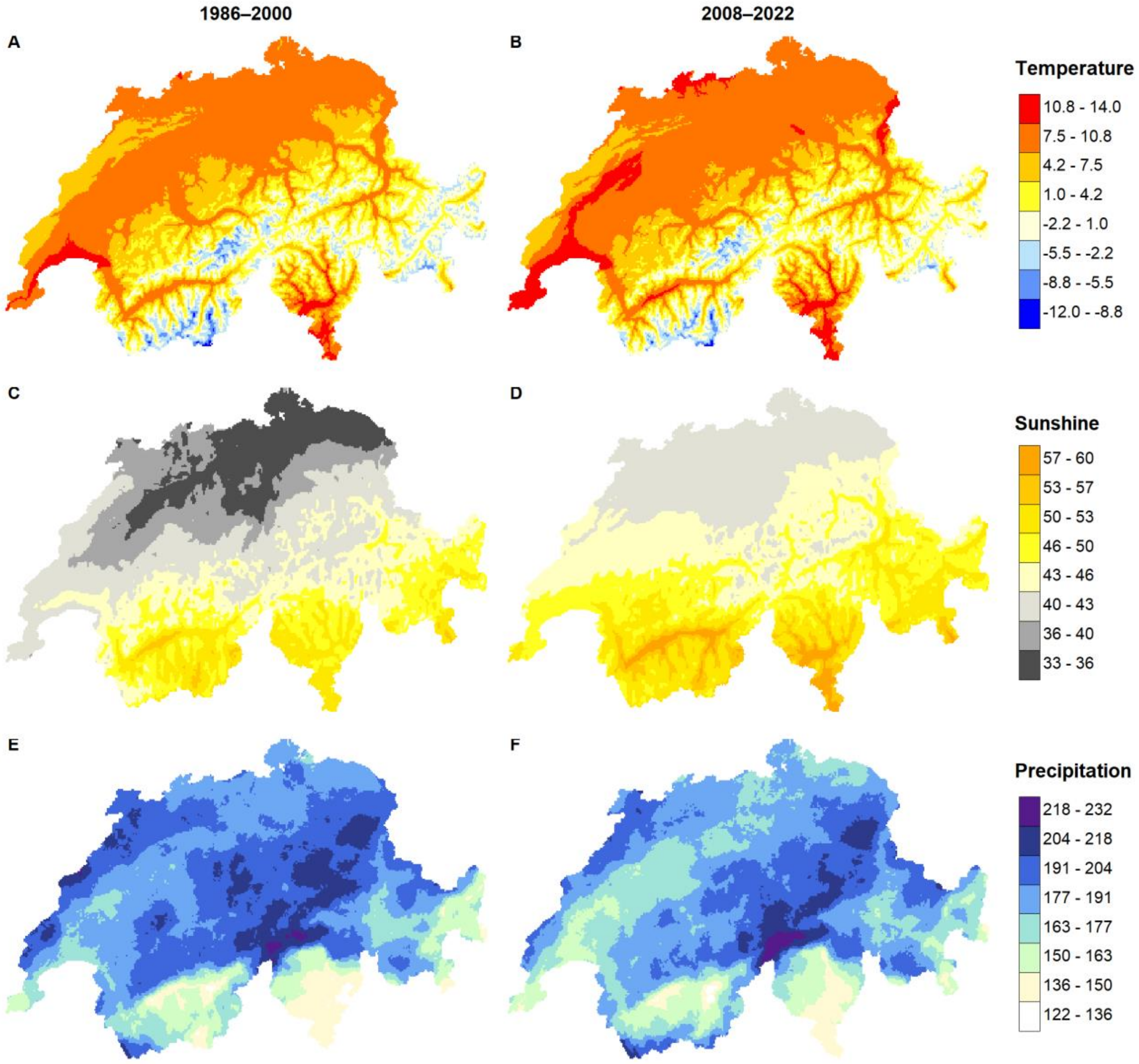

Fig. 5 Climatic changes in Switzerland over 20 years. The left-hand panels illustrate the median values across the period 1986–2000, and the right-hand panels the median values across the years 2008–2022 for yearly mean temperature in °C (A, B), relative sunshine duration in % (C, D), and number of precipitation days per year (E, F). Data for these maps were provided by MeteoSwiss (temperature: TabsY, precipitation: RhiresD, sunshine duration: SrelY).

Lichens in open habitats have been under adverse pressures from deposition of chemical substances. In the 1970s to 1980s, large amount of acid gases, especially sulphur dioxide and nitrogen oxides, were emitted from traffic and industries and deposited on the bark of the surrounding trees in tiny particles or dissolved as acid rain (BAFU, 2022; Künzle, 2022). Many lichens are very sensitive to such environmental pollutants and disappeared almost completely from European cities and industrial areas, leaving only a few acidophytic species behind (Ferry et al., 1973; Gilbert, 1969; Hawksworth & Rose, 1970; Herzig & Urech, 1991; Seaward, 1993; van Herk, 2001). Since the 1990s, the emission of these toxic gases has gradually declined thanks to stricter regulations (BAFU, 2022; Künzle, 2022), allowing bark pH to recover and lichens to recolonize trees (van Dobben & ter Braak, 1998). The emission and deposition of nitrogen, on the other hand, has declined only little over the past 20-30 years and is still exceedingly high (Rihm & Künzle, 2023). Compared to the pre-acid-rain conditions, the current environment encountered by epiphytic lichens in open landscapes is therefore much richer in nitrogen, which is likely to lead to a different set of common species than before.

Sampling errors in ecological surveys

Ecological surveys assess the distribution of species across space or time. They collect data on occurrence (presence/absence) or abundance (number of individuals), either focussing on a single species or on entire species communities. Unfortunately, however, neither occurrence nor abundance are always measured without error. Two types of errors can occur: false-negative and false-positive sampling errors (Kéry & Royle, 2016, 2021; MacKenzie et al., 2018; Royle & Dorazio, 2008; Williams et al., 2002). False-negative sampling errors (*false negatives*) occur when a species or an individual is overlooked. This error is usually due to imperfect detection, i.e., the failure to detect a species or individual, and it implies that the *detection probability* is less than 1. False-positive sampling errors (*false positives*) are usually the result of misidentification or double-counting and describe the recording of a species or individual that was not actually there. In most applications, false negatives are likely to be more common than false positives, because the former usually result from limited sampling effort (Garrard et al., 2008; McArdle, 1990), while the latter depend more on people's ability to identify or count (p. 84, Royle & Dorazio, 2008), and standardised sampling protocols can keep them to a minimum. In practice, it is therefore a lot more common that researchers account for false negatives in their data than for false positives, which are often just assumed to be absent or negligible (but see Bailey et al., 2013; Banner et al., 2018; Ferguson et al., 2015; Guillera-Arroita et al., 2017; Louvrier et al., 2018; Miller et al., 2011; Royle & Link, 2006; Ruiz-Gutiérrez et al., 2016). This is also the case here, as I assume the absence of false positives in all the data I present in this thesis, and I explain possible consequences of a violation of this assumption in the Discussion. My focus in this thesis is the more common sampling error imperfect detection.

Imperfect detection of animals and plants

Awareness of imperfect detection and development of statistical tools to account for it have seen a tremendous increase over the last 40 years. The core idea was born in the field of animal capture-mark-recapture studies (Otis et al., 1978; Pollock et al., 1990; Seber, 1982; White et al., 1982). By marking individuals, releasing them, and attempting to capture them again, it was possible to estimate the size of a population, because the ratio of marked vs. previously unmarked individuals during later capture occasions as well as the individual *detection histories* would allow insight into the number of undetected individuals.

The estimation of imperfect detection was then applied to distance sampling (Buckland et al., 1993, 2001), making use of the fact that detection probability of individuals is related to their distance from the observer. Around the year 2000, researchers first started estimating detection probability in studies of patch occupancy of single species (Bayley & Peterson, 2001; Gu & Swihart, 2004; MacKenzie et al., 2002; Moilanen, 2002; Tyre et al., 2003; Wintle et al., 2004). Estimates of local abundance (Alexander et al., 1997; Royle et al., 2005) and estimates of species richness (Boulinier et al., 1998; Dorazio et al., 2006; Yoccoz et al., 2001) could also be corrected for imperfect detection following the same statistical approach. More recent modifications extended analyses to population dynamics over time (Fukaya et al., 2017; Kéry et al., 2009; MacKenzie et al., 2003, 2009; Peach et al., 2017; Rossman et al., 2016; Royle & Kéry, 2007) and to dynamics of entire species communities (Dorazio et al., 2010; Rossman et al., 2016; Ruiz-Gutiérrez et al., 2010; Ruiz-Gutiérrez & Zipkin, 2011; Yamaura et al., 2011).

Most animals move around and may exhibit activity patterns dependent on weather, season, or time of day that make them particularly prone to imperfect detection and variation in detectability. Due to the ubiquity of imperfect detection in animal studies, many researchers nowadays systematically estimate and account for it in their surveys, including numerous recent studies of amphibians (Amburgey et al., 2021; Moor et al., 2022; Siffert et al., 2022; Takahara et al., 2020), reptiles (Amburgey et al., 2021; Boback et al., 2020; Mitrovich et al., 2018; Turner et al., 2022), mammals (Collins et al., 2021; Gomez et al., 2018; Hogg et al., 2021; Magle et al., 2021; Paniccia et al., 2018), and birds (Briscoe et al., 2021; Henckel et al., 2020; Henry et al., 2020; Iknayan & Beissinger, 2018; Maphisa et al., 2019; Şen & Akçakaya, 2022; Strebel et al., 2021).

Plants cannot avoid detection by running away or hiding. This fact has led botanist John L. Harper to write into his book on plant biology: “plants stand still to be counted and do not have to be trapped, shot, chased, or estimated” (Harper, 1977). Due to their sessile nature, plants are therefore expected to be easier to detect and survey than animals. There are much fewer studies on detection probability of plants (or other sessile organisms) than of animals, but the existing evidence does not confirm the expectation. The first studies on plants that explicitly estimated detection probability found that it correlated both with plant size and life state, i.e., whether the individual was in a dormant, vegetative, or flowering state, but that it was rarely perfect (Alexander et al., 1997; Gregg & Kéry, 2006; Kéry & Gregg, 2003; Shefferson et al., 2001; Slade et al., 2003). Later studies found that detection probability of plants generally varied between species and often also between habitats, and that it was always correlated with local abundance (Al-Chokhachy et al., 2013; Chen et al., 2009, 2013; Dennett et al., 2018; Dennett & Nielsen, 2019; Garrard et al., 2013; Middleton & Vining, 2022; Moore et al., 2014; Perret et al., 2023). Additional evidence for imperfect detection of plants comes from numerous studies that report differences in species lists by different observers but without explicitly accounting for them (Boch et al., 2022; Burg et al., 2015; Futschik et al., 2020; e.g., Lepš & Hadincová, 1992; Vittoz et al., 2010). The consideration of detection probability in plant studies was reviewed multiple times in recent years (Chen et al., 2009, 2013; Dennett et al., 2018; Middleton & Vining, 2022; Perret et al., 2023). The authors of these studies conclude that in virtually all plant surveys, detection probability was considerably smaller than 1. Plants, it seems, are not quite as easy to detect as their sessile nature may suggest. In spite of its evident omnipresence, however, the authors note that imperfect detection is not commonly accounted for in the majority of plant surveys and monitoring programs.

Imperfect detection of lichens

Not only plants “stand still to be counted”; fungi and lichens and many other organisms do too. And while most fungi and plants show seasonal variation in morphology, most lichens do not. Lichenologists Jessica Allen and James Lendemer phrase it like this: “Surveys for total diversity [of lichens] do not suffer from the incomplete sampling due to variation in flowering or fruiting times that affect inventories of plants and other fungi, or low detectability due to unusual weather patterns that can impact animal surveys” (Allen & Lendemer, 2016). Lichens could thus be expected to be yet easier to survey than plants.

Imperfect detection of lichens has been studied even less than imperfect detection of plants. As for plants, however, the evidence that does exist fails to confirm this expectation. McCune et al. (1997) were the first to state their awareness that lichens may not be perfectly detected. They conducted several independent surveys of the same sampling sites (area: 3780 m^2) by multiple lichenologists and found that no observer found more than 63 % of all detected lichen species and that estimates of species richness would be strongly biased if data from only one observer were taken into account. A similar comparative study by Vondrák et al. (2016) with much larger survey areas confirmed these findings. In their sites of 12.5 ha, only 23 % of all detected lichen species were found by all eight lichenologists, 20 % were found by only one person. Even when sampling was standardised so that all observers would walk along the same transect, there were considerable differences between observers (Britton et al., 2014). The ratio of plot size to time spent searching for lichens is likely to affect detection probability, with smaller plot size and greater time effort logically leading to higher probabilities of detection. However, no plot size seems to be small enough to guarantee perfect detection of species, as Brunialti et al. (2012) discovered when they compared biomonitoring data from different teams collected on the same trees. Their sampling units were grid cells of 10 x 10 cm and yet there was a difference of ten species between the group with the lowest and the group with the highest species count across all cells.

Several lichen studies have approached the issue of imperfect detection in a rather indirect way. Indirect, because they focussed on the *proportion of species* that is detected instead of estimating the detection probability of individual lichen species. Data on epiphytic lichens is commonly collected by searching the lowest two metres of the stem, either of individual trees (when trees are the sampling unit; Kiebacher et al., 2016; Marmor et al., 2013) or of a subset or all trees within a plot (when plots are the sampling unit; Boch et al., 2013; Dymytrova et al., 2013). Restricting the search to the lowest two metres of the trunk is merely a question of logistic convenience and not a decision based on lichen biology. In fact, Marmor et al. (2013) and Boch et al. (2013) showed that of all lichen species present on a tree in the middle of the forest, only 34-46 % could be found on its stem below 2 m from the ground. This proportion is similar for free-standing trees (39 %; Kiebacher et al., 2016). When species richness is measured not at tree-level but at plot- or stand-level, the observed proportion is higher but still only represents 58-62 % of the actual species richness (Boch et al., 2013; Kiebacher et al., 2016). Importantly, some species seem to have a preference for positions above 2 m from the ground (Fritz, 2009; Kiebacher et al., 2016; Marmor et al., 2013) and these species are therefore more likely than others to remain undetected by this sampling method. When population estimates of lichens are based on lower-stem sampling, they may therefore be biased low.

The earliest study to explicitly estimate detection probability of individual lichen taxa was conducted by Casanovas et al. (2014). They estimated the sampling error of citizen scientists who were asked to photograph morphologically dissimilar macrolichens. A few years later, Outhwaite et al. (2019, 2020) accounted for imperfect detection in an estimation of large-scale trends of lichens and many other species groups in the UK. Bhatti (2020) set up several experiments with artificial “look-a-lichens” to be able to investigate detection probability more thoroughly by varying lichen density or number of observers, and by testing various modelling approaches. He found that detection probability varied between observers and that common species were more easily detected than rare species. Estimates of species occurrence became much more precise with four instead of two surveys/observers, but there was generally some heterogeneity in detection probability between sampling units (i.e., trees) which caused a bias in estimates of lichen occurrence when it was not accounted for. Cáceres et al. (2008) also found an effect of abundance and conspicuousness of species on their detection probability, albeit under an opportunistic sampling design. Although these studies vary in their sampling designs and the variables investigated, their common feature is that detection was never perfect in either.

Consequences of ignoring imperfect detection

When imperfect detection occurs but is ignored in the analysis of survey data, biases are introduced to the estimates of the variables of interest. Occupancy, area of distribution, and abundance are, sometimes severely, underestimated (Guillera-Arroita et al., 2014; Kéry & Schmidt, 2008; MacKenzie et al., 2002; Mosher et al., 2018; Royle, 2004; Tyre et al., 2003). As a result of species-specific biases, diversity metrics like species richness are also biased low (Broms et al., 2014; Guillera-Arroita et al., 2019; Iknayan et al., 2014; Jarzyna & Jetz, 2016). When only occurrence data are available without additional information on local abundance, imperfect detection will weaken the estimated effect of habitat covariates on occurrence (Gu & Swihart, 2004; Kéry, 2004; Lahoz-Monfort et al., 2014; Tyre et al., 2003). Yet larger biases in parameter estimates may occur when detection probability is affected by an environmental or habitat covariate that is at the same time correlated with the occurrence of the species. In these situations, habitat effects on detectability may be confounded with habitat effects on occurrence if detection probability is not accounted for (Buckland et al., 2008; Chen et al., 2013; Gu & Swihart, 2004; Kéry, 2004; Tyre et al., 2003).

When detection probability varies over time, it can be difficult to detect underlying population trends. A different set of observers or different sampling intensities at two different points in time may be enough to lead to spurious patterns of population change that are in fact due to differences in detection (Archaux et al., 2012; Britton et al., 2014; Kendall et al., 1996; Kéry et al., 2009). Revisitation studies, which aim to confirm the persistence of populations at known localities, are particularly prone to biased estimates. Given that revisitation sites were selected conditional on past detection, any failure to detect the species during the revisitation will lead to an overestimation of extinction rates (Kéry, 2004; Kéry et al., 2006). However, sampling designs that do not start with a conditional selection of sites may likewise be unable to avoid biased estimates. When changes in observed occupancy or abundance are exclusively assigned to changes in the population, dynamic rates of colonization and extinction are usually overestimated (MacKenzie et al., 2003; Manna et al., 2017; Rossman et al., 2016; Sutherland et al., 2014). In addition to a general bias in estimates of occurrence and population dynamics, a review by Guillera-Arroita (2017) also points out that the precision of these estimates is generally too high, making inferences stronger than they should be.

Occupancy models

Occupancy models have become the most widely used method to estimate occurrence (presence/absence) of species while accounting for imperfect detection (Kéry & Royle, 2016, 2021; MacKenzie et al., 2018). They were independently proposed by MacKenzie et al. (2002) and Tyre et al. (2003). The original models were suited to data from single species that were collected over repeated visits to the same sites within the same season. The repeated visits in occupancy models are the equivalent to recapture occasions in capture-recapture designs, from where the idea was adapted. During each visit to a site, the species can either be detected (1) or not (0). Over *J* repeated visits, the site thus accumulates what is called a *detection history* of length *J*. With *J*=4, for example, the detection history may be [1 0 0 1], meaning that the species was detected during the first and last visits, but not during the second and third visits.

Occupancy models account for detection probability with the help of a two-level *hierarchical* model structure. The two hierarchies describe the two processes that produced the observed data *y*. The first level represents the *ecological process* of occupancy, which determines the true occupancy state *z* of site *i* (1 if occupied, 0 if unoccupied). The variable z_i follows a Bernoulli distribution with a probability of occupancy Ψ_i:

$$z_i \sim \mathrm{Bernoulli}(\Psi_i).$$

Ψ_i can depend on covariates that are specific to the site *i*, e.g., local climate or habitat type. Commonly, the relationship between the probability Ψ_i and the covariates is described with a logistic regression, i.e., a linear regression model connected to Ψ_i via a logit-link function:

$$\mathrm{logit}(\Psi_i) = \alpha_0 + \alpha_{1-n} \times X_{\Psi,i,1-n}$$

where α_0 is the intercept and α_{1-n} are the coefficients for the site-specific occupancy covariates $X_{\Psi,i,1-n}$. As the model allows for imperfect detection, *z* is not directly (or only partially) observed, i.e., it is a latent variable.

The second level of hierarchy describes the *observation process* of detecting or missing the species. It is conditional on the first level because the detection of a species depends on its occurrence. Under the assumption of no false-positive sampling errors, a species can therefore only be detected at a site that is occupied (z = 1). For an occupied site *i*, the observed data $y_{i,j}$ from visit *j* will be Bernoulli distributed with a detection probability $p_{i,j}$:

$$y_{i,j} \sim \mathrm{Bernoulli}(z_i \times p_{i,j})$$

When a site is not occupied (z = 0), the term in brackets becomes zero, and *y* will then also be zero. Reversely, when the observed *y* is 1, *z* must also be 1.

Detection probability $p_{i,j}$ can also depend on covariates, which may be site- or visit-specific. This relationship is again described with a logistic regression model:

$$\mathrm{logit}(p_{i,j}) = \beta_0 + \beta_{1-m} \times X_{p,i,j,1-m}$$

where β_0 is the intercept and β_{1-m} are the coefficients for the site- or visit-specific detection covariates $X_{p,i,j,1-m}$.

Occupancy models can be fitted using Maximum Likelihood or Bayesian approaches. A lot of software has been developed for either like Stan (https://mc-stan.org), BUGS (Lunn et al., 2013; Spiegelhalter et al., 2003), JAGS (Plummer, 2003, 2017), TMB (Kristensen et al., 2016), and countless R-packages incl. R2WinBUGS (Sturtz et al., 2005), rjags (Plummer, 2022), jagsUI (Kellner, 2021), nimble (de Valpine et al., 2017; NIMBLE Development Team, 2023), glmmTMB (Brooks et al., 2017), ubms (Kellner et al., 2022), and spOccupancy (Doser et al., 2022).

Most Bayesian software use Markov chain Monte Carlo (MCMC) simulations to estimate model parameters (Gamerman & Lopes, 2006). The output of an MCMC is a large number of values, called the *posterior* or *posterior distribution* of the parameter. The posterior allows direct estimation of the probability of a hypothesis given the data, model, and prior assumptions. This approach to drawing inferences is distinct from standard significance testing in maximum likelihood statistics. In significance testing, inference is based on the p-value, a measure of the probability of obtaining the observed data or data more extreme given the null hypothesis (Greenland et al., 2016).

Since occupancy models were first proposed, numerous extensions have been developed. Not only single species but entire species assemblages can now be modelled in community or multi-species occupancy models (Dorazio et al., 2006; Dorazio & Royle, 2005; Chapter 11 in Kéry & Royle, 2016; Chapter 15 in MacKenzie et al., 2018). These models often make use of an additional hierarchical level that describes the variation between species as coming from a common distribution with a mean and a standard deviation. Fitting such a species random effect allows inferences also about species with very few observations, or even with no observations at all, in order to include never-detected species in estimates of species richness (Royle et al., 2007). Other extensions allow the estimation of occupancy dynamics over time, either for single species (Chapter 4 in Kéry & Royle, 2021; MacKenzie et al., 2003; Chapter 8 in MacKenzie et al., 2018) or entire communities (Dorazio et al., 2010; Chapter 5 in Kéry & Royle, 2021). These dynamic, or multi-season, models either allow occupancy to vary over time using a fixed or a random effect, or they explicitly estimate the rates of colonization and extinction which lead to changes in occupancy. Further extensions include application of occupancy models to data that use time to first detection to inform estimates of detection probability (Garrard et al., 2008), to data collected along transects (Guillera-Arroita et al., 2012; Hines et al., 2010), or to data from different sampling methods (Nichols et al., 2008). A book by MacKenzie et al. (2018) offers an excellent introduction to occupancy modelling with a thorough review of available methods. Two book volumes by Kéry & Royle (2016, 2021) give equally excellent and pedagogic instructions on how to fit these models in R.

Aims

Towards revising the national Red List of epiphytic lichens for Switzerland

In 2018, Stofer et al. (2019b) began the revision of the existing national Red List of epiphytic lichens in Switzerland. The field work was completed in October 2022, but the analysis will not be finished until 2024. The sampling strategy for the revision was very similar to the one used in the first Red List (Scheidegger et al., 2002), though the sample size had to be reduced by nearly 30% because of budget restrictions. The most time-consuming sampling method was the thorough survey of standardised sampling plots of 500 m^2 on which observers recorded all epiphytic lichens. These plots served two main purposes: 1) to estimate the present area of occupancy (AOO) of the species, and 2) to estimate the change in AOO over the last 20 years by comparing the current data with the data from the first Red List. These metrics (AOO, and change in AOO) will be very useful when applying criteria during the actual Red List assessment next year (IUCN, 2012).

In addition to the standard plot surveys, independent repeated visits were conducted on a subset of these sites to assess the reproducibility of the species lists. Conducting repeated visits and having to identify the additional collected material, even if only from a subset of the plots, is costly. One may therefore legitimately ask whether this effort is necessary. With respect to Red List assessments, there are two aspects to consider. The first one is that imperfect detection, if not accounted for, leads to an underestimation of the static occupancy (and thus AOO) and distribution of a species at any given point in time (Kéry & Schmidt, 2008). The second aspect is that estimates of population change over time can be biased in different directions if detection probability varies over time (Archaux et al., 2012; Kendall et al., 1996). In this case, detection probability must be estimated separately for each point in time to unambiguously separate between occupancy and detection. Before the data are collected and detection probability is estimated, it is thus impossible to know whether it was necessary to repeat visits for all time points to obtain unbiased estimates of population changes over time.

A preliminary analysis of the data collected during repeated visits in the first Red List suggests that these data are likely to contain false negatives (Scheidegger et al., unpublished data). If detection probability was imperfect during the first Red List, it is likely to be imperfect now. Whether imperfect detection occurs at the same rate, is less clear. However, there are reasons to not assume a constant detection probability over time. First, the set of observers employed in field work and identification of specimens differed between the two Red Lists. Second, the only two team members who participated in both must have gained much experience over the 20 years that passed between them. And third, the sampling strategy was also slightly different. Observers of the first Red List followed a strict order of substrates to search (stems below 2 m of larger trees first, followed by stems of smaller trees, followed by branches) and compiled species lists for each tree species on the plot. Observers of the second Red List, on the other hand, did not have to follow any order and compiled only one list of epiphytic lichens for the entire plot. The possibility that detection probability changed over time can therefore not be excluded, and accounting for it is a prerequisite to assign species to the correct Red List category.

Thesis structure

The ultimate goal of this thesis is to assess the change that epiphytic lichen communities in Switzerland have undergone over the past 20 years while correcting for imperfect detection of species. Until now, however, there have been rather few studies on imperfect detection of lichens. The accomplishment of my ultimate goal therefore requires additional prior investigation, which has led me to the three chapters that I describe in the following.

In **Chapter 1**, I test whether the structure of the lichen data is suitable for occupancy modeling. While the conventional occupancy model (sensu MacKenzie et al., 2002; Tyre et al., 2003) was designed for observation data from multiple visits to all sampling sites, our lichen data consist of predominantly single-visit sites; only 46 sites have data from a second visit. I explore through simulation whether such data are best analysed using only the multi-visit portion of the data or whether it benefits the estimators to include also the single-visit data in the analysis. As this chapter focusses on methodology and data structure, it not only applies to lichens, but is relevant for all surveys and monitoring programs that collect data with a design that consists of a mix of single- and multi-visit sites.

In **Chapter 2**, I estimate the variation in detection probabilities in the lichen dataset collected 1995–2000 for the purpose of the first Red List assessment (Scheidegger et al., 2002). I also investigate potential covariates of detection like lichen conspicuousness or differences between observers, and I discuss the implications that imperfect detection can have on estimates of species frequency. This is one of very few studies that explicitly estimate and discuss detection probability of lichens and how it may affect estimates of species occurrence and species richness. Although this study is based on lichens, the conclusions are likely to apply also to other sessile species like plants or fungi.

In **Chapter 3**, I combine the standardised survey data from 1995–2000 with the recent data from 2018–2022. The focus here lies on estimating changes in the frequency of epiphytic lichen species over these 20 years while accounting for imperfect detection. To suggest potential drivers behind changes in epiphytic lichen communities, species are divided into ecological guilds based on common preferences for substrate, habitat, climatic or chemical conditions. The dataset I analyse in this chapter is exceptionally rich compared to data availability in other European countries, and the resulting inferences are likely to extend beyond the national borders, and also beyond lichens.

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1 “MIXED” OCCUPANCY DESIGNS: WHEN DO ADDITIONAL SINGLE-VISIT DATA IMPROVE THE INFERENCES FROM STANDARD MULTI-VISIT MODELS?

Gesa von Hirschheydt, Silvia Stofer, Marc Kéry

Abstract

Estimating occupancy while accounting for imperfect detection typically requires repeated surveys at sampling units. However, mixed sampling designs are very common, where only a subset of sites is visited repeatedly, while the remainder are visited only once, providing single-visit (SV) data. It is unclear whether SV data contribute to parameter estimates. Consequently, they have often been discarded in occupancy analyses. We conducted two simulation studies to understand the degree to which SV data contribute information to the estimation of occupancy and detection probability. In Simulation 1, we simulated detection/non-detection data under different scenarios of repeated sampling and varying magnitudes of occupancy and detection probabilities. In Simulation 2, we included continuous covariates, to see whether these could enhance the information content of SV data. To each simulated dataset, we fitted models containing between 0 and 5000 SV sites and compared the standard errors of the occupancy and detection estimates. We found that SV data always contributed some information to the estimation of both occupancy and detection in a mixed design. Their relative contribution was greatest when > 2 visits were conducted at the repeated-visit sites, and for species with higher detection probabilities. These results suggest that SV data are valuable when combined with repeated-visit data and lead to more precise estimates than when repeated-visit data are used alone. Including suitable continuous covariates into the analysis of the simulated data increased the contribution of SV data even more. This suggests that, in a mixed design, occupancy estimation could be optimized by measuring and modelling continuous covariates that explain at least some heterogeneity in occupancy and detection amongst sites. Thus, we recommend that for mixed-design data all the available information be used in a joint model to obtain the most precise detection-corrected occupancy estimates.

Introduction

Species distributions and the factors driving them have long fascinated ecologists. Species distributions are often expressed by occupancy probability, which is the probability with which a species occurs at a site (or any spatial unit), given the value of measured environmental and other variables at the site. Assessment of this probability is challenging due to the presence of measurement errors, the dominant one being the failure to detect individuals that are present, leading to false negatives. MacKenzie et al. (2002) and Tyre et al. (2003) proposed a simple, intuitive modelling framework that enables estimation of and correction for false-negative sampling errors. The error is represented as a parameter for detection probability, i.e., the probability that a species is detected during a survey given that it occurs at the site. The standard occupancy model requires a dataset with multiple (i.e., replicated) observations for at least some of the sites, in the form of binary detections and non-detections. If the occupancy status of a site is constant across all observations (i.e., the assumption that the population is closed is not violated), the model permits estimation of the probability of occurrence and of detection separately. The former is of direct interest in a species distribution model, while the latter is typically treated as a nuisance parameter that must be accounted for to avoid bias in the primary estimation target. However, conducting multiple surveys is usually costly. It may be necessary to employ several field technicians simultaneously or to visit a site on different occasions. This requires additional resources that may not always be available.

The trade-off between a need for repeated visits for reliable estimation of detection probability and the desire to cover as many sites as possible is sometimes solved with a *mixed design*, where only a subset of all sites is surveyed multiple times while the remainder (often the vast majority) is visited only once. Contrary to integrated occupancy models, which combine data from different sources or sampling methods (e.g., Koshkina et al., 2017; Miller et al., 2019), under the mixed design all data are collected with the same method. Sites to be surveyed repeatedly may be chosen randomly (or according to some strata) among all sites or in practice often also haphazardly. For instance, in and around Switzerland alone, several monitoring programs use this strategy, including major contributors to the national Biodiversity Monitoring Switzerland (www.biodiversitymonitoring.ch), the Swiss National Forest Inventory (www.lfi.ch), and the Global Observation Research Initiative in Alpine environments GLORIA (www.gloria.ac.at), and without a doubt, there are countless others. The primary goal of these schemes is often not to obtain detection-corrected occupancy estimates but presumably to cover as much heterogeneity of the landscape as possible in order to detect large-scale patterns or community changes over time. In many such schemes, repeated-visit data have not been used to estimate (or account for) species-specific detection probabilities, but merely to assess the reproducibility of the measurements (Nilsson & Nilsson, 1983). If it is deemed satisfactory, the real parameter of interest, i.e., occupancy or abundance, is then typically assessed using only the data from the first surveys (i.e., SV data only) and resulting estimates remain uncorrected for detection errors. However, whenever detection errors occur, estimates from these procedures will be biased (Guillera-Arroita, 2017; Guillera-Arroita et al., 2014; Kéry & Schmidt, 2008; Lahoz-Monfort et al., 2014; Ruiz-Gutiérrez & Zipkin, 2011). Instead of conducting separate analyses of data reproducibility and species distribution, we suggest that both can and should be achieved simultaneously by simply fitting an occupancy model (MacKenzie et al., 2002; Tyre et al., 2003) to the mixed data. Surprisingly though, there is a dearth of research on the efficiency of occupancy models that combine multi-visit (MV) data and single-visit (SV) data in a single model. MacKenzie and Royle (2005) investigated whether surveying a small number of sites with equal number of visits (standard design) was more efficient in terms of precision of the occupancy estimator than surveying a larger number of sites, but only some of them repeatedly and the rest only once (mixed design). They found that the standard design, with identical replication, is almost always more efficient for a given total number of surveys. However, they did not address the question of whether it pays, in terms of estimator precision, to add SV data into an analysis of an otherwise MV-only dataset. Our aim with this study was to identify whether, how much and under which conditions the addition of such SV data in a mixed design improves estimator precision. Additionally, we wanted to see whether adding continuous covariates to the model would further improve precision, since they have been shown to aid estimation in the case in which only SV data are available (Lele et al., 2012).

We addressed these questions using simulation, so that truth was known (Chapter 4 in Kéry & Royle, 2016). We conducted two simulation studies in which we generated detection/non-detection data under a mixed design and for widely varying scenarios defined by the number of SV sites as well as the magnitude of the probability of occupancy and detection. In Simulation 1, we focus on the effects of the number of MV sites and the number of SV sites in the simplest possible model without covariates. In Simulation 2, we investigate whether the utility of SV data can be enhanced by incorporation of continuous covariates.

Materials and methods

Data simulation

We used function `simOcc` in the R package `AHMbook` (Kéry et al., 2021) to simulate detection/non-detection datasets under a wide range of conditions and with or without the effects of a continuous covariate in either the occupancy or the detection portions of the model. Function `simOcc` first generates true presence/absence z at M sites based on a defined probability of occupancy Ψ, where Ψ can vary with environmental covariates in the form of a logistic regression. After generating true presence/absence data z, the function simulates detection/non-detection data y for J visits to each site, with a probability p of detecting the species during a visit to an occupied site, and a probability of 0 of detecting it at an unoccupied site. Variation in sampling conditions that may affect p can again be modelled with a logistic regression. We used this scheme to generate data in our two simulation studies.

Simulation 1

Here, we investigated under which conditions SV data contribute any information to the estimation of Ψ and p in a mixed design when no covariates are included in a model. We compared three schemes of repeated sampling:

- *Case2×150* with 2 visits each to 150 sites (i.e., number of visits J=2, number of sites M=150)
- *Case2×300* with 2 visits each to 300 sites
- *Case4×150* with 4 visits each to 150 sites

We chose these numbers to reflect designs from moderately small to medium sample sizes. We further varied conditions by selecting a gradient for occupancy probability Ψ and detection probability p between 0.1 and 0.9 in steps of 0.02, and by considering five levels for the number of SV sites S added to the multi-visit (MV) data: 0, 150, 500, 1000, and 5000. For each combination of J, M, Ψ, and p, we initially simulated 1000 datasets with J visits and a total number of N (= 5000 + M) sites. We then defined the first M sites of each dataset to be the repeated-visit sites and turned observations from visits $J \geq 2$ in all remaining sites into NAs, so they became SV data. The full SV portion was then subset five-ways to produce the five levels of factor *S*, i.e., for each of the 1000 original datasets, we created a total of five variants corresponding to the five levels of the factor *S*. When a simulated dataset contained either only detections or not a single detection among all MV sites, it was discarded (to avoid boundary estimates for the probability parameters in the model) and replaced by a new dataset.

Simulation 2

In this set of simulations, we evaluated whether continuous covariates in occupancy or detection affect the degree to which SV sites contribute useable information in an occupancy model. We based all simulations on *Case2×150* above, i.e., where we assumed 2 visits each to 150 sites (i.e., J=2, M=150) and varied Ψ, *p*, and *S* in the same way as in Simulation 1. With covariates, Ψ and *p* here represent the intercepts expressed on the probability scale. Data under each parameter combination were simulated under four different covariate settings:

- *CovNull* without any covariates (identical to *Case2×150*)
- *CovOcc* with one continuous site-specific covariate for occupancy and none for detection
- *CovDet* with one continuous visit-specific covariate for detection and none for occupancy
- *CovBoth* with one continuous site-specific covariate for occupancy and one visit-specific covariate for detection

Each covariate was randomly drawn from a standard normal distribution and was linked to the respective probability via a logistic regression model. The logit-scale effect of the occupancy covariate was simulated as -1, while the effect of the detection covariate was set at 1. We simulated 1000 datasets for each scenario and parameter combination.

Analysis of simulated data

Simulations and analyses were run in R (version 4.1.1; R Core Team, 2021) and static occupancy models (MacKenzie et al., 2002; Tyre et al., 2003) were fitted by maximum likelihood using function `occu` in the R package `unmarked` (Fiske & Chandler, 2011). We identified numerical failures in model fitting by the presence of either missing (NA), unreasonably large (> 3 on the logit scale) or unreasonably small (< 0.005) estimated standard errors ($\widehat{\mathrm{SE}}$). Beyond a standard error of 3 confidence intervals of probabilities cover essentially the full range of values from 0 to 1, while standard errors below 0.005 unrealistically suggest near-perfect estimation and were always associated with boundary estimates (either occupancy or detection was estimated at 0 or 1). For datasets where the simulated detection and occupancy probabilities were low, the proportion of models with such numerical failures was substantial (up to 89%). These cases were ignored in the description of our results below, but we tally their frequency in Appendix 1. All analyses are based on $\widehat{\mathrm{SE}}$s associated with the estimates on the original logit scale.

In Simulation 2, each dataset was analysed with an occupancy model with identical covariate structure as in the data-generating model. To assess the amount of information contributed by the SV data in an occupancy fit, we analysed the magnitude of the $\widehat{\mathrm{SE}}$, on the logit scale, and the rate of change in $\widehat{\mathrm{SE}}$ as we went from 0 SV sites added to 5000 SV sites added to a given number of MV site data.

For each combination of Ψ and *p*, we used $\widehat{\mathrm{SE}}$ of the logit-scale $\hat{\Psi}$ and $\hat{p}$ to fit a generalized linear mixed model across all 1000 simulations using the function `lmer` in the R package `lme4` (version 1.1-29; Bates et al., 2015) to investigate how logit-scale $\widehat{\mathrm{SE}}$ changes with increasing number of SV sites:

$$\widehat{\mathrm{SE}}(\hat{\Psi}_{k,l}) = \gamma_0 + \gamma_1 * l_s + \delta_k + \varepsilon_{k,l}$$

where $\widehat{\mathrm{SE}}(\hat{\Psi}_{k,l})$ is the estimated standard error associated with the maximum likelihood estimate of Ψ for dataset *k* and *S* factor level *l*, γ_0 is the intercept, γ_1 is the coefficient for the factor level *l* of *S*, δ_k is the random effect associated with the *k*=1...1000 simulated datasets, and $\varepsilon_{k,l}$ is the residual. We then conducted the analogous analysis also for $\widehat{\mathrm{SE}}(\hat{p}_{k,l})$. Note that we regressed the estimated SEs on the factor levels [0, 1, 2, 3, 4] of variable *S* instead of directly using the numbers [0, 150, 500, 1000, 5000]. Our reason for this is that we wanted a simple indicator for the magnitude of the change, and when plotting the SEs against different versions of the number of SV sites (e.g., raw numbers, log-transformed numbers, factor levels), the relationship to levels of factor *S* was most nearly linear. In this regression, the estimated intercept $\hat{\gamma}_0$ represents the $\widehat{\mathrm{SE}}$ of an estimate when *S*=0, i.e., when the model is fit to data with repeated visits only.

We assessed the contribution of SV data to estimator precision in two ways. The first one was to identify that part of the examined parameter space (if any) of occupancy and detection probability for which the precision of the estimated parameters was improved when SV data were added, i.e., where $\widehat{\mathrm{SE}}$ become smaller. The second was to compare the magnitude of that improvement between different sampling schemes and covariate structures, wherein we define improvement as a negative estimated slope $\hat{\gamma}_1$ in the regression on the level of *S* described above.

In this paper, we focus on the precision of occupancy and detection estimators. The effect of SV data on the precision of covariate coefficients is discussed in Appendix 2. In order to keep within the scope of the paper, we only briefly discuss the accuracy of the estimates and refer the reader to the appendices for figures and a short discussion of the effect of SV data on estimator bias (Appendix 3) and root mean squared error (Appendix 4).

Results

Simulation 1

Of the 1000 simulated datasets generated for each parameter combination, 907 on average resulted in valid estimates (range: 111 - 1000; see Appendix 1 for the number of non-valid estimates). We found that the addition of SV data was always beneficial in terms of precision of the occupancy and detection estimates for all sampling schemes examined in Simulation 1 (Fig. 1 and Fig. 2). Regression slopes $\hat{\gamma}_1$ of $\widehat{\mathrm{SE}}(\widehat{\Psi})$ against SV sites were consistently negative, i.e., the precision of estimates improved, for all combinations of Ψ and *p* and for all sampling schemes of the MV data (Fig. 1A). This improvement was greatest when Ψ was small and *p* was large.

For $\widehat{\mathrm{SE}}(\hat{p})$ too, the addition of SV data in an occupancy model always paid in terms of estimator precision: regression slopes were consistently negative for all combinations of Ψ and *p* (Fig. 1B). However, unlike for $\widehat{\mathrm{SE}}(\widehat{\Psi})$, the contribution of SV data was greatest when both Ψ and *p* were low. Doubling the number of repeated-visit sites (*Case2×300*) reduced the relative contribution of additional SV data compared to *Case2×150* for the entire parameter space. Doubling the number of visits (*Case4×150*) on the other hand increased the contribution of SV data on the estimation of $\widehat{\Psi}$, especially when the detection probability was high, as illustrated by the more negative slopes of $\widehat{\mathrm{SE}}(\widehat{\Psi})$ with additional SV data (Fig. 1 and 2). Both *Case2×300* and *Case4×150* show considerably lower absolute $\widehat{\mathrm{SE}}$ compared to *Case2×150* (see the intercepts in Fig. 2) due to the greater information content of the MV data.

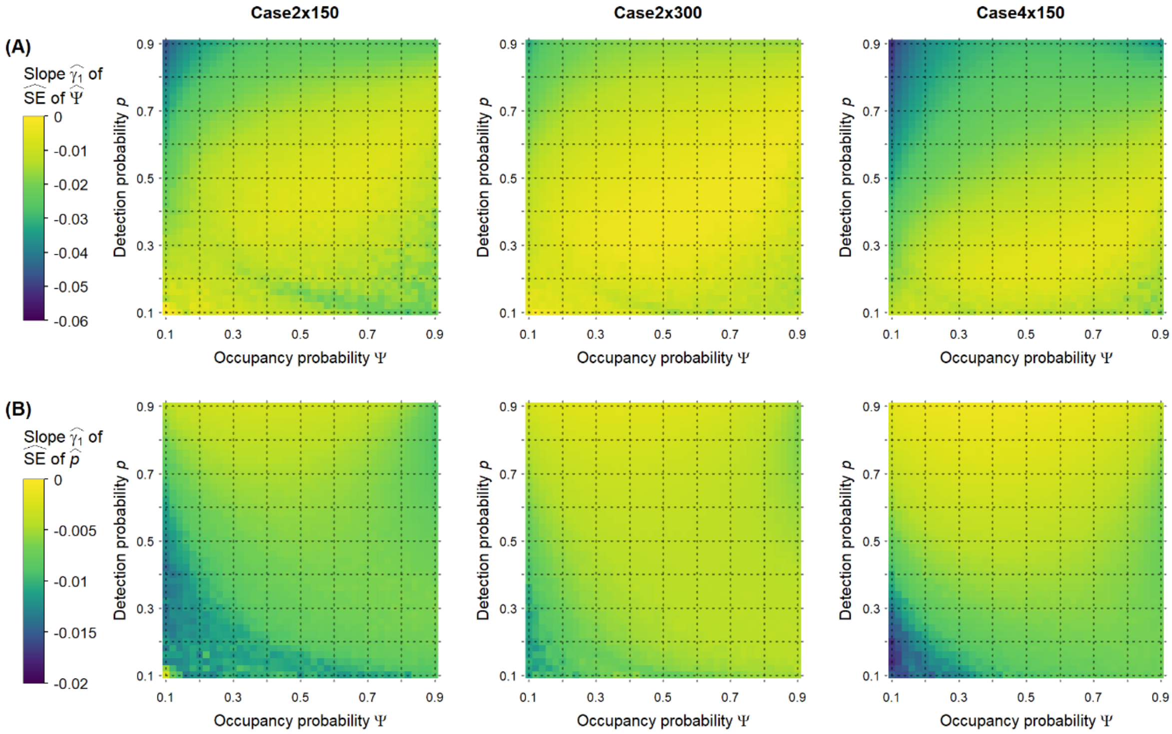

Fig. 1 Heatmaps showing slope $\hat{\gamma}_1$ of linear regressions of the estimated standard errors of $\widehat{\Psi}$ (A) and of $\hat{p}$ (B) against the number of single-visit sites l_S in relation to true occupancy Ψ and detection probability *p* (along the axes). Columns represent the different cases of repeated sampling with (left) 2 visits each to 150 sites (in addition to 0 – 5000 SV sites), (middle) 2 visits each to 300 sites, and (right) 4 visits each to 150 sites. Note that a negative slope indicates an improvement of estimator precision with increasing numbers of single-visit sites added.

Overall, the $\widehat{\mathrm{SE}}$ of $\widehat{\Psi}$ improved a lot more than the $\widehat{\mathrm{SE}}$ of $\hat{p}$ for the same number of additional SV sites. For example, for a moderately common species (Ψ = 0.5) which is easily detected (*p* = 0.8) and a repeated sampling scheme of *Case2×150*, the addition of data from only 500 SV sites reduced the $\widehat{\mathrm{SE}}(\widehat{\Psi})$ from 0.175 to 0.121 (Fig. 2A), which represents a reduction of 31%. For the same settings, the $\widehat{\mathrm{SE}}(\hat{p})$ decreased only by 5%, from 0.253 to 0.240. Even for combinations of Ψ and *p* for which the contribution of SV data on $\widehat{\mathrm{SE}}(\hat{p})$ is greater, adding 500 SV sites never reduced the $\widehat{\mathrm{SE}}(\hat{p})$ by more than 14% (results not shown).

In terms of accuracy, both estimates showed negligible deviations from the truth for species with $p \geq 0.5$ for *Case2x150*. Below this threshold, occupancy was slightly under- and detection probability slightly overestimated which confirms previous findings (e.g., MacKenzie et al., 2002). The magnitude of the bias decreased with additional MV sites or greater number of repeated visits but was not affected by the number of SV sites (Appendix 3).

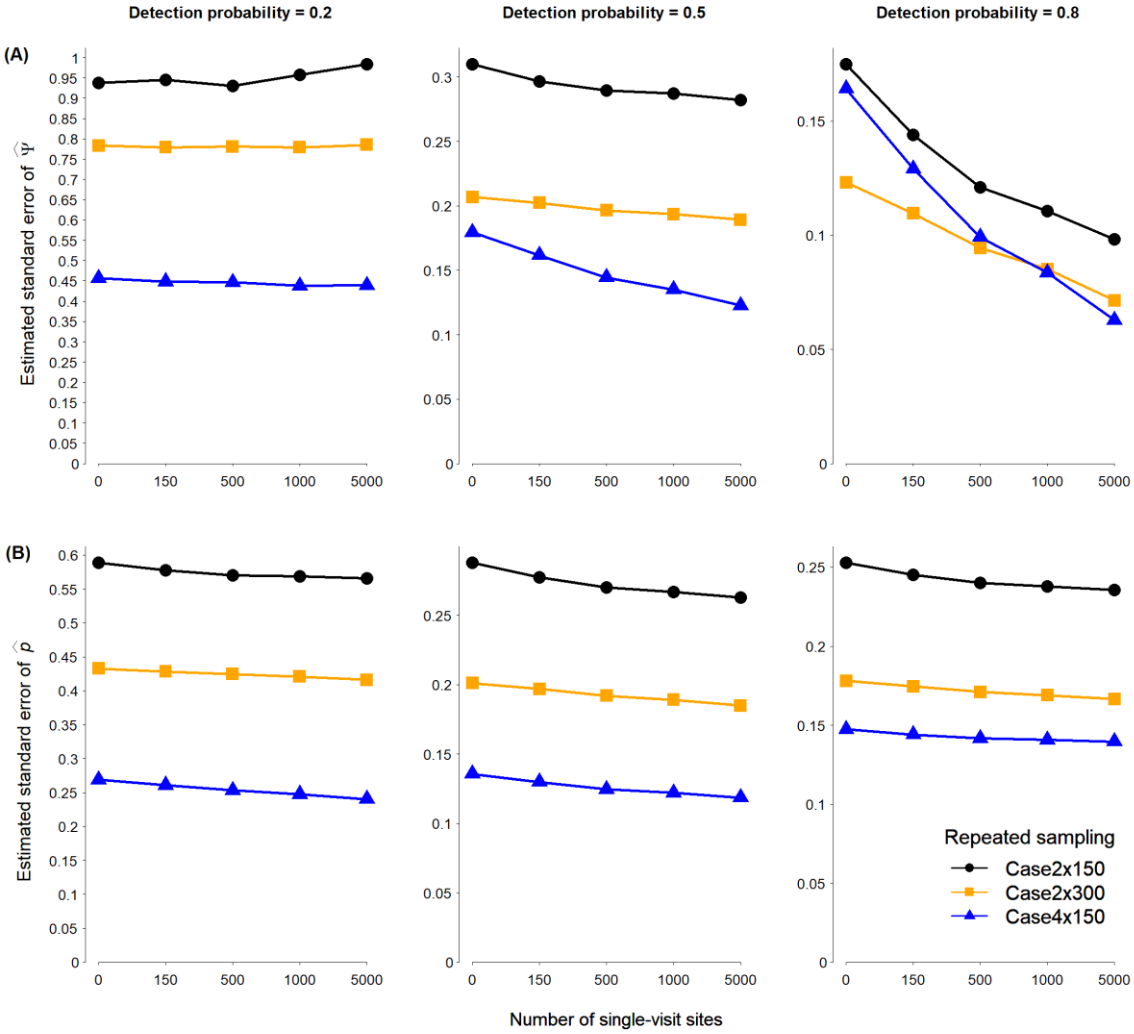

Fig. 2 Plots showing (on the y axis) the average magnitude across simulations of the estimated standard error of $\widehat{\Psi}$ (A) and of $\hat{p}$ (B) as more single-visit sites (on the x axis) are added to the analysis (Simulation 1). Columns represent different combinations of data-generating rates where Ψ is kept constant at 0.5 and p is set to 0.2 (left), 0.5 (middle), and 0.8 (right). Note that the scale of the y-axes varies, but ticks are drawn consistently at intervals of 0.05.

Simulation 2

On average, 905 simulations per parameter combination resulted in valid estimates (range: 111 - 1000). We found that the inclusion of a site-specific occupancy covariate (in scenarios *CovOcc* and *CovBoth*) strongly enhanced the contribution of SV data to the estimation of occupancy (Fig. 3A) but did only slightly do so in the estimation of detection (Fig. 3B). The steepest slope, i.e., the greatest improvement in $\widehat{\mathrm{SE}}$, was found for species with low detection probability and moderate occupancy probability (Fig. 4). Precision of the covariate coefficients improved likewise with the occupancy covariate showing a pattern similar to that of the occupancy estimate, and the detection covariate showing a pattern similar to that of the detection estimate (Appendix 2).

Adding a visit-specific covariate of detection into the model (*CovDet*) slightly increased the usable information content of SV data for the estimation of detection, but only for species with very low Ψ and p. However, it had little effect on the occupancy estimate.

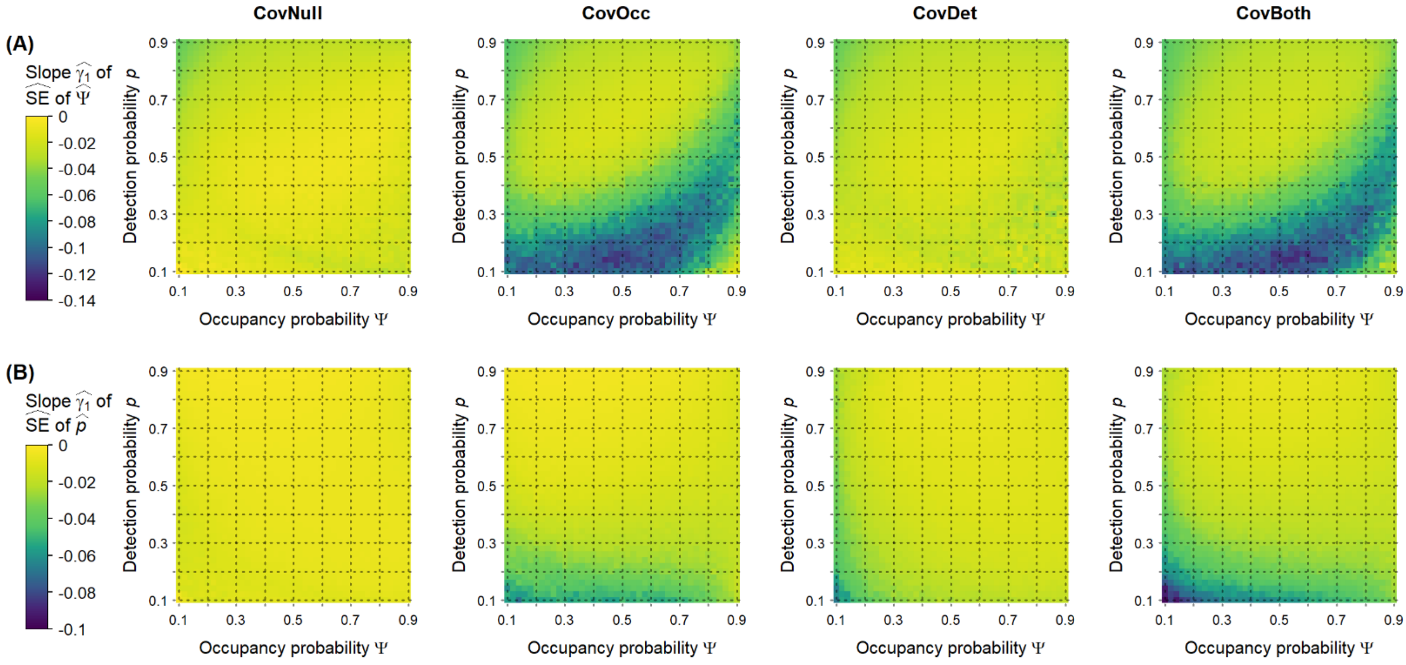

Fig. 3 Heatmaps showing slope $\hat{\gamma}_1$ of linear regressions of the estimated standard errors of $\hat{\Psi}$ (A) and of $\hat{p}$ (B) against the number of single-visit sites I_S in relation to true occupancy Ψ and detection probability p (along the axes). Columns represent the different covariate settings: *CovNull* is the intercept-only model and is identical with *Case2×150* in Simulation 1, *CovOcc* has one covariate for occupancy and none for detection, *CovDet* has one covariate for detection and none for occupancy, and *CovBoth* has one continuous covariate each. Colour indicates the magnitude of the regression slope for each combination of values of Ψ and p in the parameter space for 1000 simulated datasets each. Note that the colour scales differ from those in Fig. 1. All models include 150 sites visited twice.

In terms of accuracy, the coefficient of the occupancy covariate showed some bias when detection probability was low in combination with very low or high values of occupancy probability (i.e., near 0.1 or 0.9; Appendix 3). The coefficient of the detection covariate showed a slight positive value for all parameter combinations. For both covariates, accuracy improved substantially when SV data were added to the dataset (Appendix 3).

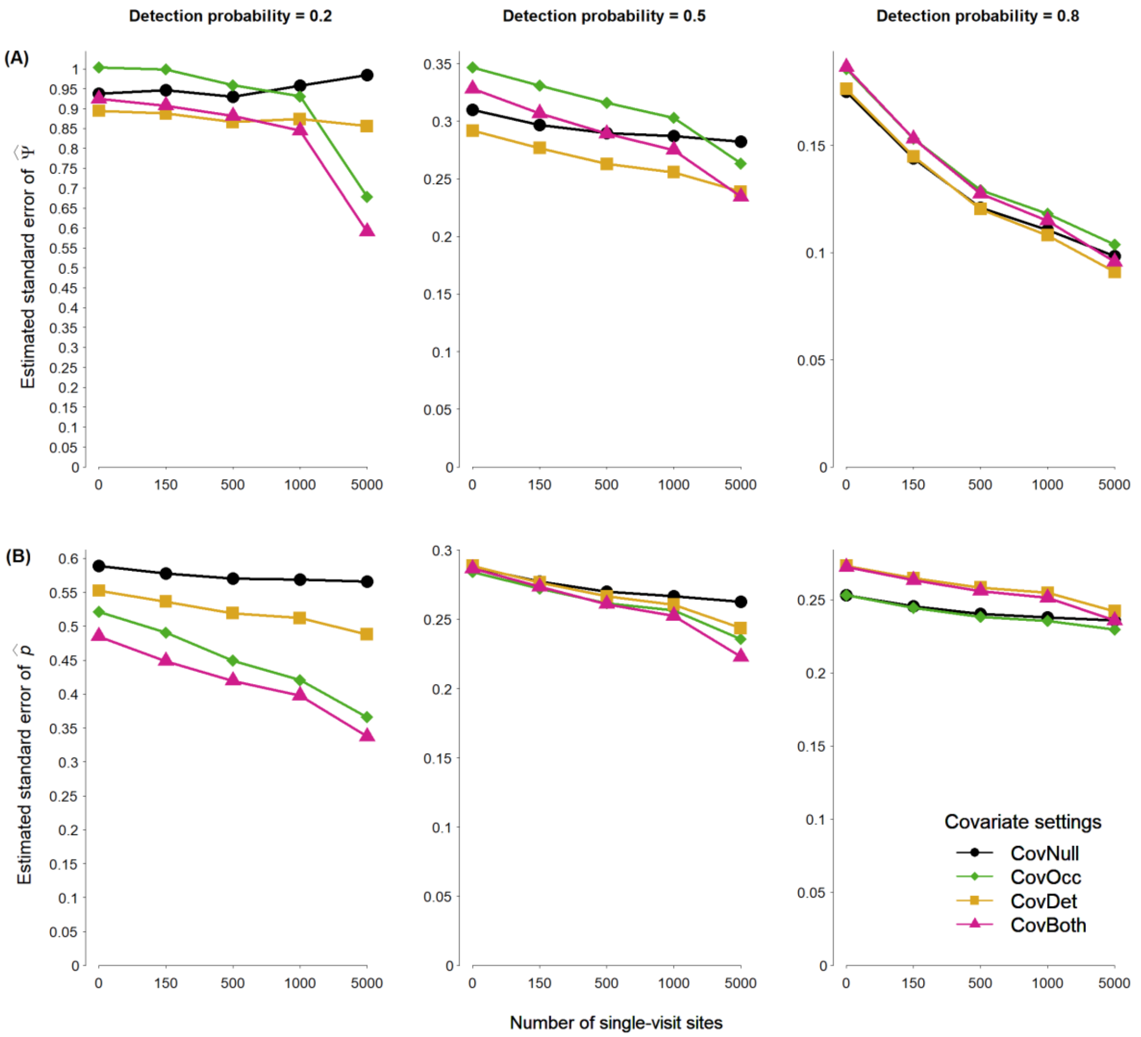

Fig. 4 Plots showing the average magnitude across simulations of the estimated standard error of $\hat{\Psi}$ (A) and of $\hat{p}$ (B) against the number of single-visit sites and with or without covariates in the model (Simulation 2). Columns represent different combinations of data-generating rates where Ψ is kept constant at 0.5 and p is set to 0.2 (left), 0.5 (middle), and 0.8 (right). The four lines illustrate different covariate settings. Note that the scale of the y-axes varies, but ticks are drawn consistently at intervals of 0.05.

Discussion

We explored what we call "mixed sampling designs" in an occupancy modelling framework. That is, where one portion of the sites is sampled multiple times, as in the standard occupancy design (MacKenzie et al., 2002; Tyre et al., 2003), and the other portion is sampled only once. Across the scenarios examined, we found that the addition of SV data always improves estimator precision for both occupancy and detection probability when compared to the analysis of data from the MV sites alone. However, the magnitude of this gain in precision varied, and depended on the magnitude of species occupancy and detection, as well as on the type of covariate included. In general, estimates of occupancy $\widehat{\Psi}$ benefited more from adding SV data than did estimates of detection probability $\hat{p}$.

Different repeated-sampling schemes

The standard occupancy design uses the MV portion of the data to provide information on detection probability. Expanding the starting dataset from 150 sites visited twice (*Case2×150*) with additional visits or additional MV sites should therefore improve overall estimator precision. As expected, we found that doubling the number of sites with two visits (*Case2×300*) improved estimates in terms of precision, but it reduced the relative improvement of precision that was observed when SV data were added to the analysis.

Doubling the number of visits (*Case4×150*) strongly improved precision of the estimates, especially when detection probability was low, as has previously been reported (MacKenzie & Royle, 2005; Reich, 2020). An interesting and new finding from our study is that a larger number of visits in the repeated portion of the data also has benefits for the relative contribution of SV data: when MV sites are visited four times, additional SV data carry relatively more information (and hence precision is improved relatively more) than when MV sites are visited only twice. In other words, greater precision in the detection estimate obtained through greater number of visits allows the model to make better use of the information on occupancy contributed by the SV data.

Different covariate structures

Covariates may carry valuable additional information on the probability that a site is occupied or not. One may therefore expect that the inclusion of one, or better two, continuous covariates (i.e., at least one at site level and another at the visit level) would make it easier for the model to utilize additional SV data. Our simulations clearly confirmed this for the estimation of occupancy: Incorporating a covariate for occupancy strongly improved the contribution of SV data to estimation of $\widehat{\Psi}$ for species with low to moderate detection probabilities. We further found that covariates also improved estimates of detection $\hat{p}$, but here the improvement was less pronounced and restricted to cases where detection probabilities were low. As standard occupancy models require repeated visits to estimate detection probability, it may seem counterintuitive that SV data should improve estimates of detection at all. In fact, MacKenzie et al. (2003) write "repeated surveys may be restricted to a subsample of sites in order to collect sufficient information for estimating detection probabilities, which can then be applied to those sites only visited once" suggesting that the detection estimate is informed only by the MV data. Our results show, however, that SV data can actually improve estimates of detection probabilities, especially when the model includes an occupancy covariate and when overall detection probability is low. This means that by adding information about the occupancy status of a site, an occupancy covariate indirectly contributes information about the detection probability. Finding suitable occupancy covariates should be relatively easy. Potential covariates may be elevation, yearly mean temperatures or precipitation, vegetation density, proximity to water or to human settlements.

Adding a detection covariate that varies at the visit level had little effect on the contribution of SV data to the estimation of $\widehat{\Psi}$, but slightly improved their contribution for $\hat{p}$. As with the occupancy covariate, this effect was more prominent when detection probability was low, but the overall improvement was smaller than for the occupancy covariate. Not unexpectedly, the greatest benefits were obtained when the model contained one unique (or "private") continuous covariate each for occupancy and detection. Lele et al. (2012) and Sólymos et al. (2012) used continuous covariates to estimate detection probability (separately from occupancy) from data of single-visit sites alone. In contrast to a design with purely SV data, a mixed design does not *require* the use of continuous covariates to guarantee parameter identifiability. Therefore, it may also be more robust to assumption violations compared to a model fit to SV-only data (Knape & Korner-Nievergelt, 2015). Our results show, however, that especially analyses of difficult-to-detect species, i.e., species with a low detection probability, can be greatly improved when adequate covariates are included. Examples of possible detection covariates that may vary between visits are date, climatic conditions during sampling (temperature, rainfall, wind, cloud cover, etc.), or some continuous measure of observer experience such as the proportion of species successfully identified in a test. We note that categorical covariates such as observer identity should not be expected to be informative in this regard (Lele et al. 2012). We did not assess the effect of detection covariates that vary at site level, but we would expect it to be of similar magnitude.

Implications for survey design

Several studies have evaluated the performance of various sampling designs in occupancy studies and tried to identify optimal strategies for a constant total survey effort (e.g., Guillera-Arroita, 2017; Guillera-Arroita et al., 2010; MacKenzie & Royle, 2005; Reich, 2020). We emphasize that our goal was *not* to show that mixed designs are particularly powerful at estimating occupancy and detection rates when compared with other designs. In fact, ever since MacKenzie and Royle (2005) it has been known that a mixed design, which they called “double sampling”, is rarely the ideal solution when the aim is to obtain a precise estimate of occupancy with a fixed number of surveys. Rather, the aim of our study was to provide guidance for an analysis in the common situation *when a survey has already been conducted*, and when both SV and MV data are available. Especially in vegetation studies, there are numerous datasets that have such a mixed structure, both from past surveys and from ongoing monitoring programs and often, separate analyses are conducted of the SV and the MV data, perhaps because the mixed data does not seem ideal for any joint analysis. Our results show, however, that the MV and SV data from such studies can be analysed jointly and that this will improve the estimates of both occupancy and detection probability, even if a design was not optimized for the purpose of correcting for imperfect detection in the most efficient way. Thus, our take-home message is this: if you have additional single-visit data in the analysis of standard (i.e., repeated-visit) occupancy data, then use them all in a single occupancy model.

Data availability

All R code used in this study to simulate, analyse, and visualize the data is available on https://doi.org/10.5281/zenodo.7272029.

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Supplementary materials

Appendix 1 – Numerical failures in occupancy model fitting

We used function occu in the R package unmarked (Fiske & Chandler, 2011) to fit occupancy models to the simulated data. This function uses maximum likelihood to estimate parameters. We found that 1) optimization of parameter estimates can be sensitive to starting values, i.e., certain starting values may result in a failure of the optimization function and hence an NA in the model output, and 2) when data were generated with low detection probabilities and there were thus few detections in the data, maximum likelihood estimates often fell on the boundary of parameter space (e.g., $\Psi=1$ and $p=0$) and the estimated standard errors (on the logit scale) would either take on unrealistically small (< 0.005) or excessively large (>3, even up to >500) values. According to Ken Kellner (current maintainer of the package, pers. comm.), such standard errors indicate numerical failure of the model fitting and estimates obtained from such a model should not be trusted. We therefore excluded such cases from our analyses. Note that the failures resulting in excessively large standard errors can only be diagnosed on the "working scale" of the logit. The built-in function in unmarked that translates the estimated standard error to the probability scale transforms those excessively large values on the logit scale to values that may appear quite innocuous on the probability scale.

Numerical failures (i.e., NA, or unreasonably large or small standard errors) were distributed unevenly, but in a fairly predictable fashion, across the parameter space of Ψ and p. In the worst case, only 11 % of all 1000 fitted models for a parameter combination yielded valid estimates (Fig. S1). Such low numbers of valid estimates were always associated with low detection probability and low occupancy. Frequency of failures also varied among the simulated cases and covariate settings. *Case2×150*, being the case with the least amount of information, showed the largest number of numerical failures (Fig. S1 A), while *Case4×150* had the smallest number (Fig. S1 B).

Appendix 2 – Effect of single-visit sites on the precision of covariate coefficients

The manuscript focuses on the effect of single-visit data on the precision of the occupancy and detection probabilities, measured in form of the standard errors of their estimators. Sometimes, however, researchers are less interested in the probabilities of occupancy or detection than in the factors that affect them. In Fig. S2 and Fig. S3 we show that adding more single-visit data to an occupancy model greatly improves the precision of the covariate coefficients. In fact, the relative improvement of these standard errors is even greater than the improvement of the standard errors of the occupancy or detection probabilities. The conclusions from the manuscript do thus also apply to covariate coefficients: including single-visit data in the analysis will improve the precision of all estimates.

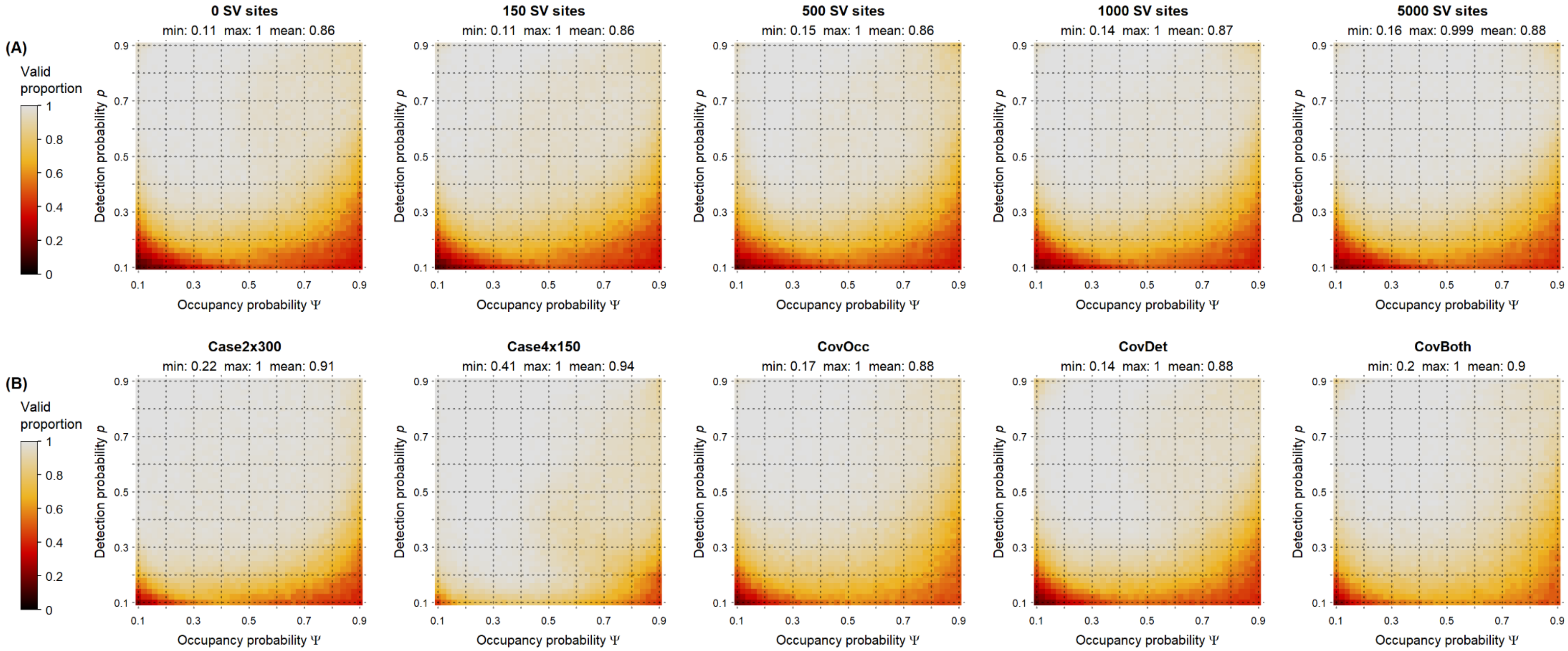

Fig. S1 Proportion of valid estimates for any given parameter combination across all five levels of *S* (i.e., number of single-visit sites) for *Case2×150* (A, top) and for 0 single-visit sites for the other cases and covariate settings (B, bottom). In all scenarios, the minimum and the mean proportion of valid estimates increased the more single-visit sites were included.

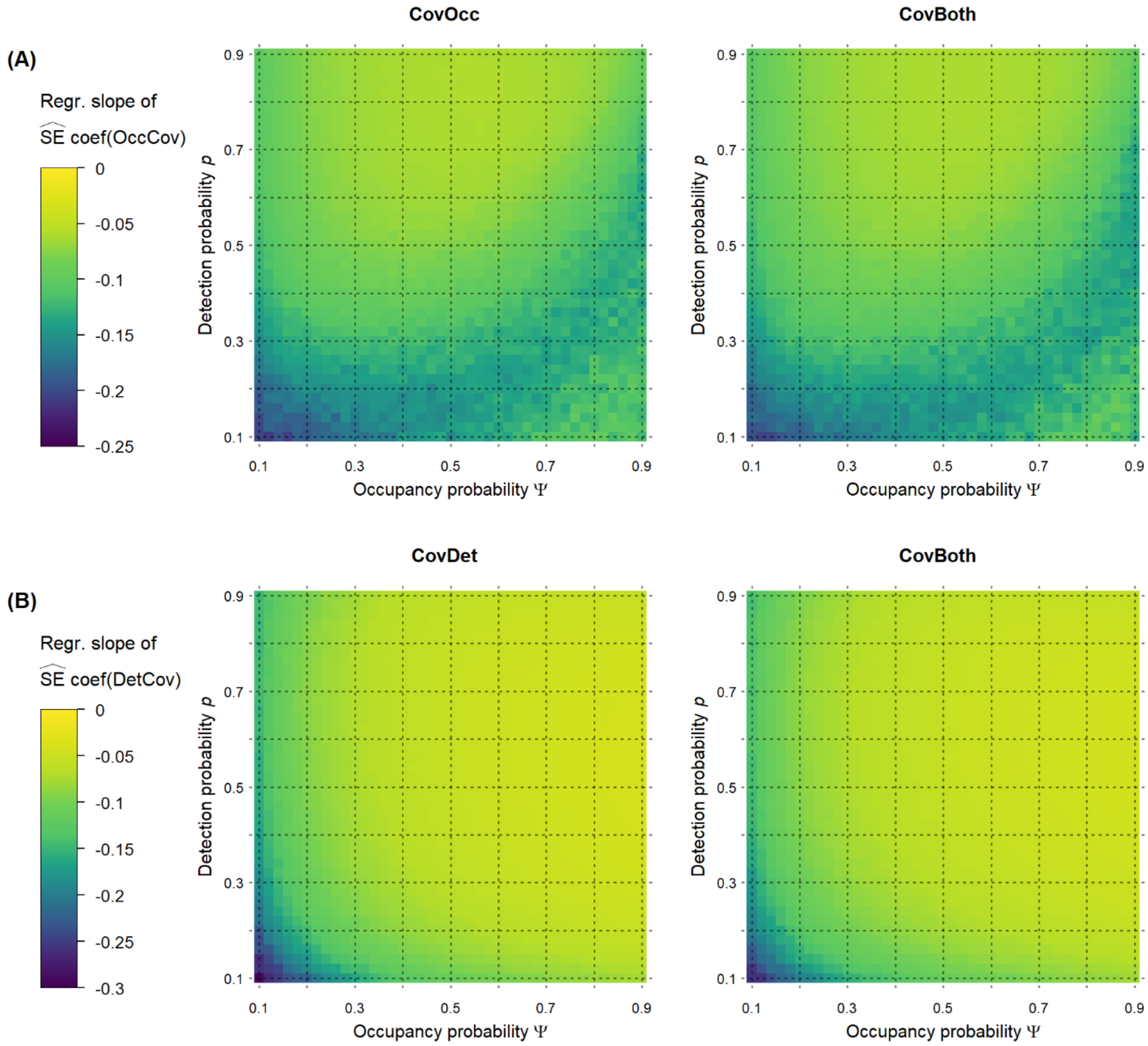

Fig. S2 Heatmaps showing the slope of linear regressions of the estimated standard errors of the coefficients for a covariate of occupancy (A, top) and a covariate of detection (B, bottom) in relation to true occupancy Ψ and detection probability p (along the axes). The top left heatmap is created with estimates from the scenario *CovOcc*, the bottom left heatmap from the scenario *CovDet*, and the heatmaps on the right come from the scenario *CovBoth*.

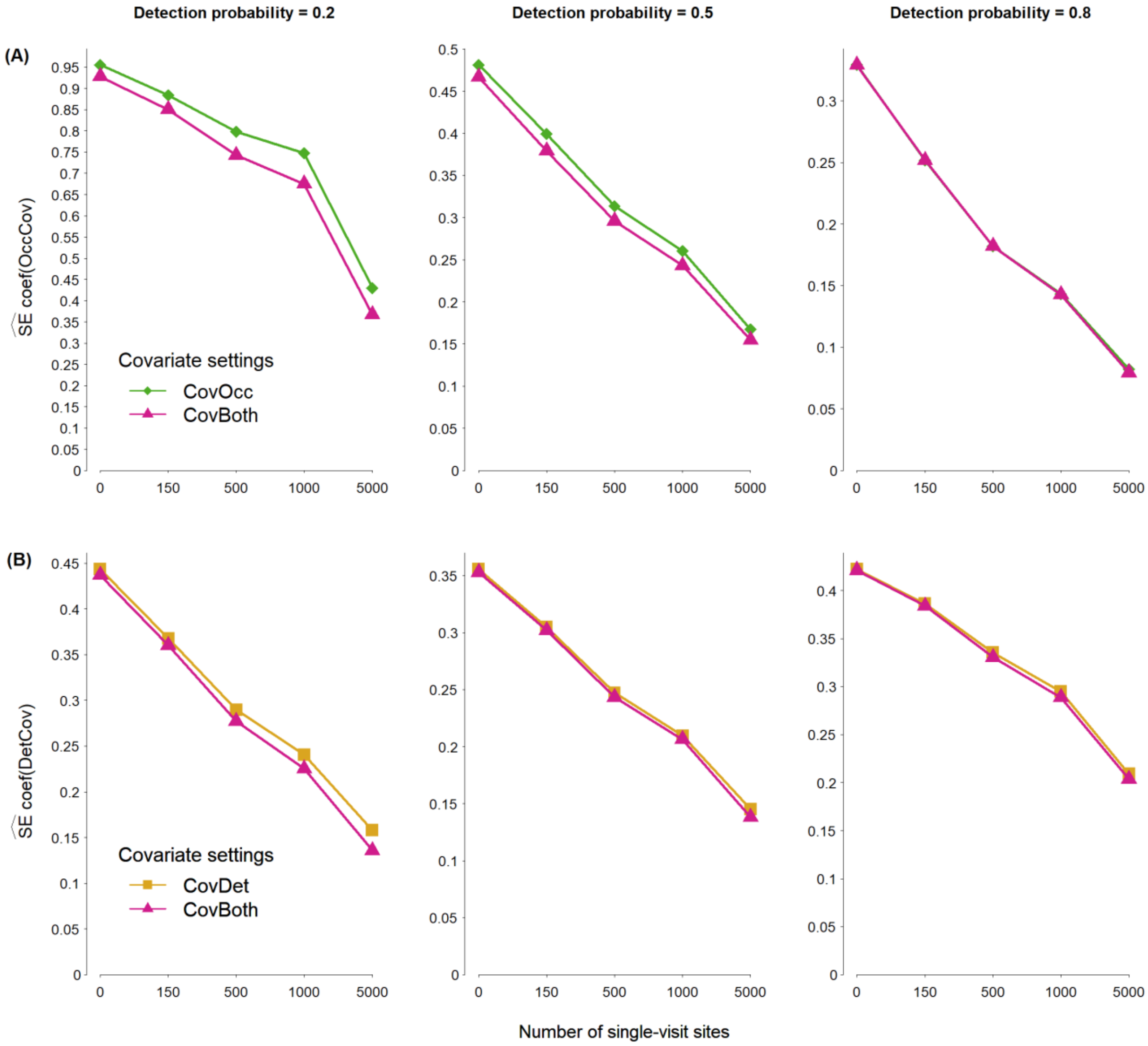

Fig. S3 Plots showing the average magnitude across simulations of the estimated standard error of the coefficients for a covariate of occupancy (A, top) and a covariate of detection (B, bottom) against the number of single-visit sites. Columns represent different combinations of data-generating rates where Ψ is kept constant at 0.5 and *p* is set to 0.2 (left), 0.5 (middle), and 0.8 (right). Line colours and symbols illustrate different covariate settings. Note that the scale of the y-axes varies, but ticks are drawn consistently at intervals of 0.05.

Appendix 3 – Accuracy of parameter estimates

Our manuscript describes how the precision of estimators from occupancy models improve when single-visit data are added to an analysis of otherwise multi-visit data. Here we check whether this addition comes at the cost of lower accuracy, i.e., whether single-visit data introduce a bias to the estimators. Other papers have already shown that estimators from occupancy models tend to be biased when detection probabilities are small and the number of repeated visits is low (e.g., MacKenzie et al., 2002; MacKenzie & Royle, 2005). We observe the same pattern in our simulated data. We do not elaborate on this observation, but we compare the bias from models with only multi-visit data (0 single-visit sites) directly to the bias that occurs in analyses with 5000 single-visit sites. In the simulation cases without covariates, i.e., where the fitted occupancy models contain only intercepts, no change in bias is apparent (Fig. S4). As expected, some bias occurs but it is restricted to the area of the parameter space where detection probability is low. The accuracy further decreases when low detection probability is combined with extreme occupancy probabilities. When covariates are added to the analysis, overall accuracy is better than without covariates, and it further improves with the addition of single-visit data (Fig. S5).

The inferences we drew from analysing the effect of single-visit data on the precision of estimates do therefore also extend to the accuracy of the estimates: 1) including single-visit data in an occupancy analysis is beneficial (or at least not harmful in intercept-only models) for estimator accuracy, and 2) including covariates (and especially an occupancy covariate) can further improve estimator accuracy.

Appendix 4 – Root mean squared error of parameter estimates

The root mean squared error (RMSE) is another metric for the performance of a model. By using the square of the prediction error, it is affected both by bias and precision of the estimator. For each combination of parameter values, we here calculated it as:

$$\text{RMSE} = \sqrt{\frac{\sum_{i=1}^{n}(\mathrm{T}_i - \mathrm{F}_i)^2}{n}}$$

where T_i is the true parameter value used in the simulation of the data, F_i is the fitted (i.e., estimated) value from simulation replicate *i*, and *n* is the total number of valid estimates obtained from running 1000 simulations with identical parameter values.

Our focus in this study is the evaluation of the effects of single-visit sites on parameter estimation in the occupancy model. Hence, we directly compared the RMSE of estimates from models with multi-visit data only (i.e., with 0 single-visit sites added) to the RMSE of estimates when 5000 single-visit sites were added in the dataset.

In the simulation cases without covariates, no change in RMSE was apparent (Fig. S6). The bias described in Appendix 3 led to high RMSE when detection probability was low. The addition of covariates hardly affected the RMSE of the occupancy and detection estimates (Fig. S7, parts A and B). The RMSE of the covariate coefficients, however, improved greatly when single-visit data were added (Fig. S7, parts C and D) as a result of improved precision (see main paper) and improved accuracy (see Fig. S5).

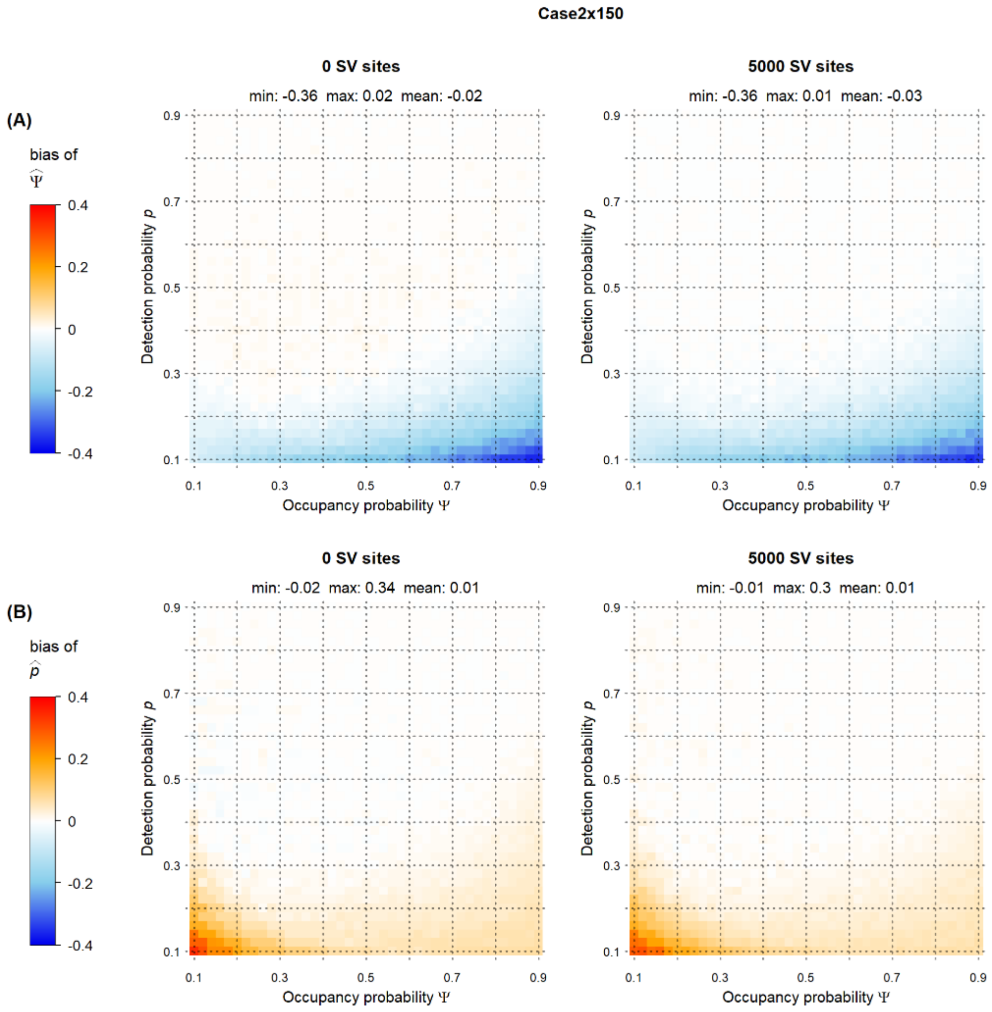

Fig. S4 Heatmaps showing the median bias of the estimated occupancy probability Ψ (A, top) and the estimated detection probability *p* (B, bottom) from the simulation *Case2x150* in relation to true occupancy Ψ and detection probability *p* (along the axes). The heatmaps to the left are created from models that use only the multi-visit portion of the data (0 single-visit sites), while the heatmaps to the right come from models that include 5000 single-visit sites. No significant difference is apparent between the left and the right heatmaps, indicating that single-visit data do neither improve nor worsen accuracy of estimates in intercept-only models.

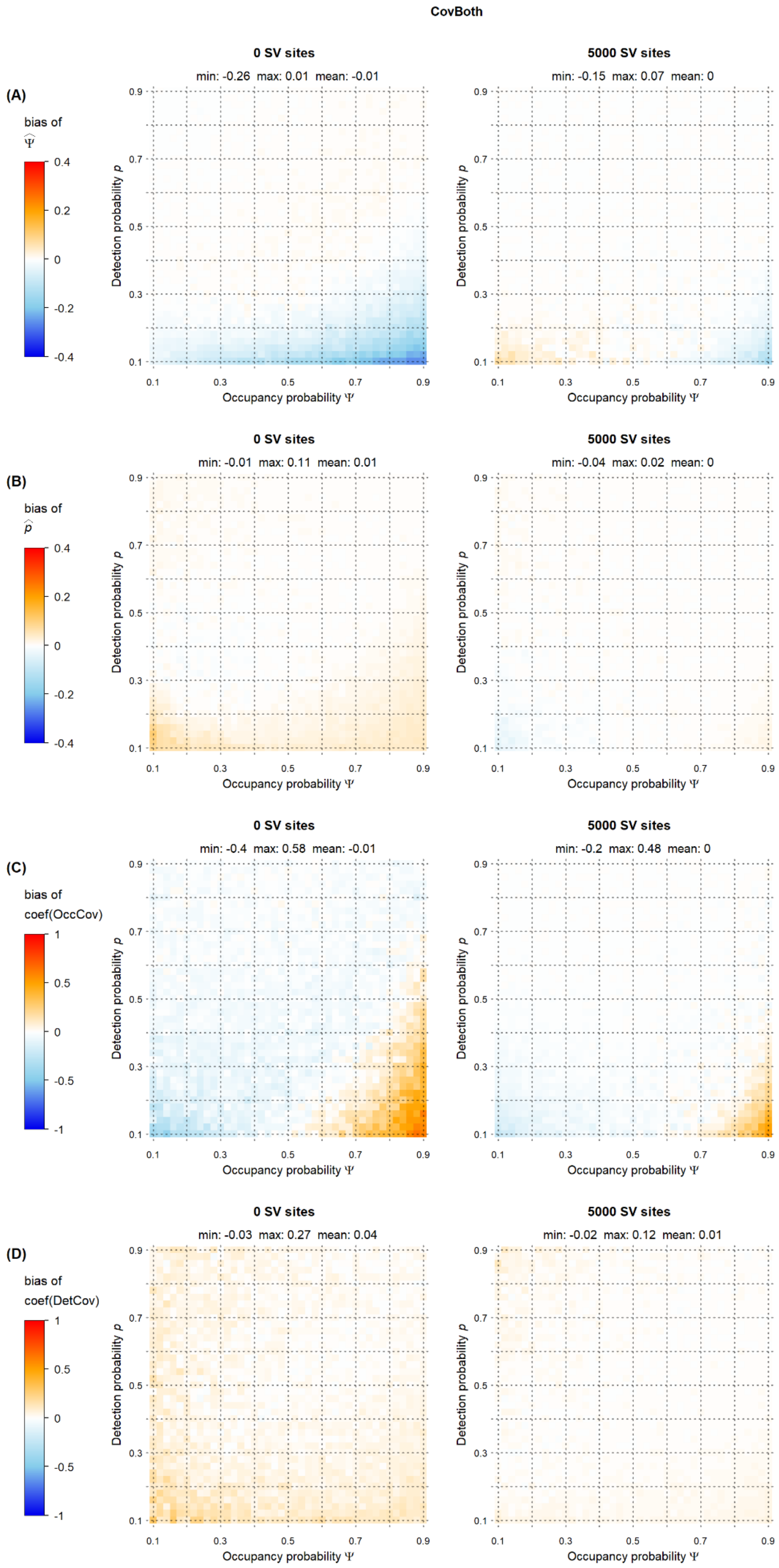

Fig. S5 Heatmaps showing the median bias of the estimated occupancy probability Ψ (A), detection probability *p* (B), coefficient for the occupancy covariate (C), and coefficient for the detection covariate (D) from the simulation *CovBoth*. The heatmap axes represent the true occupancy Ψ and detection probability *p* used to simulate the data. The heatmaps to the left are created from models that use only the multi-visit portion of the data (0 single-visit sites), while the heatmaps to the right come from models that include 5000 single-visit sites. In general, the values are closer to 0 in the heatmaps to the right than in the heatmaps to the left, indicating that single-visit data improve accuracy of estimates in models that include covariates.

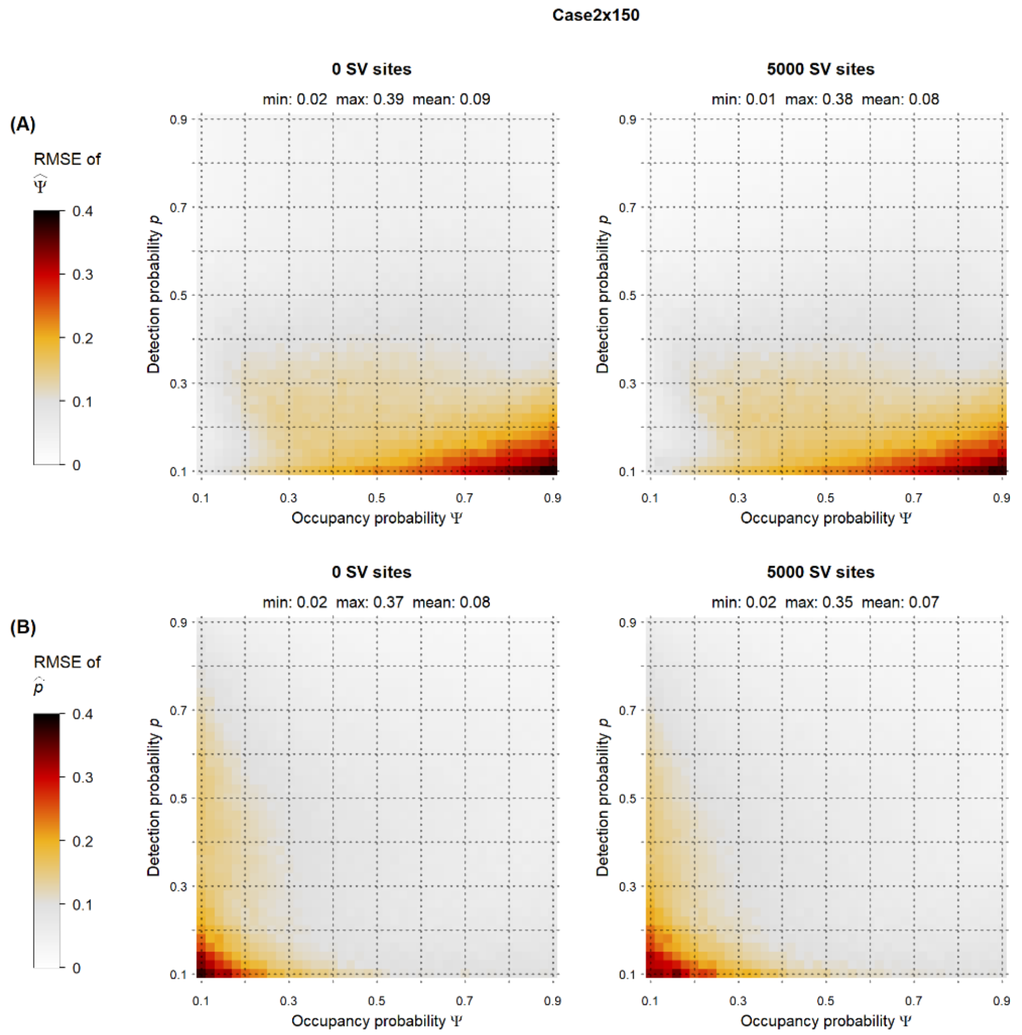

Fig. S6 Heatmaps showing the root mean squared error (RMSE) of the estimated occupancy probability Ψ (A, top) and the estimated detection probability p (B, bottom) from the simulation *Case2x150* in relation to true occupancy Ψ and detection probability p (along the axes). The heatmaps to the left are created from models that use only the multi-visit portion of the data (0 single-visit sites), while the heatmaps to the right come from models that include 5000 single-visit sites. Hardly any difference is apparent between the left and the right heatmaps, indicating that single-visit data neither improved nor deproved RMSE of estimates in intercept-only models.

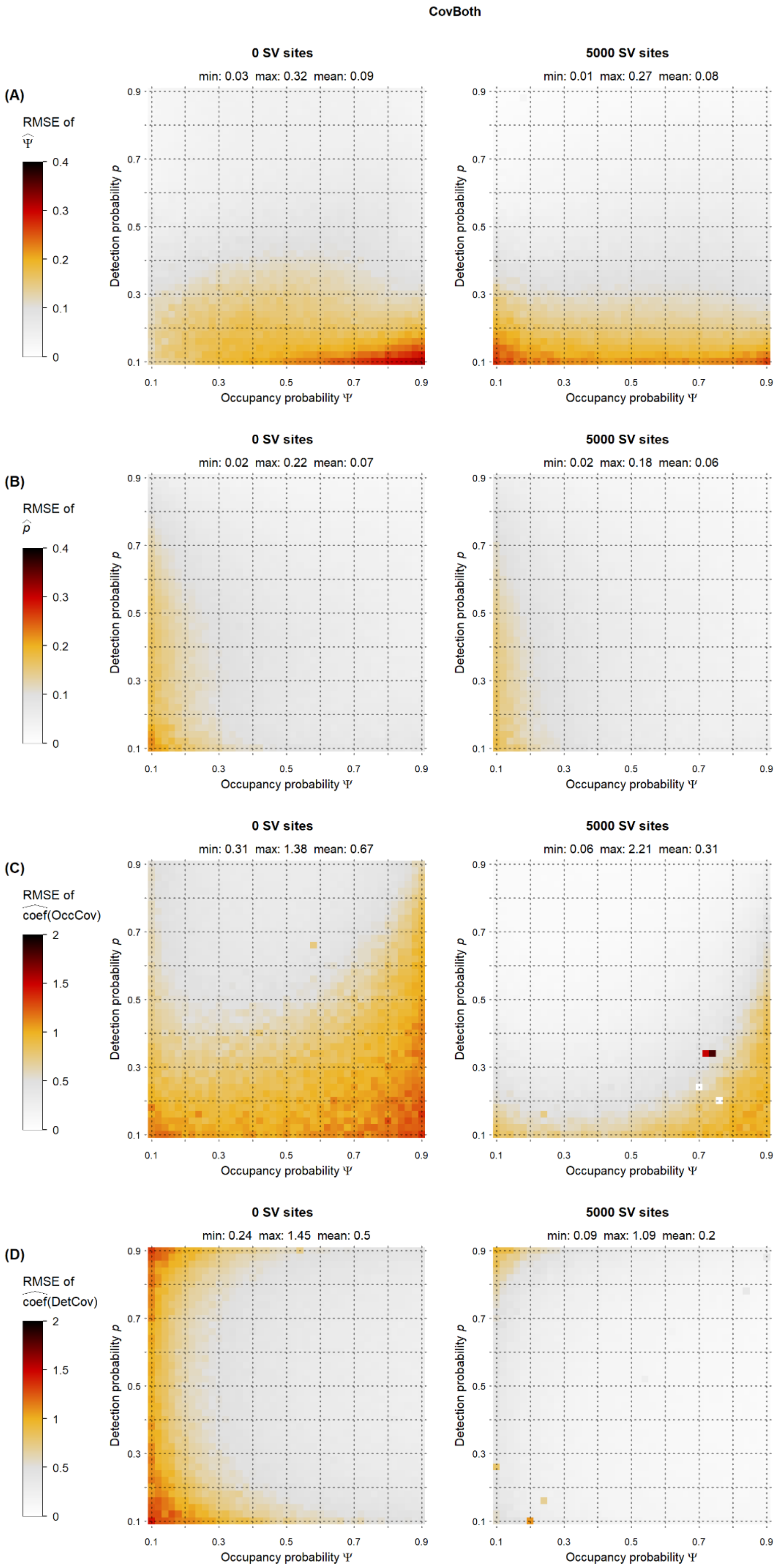

Fig. S7 Heatmaps showing the root mean squared error of the estimated occupancy probability Ψ (A), detection probability *p* (B), coefficient for the occupancy covariate (C), and coefficient for the detection covariate (D) from the simulation *CovBoth*. The heatmap axes represent the true occupancy Ψ and detection probability *p* used to simulate the data. The heatmaps to the left are created from models that use only the multi-visit portion of the data (0 single-visit sites), while the heatmaps to the right come from models that include 5000 single-visit sites. In general, RMSE does not change much for the estimates of Ψ and *p*, but is considerably smaller in the heatmaps to the right for the estimates of the covariate coefficients, indicating that single-visit data did improve RMSE of covariate effects. This improvement was consistent when only one covariate was included (figure not shown).

Note: the few extreme values are the result of some outlier estimates which strongly affect the mean of the squared errors.

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MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Royle, J. A., & Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, *83*(8), 2248–2255. https://doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2

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The following manuscript is currently under review in *Journal of Vegetation Science*. Upon publication, it should be cited with a reference to the publishing journal.

2 OCCUPANCY MODELS REVEAL LIMITED DETECTABILITY OF LICHENS IN A STANDARDISED LARGE-SCALE MONITORING

Gesa von Hirschheydt, Marc Kéry, Stefan Ekman, Silvia Stofer, Michael Dietrich, Christine Keller, Christoph Scheidegger

Abstract

Imperfect detection of mobile species (i.e., animals) is readily acknowledged and nowadays often corrected for in surveys and monitoring programs. Although evidence has accumulated over the last 20 years that also sessile organisms (plants, fungi, etc.) are imperfectly detected, this error is seldom accounted for. As lichens are not only sessile but also non-seasonal, they should be easier to survey than plants or fungi. In this study, we explore data from a standardised national lichen survey conducted by professional lichenologists on 826 sampling plots across Switzerland. We estimate mean and variation in detectability for 373 tree-living lichen species using multi-species occupancy models. Detectability is modelled as a function of species conspicuousness, identifiability, and observer experience. We found that average detectability for a single survey was only 0.49 (range across species: 0.34 - 0.63), with conspicuous species showing higher average detectability (0.53) than inconspicuous species (0.41). Identifiability and previous experience with a species substantially increased the probability of a person detecting it. Observers also differed generally, regardless of experience, with detectabilities ranging from 0.33 to 0.72. Our study confirms that detectability per survey is often far below 1 also in sessile organisms, even under excellent conditions. When species are seasonal (plants, fungi, etc.), survey areas larger, or field personnel 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 design and analysis of occurrence data also for sessile organisms.

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., due to species misidentification). One way to account for such sampling errors is to adopt a repeated-measures design, i.e., to conduct multiple independent surveys to 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 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 (Guillera-Arroita et al., 2014; Kéry & Schmidt, 2008; MacKenzie et al., 2002; Royle, 2004), biodiversity metrics (Broms et al., 2014; Guillera-Arroita et al., 2019; Iknayan et al., 2014; Jarzyna & Jetz, 2016), demographic rates like (local) colonization and extinction (MacKenzie et al., 2003; Manna et al., 2017; Rossman et al., 2016), or strength of habitat associations (Gu & Swihart, 2004; Kéry, 2004; Lahoz-Monfort et al., 2014; Tyre et al., 2003).

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 (Amburgey et al., 2021; Maphisa et al., 2019; Moor et al., 2022; e.g., Mosher et al., 2018; Siffert et al., 2022). However, this is not the case for sessile organisms (for exceptions see e.g., 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 organism) cannot escape detection by movement, but does it 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, hardly possible to identify, or at least very inconspicuous. Additionally, 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 (Chen et al., 2009, 2013; Garrard et al., 2008, 2013; Perret et al., 2023). Some studies have reported observer differences in plant records (Burg et al., 2015; Klimeš et al., 2001; Nilsson & Nilsson, 1985; Vittoz et al., 2010), and species differed in their detectability based on their morphological (Chen et al., 2009; Garrard et al., 2013; Gregg & Kéry, 2006) or seasonal reproductive state (Abrego et al., 2016; Halme & Kotiaho, 2012; 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 (e.g., Bjorkman et al., 2020; Jönsson et al., 2022; Kolb et al., 2010; Newman et al., 2015; Perring et al., 2018; Staude et al., 2022; Zhang et al., 2014).

Although detectability may vary greatly between species, observers, or sampling schemes, and should thus be estimated at 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; Lõhmus, 2009), or that previous experience of an observer with a species increases the chance that s/he will find it again (Brunialti et al., 2012; Erickson & Smith, 2021; McCune et al., 1997). Conspicuousness, identifiability and observer experience have the potential to be relevant for many species groups, but the generalizability across sampling schemes remains to be tested.

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 should be easier to assess than 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 (Britton et al., 2014; Cáceres et al., 2008; Vondrák et al., 2016). However, none of these studies explicitly estimated detectability at the species level. Casanova et al. (2014) were, to the best of our knowledge, the first ones to systematically collect data in order to estimate detectability of individual lichen taxa using multiple independent observers. A second study by Outhwaite et al. (2020) also estimated detectability of lichens, but they extracted multiple-visit-type data from presence-only observations in a data-base, following an approach suggested by Kéry et al. (2010). Although Casanova et al. (2014) stress the usefulness and importance of their results for future lichen surveys, we are not aware of any published studies that followed their suggestion.

The purpose of the present study is to estimate 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 is to (1) estimate the average detectability of tree-living lichen species in a large-scale, standardised survey, (2) quantify the variation of detectability among species, e.g., based on their conspicuousness or identifiability, and (3) quantify differences in detectability among observers depending on their previous experience with each species. We also illustrate the effect of ignoring imperfect detection in our data and discuss the requirements that must be fulfilled to be able to account for detectability in lichens.

Materials and methods

Lichen data

The lichen dataset was collected between 1995 and 2000 for the national Red List of corticolous lichens ("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 1km-coordinate grid. Stratification was based on combinations of biogeographic region (5 strata), elevational belt (6), 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 12.62 m radius centered on an intersection point (area 500 m^2). After inspecting the selected locations on a map, 185 were excluded as either unsuitable for tree lichens (e.g., lakes, glaciers, intensive agricultural fields without trees or shrubs), or as inaccessible. For our analysis, we further excluded sites without any tree substrate, resulting in a final dataset of 416 sites (Fig. 1). These were surveyed by one of six lichen experts (observers 1-6) with the aim to detect as many lichen species as possible on each species of substrate tree (i.e., one list for *Abies alba*, one for *Acer pseudoplatanus*, etc.). More details on the sampling protocol are given in Scheidegger *et al.* (2002). Survey duration was loosely restricted by the expectation that every person should survey two sites per day on average. A second survey was conducted on 46 sites, all by a single person (observer 7). Time was not restricted in this second survey, and this surveyor typically spent considerably more time on the site than the first surveyor. When a lichen specimen could not be identified in the field with certainty, a small part of it was collected for later identification with microscope and/or chemistry.

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 of our main analysis, i.e., they are independent from our estimates of detectability.

Species conspicuousness

Our conspicuousness score 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, while 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.,

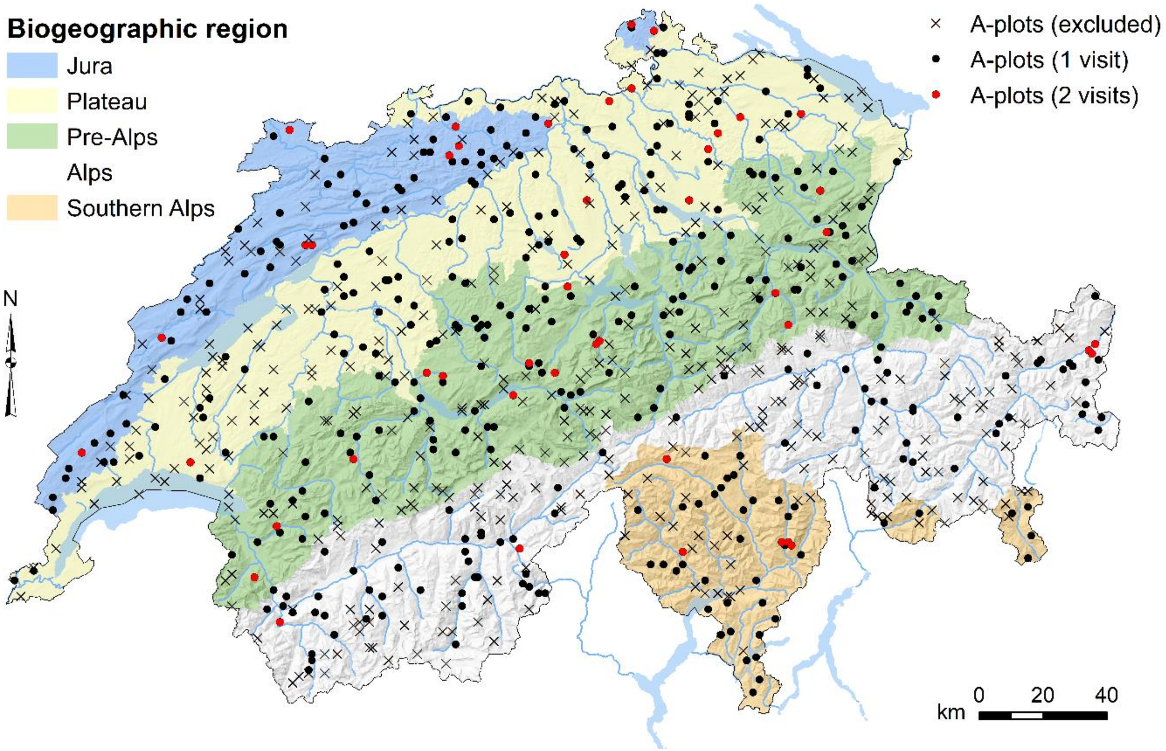

Fig. 1 Map of Switzerland with the location of the sampling points. Among all 826 sampling sites, 410 were excluded because they did not contain any substrate for tree lichens. Of the remaining 416 sites, 46 were surveyed twice. Background colours illustrate different biogeographic regions. The topographic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

2008). The assignment to either group was based on the majority judgement of five field-experienced lichenologists (GH, MD, CK, SE, CS).

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. Possible index values are -1, -0.5, 0.5, 1, where 1 is given to a species that can be identified in the field with a hand lens, and -1 is given to a species that requires advanced microscopy and/or thin layer chromatography to identify it. Cáceres et al. (2008) used a similar index and called it “distinctiveness”.

Observer experience

We defined experience as the presence of a report of the same species by the same observer to the national lichen database SwissLichens (Stofer et al., 2019) in any previous year. Before any first report, the experience of the observer-species pair was set to zero. 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).

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 (von Hirschheydt et al., 2023). This occupancy model estimates the occupancy probability of each species separately from its detectability, i.e., the probability to detect a species given its presence, while assuming that no species is detected mistakenly. Under this "no-false-positives" assumption, the true occupancy state *z* of site *i* (*i* = 1, 2, …, 416) for species *k* (*k* = 1, 2, …, 373) is modelled as a function of occupancy probability Ψ, which is described by covariates in the form of a logistic regression:

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

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

$$\alpha_{x,k} \sim \mathrm{Normal}\left(\mu_{\alpha_x}, \sigma_{\alpha_x}^2\right), \text{ for } x = 1, 2, \ldots, 7$$

where μ_{α_x} and $\sigma_{\alpha_x}^2$ are the hyperparameters that describe the random species effect. The variable *substrate* 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 to be suitable. The 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.

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

$$y_{ijk} \sim \mathrm{Bernoulli}\left(z_{ik} \times p_{ijk}\right)$$

$$\mathrm{logit}\left(p_{ijk}\right) = \beta_{1,ijk} + \beta_2 \times \mathrm{conspicuousness}_k + \beta_3 \times \mathrm{identifiability}_k + \beta_4 \times \mathrm{experience}_{ijk}$$

$$\beta_{1,ijk} \sim \mathrm{Normal}\left(\mu_{\beta_o}, \sigma_{\beta_o}^2\right)$$

Each observer *o* thus has their own mean detectability (fixed observer effect) and associated variance over which the species can vary (random species effect). The other coefficients (β_2, β_3, β_4) are constants.

Software, settings, model validation

We carried out all analyses in R Version 4.1.2 (R Core Team, 2021). The occupancy model was fitted in JAGS (Plummer, 2003) using 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 a standard deviation (sd) of 2.5 for regression coefficients (Gelman et al., 2008), and half-Cauchy priors with a 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 (Supplementary Materials). We ran 5 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 $\widehat{\mathrm{R}}$ was < 1.1 for all parameters (p.285 in Gelman et al., 2013; Gelman & Rubin, 1992) and when traceplots showed good mixing of the MCMC chains. Overall goodness-of-fit of the model was assessed at species level using posterior predictive checks (Gelman et al., 1996).

Results

Mean occupancy probability 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 was expected, partly because the majority of lichen species tend to be rare (Edwards et al., 2004; Fisher et al., 1943), and partly because tree lichens can only grow where suitable bark substrate is available. Not surprisingly therefore, the availability 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]. This result emphasizes the importance of including this parameter as a covariate in the model. Our dataset included 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 coarser resolution from forestry data. 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 (Fig. 2A, from Table 1). Interestingly, observers also differed in the consistency with which they detected different species, as measured by the species-specific random effect variance σ^2 which was estimated separately for each observer. Observers 4 and

Table 1 Parameter estimates obtained as posterior means from the community occupancy analysis. All estimates (and associated Bayesian 95% credible intervals CRI) are given on the logit scale.

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_{elev2}	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_{precip2}	-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_{solar2}	-0.22 [-0.28, -0.17]	0.25 [0.19, 0.31]
Detection process		
Observer 1 μ_{obs1}	-0.73 [-1.00, -0.45]	0.71 [0.52, 0.91]
Observer 2 μ_{obs2}	-0.43 [-0.71, -0.16]	0.63 [0.46, 0.82]
Observer 3 μ_{obs3}	-0.54 [-0.81, -0.27]	0.79 [0.61, 0.99]
Observer 4 μ_{obs4}	-0.90 [-1.19, -0.61]	1.09 [0.88, 1.31]
Observer 5 μ_{obs5}	-0.43 [-0.75, -0.11]	1.08 [0.70, 1.53]
Observer 6 μ_{obs6}	0.26 [-0.04, 0.56]	0.54 [0.12, 0.86]
Observer 7 μ_{obs7}	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]	-

5 had considerably greater, and observer 6 considerably lower, among-species variation of detectability than the others (Fig. 2B). Modelling species-random effects separately for each observer allowed species to have very different (or very similar) detectabilities for different observers (Table S1). For instance, while *Pseudevernia furfuracea* had estimated mean detectabilities between 0.502 and 0.659 for all observers, estimates for *Lecanora barkmaniana* ranged from 0.163 to 0.851 in different observers (Table S1). Identifiability and experience had equally strong positive effects on detectability with 95% CRI not overlapping zero (Table 1, Fig. 3). The effect of conspicuousness was likewise positive with the entire 95% CRI above zero, but it was slightly weaker (Table 1). Species that

were easier to detect also tended to be more common, but with considerable variation (Fig. 4). For example, the conspicuous shrubby lichen *Pseudevernia furfuracea* was very easy to detect and more common than all inconspicuous species. However, the inconspicuous crust *Violella fucata* was more common than the conspicuous *Graphis scripta*, and *Myriolecis persimilis*, which had the lowest detectability of all species, was still more common than the conspicuous *Lecanora barkmaniana*. Taking conspicuousness, identifiability, and the time-varying observer experience into account, mean detectability across all species for a single first survey was estimated at 0.482 [0.460, 0.504] at the beginning of the study period, and increased to 0.507 [0.487, 0.527] at the end of the study period. On average, over all 373 species, detectability was 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 (Fig. 5). The same was true for species richness which was always estimated at a higher value than what was observed (see Supplementary Materials).

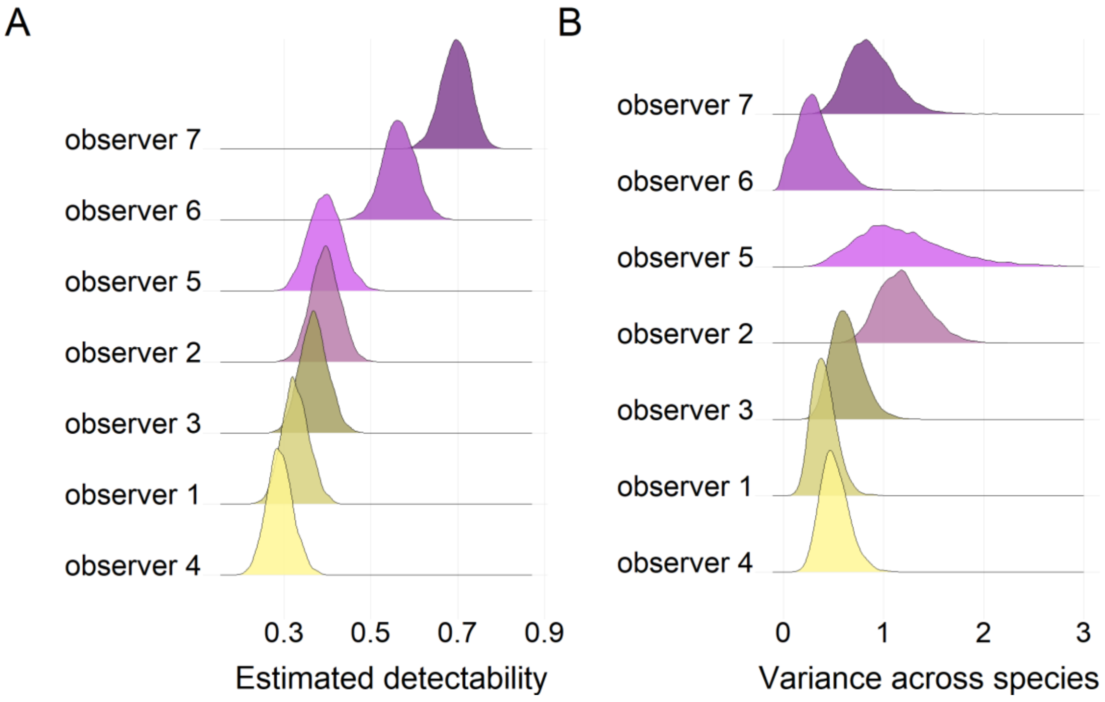

Fig. 2 Posterior densities of observer-specific detection intercepts with a random species effect. The left panel (A) illustrates the estimated mean per observer, i.e., the expected probability that an observer finds a species that is inconspicuous and without prior experience. The right panel (B) shows the estimated variance across species, where a small variance means that species cluster closer around the observer's mean detectability, and a large variance means that species vary greatly within that observer.

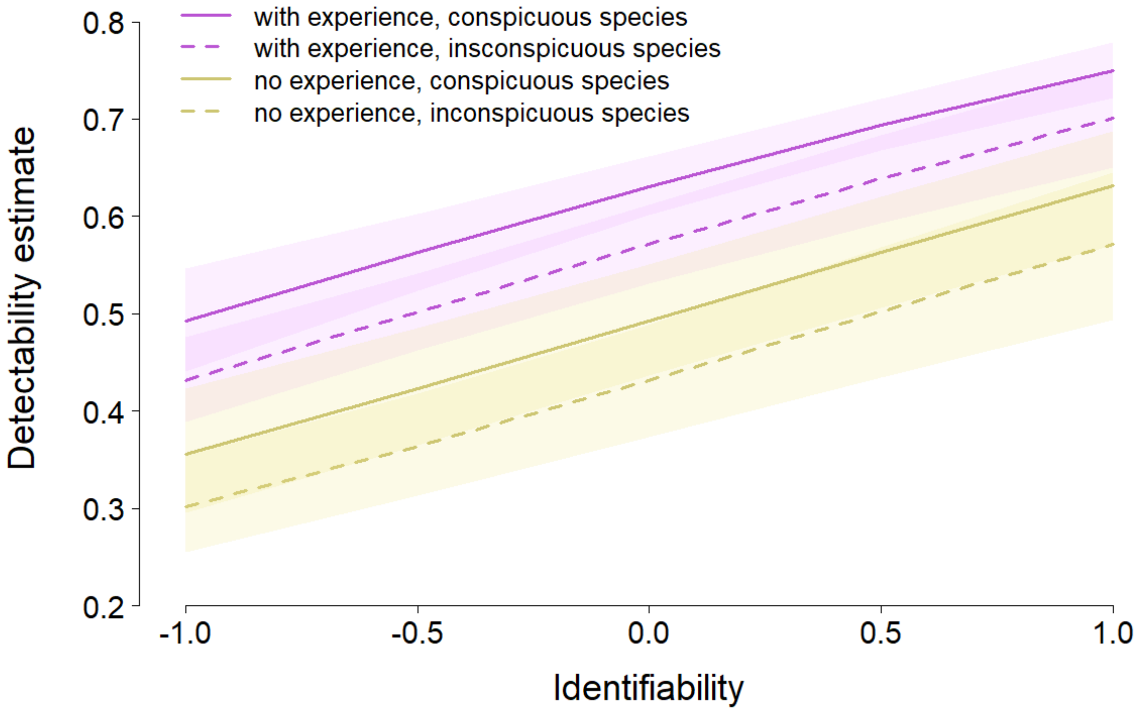

Fig. 3 Posterior detectability estimates in relation to identifiability, observer experience (purple: with observer experience, beige: without experience), and species conspicuousness (solid lines: conspicuous species, dashed lines: inconspicuous species). The shaded areas represent Bayesian 95% CRI.

Discussion

Our study explicitly estimates 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 improved the detectability for observers over the course of the study slightly 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. Detectability varied largely among observers, which has been documented many times before (McCune et al., 1997; Vondrák et al., 2016), and also among species (Casanovas et al., 2014). 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

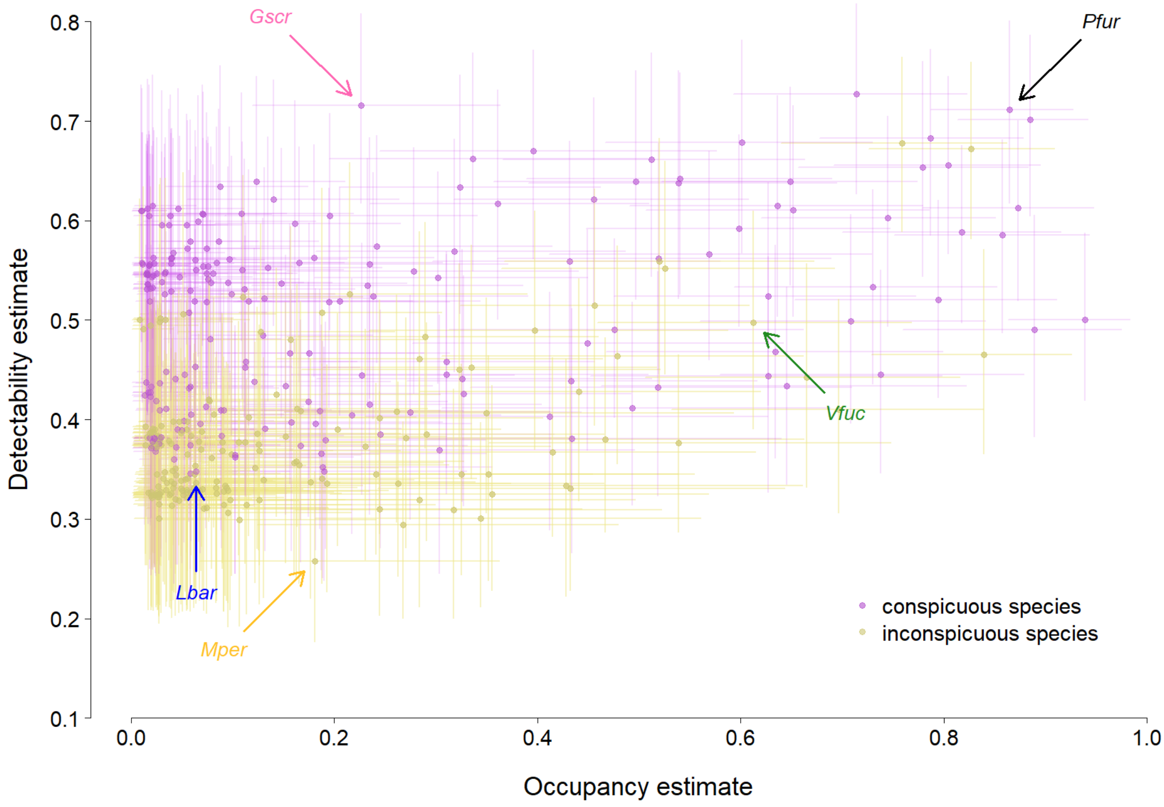

Fig. 4 Species-specific estimates of detectability against estimates of occupancy probability obtained from the community occupancy model fit to survey data from 373 Swiss tree lichens. Points represent the posterior means and bars the Bayesian 95% CRI. Detectability estimates are averaged across all 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: *Pseudevernia furfuracea* (black), *Graphis scripta* (pink), *Violella fucata* (green), *Myriolecis persimilis* (orange), and *Lecanora barkmaniana* (blue).

and subsequent microscopic analysis of most specimens that could not be identified in the field. In some way, our survey thus represents a best-case scenario 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; Lõhmus, 2009).

Although we were aware of some detection errors in our data, we would *a priori* have expected a much higher average detectability for several reasons: 1) 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, 2) all surveyors in this study were experienced lichen specialists, and 3) the sampling protocol was intended to be exhaustive, i.e. survey time per site was not strictly limited, and specimens collected in the field were all later identified in the lab. Although the sampled area per site was relatively large (500 m^2), we had hoped that the generous allowance of survey time would have counter-balanced this less favourable aspect. With an average detectability 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 detectability 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 et al., 2006; Supplementary Materials; Dorazio & Royle, 2005). A few studies have assessed the indirect effects of detectability on estimated species richness in lichens (Britton et al., 2014; Cáceres et al., 2008; McCune et al., 1997; Vondrák et al., 2016), but this is the first study to formally estimate species-specific detectability using standardised data from a nation-wide 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 in a best case when observers are experts, search area is limited, and time is not limiting. It is likely that under less favourable conditions (i.e., larger search areas, tighter time restrictions, or less experienced observers), detectability 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 (Berberich et al., 2016; Brown et al., 2017; Cáceres et al., 2008; Casanovas et

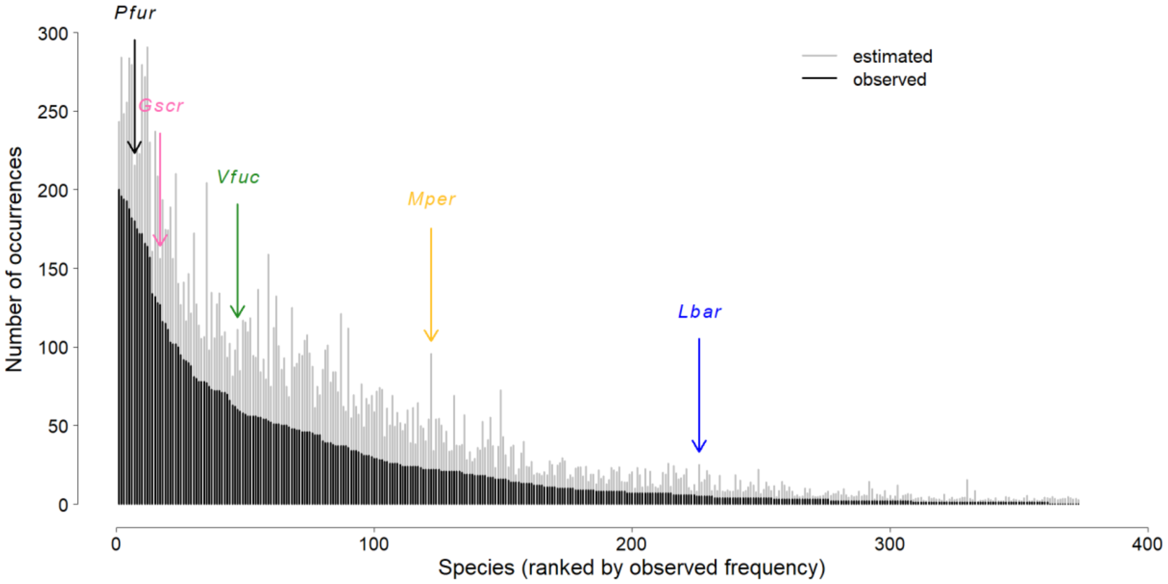

Fig. 5 Number of occurrences per species that were observed (black bars) or estimated by the occupancy model (grey bars) for 373 tree lichen species at a total of 416 surveyed sites. No species was observed at more than 200 sites, but 17 species were estimated to occur at more than 200 sites. Five example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

al., 2014; Chen et al., 2009, 2013; Dennett et al., 2018; Dennett & Nielsen, 2019; Garrard et al., 2008, 2013; Iles et al., 2019; Kéry & Gregg, 2003; Middleton & Vining, 2022; Morrison, 2016; Perret et al., 2023; Vittoz et al., 2010; Vondrák et al., 2016). Yet, detectability 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) 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, on the other hand, do both, which is why they have become so popular (Guillera-Arroita, 2017). Like other authors (Casanovas et al., 2014; Chen et al., 2009, 2013; Middleton & Vining, 2022; Perret et al., 2023), we believe that we do not yet realize 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 and some experience in model fitting, but where detectability is considerably < 1, the benefits of more accurate estimates of species occupancy will arguably outweigh the costs of such an undertaking. Normally, a few repeated visits to a subset of the sampling sites is enough to allow the explicit modelling of detection errors (MacKenzie & Royle, 2005; von Hirschheydt et al., 2023). Recall that in our study we had two replicated visits in only 46 out of 416 sites.

There are a few limitations to our study. First, the sampling protocol targeted only lichens growing up to two meters 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. For lichen species that prefer the crown of trees, our estimates may thus still be biased low (Boch et al., 2013; Kiebacher et al., 2016; Marmor et al., 2013). Second, 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, habitat structure or slope exposure would be desirable variables to include in the model. Third, we considered only false-negative detection errors (imperfect detection) and assumed that false-positive errors (i.e., typically due to species misidentification) were absent. The way the sampling was standardised convinced us that the latter would be negligible, but we cannot exclude the possibility that some small false-positive error may have affected our estimates (Miller et al., 2011; Royle & Link, 2006).

Conclusions

It is tempting to assume that sessile organisms are easy to detect because they cannot move. Among all sessile organisms, lichens in particular should be easy to assess, as they do not show any seasonality in morphology, in contrast to plants or fungi. Alas, the reality is different. Here, 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 missed with a probability of 0.48 during a single survey. We believe that equally considerable imperfect detection is at work in other surveys of lichens but also of other sessile organisms such as plants and fungi, even when data are collected with a standardised protocol and not by opportunistic sampling that poses even greater challenges to analysis. 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.

Data availability

All cleaned data used in this study and all R code to reproduce the presented results and figures in this study will be made available on EnviDat (https://envidat.ch) upon acceptance of the manuscript. Until then, data and code are available on a temporary GitHub repository: https://github.com/gesahirsch/lichen_detectability.git. In the published data, observers are anonymized, and sites are given without their geographic coordinates to preserve the local populations of protected and rare species.

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Supplementary materials

Appendix 1 - Prior sensitivity analysis

The model we present in the main manuscript of this publication uses three different sets of priors for three types of parameters:

1) priors for intercepts of the logistic regression models (occupancy and detection)
2) priors for the regression coefficients
3) priors for the variance terms (or standard deviations SD) of the species random effects

Here, we test whether our relatively informative priors on the regression coefficients and standard deviations of the random effects could have influenced the posterior distribution of the main parameters. The priors tested in this sensitivity analysis are summarized in Table S1. In Fig. S1 and Fig. S2 we visualize the priors themselves, comparing the prior we used in the final analysis to a less informative prior. In Fig. S3 we then illustrate the posterior distribution of the main parameters across the three sets of priors.

Conclusions

In comparison to the alternative priors tested here, the priors we used in the final model seem relatively informative (Fig. S1 and S2). When comparing the posterior distributions of the main parameters, however, we cannot perceive any major difference in any parameter, neither in their mean nor in their uncertainty (Fig. S3) and therefore conclude that our results are robust to prior specification.

Table S1 Priors used in the final and in two additional model runs. For each alternative set of priors, only the priors for one set of parameters were changed. Where the field is empty, we used the same priors as in the final model run. Green code shows the syntax used to define this prior in JAGS (Plummer, 2003). The two prior distributions for the regression coefficients are shown in Fig. S1, the two prior distributions for the standard deviations of the random effects in Fig. S2.

Parameters		**Priors used**	**Alternative priors 1**	**Alternative priors 2**

Intercepts	`mu.alpha0`
	`mu.beta1[1:7]`
		Uniform on the probability scale, transformed to logit scale[1]:
		`param.prob ~ dunif(0, 1)`
		`param <- logit(param.prob)`		

Regression coefficients	`mu.alpha1`
	`mu.alpha2`
	`alpha3`
	`beta2`
	`beta3`
		Cauchy with SD=2.5 (Gelman et al., 2008):
		`param ~ dt(0, 1/2.5^2, 1)`
			Normal with SD=10 (tau=0.01):
			`param ~ dnorm(0, 0.01)`	

Standard deviations of random effects	`sd.alpha0`
	`sd.alpha1`
	`sd.alpha2`
	`sd.beta1[1:7]`
		Half-Cauchy with SD=2.25 (Broms et al., 2016):
		`param ~ dt(0, 1/2.25^2, 1) T(0, )`
				Half-Cauchy with SD=25 (Gelman, 2006):
				`param ~ dt(0, 1/25^2, 1) T(0, )`

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[1] Note that this is equivalent to defining a logistic prior on the intercept directly, computed in JAGS as: `param ~ dlogis(0, 1)`

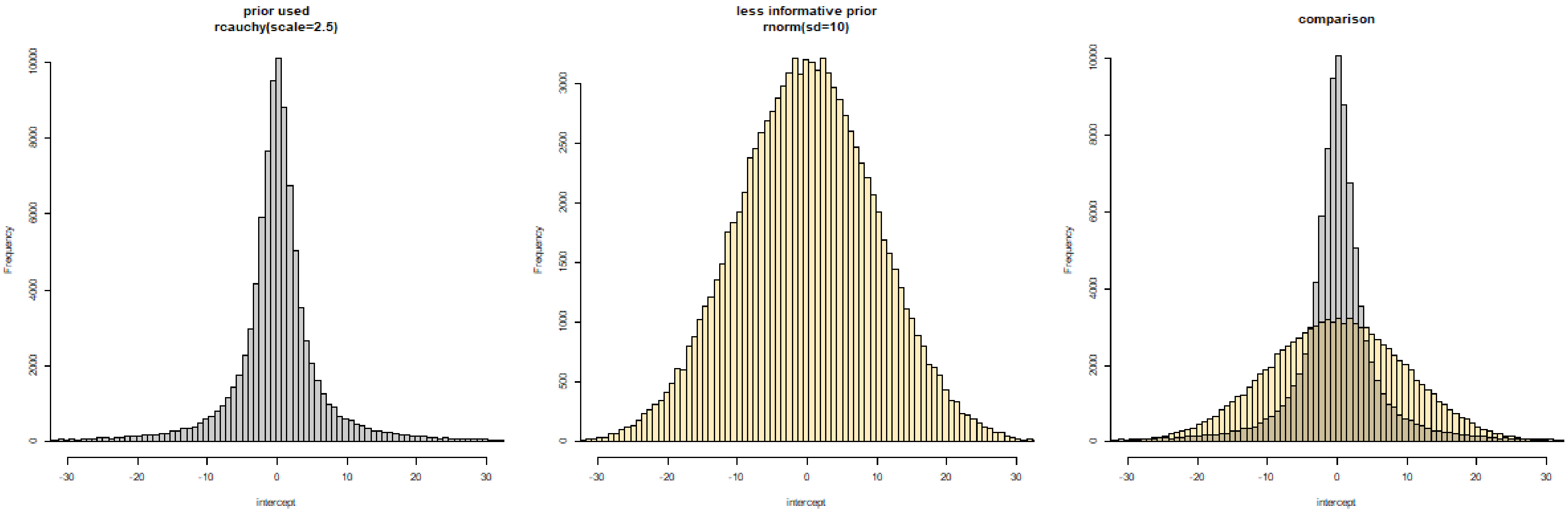

Fig. S1 Comparison of the prior distributions used in the final model (grey) vs. the alternative, less informative prior 1 (beige). Note that the tails of the distributions are cut off.

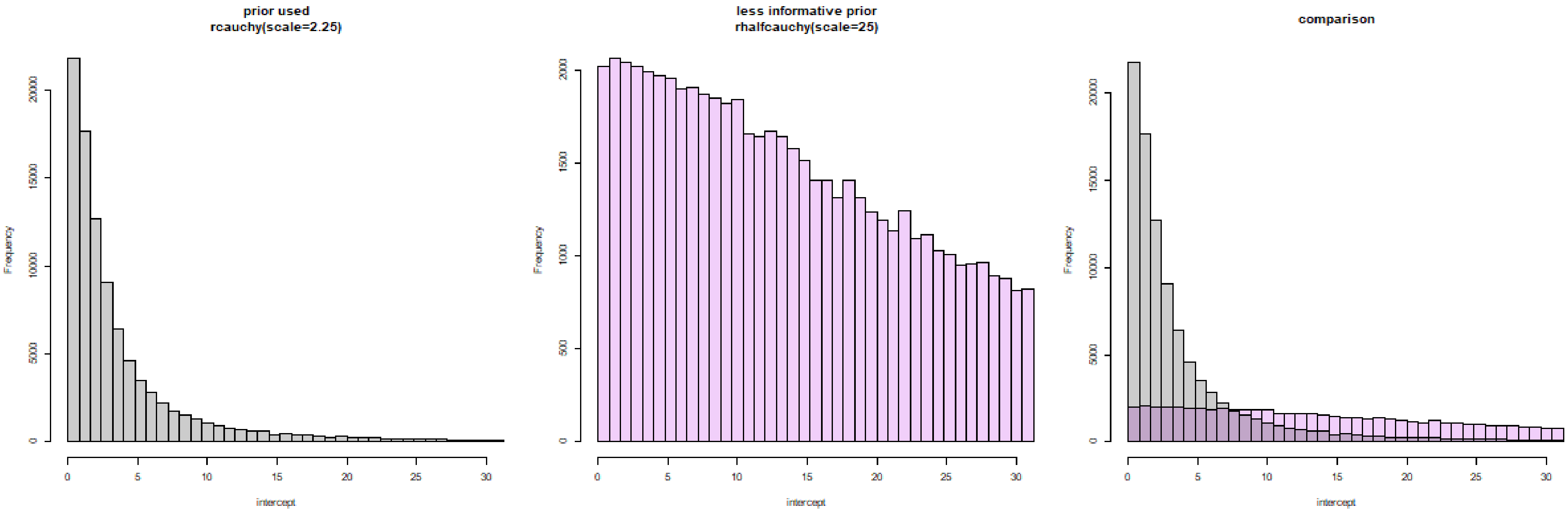

Fig. S2 Comparison of the prior distributions used in the final model (grey) vs. the alternative, less informative prior 2 (purple). Note that the tails of the distributions are cut off.

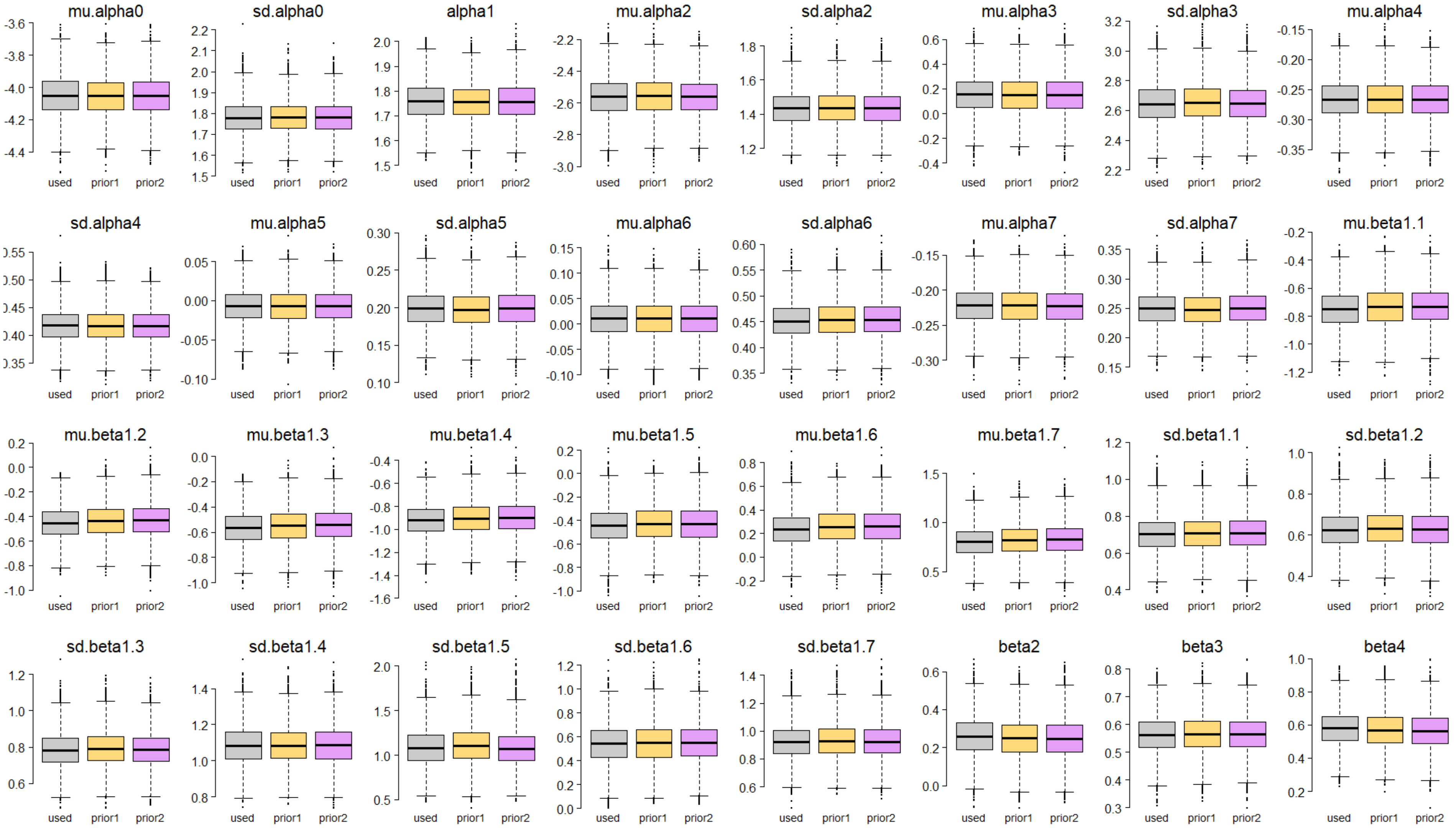

Fig. S3 Comparison of the posterior distributions of the 32 main parameters. In each boxplot, the left-hand boxplot (grey) is the result obtained in our final model run which uses a Cauchy prior with SD=2.5 for regression coefficients and a half-Cauchy prior with SD=2.25 for the standard deviation of the random effects. The middle boxplot in each panel (beige) uses a normally distribution prior for the regression coefficients with SD=10 (all other priors being equal). The right boxplot in each panel (purple) uses a half-Cauchy prior with SD=25 for the random effects (all other priors being equal).

Appendix 2 – Species- and observer-specific detectabilities

Table S2 Species- and observer-specific detectabilities. Estimates represent the predicted probability that an observer would find a species at a site where it occurs, taking into account the conspicuousness and the taxonomic identifiability of that species. Note that these estimates assume that the observer has never detected the species previously (i.e., experience=0), because individual experience values changed over the course of the field study and this table thus shows observer differences corrected for differences in experience.

	Observer						
species	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Acolium inquinans	0.391	0.491	0.398	0.273	0.440	0.610	0.737
Acolium karelicum	0.379	0.402	0.332	0.246	0.418	0.627	0.800
Acrocordia cavata	0.312	0.381	0.346	0.269	0.391	0.584	0.689
Acrocordia gemmata	0.302	0.416	0.275	0.365	0.380	0.548	0.724
aff. Lecania cyrtellina	0.446	0.347	0.314	0.337	0.371	0.541	0.557
aff. Pyrrhospora quernea	0.309	0.367	0.333	0.415	0.381	0.590	0.666
Agonimia allobata/repleta	0.330	0.309	0.336	0.156	0.319	0.526	0.777
Agonimia octospora	0.299	0.465	0.290	0.238	0.377	0.546	0.733
Agonimia tristicula	0.283	0.387	0.377	0.551	0.358	0.587	0.773
Alectoria sarmentosa	0.359	0.511	0.399	0.268	0.441	0.617	0.740
Alyxoria varia aggr.	0.296	0.447	0.225	0.600	0.459	0.553	0.691
Amandinea punctata	0.213	0.449	0.618	0.449	0.256	0.683	0.589
Anaptychia ciliaris	0.381	0.490	0.397	0.327	0.279	0.634	0.615
Anisomeridium polypori	0.162	0.285	0.301	0.205	0.321	0.633	0.829
Arthonia atra	0.334	0.441	0.189	0.407	0.419	0.670	0.748
Arthonia didyma	0.334	0.368	0.242	0.227	0.167	0.694	0.856
Arthonia dispersa	0.317	0.381	0.346	0.261	0.392	0.589	0.687
Arthonia faginea	0.310	0.380	0.437	0.255	0.380	0.557	0.679
Arthonia fuliginosa	0.311	0.443	0.335	0.255	0.384	0.552	0.677
Arthonia mediella	0.444	0.350	0.233	0.125	0.247	0.649	0.686
Arthonia radiata	0.308	0.532	0.365	0.543	0.385	0.654	0.756
Arthonia ruana	0.208	0.203	0.286	0.352	0.462	0.629	0.840
Arthonia spadicea	0.326	0.322	0.217	0.126	0.418	0.560	0.781
Arthrosporum populorum	0.424	0.365	0.331	0.247	0.377	0.577	0.671
Bacidia absistens	0.254	0.350	0.383	0.274	0.371	0.531	0.795
Bacidia arceutina	0.276	0.397	0.363	0.182	0.467	0.552	0.775
Bacidia circumspecta	0.297	0.452	0.402	0.353	0.380	0.544	0.719
Bacidia incompta	0.375	0.432	0.336	0.248	0.386	0.548	0.681
Bacidia laurocerasi	0.405	0.500	0.273	0.249	0.426	0.595	0.703
Bacidia rosella	0.373	0.444	0.405	0.447	0.447	0.622	0.740
Bacidia rubella	0.260	0.573	0.273	0.485	0.606	0.633	0.821
Bacidia subincompta aggr.	0.291	0.400	0.373	0.292	0.570	0.684	0.861
Bacidina arnoldiana aggr.	0.322	0.341	0.305	0.477	0.436	0.601	0.663
Bacidina chloroticula	0.294	0.404	0.476	0.152	0.496	0.569	0.702
Bacidina delicata	0.323	0.365	0.329	0.258	0.337	0.559	0.731
Bacidina neosquamulosa	0.288	0.383	0.285	0.200	0.312	0.633	0.646
Bacidina phacodes	0.368	0.422	0.332	0.353	0.382	0.542	0.660
Bactrospora dryina	0.371	0.490	0.409	0.313	0.446	0.621	0.740
Biatora beckhausii	0.331	0.376	0.482	0.160	0.353	0.563	0.713
Biatora chrysantha	0.540	0.635	0.589	0.517	0.515	0.604	0.786
Biatora efflorescens	0.219	0.490	0.539	0.189	0.533	0.531	0.701

Table S2 continued

	Observer						
species	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Biatora fallax	0.505	0.476	0.411	0.213	0.561	0.618	0.687
Biatora flavopunctata	0.325	0.366	0.346	0.637	0.339	0.594	0.654
Biatora globulosa	0.282	0.520	0.183	0.178	0.481	0.570	0.736
Biatora helvola	0.336	0.454	0.547	0.208	0.351	0.518	0.690
Biatora ocelliformis	0.315	0.380	0.348	0.209	0.385	0.554	0.740
Biatora rufidula	0.285	0.374	0.345	0.257	0.382	0.554	0.750
Biatora subduplex	0.511	0.364	0.517	0.432	0.393	0.632	0.712
Biatora vacciniicola	0.352	0.359	0.329	0.366	0.372	0.585	0.676
Biatora veteranorum	0.374	0.415	0.297	0.223	0.390	0.541	0.651
Biatoridium monasteriense	0.274	0.379	0.423	0.347	0.369	0.604	0.768
Bryobilimbia sanguineoatra	0.359	0.437	0.430	0.234	0.394	0.614	0.788
Bryoria capillaris	0.636	0.608	0.516	0.184	0.267	0.651	0.807
Bryoria fuscescens	0.375	0.446	0.585	0.439	0.363	0.687	0.775
Bryoria implexa	0.476	0.470	0.680	0.327	0.666	0.575	0.813
Bryoria nadvornikiana	0.353	0.469	0.379	0.584	0.436	0.611	0.724
Bryoria subcana	0.309	0.374	0.439	0.254	0.380	0.552	0.589
Bryostigma muscigenum	0.354	0.368	0.341	0.224	0.379	0.588	0.686
Buellia arborea	0.228	0.339	0.384	0.174	0.351	0.622	0.781
Buellia disciformis	0.258	0.379	0.479	0.218	0.478	0.658	0.766
Buellia erubescens	0.346	0.478	0.383	0.182	0.399	0.647	0.780
Buellia griseovirens	0.321	0.399	0.380	0.253	0.343	0.650	0.723
Buellia schaereri	0.663	0.419	0.300	0.390	0.671	0.403	0.832
Byssoloma marginatum	0.312	0.380	0.309	0.257	0.388	0.555	0.742
Calicium adspersum	0.366	0.479	0.400	0.411	0.441	0.616	0.740
Calicium glaucellum	0.307	0.375	0.351	0.255	0.388	0.588	0.681
Calicium lenticulare	0.295	0.377	0.436	0.240	0.534	0.550	0.682
Calicium montanum	0.378	0.522	0.275	0.243	0.565	0.589	0.677
Calicium parvum	0.314	0.442	0.346	0.253	0.381	0.556	0.680
Calicium salicinum	0.314	0.380	0.352	0.418	0.380	0.555	0.687
Calicium trabinellum	0.297	0.310	0.481	0.192	0.564	0.545	0.685
Calicium viride	0.270	0.457	0.426	0.573	0.588	0.642	0.766
Caloplaca alnetorum/pyracea	0.465	0.464	0.451	0.287	0.434	0.606	0.768
Caloplaca cerina aggr.	0.318	0.397	0.254	0.305	0.191	0.645	0.502
Caloplaca cerinella	0.379	0.421	0.420	0.291	0.424	0.635	0.488
Caloplaca cerinelloides	0.331	0.380	0.444	0.250	0.257	0.573	0.600
Caloplaca chlorina	0.376	0.424	0.251	0.539	0.332	0.506	0.694
Caloplaca chrysophthalma	0.368	0.441	0.404	0.236	0.444	0.618	0.776
Caloplaca ferruginea/hungarica	0.329	0.627	0.296	0.190	0.435	0.581	0.801
Caloplaca herbidella aggr.	0.413	0.406	0.357	0.114	0.379	0.471	0.638
Caloplaca holocarpa	0.588	0.292	0.589	0.316	0.309	0.685	0.416
Caloplaca isidiigera	0.296	0.410	0.459	0.392	0.389	0.538	0.553
Caloplaca lucifuga	0.313	0.367	0.410	0.254	0.385	0.580	0.687
Caloplaca obscurella	0.378	0.413	0.327	0.372	0.377	0.544	0.554
Caloplaca sorocarpa	0.313	0.285	0.267	0.587	0.317	0.615	0.705
Caloplaca sp.1	0.349	0.443	0.361	0.388	0.330	0.558	0.741
Caloplaca ulcerosa	0.314	0.379	0.347	0.432	0.390	0.556	0.685
Candelaria concolor/pacifica	0.359	0.302	0.437	0.356	0.337	0.665	0.579
Candelariella antennaria/viae-lacteae	0.310	0.381	0.351	0.265	0.388	0.578	0.689

Table S2 continued

	Observer						
species	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Candelariella reflexa	0.382	0.418	0.559	0.463	0.340	0.734	0.846
Candelariella vitellina	0.535	0.355	0.206	0.115	0.314	0.645	0.819
Candelariella xanthostigma	0.212	0.446	0.467	0.676	0.276	0.608	0.488
Catillaria nigroclavata	0.276	0.331	0.446	0.241	0.570	0.598	0.790
Catinaria atropurpurea	0.308	0.435	0.290	0.238	0.381	0.551	0.744
Cetraria sepincola	0.417	0.444	0.416	0.316	0.444	0.616	0.746
Cetrelia olivetorum aggr.	0.350	0.476	0.463	0.331	0.436	0.606	0.797
Chaenotheca brachypoda	0.405	0.435	0.383	0.409	0.427	0.631	0.758
Chaenotheca brunneola	0.314	0.378	0.310	0.257	0.386	0.556	0.730
Chaenotheca chrysocephala	0.370	0.560	0.326	0.632	0.628	0.504	0.781
Chaenotheca ferruginea	0.276	0.397	0.360	0.166	0.684	0.512	0.849
Chaenotheca furfuracea	0.522	0.390	0.194	0.554	0.445	0.553	0.744
Chaenotheca gracilenta	0.314	0.352	0.344	0.254	0.386	0.556	0.732
Chaenotheca laevigata	0.312	0.380	0.309	0.254	0.390	0.555	0.731
Chaenotheca phaeocephala	0.447	0.452	0.373	0.441	0.436	0.617	0.597
Chaenotheca stemonea	0.400	0.358	0.351	0.471	0.593	0.575	0.790
Chaenotheca subroscida	0.320	0.380	0.435	0.255	0.383	0.559	0.686
Chaenotheca trichialis	0.457	0.463	0.340	0.552	0.640	0.594	0.866
Chrysothrix candelaris	0.559	0.447	0.270	0.544	0.536	0.616	0.663
Cladonia cenotea	0.355	0.498	0.528	0.111	0.627	0.604	0.660
Cladonia coniocraea aggr.	0.401	0.350	0.491	0.795	0.682	0.560	0.864
Cladonia digitata	0.307	0.455	0.475	0.647	0.665	0.591	0.866
Cladonia fimbriata	0.313	0.405	0.660	0.483	0.588	0.650	0.847
Cladonia squamosa	0.393	0.453	0.293	0.677	0.401	0.610	0.620
Cliostomum corrugatum	0.352	0.427	0.395	0.585	0.438	0.616	0.738
Cliostomum haematommatis/ Loxospora cristinae	0.327	0.481	0.439	0.287	0.414	0.640	0.845
Cliostomum pallens	0.310	0.440	0.349	0.258	0.383	0.549	0.683
Coenogonium luteum	0.318	0.430	0.349	0.264	0.389	0.560	0.730
Coenogonium pineti	0.487	0.530	0.638	0.494	0.723	0.632	0.893
Collema flaccidum	0.392	0.451	0.467	0.451	0.438	0.625	0.778
Collema nigrescens aggr.	0.365	0.440	0.454	0.400	0.449	0.637	0.740
Coniocarpon cinnabarinum aggr.	0.388	0.348	0.447	0.333	0.415	0.660	0.778
Eopyrenula leucoplaca	0.242	0.284	0.519	0.350	0.343	0.542	0.770
Evernia divaricata	0.442	0.443	0.643	0.426	0.560	0.588	0.553
Evernia mesomorpha	0.416	0.549	0.344	0.205	0.391	0.579	0.694
Evernia prunastri	0.275	0.588	0.276	0.222	0.619	0.658	0.472
Fellhanera bouteillei	0.310	0.371	0.334	0.374	0.502	0.553	0.679
Fellhanera gyrophorica	0.316	0.378	0.434	0.259	0.387	0.558	0.733
Fellhanera viridisorediata	0.310	0.380	0.340	0.219	0.374	0.556	0.746
Flavoparmelia caperata	0.428	0.359	0.511	0.346	0.397	0.648	0.699
Flavopunctelia flaventior	0.365	0.469	0.389	0.420	0.434	0.628	0.598
Frutidella furfuracea	0.285	0.567	0.296	0.290	0.535	0.622	0.653
Fuscidea pusilla	0.279	0.362	0.320	0.353	0.373	0.588	0.726
Graphis scripta	0.433	0.620	0.612	0.526	0.645	0.621	0.823
Gyalecta fagicola	0.411	0.407	0.324	0.228	0.380	0.571	0.550
Gyalecta flotowii	0.315	0.443	0.352	0.257	0.383	0.557	0.690
Gyalecta truncigena aggr.	0.386	0.339	0.255	0.412	0.357	0.541	0.774
Haematomma ochroleucum	0.358	0.418	0.567	0.406	0.437	0.603	0.801

Table S2 continued

				Observer			
species	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Halecania viridescens	0.286	0.309	0.369	0.204	0.507	0.586	0.741
Hyperphyscia adglutinata	0.357	0.276	0.446	0.200	0.442	0.598	0.753
Hypocenomyce scalaris	0.314	0.434	0.495	0.271	0.480	0.616	0.835
Hypogymnia austerodes	0.457	0.432	0.403	0.293	0.437	0.609	0.737
Hypogymnia bitteri	0.448	0.458	0.439	0.406	0.512	0.641	0.755
Hypogymnia farinacea	0.376	0.566	0.514	0.455	0.413	0.627	0.674
Hypogymnia physodes	0.490	0.578	0.700	0.467	0.653	0.702	0.531
Hypogymnia tubulosa	0.482	0.465	0.681	0.115	0.157	0.497	0.439
Hypogymnia vittata	0.463	0.482	0.366	0.410	0.428	0.601	0.592
Hypotrachyna revoluta aggr.	0.314	0.381	0.329	0.509	0.415	0.641	0.681
Imshaugia aleurites	0.372	0.305	0.525	0.519	0.321	0.647	0.827
Jamesiella anastomosans	0.257	0.352	0.153	0.184	0.270	0.551	0.798
Japewia subaurifera	0.502	0.361	0.326	0.230	0.374	0.537	0.670
Japewia tornoensis	0.291	0.498	0.374	0.164	0.503	0.508	0.709
Lecania cyrtella	0.431	0.286	0.496	0.225	0.449	0.578	0.675
Lecania fuscella	0.305	0.367	0.324	0.366	0.539	0.583	0.676
Lecania naegelii	0.259	0.358	0.339	0.254	0.153	0.631	0.685
Lecanora aff. expallens	0.299	0.361	0.398	0.536	0.370	0.543	0.671
Lecanora albella	0.384	0.409	0.433	0.390	0.415	0.561	0.806
Lecanora allophana	0.449	0.393	0.374	0.393	0.361	0.656	0.803
Lecanora anopta	0.382	0.373	0.349	0.254	0.381	0.554	0.691
Lecanora argentata	0.162	0.490	0.507	0.168	0.629	0.687	0.801
Lecanora barkmaniana	0.417	0.353	0.282	0.163	0.455	0.596	0.851
Lecanora boligera	0.345	0.459	0.307	0.213	0.362	0.574	0.680
Lecanora cadubriae	0.360	0.408	0.497	0.081	0.566	0.520	0.796
Lecanora carpinea	0.438	0.502	0.397	0.247	0.466	0.621	0.863
Lecanora chlarotera	0.568	0.360	0.336	0.495	0.360	0.438	0.398
Lecanora circumborealis	0.295	0.553	0.710	0.339	0.582	0.511	0.415
Lecanora conizaeoides	0.484	0.472	0.577	0.114	0.571	0.635	0.759
Lecanora expallens	0.311	0.426	0.424	0.239	0.373	0.546	0.679
Lecanora expersa	0.371	0.473	0.420	0.156	0.568	0.580	0.762
Lecanora fuscescens	0.388	0.347	0.319	0.208	0.359	0.614	0.680
Lecanora gisleri	0.353	0.496	0.413	0.303	0.443	0.614	0.741
Lecanora hagenii aggr.	0.400	0.383	0.535	0.344	0.460	0.572	0.392
Lecanora horiza aggr.	0.351	0.471	0.450	0.532	0.444	0.605	0.805
Lecanora hypopta	0.248	0.350	0.315	0.210	0.362	0.535	0.792
Lecanora intumescens	0.376	0.477	0.471	0.288	0.289	0.665	0.736
Lecanora leptyrodes	0.344	0.365	0.736	0.239	0.367	0.525	0.533
Lecanora mughicola	0.347	0.434	0.396	0.295	0.444	0.671	0.738
Lecanora phaeostigma	0.236	0.304	0.277	0.680	0.499	0.500	0.630
Lecanora praesistens	0.342	0.412	0.509	0.268	0.436	0.661	0.771
Lecanora pulicaris	0.256	0.549	0.307	0.289	0.628	0.698	0.601
Lecanora salicicola	0.444	0.483	0.384	0.404	0.427	0.603	0.731
Lecanora saligna	0.350	0.443	0.639	0.192	0.322	0.667	0.631
Lecanora strobilina aggr.	0.204	0.355	0.286	0.384	0.623	0.653	0.887
Lecanora subcarpinea	0.325	0.509	0.585	0.521	0.408	0.581	0.712
Lecanora subintricata	0.363	0.372	0.273	0.361	0.475	0.584	0.819
Lecanora symmicta aggr.	0.369	0.359	0.380	0.204	0.509	0.644	0.608
Lecanora varia	0.435	0.418	0.461	0.133	0.365	0.681	0.727

Table S2 continued

	Observer						
species	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Lecidea erythrophaea	0.496	0.359	0.326	0.230	0.363	0.544	0.762
Lecidea leprarioides	0.339	0.444	0.299	0.322	0.359	0.538	0.732
Lecidea nylanderi	0.173	0.236	0.259	0.320	0.368	0.561	0.838
Lecidea turgidula	0.311	0.376	0.349	0.271	0.388	0.522	0.750
Lecidella aff. leprothalla	0.268	0.350	0.309	0.182	0.362	0.598	0.760
Lecidella albida	0.343	0.424	0.277	0.465	0.531	0.555	0.869
Lecidella elaeochroma aggr.	0.424	0.423	0.451	0.347	0.205	0.626	0.730
Lecidella flavosorediata	0.233	0.311	0.323	0.426	0.203	0.589	0.742
Lecidella sp.3	0.293	0.437	0.354	0.338	0.359	0.564	0.704
Lecidella subviridis	0.416	0.598	0.338	0.685	0.385	0.650	0.669
Lepra albescens	0.508	0.380	0.574	0.299	0.425	0.614	0.687
Lepra amara	0.408	0.493	0.296	0.603	0.533	0.614	0.740
Lepra multipuncta	0.372	0.437	0.501	0.301	0.441	0.620	0.735
Lepra opthalmiza	0.373	0.439	0.403	0.450	0.442	0.618	0.743
Lepraria eburnea	0.338	0.549	0.601	0.210	0.766	0.574	0.830
Lepraria elobata	0.517	0.616	0.425	0.324	0.826	0.726	0.727
Lepraria finkii	0.454	0.310	0.371	0.692	0.566	0.495	0.825
Lepraria incana	0.351	0.679	0.379	0.221	0.687	0.673	0.758
Lepraria jackii	0.392	0.585	0.516	0.557	0.555	0.606	0.811
Lepraria obtusatica	0.355	0.424	0.313	0.400	0.440	0.605	0.816
Lepraria rigidula	0.550	0.586	0.588	0.613	0.650	0.573	0.867
Lepraria vouauxii	0.355	0.281	0.312	0.483	0.156	0.582	0.760
Leptogium saturninum	0.349	0.407	0.494	0.347	0.438	0.625	0.772
Letharia vulpina	0.300	0.485	0.518	0.211	0.491	0.648	0.799
Lobaria pulmonaria	0.375	0.447	0.418	0.408	0.453	0.620	0.746
Lopadium disciforme	0.298	0.401	0.238	0.213	0.372	0.570	0.757
Loxospora cismonica	0.311	0.381	0.429	0.260	0.387	0.555	0.692
Loxospora elatina	0.345	0.503	0.431	0.663	0.387	0.491	0.670
Megalaria pulverea	0.319	0.367	0.390	0.495	0.361	0.513	0.812
Melanelixia glabra	0.312	0.533	0.358	0.380	0.415	0.656	0.572
Melanelixia glabratula aggr.	0.539	0.499	0.511	0.337	0.566	0.664	0.760
Melanelixia subargentifera	0.416	0.417	0.451	0.227	0.516	0.653	0.771
Melanelixia subaurifera	0.227	0.467	0.236	0.302	0.294	0.622	0.472
Melanohalea elegantula	0.414	0.471	0.381	0.286	0.437	0.632	0.766
Melanohalea exasperata	0.369	0.458	0.442	0.119	0.376	0.586	0.432
Melanohalea exasperatula	0.403	0.501	0.512	0.151	0.422	0.690	0.381
Menegazzia terebrata	0.367	0.440	0.489	0.301	0.442	0.619	0.748
Micarea adnata	0.314	0.431	0.349	0.262	0.383	0.559	0.689
Micarea cinerea f. cinerea	0.315	0.379	0.422	0.255	0.381	0.556	0.730
Micarea coppinsii	0.310	0.377	0.347	0.256	0.384	0.598	0.682
Micarea denigrata	0.334	0.351	0.265	0.087	0.576	0.569	0.792
Micarea melaena	0.286	0.402	0.421	0.308	0.532	0.537	0.662
Micarea nitschkeana	0.389	0.367	0.336	0.237	0.543	0.550	0.670
Micarea peliocarpa	0.427	0.462	0.304	0.414	0.422	0.545	0.712
Micarea prasina aggr.	0.522	0.524	0.559	0.607	0.772	0.629	0.719
Micarea sp.1	0.311	0.372	0.335	0.498	0.382	0.550	0.669
Mycobilimbia epixanthoides/ Lecania croatica	0.393	0.561	0.240	0.141	0.347	0.503	0.579
Mycobilimbia pilularis	0.370	0.443	0.492	0.313	0.441	0.618	0.738

Table S2 continued

	Observer						
species	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Mycoblastus affinis	0.425	0.479	0.396	0.278	0.433	0.616	0.611
Mycoblastus alpinus	0.236	0.420	0.379	0.300	0.349	0.522	0.700
Myochroidea porphyrospoda	0.360	0.367	0.402	0.284	0.527	0.555	0.718
Myochroidea rufofusca	0.281	0.367	0.340	0.375	0.379	0.589	0.688
Myriolecis persimilis	0.188	0.289	0.169	0.073	0.255	0.692	0.696
Myriolecis sambuci	0.494	0.338	0.418	0.384	0.446	0.577	0.737
Nephroma bellum	0.409	0.471	0.402	0.288	0.447	0.619	0.745
Nephroma parile	0.320	0.456	0.533	0.229	0.429	0.616	0.742
Nephroma resupinatum	0.374	0.478	0.409	0.307	0.451	0.622	0.744
Nephromopsis laureri	0.301	0.476	0.403	0.282	0.438	0.620	0.767
Normandina acroglypta	0.283	0.317	0.538	0.134	0.349	0.473	0.831
Normandina pulchella	0.370	0.448	0.273	0.394	0.128	0.612	0.780
Ochrolechia alboflavescens	0.403	0.587	0.586	0.255	0.559	0.684	0.815
Ochrolechia androgyna aggr.	0.606	0.476	0.481	0.518	0.264	0.550	0.628
Ochrolechia arborea	0.184	0.494	0.506	0.285	0.343	0.596	0.767
Ochrolechia microstictoides	0.283	0.554	0.345	0.188	0.547	0.586	0.786
Ochrolechia pallescens	0.367	0.443	0.353	0.310	0.450	0.619	0.778
Ochrolechia szatalaensis	0.360	0.468	0.526	0.188	0.399	0.603	0.814
Ochrolechia turneri	0.280	0.431	0.357	0.299	0.392	0.689	0.802
Opegrapha sp.1	0.307	0.377	0.328	0.246	0.375	0.605	0.678
Opegrapha vermicellifera	0.338	0.438	0.386	0.511	0.374	0.621	0.786
Opegrapha vulgata aggr.	0.369	0.499	0.337	0.558	0.226	0.602	0.802
Pannaria conoplea	0.372	0.440	0.414	0.424	0.448	0.622	0.745
Parmelia saxatilis aggr.	0.350	0.513	0.537	0.638	0.554	0.654	0.746
Parmelia submontana	0.423	0.487	0.446	0.198	0.417	0.640	0.657
Parmelia sulcata	0.407	0.473	0.556	0.193	0.304	0.602	0.726
Parmeliella triptophylla	0.362	0.467	0.455	0.399	0.438	0.618	0.737
Parmelina pastillifera	0.407	0.439	0.520	0.460	0.430	0.629	0.754
Parmelina quercina aggr.	0.384	0.494	0.446	0.237	0.433	0.561	0.514
Parmelina tiliacea	0.373	0.459	0.480	0.458	0.306	0.606	0.617
Parmeliopsis ambigua	0.487	0.575	0.581	0.649	0.598	0.687	0.801
Parmeliopsis hyperopta	0.399	0.547	0.556	0.332	0.636	0.644	0.830
Parmotrema crinitum	0.368	0.444	0.460	0.317	0.449	0.620	0.745
Parmotrema perlatum	0.374	0.442	0.462	0.314	0.453	0.619	0.598
Peltigera collina	0.362	0.432	0.453	0.477	0.449	0.617	0.734
Pertusaria alpina	0.366	0.433	0.354	0.434	0.443	0.617	0.803
Pertusaria coccodes	0.303	0.493	0.442	0.301	0.389	0.624	0.653
Pertusaria coronata	0.309	0.455	0.484	0.425	0.402	0.551	0.687
Pertusaria leioplaca	0.349	0.497	0.467	0.241	0.386	0.678	0.834
Pertusaria pupillaris	0.235	0.345	0.523	0.114	0.436	0.553	0.814
Pertusaria sommerfeltii	0.436	0.437	0.402	0.299	0.444	0.615	0.735
Phaeophyscia ciliata	0.414	0.439	0.404	0.412	0.452	0.616	0.742
Phaeophyscia endophoenicea	0.289	0.504	0.428	0.280	0.233	0.655	0.815
Phaeophyscia hirsuta	0.416	0.445	0.409	0.325	0.453	0.617	0.744
Phaeophyscia orbicularis	0.446	0.262	0.434	0.590	0.602	0.696	0.785
Phaeophyscia poeltii	0.373	0.437	0.404	0.316	0.451	0.638	0.742
Phlyctis agelaea	0.361	0.429	0.373	0.387	0.447	0.659	0.594
Phlyctis argena	0.579	0.619	0.492	0.557	0.406	0.671	0.880
Physcia adscendens	0.515	0.261	0.640	0.390	0.397	0.597	0.730

Table S2 continued

	Observer						
species	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Physcia aipolia	0.547	0.357	0.375	0.450	0.528	0.615	0.796
Physcia stellaris	0.182	0.380	0.381	0.132	0.295	0.675	0.487
Physcia tenella	0.230	0.463	0.275	0.324	0.374	0.633	0.700
Physciella chloantha	0.321	0.420	0.401	0.439	0.414	0.670	0.748
Physconia distorta	0.426	0.450	0.468	0.291	0.488	0.637	0.789
Physconia enteroxantha	0.408	0.433	0.371	0.291	0.445	0.614	0.767
Physconia grisea	0.348	0.409	0.491	0.530	0.519	0.607	0.583
Physconia perisidiosa	0.346	0.510	0.363	0.507	0.437	0.626	0.731
Piccolia ochrophora	0.291	0.392	0.454	0.336	0.356	0.586	0.668
Placynthiella dasaea	0.227	0.419	0.357	0.076	0.514	0.605	0.784
Placynthiella icmalea	0.261	0.334	0.329	0.082	0.447	0.448	0.807
Platismatia glauca	0.328	0.577	0.523	0.624	0.468	0.579	0.750
Pleurosticta acetabulum	0.411	0.478	0.433	0.133	0.532	0.627	0.781
Polycauliona candelaria	0.311	0.384	0.532	0.047	0.257	0.604	0.664
Polycauliona polycarpa	0.315	0.335	0.433	0.214	0.442	0.639	0.665
Porina leptalea	0.357	0.337	0.278	0.220	0.468	0.629	0.701
Protoparmelia hypotremella	0.317	0.576	0.199	0.095	0.445	0.603	0.758
Pseudevernia furfuracea	0.568	0.623	0.659	0.502	0.592	0.653	0.597
Pseudosagedia aenea	0.377	0.557	0.329	0.413	0.433	0.559	0.762
Pseudoschismatomma rufescens	0.453	0.630	0.298	0.171	0.245	0.511	0.736
Punctelia subrudecta aggr.	0.391	0.345	0.378	0.549	0.286	0.490	0.747
Pycnora sorophora	0.232	0.420	0.289	0.411	0.449	0.502	0.795
Pyrenula laevigata	0.352	0.417	0.434	0.490	0.435	0.603	0.792
Pyrenula nitida	0.328	0.465	0.400	0.514	0.372	0.658	0.790
Pyrenula nitidella	0.369	0.442	0.404	0.443	0.442	0.619	0.742
Ramalina dilacerata	0.434	0.441	0.407	0.310	0.450	0.620	0.601
Ramalina europaea/pollinaria	0.222	0.412	0.544	0.175	0.467	0.681	0.773
Ramalina farinacea	0.450	0.485	0.279	0.312	0.484	0.603	0.819
Ramalina fastigiata	0.361	0.468	0.447	0.279	0.433	0.635	0.596
Ramalina fraxinea	0.350	0.483	0.435	0.349	0.432	0.640	0.739
Ramalina obtusata aggr.	0.522	0.501	0.432	0.152	0.526	0.607	0.774
Ramalina thrausta	0.420	0.439	0.411	0.313	0.449	0.620	0.740
Reichlingia leopoldii	0.439	0.391	0.307	0.492	0.402	0.637	0.805
Rinodina albana	0.308	0.342	0.408	0.470	0.364	0.548	0.772
Rinodina archaea	0.239	0.441	0.388	0.214	0.358	0.568	0.723
Rinodina capensis	0.607	0.493	0.413	0.251	0.361	0.609	0.614
Rinodina conradii	0.309	0.373	0.348	0.258	0.389	0.589	0.689
Rinodina efflorescens	0.297	0.301	0.309	0.220	0.363	0.607	0.808
Rinodina exigua	0.265	0.417	0.349	0.431	0.356	0.546	0.603
Rinodina freyi	0.516	0.347	0.402	0.275	0.341	0.528	0.444
Rinodina griseosoralifera	0.310	0.372	0.415	0.201	0.382	0.552	0.771
Rinodina malangica	0.346	0.426	0.475	0.494	0.442	0.613	0.740
Rinodina orculata	0.364	0.485	0.248	0.275	0.261	0.637	0.689
Rinodina polysporoides	0.363	0.352	0.340	0.355	0.382	0.567	0.670
Rinodina pyrina	0.270	0.420	0.380	0.523	0.438	0.623	0.744
Rinodina sophodes	0.409	0.447	0.440	0.478	0.428	0.624	0.767
Ropalospora viridis	0.449	0.391	0.315	0.238	0.329	0.592	0.581
Schismatomma pericleum	0.299	0.348	0.211	0.379	0.579	0.370	0.831
Sclerophora pallida	0.317	0.386	0.430	0.263	0.393	0.558	0.689

Table S2 continued

	Observer						
species	**1**	**2**	**3**	**4**	**5**	**6**	**7**
Scoliciosporum chlorococcum	0.290	0.407	0.250	0.262	0.576	0.580	0.477
Scoliciosporum gallurae	0.278	0.386	0.395	0.153	0.467	0.599	0.806
Scoliciosporum sarothamni	0.195	0.536	0.489	0.087	0.643	0.587	0.345
Scoliciosporum umbrinum	0.319	0.459	0.329	0.195	0.403	0.579	0.482
Sticta sylvatica	0.374	0.446	0.417	0.419	0.452	0.618	0.742
Strangospora moriformis	0.371	0.367	0.393	0.197	0.346	0.637	0.660
Strangospora pinicola	0.314	0.340	0.343	0.259	0.383	0.553	0.737
Strigula glabra	0.371	0.413	0.414	0.239	0.382	0.549	0.758
Strigula jamesii	0.319	0.342	0.350	0.270	0.394	0.559	0.731
Strigula stigmatella	0.324	0.438	0.350	0.242	0.287	0.508	0.756
Tephromela atra	0.431	0.445	0.473	0.332	0.424	0.620	0.590
Tetramelas chloroleucus	0.426	0.423	0.483	0.262	0.436	0.644	0.612
Thelenella muscorum	0.319	0.382	0.345	0.431	0.383	0.552	0.679
Thelopsis rubella	0.317	0.431	0.356	0.266	0.392	0.559	0.724
Thelotrema lepadinum	0.372	0.443	0.452	0.397	0.446	0.621	0.759
Trapelia corticola	0.305	0.372	0.485	0.243	0.384	0.551	0.789
Trapeliopsis flexuosa	0.403	0.616	0.299	0.124	0.430	0.617	0.653
Tuckermannopsis chlorophylla	0.432	0.388	0.548	0.110	0.602	0.621	0.801
Usnea barbata	0.602	0.517	0.691	0.241	0.357	0.635	0.722
Usnea cavernosa	0.387	0.436	0.416	0.413	0.405	0.617	0.783
Usnea dasopoga	0.350	0.468	0.378	0.585	0.434	0.608	0.612
Usnea diplotypus	0.354	0.523	0.608	0.275	0.523	0.591	0.741
Usnea hirta	0.393	0.510	0.507	0.281	0.608	0.588	0.689
Usnea intermedia	0.375	0.465	0.459	0.289	0.562	0.608	0.691
Usnea perplexans	0.413	0.415	0.661	0.164	0.511	0.626	0.682
Usnea scabrata	0.415	0.429	0.494	0.304	0.441	0.611	0.734
Usnea subfloridana	0.423	0.334	0.382	0.522	0.629	0.600	0.696
Usnea substerilis	0.362	0.371	0.490	0.468	0.332	0.591	0.660
Usnocetraria oakesiana	0.376	0.439	0.414	0.424	0.457	0.619	0.744
Varicellaria hemisphaerica	0.366	0.441	0.410	0.455	0.442	0.618	0.734
Vezdaea aestivalis	0.304	0.375	0.325	0.387	0.378	0.553	0.726
Violella fucata	0.173	0.394	0.255	0.473	0.477	0.572	0.723
Vulpicida pinastri	0.536	0.471	0.642	0.346	0.602	0.596	0.641
Xanthomendoza fallax aggr.	0.369	0.452	0.456	0.319	0.380	0.646	0.751
Xanthomendoza fulva	0.340	0.442	0.333	0.688	0.428	0.625	0.724
Xanthomendoza ulophyllodes	0.468	0.463	0.371	0.534	0.443	0.598	0.727
Xanthoria parietina	0.460	0.418	0.589	0.429	0.333	0.694	0.731
Xylographa parallela	0.306	0.376	0.343	0.409	0.383	0.550	0.686
Xylopsora caradocensis	0.307	0.365	0.336	0.399	0.540	0.551	0.680
Xylopsora friesii	0.313	0.444	0.349	0.260	0.389	0.556	0.681
Zwackhia viridis	0.305	0.345	0.378	0.572	0.292	0.607	0.799

Appendix 3 – Species richness per site

In the main manuscript of our study, we focus on species-specific estimates and the bias introduced to these when ignoring imperfect detection in lichens. Occupancy models (MacKenzie et al., 2002; Tyre et al., 2003) are a powerful tool to account for such detection errors for estimates of species-specific occupancy (and in some measure their frequency). They can, however, also be used to estimate species richness, both at site-level (local community) and globally across the study region (meta-community; Dorazio et al., 2006; Dorazio & Royle, 2005). Where one really wants to estimate global species richness, it is usually recommended to augment the data with species that are known to occur in the study region but that were never observed at any field site (chapter 11 in Kéry & Royle, 2016). We did not augment the data for our models with any species, although more corticolous lichen specis are known from Switzerland than we modelled in the analysis, and we also did not optimize the model in a way to obtain as accurate and precise estimates of species richness as possible. We nevertheless visualize the observed and estimated species richness per site here (Fig. S4) and discuss our interpretation of it.

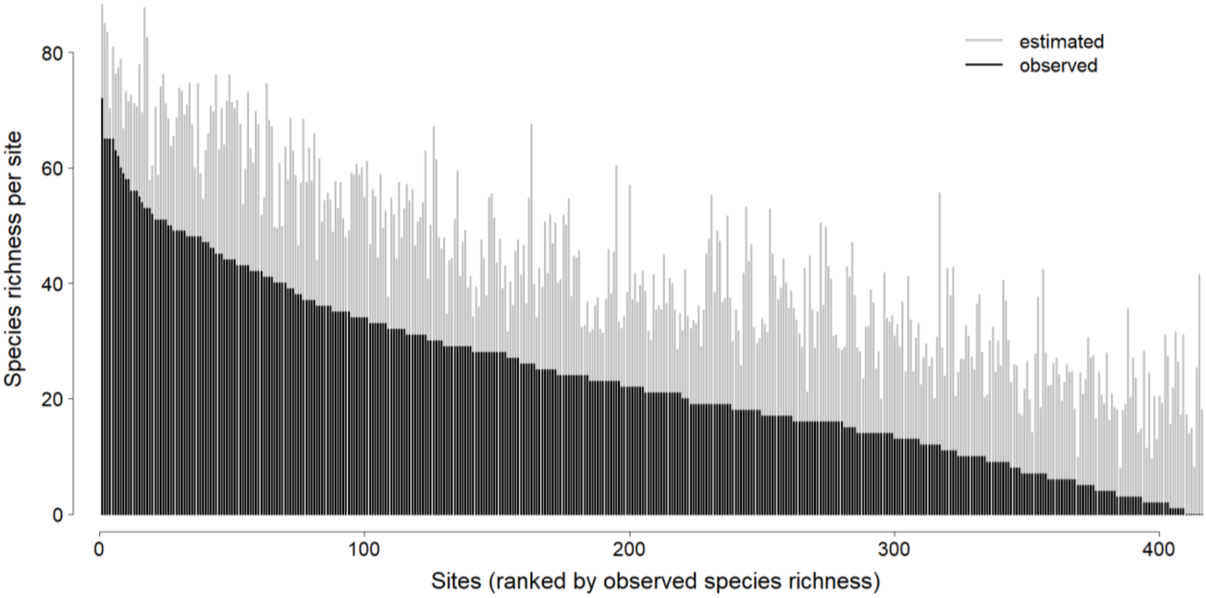

Fig. S4 Species richness per site. Black bars represent the observed number, grey bars on top the estimated additional number of species as predicted by the occupancy model. There were 416 sites and a total of 373 species in the data.

Conclusions

The occupancy model predicted greater species richness than what was observed for all sites. We note, however, that the model predicts roughly the same number of not-observed species for all sites, independent of the observed richness of the site (the average height of the grey bar remains the same across the entire x-axis in Fig. S4). We believe that this is a bias in the model. We are nearly certain that sites with 1-10 observed species do not harbour 10 additional species which we failed to detect. On the other hand, we believe it very likely that sites with many observed species may harbour many species more that we did not find. The model can thus not distinguish very well between highly suitable and much less suitable sites based on the covariates we used. We believe that this bias is largely due to the limited amount of environmental heterogeneity across sites that is described by the covariates. Had the covariates caught more of the spatial heterogeneity, we would expect the number of not-observed species to be greater at sites with high species richness and smaller at sites with low species richness. We are certain that the inferences we drew on overall detectability, and of the differences between species and observers would not be considerably different without this bias.

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3 CHANGES IN EPIPHYTIC LICHEN COMMUNITIES IN SWITZERLAND ARE RELATED TO FOREST MANAGEMENT, NITROGEN EXCESS AND CLIMATE CHANGE

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Abstract

Biological communities across the globe are currently experiencing major alterations in species number and composition. So far, however, very few studies have analysed standardised data from large-scale surveys to assess changes in lichen communities. We here compare detection-corrected occupancy rates of 329 epiphytic lichen taxa across Switzerland between the periods 1995–2000 and 2018–2022. Data were collected with a standardised procedure on a total of 446 long-term monitoring sites, of which 46 were visited twice in each period to estimate and account for detection probability. Systematic changes were analysed for 17 ecological guilds that relate to habitat preference (free-standing deciduous trees, humid forests, old trees), photobiont type (cyanobacteria, *Trentepohlia*), or high and low ecological indicator values for eutrophication, bark pH, temperature, precipitation, continentality, and light. We found systematic declines among species associated with old trees, humid forests, oligotrophic conditions, low pH, and high precipitation. Systematic increases were revealed for species with high eutrophication-tolerance, high pH, low precipitation, high temperature and high light availability. Comparing these patterns to environmental changes in Switzerland and Central Europe in the last decades, we hypothesize three major drivers: 1) forest management which in the past reduced the number of old trees suitable for specialists, 2) environmental pollutants with a simultaneous decrease in acid and an increase in nitrogen deposition which led to a replacement of acidophytic-oligotrophic species with acid-sensitive-nitrophytic species, and 3) climate change which has favoured species tolerant to high temperatures and low precipitation at the expense of wetness indicators and species that prefer cooler temperatures. The large-scale alterations of the climate and environmental pollutants that drive these community changes are likely to continue to affect lichen communities in Europe and indeed worldwide. It remains to be seen whether the species currently declining can shift their distribution or persist at lower densities in local or microclimatic refugia.

Introduction

Human impact has led to major alterations of the natural environment worldwide. The urban or agricultural land area has increased nearly 80-fold between 1700 and 2000 (Ellis et al., 2010). This expansion happened largely at the expense of wildlands (land largely unchanged by human activity) which declined to only 22 % of the ice-free land area, much of it restricted to cold or dry biomes (Ellis et al., 2010; Kennedy et al., 2019). These major landscape changes have triggered the beginning of a global biodiversity crisis (Newbold et al., 2015). In addition to these land-use changes and the associated habitat loss, climate warming also puts pressure on the distribution of many species (Harrison et al., 2020; Thomas et al., 2004; Urban, 2015), and increased deposition of fertilizers or pesticides have also been associated with species loss (De Schrijver et al., 2011; Gibbs et al., 2009; Sánchez-Bayo & Wyckhuys, 2019; Stevens et al., 2010).

Many of the recent human-induced changes to plant and animal communities are well documented. Plant communities in grasslands, for example, have lost much of their species richness due to an increase in nitrogen deposition, making them more homogeneous with nitrogen-favoured, competitive species dominating (Stevens et al., 2010; Wesche et al., 2012). Bobbink et al. (2010) go as far as to say that nitrogen deposition is the main driver of change in plant community composition across Europe and North America. Also birds, mammals, amphibians, and arthropods have been affected by land-use changes and/or climate warming (Gallant et al., 2007; Hof et al., 2011; Neff et al., 2022; Outhwaite et al., 2022; Seibold et al., 2019; Spooner et al., 2018).

Evidence for changes in community composition of lichens or other cryptogams is scarcer. Although lichen species are frequently used for biomonitoring of air quality (Belguidoum et al., 2022; Boonpeng et al., 2023; e.g., Kłos et al., 2018; Kousehlar & Widom, 2020; Sujetovienė & Česynaitė, 2021), entire lichen communities are rarely tracked over time for the effect of other factors. Some evidence points towards declines or shifts in distribution range with climate change (Nascimbene et al., 2016), especially for terricolous lichens (Allen & Lendemer, 2016; Rubio-Salcedo et al., 2017; Vallese et al., 2021). In Great Britain, bioclimatic envelope models also predicted negative trends for species of montane and boreal regions (Ellis et al., 2007). However, these studies used only a limited number of species (< 50) and have the additional limitation that their conclusions are drawn from current relationships between species occurrence and climate rather than tracing a change over time. Observations of community-wide changes that include a majority of all species and that are based on high-quality data from both a historic and a present period are largely lacking. To our knowledge the only country with such a record are the Netherlands (Aptroot & van Herk, 2007; van Herk et al., 2002).

In this study, we estimate nation-wide changes in epiphytic lichen communities in Switzerland over the last 20 years using systematically collected detection/non-detection data on 329 species. We summarize trends for all species, and for threatened (species classified as Vulnerable, Endangered, or Critically Endangered in the national Red List by Scheidegger et al., 2002) and non-threatened species separately. We also want to draw conclusions about the potential drivers behind major community changes. For this purpose, we group species into ecological guilds based on 1) their association with certain substrate or habitat types (e.g., old trees), 2) photobiont (cyanobacteria, *Trentepohlia*), and 3) their sensitivity to environmental variables (e.g., nitrogen content, temperature, etc.). We describe systematic changes guided by the following main research questions:

- What is the general direction of change for epiphytic lichen species in Switzerland? Is there a different pattern for threatened species?
- Which ecological guilds tend to increase/decline?
- How are these changes related to environmental (climatic or land-management) changes?

Methods

Data collection

Lichen data

Data for this project were collected during two sampling periods, 1995–2000 and 2018–2022, as part of the fieldwork conducted for the first and the ongoing second national Red List assessments for epiphytic lichens (Scheidegger et al., 2002; Stofer et al., 2019a). The original datasets included 826 and 500 sampling sites, respectively, but we here only analyse data from sites with at least one epiphytic lichen in one of the periods (Table 1). The final dataset thus consists of 446 sites, of which 268 were surveyed in both periods, 167 only in the first and 11 only in the second period. In addition to this regular survey, a second survey was conducted on a subset of 46 sites in each period. The design is therefore robust according to Pollock (1982), with two primary sampling periods (1995–2000 and 2018–2022) and two secondary sampling periods each, represented by the subset of 46 repeated-visit sites. The permanent sampling sites are distributed across Switzerland following a stratified random sampling design, where a stratum is the combination of biogeographic region (Jura, Plateau, Pre-Alps, Alps, Southern Alps), altitudinal belt (submontane, lower and upper montane, lower and upper subalpine, alpine) and vegetation type (forest, open). A sampling site consists of a circular area of 500 m^2 (radius 12.62 m) around the intersection point of the Swiss 1-km coordinate grid. After excluding sites as substrate-free or inaccessible based on maps or aerial photographs, the remaining sites were surveyed without strict time limit until the observer had as complete a list of epiphytic lichen species as possible. All accessible bark substrate (most of it below 2 m above ground) was searched. For further details on field sampling, see the original publications (Scheidegger et al., 2002; Stofer et al., 2019a).

We excluded ambiguous taxa, species that were predominantly non-epiphytic, and due to time restrictions also those belonging to the genera *Bryoria, Cladonia, Lepraria,* and *Usnea*. The final dataset then contained 329 species that were detected at least once on a sampling site.

Ecological guilds

Not all lichens are equally affected by the same environmental change. We therefore focus on 17 ecological guilds that were defined *a priori* (Appendix 1), assuming that species belonging to the same guild would react similarly to a stressor and may therefore experience a similar change. Three guilds describe the combination of substrate and habitat: species growing preferably on old trees (*old trees*, n=54), in high-humidity forests (*humid forests*, n=45), or on free-standing trees of *Acer pseudoplatanus*, *Quercus*, or *Fraxinus* (*free-standing trees*, n=28). The choice of species for these guilds was based on expert judgement by MD, CK, and CS. Two guilds describe the nature of the photobionts: cyanobacteria (*cyano*, n=10), and trentepohlioid green algae (*trentepohlioid*, n=43). The other twelve guilds describe the preference/tolerance of species to continuous environmental parameters (a *low* guild and a *high* guild each for *eutrophication, continentality, temperature, precipitation, pH,* and *light conditions*). The choice of species for these guilds was based on the ecological indicator values defined by Wirth (2010): Members belonging to the 2–3 classes at each end of the indicator scale ranging from 1 to 9 were assigned to the *low* or *high* guild, respectively. Species belonging to any of the intermediate classes, species with a wide amplitude, and species without any value were ignored in the classification. Except for the photobiont, a species may belong to multiple guilds — creating some overlap between them — or to none. Such a guild-specific approach has proven very valuable in the past to draw inference on species composition (Aptroot & van Herk, 2007; Koelemeijer et al., 2022; Pinho et al., 2012).

Environmental data

We used four variables to describe the occurrence of species across space and time (Appendix 2). Precipitation was defined as the number of days per year in which the interpolated daily precipitation exceeded 0.1 mm. Data were obtained from MeteoSwiss (precipitation grid data RhiresD), calculated from the median across 15 years of data prior to and including the sampling periods. For the first time period, the median is thus based on the years 1986 to 2000, for the second time period on the years 2008 to 2022. Nitrogen deposition data [kg N/ha/year] were kindly provided by the Federal Office for the Environment (FOEN, Abt. Luftreinhaltung und Chemikalien; based on Rihm & Künzle, 2023). Vegetation type (forest/open) was based on the assessment of the Swiss National Forest Inventory (www.lfi.ch). Availability of suitable bark substrate was defined for each lichen species, based on our own observations of available tree/shrub species per site, and a list of which bark-pH classes are suitable for each lichen species. All pH classes (based on Barkman, 1958) were deemed suitable that hosted more than ten percent of that species' records in the database SwissLichens (Stofer et al., 2019b, accessed 12.03.2023).

Table 1. Data structure. The original sampling design for the first Red List assessment of epiphytic lichens in Switzerland from 1995–2000 comprised 826 sites of which 435 were found to contain epiphytic lichens. The original 500 sampling sites for the second Red List assessment in 2018–2022 were a subset of the 826 sites. Because 11 sites could not be relocated without doubt, these sites were modelled as being independent of the surveys in 1995–2000.

	1995–2000			**2018–2022**		
	Original	**Standard survey**	**Repeated survey**	**Original**	**Standard survey**	**Repeated survey**
Sites only visited 1995–2000	826	167	17	-	-	-
Sites visited in both periods		268	29	500	268	46
Sites only visited 2018–2022	-	-	-		11	0
Total = 446		**435**	**46**		**279**	**46**

Analysis

Model

Data were analysed with a Bayesian multi-species occupancy model with a fixed effect for the time period (Dorazio & Royle, 2005; Kéry & Royle, 2016; MacKenzie et al., 2018). Occupancy models describe the observed detection/non-detection history of each species at each site and for each period as the result of two processes that are modelled separately but linked via conditional probability (MacKenzie et al., 2002; Tyre et al., 2003). The first (ecological) process is the occurrence $z_{k,i,t}$ of species *k* at site *i* during period *t*, a Bernoulli random variable where 1 indicates presence and 0 absence of the species. Commonly in field situations, the true occupancy state *z* is only partially observed via the second (detection) process which generates the observed detection/nondetection data *y*. For example, species can be missed and are therefore not recorded on a site where they occur. With a maximum of two visits (j = 1, 2) per site within the same period *t*, a site *i* occupied by species *k* (i.e., $z_{k,i,t}$ = 1) could thus yield four possible detection histories $y_{k,i,t,1\text{-}2}$: 11, 10, 01, or 00. We assume that species are not falsely detected, so when the species is detected during at least one of the two surveys (cases 1-3), the model assumes the presence of the species on that site during that period ($z_{k,i,t}$ = 1). The model then also has information about the detection process, because with the known occupancy status, also the detection "success" is known. However, when the species is not observed on any of the surveys (case 4), the model has no unambiguous information at all and can only estimate the probability for the two possible cases: either the species was truly absent from the site, or it was present but missed during both surveys. The availability of repeated-visit data to at least some of the sites in each period is thus a prerequisite to distinguish between the ecological and the detection process. Both processes can be described as a function of site-specific — and in the case of detection also survey-specific — covariates. We describe the model and the used covariates in Appendix 2. By automatically correcting for the imperfect-detection error, the model avoids the bias inherent to logistic regression, Maxent, boosted regression trees that use detection/non-detection data from single visits as if they were true presence/absence data.

Software, priors, and MCMC settings

Analyses were run in R Version 4.1.2 (R Core Team, 2021) using the R package nimble Version 1.0.0 (NIMBLE Development Team, 2023). The software nimble (de Valpine et al., 2017) compiles priors and likelihood into C++ code for fast computation of posterior Markov Chain Monte Carlo (MCMC) samples. Species random effects were modelled as coming from a Student-*t* distribution with a mean, a standard deviation, and four degrees of freedom to allow more species to have extreme values than under a normal distribution (p. 107–109, Lunn et al., 2013). We used logistic priors for the intercepts (Northrup & Gerber, 2018), normal priors with a standard deviation (SD) of 10 for regression coefficients, and half-Cauchy priors (SD=1) for the SD-terms of the random effects (Outhwaite et al., 2018). This choice was largely based on computational efficiency, but we confirmed the robustness of our results to prior definition in a sensitivity analysis (Appendix 3). Inferences are based on a posterior sample of 2000 values which resulted from running 4 MCMC chains with 35 000 iterations each, discarding the first 10 000 values as burn-in, and a thinning of 50. We inferred MCMC convergence based on visual checks of traceplots and a scale-reduction factor $\hat{R} < 1.1$ for all parameters (p.285 in Gelman et al., 2013; Gelman & Rubin, 1992).

The output from an occupancy model fitted using Bayesian MCMC simulation is the posterior probability distribution of the estimated parameters, which allows inferences based on probability statements rather than p-values. To illustrate the sensitivity of inference to the choice of the probability threshold applied, we present summary statistics using three thresholds (95%, 90%, 80%). All result figures use a threshold of 95% probability to indicate a very high probability of change. Where changes are estimated at the guild-level, we use the median across all species as an indicator for how the guild has changed as a whole. By using the median instead of the mean, the results are less sensitive to individual species that have experienced a strong change, and they are more indicative of the direction towards which the majority of species in the guild have changed.

Results

A summary of species trends depends strongly on the threshold of certainty required to infer a trend (Table 2). When using a certainty threshold of 0.95, 18% of all 329 lichen species in the model are estimated to have declined, and 16% are estimated to have increased. Using a lower probability threshold of 0.80, these percentages increase to 39% declining and 22% increasing. When contrasting the development of threatened vs. non-threatened species (according to the national Red List by Scheidegger et al., 2002), the probability threshold has even greater impact on trend summaries. With a threshold of 0.95, it looks as if more non-threatened species were declining (20%) than threatened species (13%). However, a probability threshold of 0.95 is rather restrictive when it comes to assessing species declines, especially of threatened (and thus often rare) species, because they tend to have fewer records which makes it difficult to reach a level of certainty > 0.95 even if they may be experiencing the same decline as more common species. With a threshold of 0.90, the proportion of declining threatened species already increases to 18% (26% for non-threatened species), and it is considerably higher than for non-threatened species when using a probability threshold of 0.80, with 51% and 36% declining, respectively.

Table 2 Trends of change for 329 epiphytic lichen species from 1995–2000 to 2018–2022. The percentage of species that are experiencing a certain change depends on the threshold used to define certainty. Among the 78 threatened species, one is considered Critically Endangered, 26 Endangered, and 51 Vulnerable on the Swiss Red List.

Probability threshold	Species group	% Species declining	% Species without change	% Species increasing
95%	threatened	13	80	8
	not threatened	20	62	19
	all	**18**	**66**	**16**
90%	threatened	18	72	10
	not threatened	26	51	23
	all	**24**	**56**	**20**
80%	threatened	51	35	14
	not threatened	36	40	24
	all	**39**	**39**	**22**

To illustrate our approach of drawing species- and guild-specific inference, we show species-specific estimates for all members of the *high-precipitation* guild (n=32) in Fig. 1. In this guild, 24 species are estimated to have declined (midpoint of their posterior distribution < 0), three of them with a probability > 0.95 (95% CRI does not include 0), while eight are estimated to have increased, three of which with a probability > 0.95. The posterior median across the species' midpoints centers at -0.004 with a CRI of [-0.007, -0.002], indicating a weak, overall negative trend for the guild. Separate figures with species-specific estimates for all guilds can be found in Appendix 4.

A summary of species-specific changes per guild (based on the median across all species of a guild, see Fig. 1) indicates an unambiguous decline for the guilds *humid forests, old trees, low eutrophication, low temperature, high precipitation,* and *low pH* (Fig. 2). A distinct increase occurred in the guilds *high eutrophication, low precipitation, high pH,* and *high light conditions*. The remaining guilds (*free-*

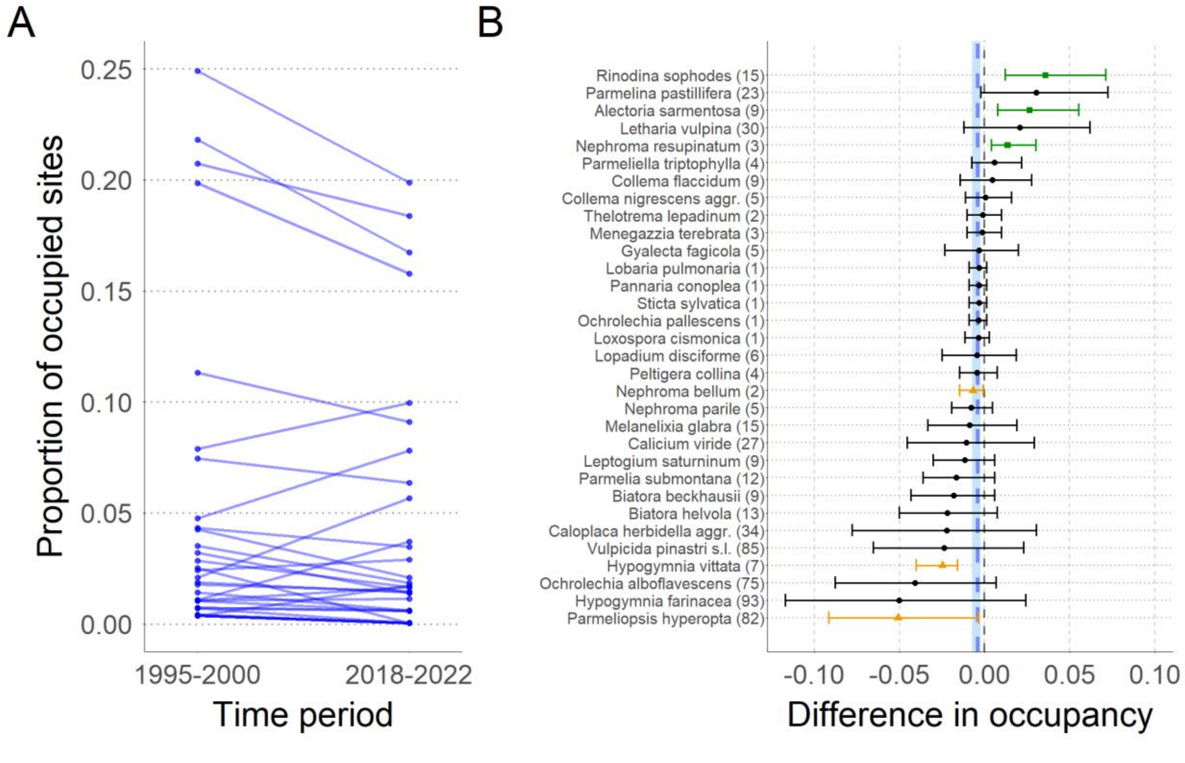

Fig. 1 Estimated change in occupancy across 446 sites for species of the *high precipitation* guild (n=32). Each line in the left panel (A) illustrates how the occupancy estimate of each species changes from one sampling period to the next. The right panel (B) shows the posterior distribution of the difference between these two estimates, given by midpoints (median) and the 95% credible interval (CRI). Values > 0 show an estimated increase, values < 0 an estimated decline. Orange colour and triangular symbols indicate that the entire CRI lies below zero, green colour and squared symbols that it lies above zero. The blue dashed line marks the posterior median across all midpoints, which lies slightly below 0 in this case and the light blue shaded area marks the CRI of this median. The number in brackets represents the number of sites on which a species was detected.

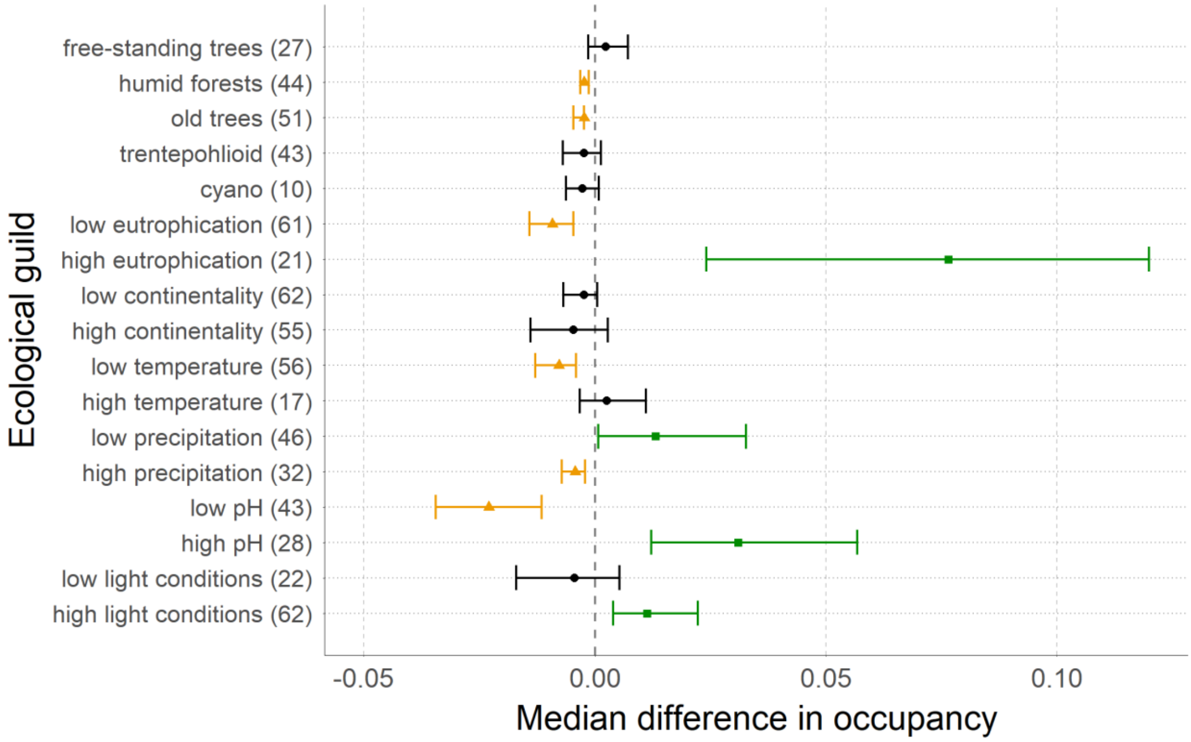

Fig. 2 Population trends of epiphytic lichen species across Switzerland separated by ecological guild. This plot illustrates the posterior distribution (given by midpoints and the 95% CRI) of the median difference in occupancy across all species within a guild. Orange colour and triangular symbols indicate that the guild is experiencing a negative trend with > 95% probability, green colour and squared symbols indicate a positive trend with > 95% probability. The number in brackets represents the number of species belonging to a guild.

standing trees, trentepohlioid, cyano, low continentality, high continentality, high temperature, and *low light conditions*) may also experience changes, but the probability of the direction (decline or increase) is less than 0.95.

Changes vary somewhat between biogeographic regions (Fig. 3). Species adapted to high eutrophication or high pH increase everywhere, but their increase is strongest in the Jura, Plateau, and Southern Alps and weakest in the Pre-Alps. Climate-related changes are most evident in the Alps where species associated with high temperature and low precipitation show a certain increase.

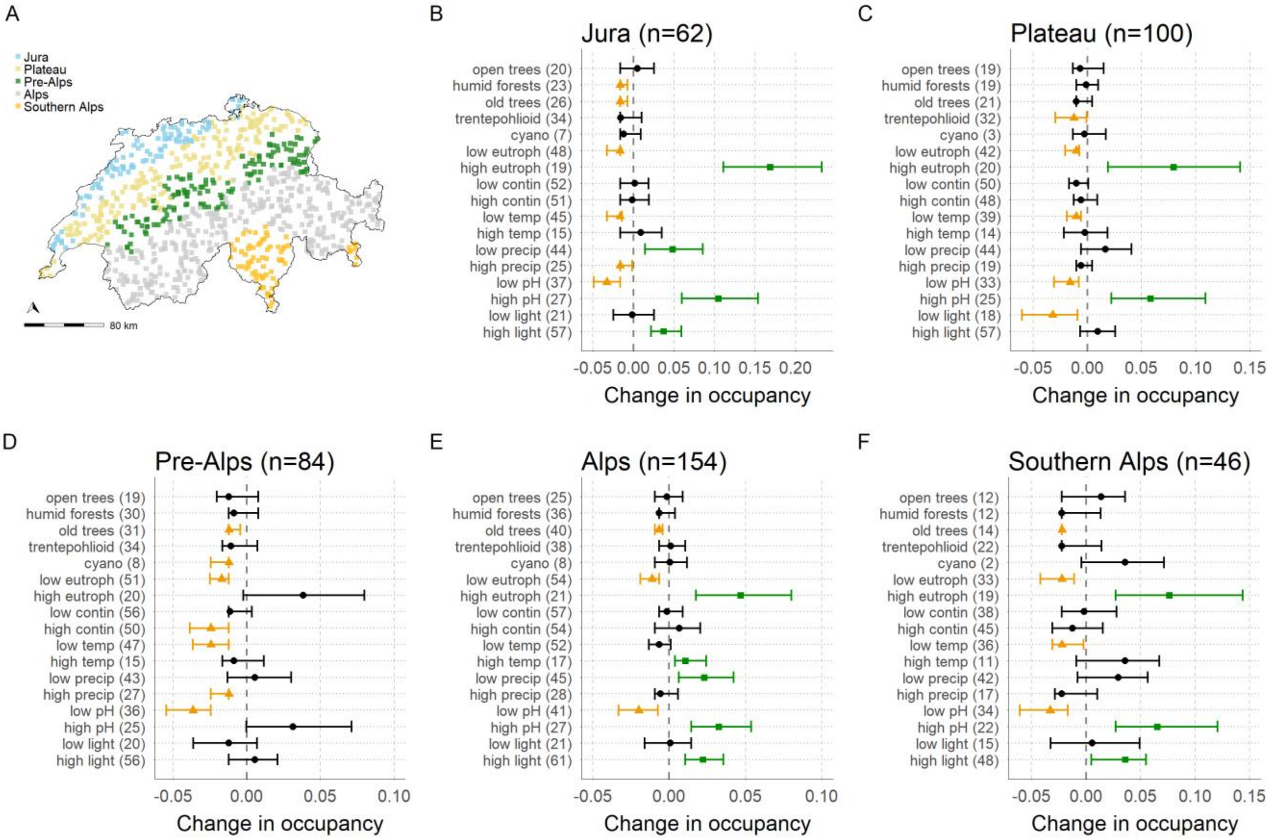

Fig. 3 Population trends of epiphytic lichen guilds separated by biogeographic region. The map (A) illustrates the distribution of the sampling sites across Switzerland, with colours indicating the five biogeographic regions. Panels B to F represent estimates across all sites that fall into the respective biogeographic region. Guild-specific values are calculated based only on species that are estimated to occur in that region, the number in brackets behind the guild gives the average number of species. Orange colour and triangular symbols indicate that the guild is experiencing a negative trend with > 95% probability, green colour and squared symbols indicate a positive trend with > 95% probability.

Discussion

In this study, we estimated changes in site occupancy over the last 20 years for 329 epiphytic lichen species in Switzerland. We interpret the changes by 1) summarizing species-specific trends, and 2) interpreting trends of ecological guilds. Conclusions about species-specific trends depend strongly on the probability threshold used to infer a trend, especially when contrasting threatened and non-threatened species. With a probability threshold of 0.95, fewer threatened species decline (13%) than non-threatened species (20%), but this pattern reverses when using a threshold of 0.8, with 51% of threatened and 36% of non-threatened species declining. Given the generally low sample size of threatened species, a threshold of 0.8 may be better able to pick up trends that lack the power to be detected with greater certainty. We therefore consider a threshold of 0.8 as better adapted for species-specific estimates. Accordingly, our results indicate that 39% of all species have declined and 22% have increased.

The systematic changes of the ecological guilds were based on the median across species within a guild. This estimate is much less sensitive to the choice of probability threshold, and we have therefore used a restrictive 0.95 to infer trends. Our results suggest that three major factors may be driving the community changes in Switzerland: forest management, environmental pollution (particularly nitrogen and acid deposition), and climate change.

Forest management

Species belonging to the guild *old trees* showed a systematic decline in our data, while species in the guild *high light conditions* have increased. We see in these changes a possible effect of past and current forest practices that operate at different temporal scales. The observed decline in *old tree* species indicates a scarcity of suitable substrate in Switzerland. Over many decades, the number of old and veteran trees, tree diversity, and the amount of dead wood were systematically reduced in Swiss forests to make room for a few fast-growing tree species that could be harvested (Bürgi & Schuler, 2003). This practice led to younger, more evenly aged, and darker forests dominated by only a few tree species (Brassel & Brändli, 1999). Among the detrimental effects that followed were a loss of local species richness (Watt et al., 2007) and a decline of light-dependant species and those associated with old trees (Bollmann et al., 2009; Scheidegger et al., 2010; Walther & Grundmann, 2001). Having realized the extent of biodiversity loss in the Swiss forests, the Federal Office for the Environment (FOEN) implemented a new Forest Policy (FOEN, 2013) and a Swiss Biodiversity Strategy (FOEN, 2012). Two goals were to raise the number of old trees and to lighten up forests by reducing dominant species and enhancing greater heterogeneity in tree age, occasionally with artificial disturbances (Bollmann et al., 2009; Imesch et al., 2015; Wohlgemuth et al., 2002). Bringing light into forests can be accomplished a lot faster than raising the number of old trees. We therefore suspect that the increase in *high light* species in forests may be an early result of increased structural diversity (p. 203, Brändli et al., 2020), and thus a sign of a potential (and partial) recovery from the period where forests were uncommonly dense and dark. There is, however, considerable overlap between species in the *high light* and the *high eutrophication* guild. We can therefore not exclude that the increase experienced by *high light* species is due to changes in nitrogen deposition rather than a consequence of lighter forests, especially in open areas where light is not a limiting factor.

Compared to creating open spaces in forests, promoting old trees takes time. Although the number of “giant” trees (diameter > 80 cm) has increased continuously over the last decades (p. 201–202, Brändli et al., 2020), this improvement has obviously not (yet) translated into the recovery of *old tree* species. A substantial time lag must naturally be expected, because *old tree* species tend to be rather slow colonizers, but there may be other reasons too. First, a “giant” or “old” tree by forestry standards may still be too young — or otherwise unsuitable in terms of bark structure or microclimatic conditions — for *old tree* lichens (Fritz et al., 2009). Second, strongly reduced population density, limited dispersal ability, and, in some species, dependence on the presence of other species with the same photobiont may prevent some lichens from successfully establishing new populations despite the availability of suitable trees (Belinchón et al., 2015; Sillett et al., 2000; Werth et al., 2006). Adopting these forest management practices, which in themselves have led to many positive changes for lichens and biodiversity in general, may thus not be enough for some *old tree* specialists, and species-specific, possibly even population-specific, conservation actions may be necessary to prevent their further decline or extinction.

Contrary to our expectations, species in the guild *free-standing trees* did not experience a systematic decline, despite a history of intensification of alpine pastures which led to the removal of many free-standing *Acer pseudoplatanus* and other deciduous trees (Kiebacher et al., 2018; Tappeiner et al., 2003), or the dieback of *Fraxinus excelsior* trees through disease (Klesse et al., 2021). Within the guild, however, there is considerable variation which illustrates one of the limitations of such a guild-based approach. Relying on the median change across all 27 species in this guild, one may conclude that species associated with this ecological niche show stable population sizes. It is true that we could not find a *general* pattern of decline. However, six species within the guild showed a high probability of decline, and four species an equally high probability of increase, changes we could not clearly associate with any other ecological variable assessed here. Lichens respond to their environment in complex ways which may lead to contrasting responses to the same environmental change despite a similarity in current distribution patterns (Ellis et al., 2007, 2009). Lumping them together because they regularly co-occur on the same type of substrate, may thus be overly simplified and not allow much insight into the processes that govern population changes. In fact, all guilds except *high temperature* contained at least one species that showed a significant trend opposite to the overall direction of the guild. Conclusions drawn at guild-level should therefore not be used to infer species-specific responses to environmental change.

Environmental pollution

The ecological guilds *high eutrophication* and *high pH* increased substantially over the past 20 years while the guilds *low eutrophication* and *low pH* experienced a decline. This development is evident in open and forested habitats, across all biogeographic regions, and along the entire elevational gradient, not excepting the Alps. As there is correlation between nitrogen tolerance of lichens and their preference for alkaline conditions (e.g., 57% of *high eutrophication* species also belong to the *high pH* guild) as well as their preference for light availability (86% of *high eutrophication* species also prefer *high light* conditions), their respective changes cannot be fully disentangled in this observational study. Nevertheless, we are confident that two major changes in the chemical environment have contributed to this change. The first one is the drastic decline in acid deposition over the last 30 years (BAFU, 2022). Around the 1970s, highly acid and heavy-metal enriched exhaust gases from industries and traffic wiped out much of the lichen biota in European cities and industrial areas, allowing only few acidophytic (and most of them rather oligotrophic) lichens to thrive (Ferry et al., 1973; Gilbert, 1969; Hawksworth & Rose, 1970; Herzig & Urech, 1991; Seaward, 1993; van Herk, 2001). Following the implementation of the Ordinance on Air Pollution Control in Switzerland in 1986 (SR 814.318.142.1) and the European Large Combustion Plants Directive (CD 88/609/EEC) in 1988, the reduction of acid gas emissions gradually led to a recovery of bark conditions towards higher pH (van Dobben & ter Braak, 1998).

The second driver likely to have contributed to the observed pattern is the significant excess of nitrogen in our landscape (Rihm & Künzle, 2023). Though political milestones such as the above-mentioned regulations managed to stop the decade-long increase in anthropogenic nitrogen emissions in Switzerland and Europe (Liu et al., 2022; Seitler et al., 2021; Vivanco et al., 2018), deposition is still so high as to exceed critical levels in more than 67% of the Swiss landscape (EEA, 2022; Rihm & Künzle, 2023). Countless studies have described the sensitivity of lichen physiology and growth to nitrogen concentrations (e.g., Frahm, 2013; Gaio-Oliveira et al., 2005; Welch et al., 2006) or the effect of spatial or temporal variation in nitrogen deposition on lichen community composition (Belinchón et al., 2016; Frati et al., 2008; Gutiérrez-Larruga et al., 2020; Jovan et al., 2012; Mitchell et al., 2005; Pinho et al., 2008; Ruoss, 1999; van Herk, 1999, 2001; van Herk et al., 2003; Wolseley et al., 2006; Zarabska-Bożejewicz, 2020). A general trend in this direction is therefore no surprise. Our results also corroborate findings from studies on plants and fungi that species communities are undergoing a shift towards nitrogen-tolerant species (Andrew et al., 2018; Duprè et al., 2010; Mitchell et al., 2017; Peter et al., 2009; van der Linde et al., 2018), suggesting this development may be occurring at a European scale. Acidophytic-oligotrophic species no longer seem to find favourable conditions and are thus being replaced by nitrophytic species with a preference for higher pH.

Climate change

The decline in *low temperature*, *high precipitation*, and *humid forest* species together with an increase in *low precipitation* and, at least locally, *high temperature* species indicate an effect of climate change on the Swiss lichen biota. Even at our 446 sampling sites, the climatic covariates distinctly illustrate a trend towards more intense solar radiation, higher temperatures, and lower number of precipitation days (MeteoSwiss). Combined, this trend leads to faster evaporation of water and reduced air humidity which limits the time of physiological activity in lichens (reviewed in Palmqvist et al., 2008). Especially *humid forest* species and those demanding *high precipitation* are disadvantaged by this development, whereas *high temperature* and *low precipitation* species can expand their distribution. Despite the observed correlation with climate variables, there was no clear change in species with *low* or *high continentality*. As all *cyano* lichens are included in the *high precipitation* guild due to their dependence on liquid water for photosynthesis (Lange et al., 1986, 1993), we would have expected a clearer decline in the *cyano* guild (Ellis & Eaton, 2021; Koelemeijer et al., 2022; Rubio-Salcedo et al., 2017). We could not confirm the predictions made by these studies. It is possible, however, that the absence of a clear trend is due to our guild consisting only of ten species with relatively few detections (max. 9). Among these, only one species had declined with a probability > 0.95 (*Nephroma parile*), while one species had even increased with a probability > 0.95 (*Nephroma resupinatum*). We were also surprised at the absence of a general effect among the *trentepohlioid* guild. A long-term study by Aptroot & van Herk (2007) from the Netherlands found a strong general increase among these species, supposedly due to their preference for warmer temperatures (Marini et al., 2011; Phinney et al., 2022). Interestingly, the very species that increased most on Dutch sites (*Anisomeridium polypori*) showed the strongest decline of all *trentepohlioid* species in our dataset. In total, six species showed a high probability of decline and four a high probability of increase, all other members in our guild showed no certain change. We can thus not conclude that there is a general trend for species with this photobiont.

Conclusions

Epiphytic lichen communities in Switzerland have moved towards greater abundance of acid-sensitive, nitrogen-, and drought-tolerant species over the last 20 years. Oligotrophic and acidophytic species, on the other hand, as well as those indicative of cooler temperatures and higher precipitation, are declining. The nature of our data does not allow causal inference with respect to environmental variables (Sugihara et al., 2012). We are nevertheless quite confident that these are (among) the main drivers of these large-scale community changes, as similar patterns have been observed in lichen communities in the Netherlands (Aptroot & van Herk, 2007; van Herk, 2009; van Herk et al., 2002) and Germany (Hauck et al., 2013), or predicted for Scotland (Ellis et al., 2007) and even Europe (Rubio-Salcedo et al., 2017). Considering global warming, increased nitrogen input, and major land-use changes in some parts of the world, lichen communities are expected to be altered globally in the future. Whether these alterations will affect the conservation status of lichens remains to be seen.

Data availability

R code and all cleaned data used in this study will be made publicly available on the EnviDat repository (https://envidat.ch) upon acceptance of the manuscript for publication.

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Supplementary materials

Appendix 1 – Ecological guilds

Table S1 List of all species and ecological guilds. All species in this table had at least one detection on at least one of the 446 sampling sites. The guilds *free-standing trees, humid forests,* and *old trees* were defined based on expert experience. The guilds *trentepohlioid* and *cyano* describe the photobiont of the lichens. All remaining guilds were assembled based on the 2–3 lowest and highest classes of ecological indicator values by Wirth (2010). A species may belong to several or to no ecological guild.

	free-standing trees	**humid forests**	**old trees**	**trentepohlioid**	**cyano**	**low eutrophication**	**high eutrophication**	**low continentality**	**high continentality**	**low temperature**	**high temperature**	**low precipitation**	**high precipitation**	**low pH**	**high pH**	**low light conditions**	**high light conditions**
species	**27**	**44**	**51**	**43**	**10**	**61**	**21**	**62**	**55**	**56**	**17**	**46**	**32**	**43**	**28**	**22**	**62**
Acolium inquinans										1				1			
Acolium karelicum			1														
Acrocordia cavata				1													
Acrocordia gemmata s.l.				1		1		1									
Agonimia allobata/repleta								1									
Agonimia flabelliformis																	
Agonimia tristicula																	
Alectoria sarmentosa		1				1		1		1			1				1
Alyxoria varia aggr.			1	1													
Amandinea punctata							1		1			1					1
Anaptychia ciliaris	1		1												1		1
Anisomeridium polypori				1				1							1		
Arthonia atra				1													
Arthonia didyma				1													
Arthonia dispersa				1													
Arthonia faginea				1													
Arthonia fuliginosa		1		1													
Arthonia ligniaria				1													
Arthonia mediella				1													
Arthonia radiata				1												1	
Arthonia ruana				1				1								1	
Arthonia spadicea s.l.				1				1								1	
Arthrosporum populorum	1																
Bacidia absistens																	
Bacidia arceutina								1									
Bacidia circumspecta																	
Bacidia incompta																	
Bacidia laurocerasi		1	1														
Bacidia rosella																	
Bacidia rubella								1							1		
Bacidia subincompta aggr.						1		1									
Bacidina arnoldiana aggr.																	

Table S1 continues on the following pages.

Table S1 continued

species	free-standing trees	humid forests	old trees	trentepohlioid	cyano	low eutrophication	high eutrophication	low continentality	high continentality	low temperature	high temperature	low precipitation	high precipitation	low pH	high pH	low light conditions	high light conditions
Bacidina assulata																	
Bacidina chloroticula								1									
Bacidina neosquamulosa								1									
Bacidina phacodes																	
Bactrospora dryina		1	1	1		1		1						1			
Biatora beckhausii						1		1		1			1				
Biatora chrysantha																	
Biatora efflorescens																	
Biatora fallax		1	1														
Biatora flavopunctata																	
Biatora globulosa						1											
Biatora helvola						1				1			1				
Biatora ocelliformis		1															
Biatora rufidula			1														
Biatora subduplex																	
Biatora vacciniicola																	
Biatora veteranorum		1	1														
Biatorella microhaema																	
Biatoridium monasteriense																	
Bryobilimbia sanguineoatra																	
Bryostigma muscigenum				1													
Buellia arborea																	
Buellia disciformis s.l.						1		1									
Buellia erubescens																	
Buellia griseovirens																	
Buellia schaereri																	
Byssoloma marginatum		1															
Calicium adspersum			1			1								1			
Calicium glaucellum						1			1	1				1		1	
Calicium lenticulare			1														
Calicium montanum			1														
Calicium parvum																	
Calicium pinastri			1														
Calicium pinicola																	
Calicium salicinum			1			1			1	1						1	
Calicium viride						1			1	1			1	1		1	
Caloplaca alnetorum/pyracea		1							1			1			1		1
Caloplaca cerina aggr.																	
Caloplaca cerinella												1			1		1
Caloplaca cerinelloides												1			1		1
Caloplaca chlorina aggr.																	
Caloplaca chrysophthalma	1																
Caloplaca ferruginea/hungarica																	
Caloplaca herbidella aggr.								1		1			1				
Caloplaca lucifuga			1														
Caloplaca obscurella	1																
Caloplaca sorocarpa																	
Candelaria concolor/pacifica							1		1			1					1
Candelariella antennaria/viae-lacteae	1		1				1		1		1	1			1		1
Candelariella reflexa aggr.							1	1									
Candelariella xanthostigma												1					1
Catillaria nigroclavata							1					1			1		1
Catinaria atropurpurea																	

Table S1 continued

species	**free-standing trees**	**humid forests**	**old trees**	**trentepohlioid**	**cyano**	**low eutrophication**	**high eutrophication**	**low continentality**	**high continentality**	**low temperature**	**high temperature**	**low precipitation**	**high precipitation**	**low pH**	**high pH**	**low light conditions**	**high light conditions**
Cetraria sepincola						1			1	1				1			1
Chaenotheca brachypoda																	
Chaenotheca chlorella			1														
Chaenotheca chrysocephala						1			1	1				1		1	
Chaenotheca ferruginea									1			1		1			
Chaenotheca furfuracea						1				1				1		1	
Chaenotheca gracilenta						1		1								1	
Chaenotheca laevigata		1	1														
Chaenotheca phaeocephala			1											1			
Chaenotheca stemonea																	
Chaenotheca subroscida		1	1														
Chaenotheca trichialis						1										1	
Chrysothrix candelaris						1								1			
Cliostomum corrugatum			1			1		1						1			
Cliostomum																	
Cliostomum pallens																	
Coenogonium luteum		1	1	1													
Coenogonium pineti				1				1								1	
Collema flaccidum					1					1			1				
Collema nigrescens aggr.			1		1					1			1		1		
Coniocarpon cinnabarinum aggr.		1		1		1		1			1						
Eopyrenula leucoplaca				1													
Evernia divaricata						1			1	1				1			1
Evernia mesomorpha																	
Evernia prunastri									1					1			1
Fellhanera bouteillei		1						1									1
Fellhanera gyrophorica		1	1														
Fellhanera subtilis																	
Fellhanera viridisorediata																	
Flavoparmelia caperata								1			1						
Flavopunctelia flaventior	1								1		1	1					1
Frutidella furfuracea																	
Fuscidea pusilla																	
Graphis scripta aggr.				1												1	
Gyalecta fagicola			1	1		1							1				
Gyalecta flotowii			1	1													
Gyalecta truncigena aggr.		1		1													
Gyalideopsis helvetica																	
Haematomma ochroleucum s.l.						1		1									
Halecania viridescens																	
Hyperphyscia adglutinata							1	1			1	1			1		1
Hypocenomyce scalaris						1			1			1		1			
Hypogymnia austerodes																	
Hypogymnia bitteri																	
Hypogymnia farinacea						1			1	1			1	1			
Hypogymnia physodes									1			1		1			1
Hypogymnia tubulosa												1					1
Hypogymnia vittata		1	1			1			1	1			1	1			
Hypotrachyna revoluta aggr.								1			1						
Imshaugia aleurites						1			1	1		1		1			
Jamesiella anastomosans																	
Japewia tornoensis																	
Lecania cyrtella aggr.									1			1			1		1

Table S1 continued

species	**free-standing trees**	**humid forests**	**old trees**	**trentepohlioid**	**cyano**	**low eutrophication**	**high eutrophication**	**low continentality**	**high continentality**	**low temperature**	**high temperature**	**low precipitation**	**high precipitation**	**low pH**	**high pH**	**low light conditions**	**high light conditions**
Lecania naegelii							1		1			1			1		
Lecanora albella						1		1									
Lecanora allophana s.l.	1									1		1					1
Lecanora argentata																	
Lecanora barkmaniana	1																
Lecanora boligera																	
Lecanora cadubriae																	
Lecanora carpinea									1			1					
Lecanora chlarotera s.l.									1			1					
Lecanora circumborealis																	
Lecanora conizaeoides												1		1			1
Lecanora expallens								1				1					
Lecanora expersa																	
Lecanora farinaria																	
Lecanora fuscescens																	
Lecanora gisleri																	
Lecanora hagenii aggr.	1						1		1			1			1		1
Lecanora horiza aggr.																	
Lecanora intumescens						1				1							
Lecanora leptyrodes																	
Lecanora phaeostigma																	
Lecanora praesistens																	
Lecanora pulicaris									1	1		1		1			1
Lecanora salicicola																	
Lecanora sp.1		1															
Lecanora sp.3 (ticinense)																	
Lecanora strobilina aggr.																	
Lecanora subcarpinea																	
Lecanora symmicta aggr.									1	1							1
Lecidea erythrophaea																	
Lecidea leprarioides																	
Lecidea nylanderi																	
Lecidella albida																	
Lecidella elaeochroma aggr.									1			1					
Lecidella flavosorediata																	
Lecidella subviridis																	
Lepra albescens s.l.									1			1					
Lepra amara						1			1					1			
Lepra multipuncta																	
Lepra opthalmiza		1	1														
Leptogium saturninum					1			1		1			1				
Letharia vulpina						1				1			1	1			1
Lobaria pulmonaria		1	1			1				1			1				
Lopadium disciforme		1	1			1				1			1	1			
Loxospora cismonica		1				1				1			1				
Loxospora elatina						1		1		1				1			
Megalaria pulverea		1	1														
Melanelixia glabra										1			1				1
Melanelixia glabratula aggr.									1					1			
Melanelixia subargentifera	1								1						1		1
Melanelixia subaurifera																	
Melanohalea elegantula	1							1			1						1
Melanohalea exasperata										1							1

Table S1 continued

species	**free-standing trees**	**humid forests**	**old trees**	**trentepohlioid**	**cyano**	**low eutrophication**	**high eutrophication**	**low continentality**	**high continentality**	**low temperature**	**high temperature**	**low precipitation**	**high precipitation**	**low pH**	**high pH**	**low light conditions**	**high light conditions**
Melanohalea exasperatula									1			1					1
Melaspilea rhododendri				1													
Menegazzia terebrata		1	1			1		1		1			1				
Micarea adnata		1	1			1		1								1	
Micarea cinerea f. cinerea		1															
Micarea coppinsii																	
Micarea melaena						1		1		1				1			
Micarea nitschkeana																	
Micarea peliocarpa						1		1						1			
Micarea prasina aggr.										1						1	
Mycobilimbia epixanthoides/Lecania																	
Mycobilimbia pilularis		1	1														
Mycoblastus alpinus/affinis																	
Myochroidea porphyrospoda																	
Myochroidea rufofusca																	
Myriolecis sambuci	1											1			1		1
Nephroma bellum		1			1	1				1			1				
Nephroma parile					1					1			1				
Nephroma resupinatum		1	1		1					1			1				
Nephromopsis laureri			1														
Normandina acroglypta																	
Normandina pulchella								1									
Ochrolechia alboflavescens						1			1	1			1	1			
Ochrolechia arborea																	
Ochrolechia microstictoides						1				1				1			
Ochrolechia pallescens						1		1		1			1				
Ochrolechia szatalaensis																	
Ochrolechia turneri	1																1
Opegrapha vermicellifera				1				1			1					1	
Opegrapha vulgata aggr.				1													
Orcularia insperata																	
Pannaria conoplea		1	1		1	1		1		1			1				
Parmelia saxatilis aggr.									1					1			
Parmelia submontana								1					1				
Parmelia sulcata							1		1			1					1
Parmeliella triptophylla		1			1	1		1		1			1				
Parmelina pastillifera								1		1			1				
Parmelina quercina aggr.																	
Parmelina tiliacea												1					1
Parmeliopsis ambigua						1			1	1				1			
Parmeliopsis hyperopta						1			1	1			1	1			
Parmotrema arnoldii		1															
Parmotrema crinitum		1	1														
Parmotrema perlatum								1			1						
Peltigera collina					1					1			1				
Pertusaria alpina		1	1														
Pertusaria coccodes			1					1									
Pertusaria coronata		1	1			1		1									
Pertusaria leioplaca						1		1									
Pertusaria pertusa s.l.																	
Pertusaria pupillaris																	
Pertusaria sommerfeltii																	
Phaeophyscia ciliata	1																

Table S1 continued

species	**free-standing trees**	**humid forests**	**old trees**	**trentepohlioid**	**cyano**	**low eutrophication**	**high eutrophication**	**low continentality**	**high continentality**	**low temperature**	**high temperature**	**low precipitation**	**high precipitation**	**low pH**	**high pH**	**low light conditions**	**high light conditions**
Phaeophyscia endophoenicea																	
Phaeophyscia hirsuta	1																
Phaeophyscia insignis	1																
Phaeophyscia orbicularis aggr.							1		1						1		1
Phaeophyscia poeltii	1																
Phlyctis agelaea						1		1									
Phlyctis argena												1					
Physcia adscendens							1		1			1			1		1
Physcia aipolia									1			1			1		1
Physcia stellaris									1	1		1					1
Physcia tenella							1		1			1					1
Physcia vitii	1																
Physciella chloantha							1	1			1	1			1		1
Physconia distorta									1						1		1
Physconia enteroxantha	1								1	1							1
Physconia grisea s.l.	1						1		1		1	1					1
Physconia perisidiosa									1	1							1
Piccolia ochrophora																	
Placynthiella dasaea																	
Placynthiella icmalea									1			1		1			1
Platismatia glauca						1			1	1				1			1
Pleurosticta acetabulum												1			1		1
Polycauliona candelaria							1					1					1
Polycauliona polycarpa	1						1					1			1		1
Porina leptalea				1				1			1					1	
Protoparmelia hypotremella							1	1			1						
Pseudevernia furfuracea s.l.						1			1	1				1			1
Pseudosagedia aenea				1												1	
Pseudoschismatomma rufescens				1				1								1	
Punctelia subrudecta aggr.								1			1						1
Pycnora sorophora																	
Pyrenula laevigata		1		1													
Pyrenula nitida				1		1		1			1					1	
Pyrenula nitidella				1		1		1			1					1	
Ramalina dilacerata		1															
Ramalina europaea/pollinaria																	1
Ramalina farinacea									1								
Ramalina fastigiata	1		1														1
Ramalina fraxinea	1		1														1
Ramalina obtusata aggr.		1															
Ramalina thrausta		1	1														
Reichlingia leopoldii		1		1													
Rinodina albana																	
Rinodina archaea																	
Rinodina capensis																	
Rinodina conradii																	
Rinodina efflorescens			1														
Rinodina exigua							1		1			1			1		1
Rinodina freyi																	
Rinodina griseosoralifera																	
Rinodina malangica																	
Rinodina orculata																	
Rinodina polysporoides	1																

Table S1 continued

species	free-standing trees	humid forests	old trees	trentepohlioid	cyano	low eutrophication	high eutrophication	low continentality	high continentality	low temperature	high temperature	low precipitation	high precipitation	low pH	high pH	low light conditions	high light conditions
Rinodina pyrina									1	1					1		1
Rinodina sophodes								1		1			1				1
Ropalospora viridis								1									
Schismatomma pericleum				1		1				1				1		1	
Sclerophora pallida			1	1		1									1		
Scoliciosporum chlorococcum								1				1		1			
Scoliciosporum gallurae																	
Scoliciosporum sarothamni																	
Scoliciosporum umbrinum s.l.							1										1
Sticta sylvatica		1	1		1	1		1		1			1				
Strangospora moriformis																	
Strangospora pinicola			1						1			1		1			1
Strigula glabra				1													
Strigula jamesii				1													
Strigula stigmatella				1													
Tetramelas chloroleucus																	
Thelopsis flaveola				1													
Thelopsis rubella			1	1													
Thelotrema lepadinum		1	1	1		1		1					1				
Trapelia corticola																	
Tuckermannopsis chlorophylla									1	1				1			
Usnocetraria oakesiana		1	1														
Varicellaria hemisphaerica		1	1					1									
Vezdaea aestivalis																	
Violella fucata								1		1				1			
Vulpicida pinastri s.l.						1			1	1			1	1			
Xanthomendoza fallax aggr.	1										1	1			1		1
Xanthomendoza fulva	1						1		1						1		1
Xanthomendoza ulophyllodes	1																
Xanthoria parietina s.l.							1					1			1		1
Xylopsora caradocensis						1		1						1			
Zwackhia viridis				1		1		1								1	

Appendix 2 – Model description

The two-season multi-species occupancy model we fitted to the lichen data estimates the latent response variable $z_{i,t,k}$ which is the true occupancy state of site *i* during season *t* (season 1 refers to the period 1995–2000, season 2 to the period 2018–2022) and for species *k*. The probability of occupancy is described by Ψ:

$$z_{i,t,k} \sim \text{Bernoulli}(\Psi_{i,t,k})$$

Occupancy probability is allowed to vary between sites (*i* = 1,…,446), seasons (*t* = 1, 2), and species (*k* = 1,…,329). We describe variation in occupancy with the following logistic regression model on Ψ:

$$\text{logit}(\Psi_{i,t,k}) = \alpha_{0,t,k} + \alpha_{1,k} \times \text{precipitation}_{i,t} + \alpha_{2,k} \times \text{precipitation}^2_{i,t} + \alpha_{3,k} \times \text{nitrogen}_{i,t} + \alpha_{4,k} \times \text{vegetation}_i + \alpha_{5,k} \times \text{substrate}_{i,t,k} + \alpha_{6,k} \times \text{vegetation*substrate}_{i,t,k}$$

Species-specific random effects are modelled with a Student-*t* distribution with 4 degrees of freedom, a mean μ, and a standard deviation σ:

$\alpha_{0,t,k} \sim \text{T}(\mu_{\alpha_0,t}, \sigma_{\alpha_0}, 4)$, where the mean can vary between seasons *t*

$$\alpha_{1,k} \sim \text{T}(\mu_{\alpha_1}, \sigma_{\alpha_1}, 4)$$

$$\alpha_{2,k} \sim \text{T}(\mu_{\alpha_2}, \sigma_{\alpha_2}, 4)$$

$$\alpha_{3,k} \sim \text{T}(\mu_{\alpha_3}, \sigma_{\alpha_3}, 4)$$

$$\alpha_{4,k} \sim \text{T}(\mu_{\alpha_4}, \sigma_{\alpha_4}, 4)$$

$$\alpha_{5,k} \sim \text{T}(\mu_{\alpha_5}, \sigma_{\alpha_5}, 4)$$

$$\alpha_{6,k} \sim \text{T}(\mu_{\alpha_6}, \sigma_{\alpha_6}, 4)$$

The observed data *y* are then connected to *z* through conditional probability: A species can only be detected (*y* = 1) if the species is present at a site (*z* = 1). The probability of detection, given the presence of the species, is given by *p*:

$$y_{i,t,k,j} \sim \text{Bernoulli}(z_{i,t,k} \times p_{i,t,k,j})$$

Detection probability is allowed to vary between visits (*j* = 1, 2), sites, seasons, and species. We describe this variation with the following logistic regression model on *p*:

$$\text{logit}(p_{i,t,k,j}) = \beta_{0,i,k,j} + \beta_1 \times \text{conspicuousness}_k + \beta_2 \times \text{experience}_{i,t,k,j} + \beta_3 \times \text{multiple.observers}_{i,t,j}$$

The intercept $\beta_{0,i,k,j}$ is a Student-*t* random variable with 4 degrees of freedom that is governed by a mean $\mu_{\beta_0,o}$ which varies between observers *o*, and a standard deviation σ_{β_0} which is constant across observers:

$$\beta_{0,i,k,j} \sim \mathrm{T}(\mu_{\beta_0,o}, \sigma_{\beta_0}, 4)$$

In Table S2, we describe the covariates used to describe variation in occupancy and detection. The estimates of their effects, as obtained from the fitted model, are given in Table S3.

Table S2 Description of covariates used to model variation in occupancy and detection probability.

Covariate	**Description**	**Source**
Occupancy process		
precipitation	site-specific standardised number of precipitation days per year, summarized per time period *t* for the years 1986–2000 (*t* = 1) and 2008–2022 (*t* = 2)	MeteoSwiss RhiresD
precipitation^2	site-specific squared standardised number of precipitation days per year, summarized per time period *t* for the years 1986–2000 (*t* = 1) and 2008–2022 (*t* = 2)	MeteoSwiss RhiresD
nitrogen	site-specific standardised deposition of total nitrogen in kg N/ha/year for the years 1990 (used for *t* = 1) and 2015 (for *t* =2)	Bundesamt für Umwelt BAFU, Abt. Luftreinhaltung und Chemikalien; Rihm and Künzle (2023)
vegetation	site-specific indicator for the type of vegetation: forest (1) or open (0)	Swiss National Forest Inventory www.lfi.ch
substrate	species- and site-specific indicator for the presence (1) or absence (0) of suitable bark substrate for the species	SwissLichens database (Stofer et al., 2019) definition of pH classes (Barkman, 1958)
vegetation*substrate	interaction between the two above, because suitable substrate may only be colonized if it grows in the right habitat (open or forest)	see above
Detection process		
conspicuousness	species-specific indicator for conspicuous (1) or inconspicuous (0) species	we compiled this index based on the majority judgement of five experienced lichenologists
experience	species- and observer-specific indicator whether the observer who conducted the survey had previously reported this species to the national database (1) or not (0)	SwissLichens database (Stofer et al., 2019)
multiple.observers	survey-specific indicator for whether the site was surveyed alone (0) or in collaboration with another observer (1)	-

Table S3 Parameter estimates obtained from the posterior distribution of the fitted occupancy model. The posterior is described by its mean and the 95% Bayesian credible interval.

Parameter	**Posterior mean**	**2.5% quantile**	**97.5% quantile**
Occupancy process			
$\mu_{\alpha_{0},t=1}$	-1.71	-2.20	-1.20
$\mu_{\alpha_{0},t=2}$	-2.38	-2.89	-1.87
μ_{α_1}	0.19	0.11	0.26
μ_{α_2}	-0.06	-0.10	-0.01
μ_{α_3}	-0.83	-1.02	-0.64
μ_{α_4}	-1.44	-1.78	-1.14
μ_{α_5}	0.53	0.32	0.73
μ_{α_6}	0.03	-0.18	0.24
σ_{α_0}	3.75	3.45	4.04
σ_{α_1}	0.52	0.46	0.59
σ_{α_2}	0.29	0.25	0.33
σ_{α_3}	1.47	1.34	1.61
σ_{α_4}	1.49	1.24	1.79
σ_{α_5}	1.04	0.88	1.22
σ_{α_6}	1.10	0.93	1.29
Detection process			
$\mu_{\beta_0,o=1}$	0.20	-0.05	0.46
$\mu_{\beta_0,o=2}$	-0.55	-0.82	-0.28
$\mu_{\beta_0,o=3}$	-0.78	-1.02	-0.56
$\mu_{\beta_0,o=4}$	-0.40	-0.64	-0.17
$\mu_{\beta_0,o=5}$	-0.17	-0.39	0.07
$\mu_{\beta_0,o=6}$	-1.37	-1.61	-1.14
$\mu_{\beta_0,o=7}$	1.16	0.92	1.42
$\mu_{\beta_0,o=8}$	-0.05	-0.28	0.17
$\mu_{\beta_0,o=9}$	1.24	0.93	1.56
$\mu_{\beta_0,o=10}$	-0.53	-0.75	-0.31
$\mu_{\beta_0,o=11}$	0.48	0.19	0.76
$\mu_{\beta_0,o=12}$	-0.18	-0.46	0.10
μ_{β_1}	0.58	0.43	0.74
μ_{β_2}	0.13	-0.01	0.26
μ_{β_3}	0.49	0.34	0.66
σ_{β_0}	0.84	0.77	0.92

Appendix 3 – Prior sensitivity analysis

We here test the sensitivity of the main parameter estimates to prior specification. In particular two aspects in our priors could have affected the estimates. The first is that we used rather informative priors for the regression coefficients, i.e., normal priors with a standard deviation of 10 ($\tau = 0.01$), whereas it may have been more conservative to use wider priors. We therefore compare our prior to a prior with a standard deviation of 100 ($\tau = 0.001$). The second aspect is the use of very informative priors for the standard deviations of random effects, i.e., half-Cauchy priors with a standard deviation of 1, following the example of Outhwaite et al. (2018). We here compare the use of our prior to a standard deviation of 25 as suggested by Gelman (2006).

Fig. S1 illustrates the distribution of the prior pairs, and Fig. S2 shows the comparison of the posterior estimates of the 30 main parameters. As the resulting estimates show only minute differences between the priors, we conclude that the parameter estimates are not sensitive to the definition of the prior. The model with our preferred priors and the model with alternative priors 1 took a similar time to run, i.e., roughly 21 hours, the model with alternative priors 2 took 31 hours. Our choice was therefore based on computational speed in combination with our conviction that a narrower prior for regression coefficients was reasonable in this situation.

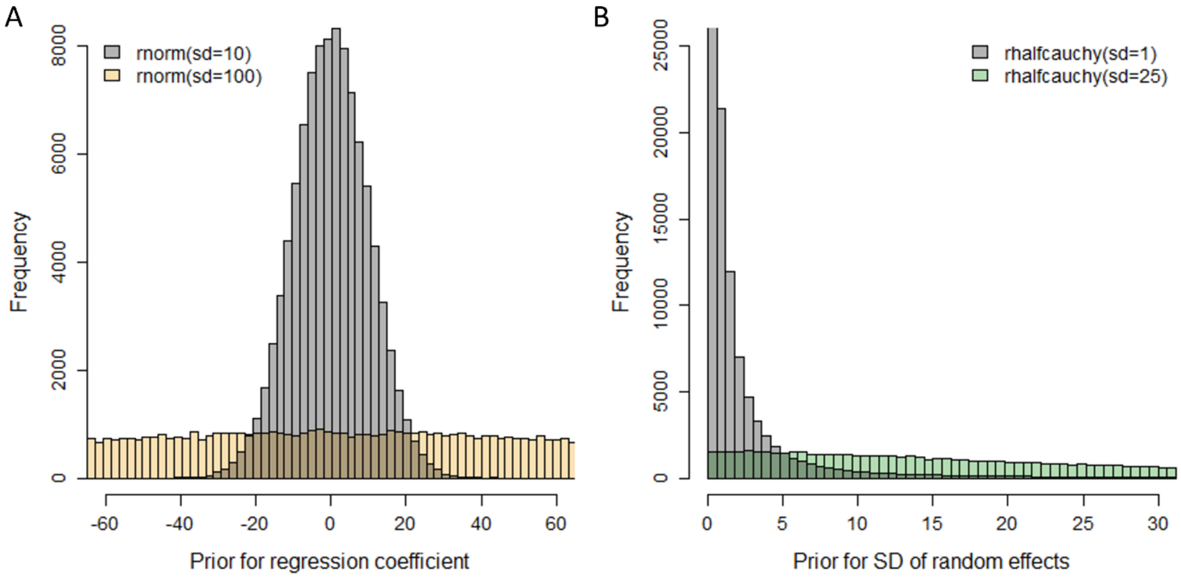


Fig. S1 Comparison of the prior distribution we used in the main manuscript with alternative, wider distributions. The first distribution was used as prior to regression coefficients (A), the second distribution was used as prior to the standard deviation of species random effects (B). Note that the y-axis in panel B is truncated.

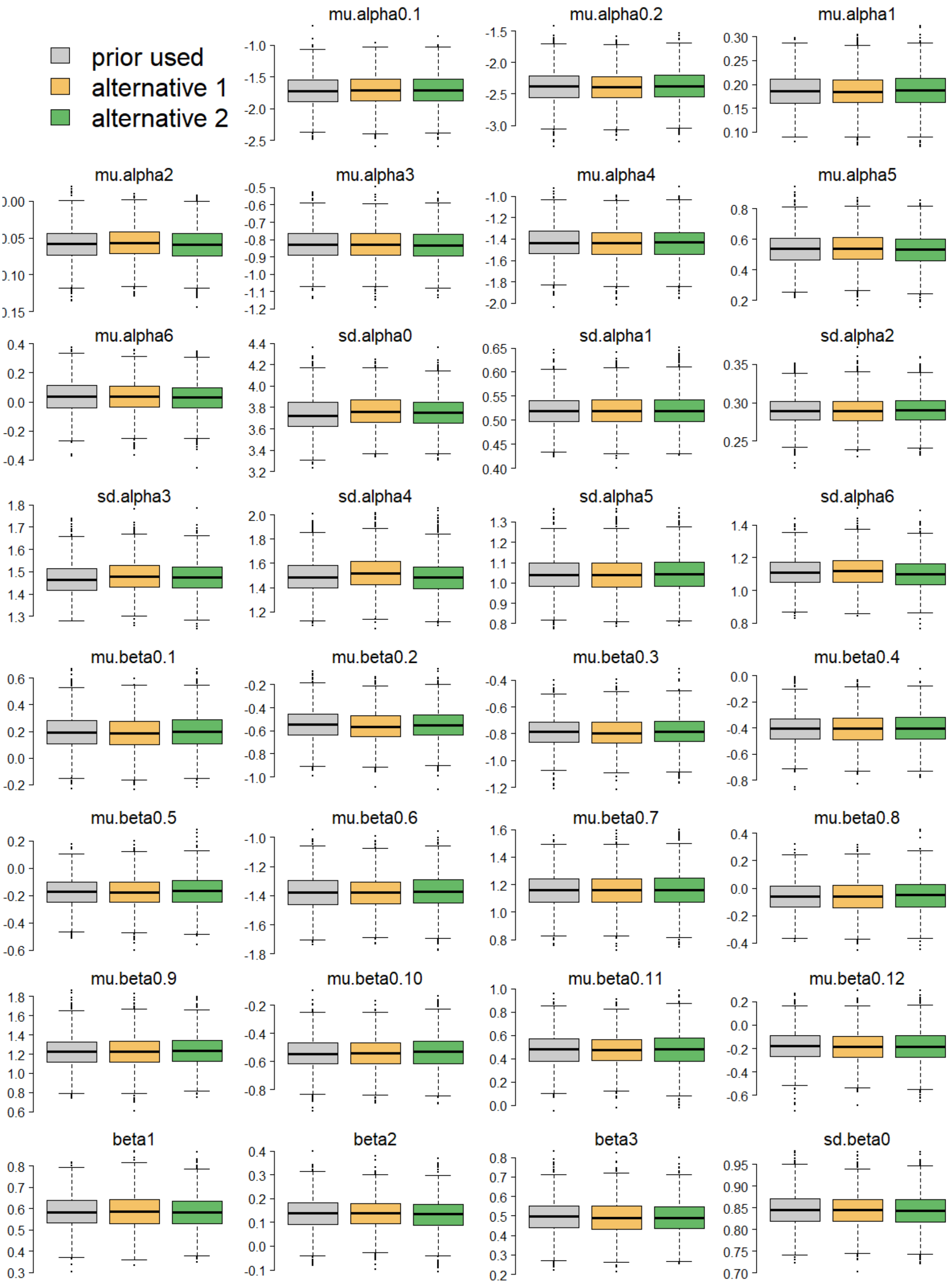
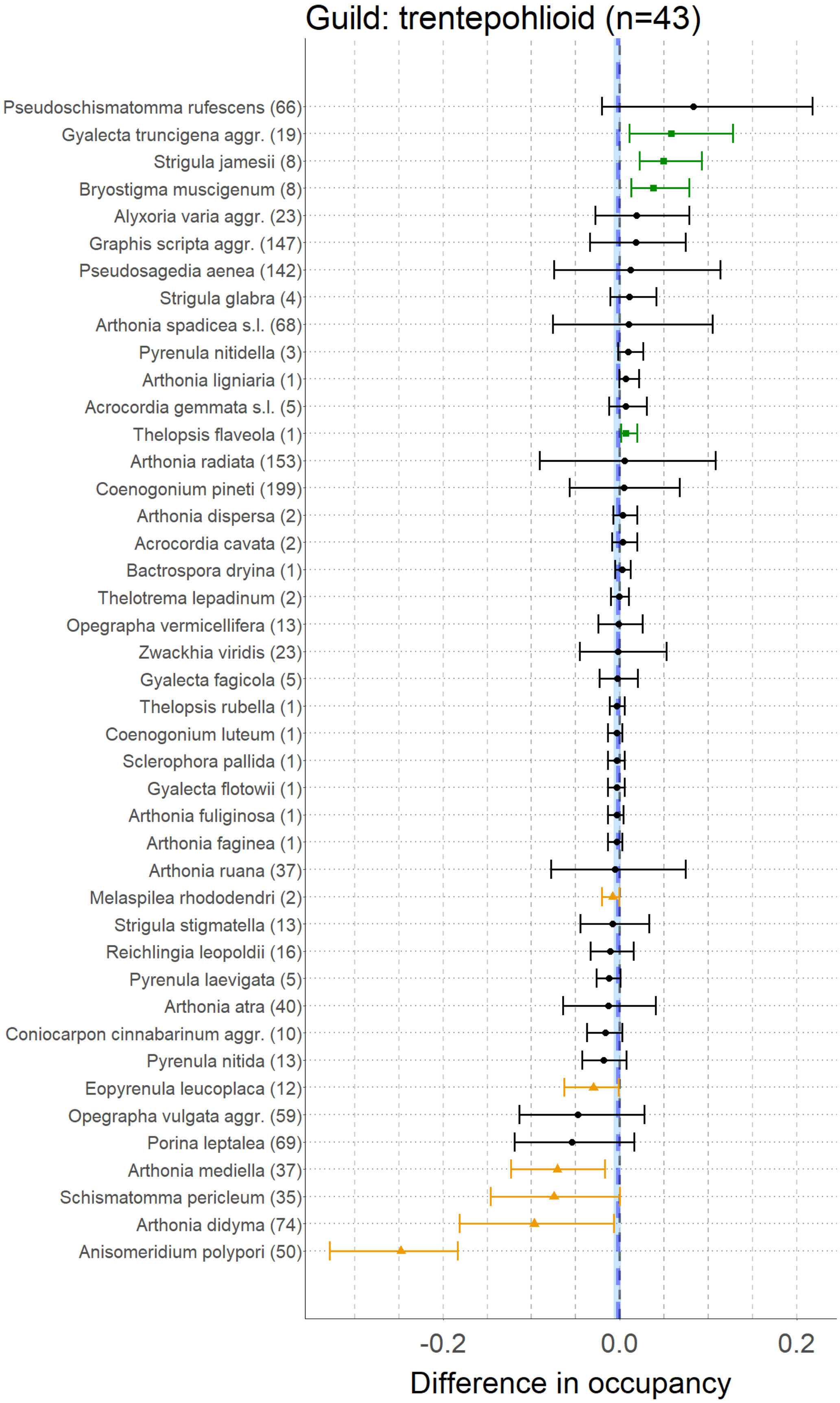
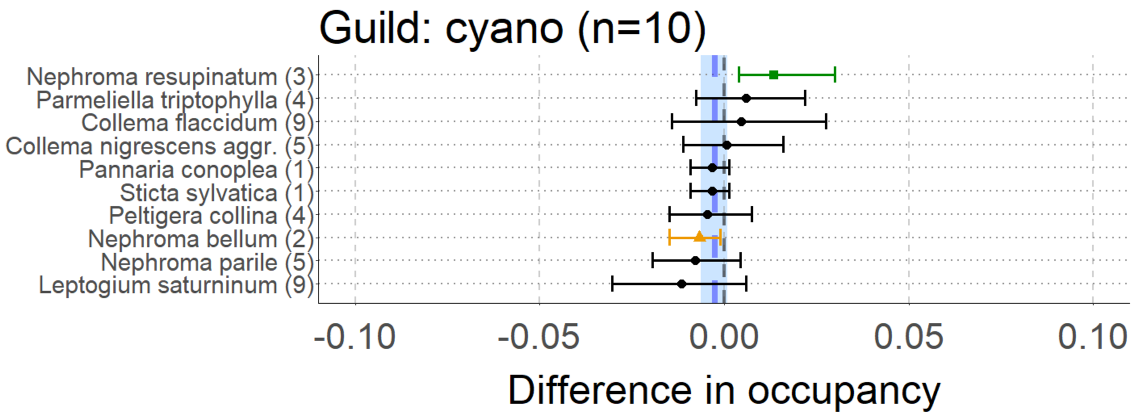
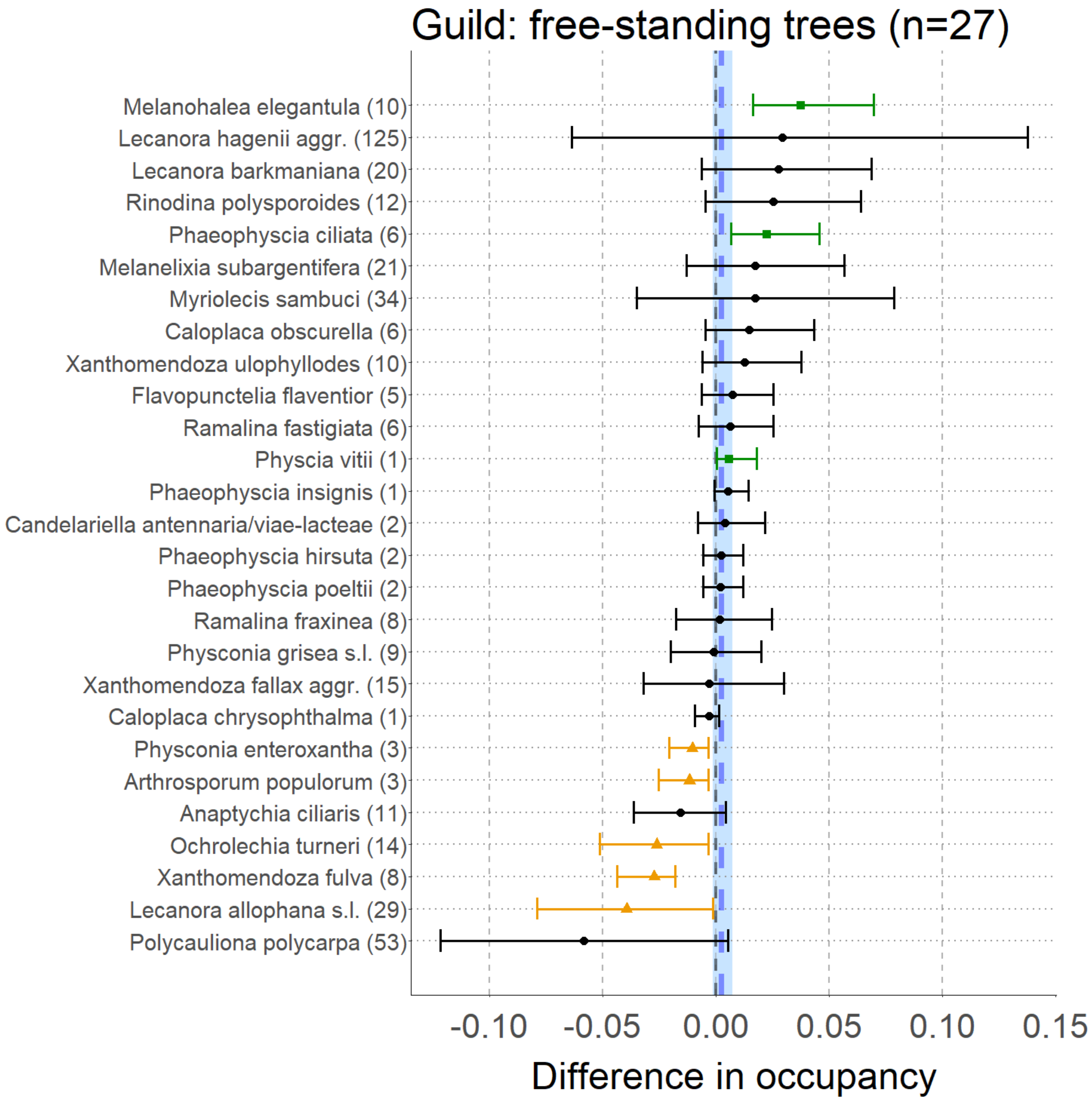


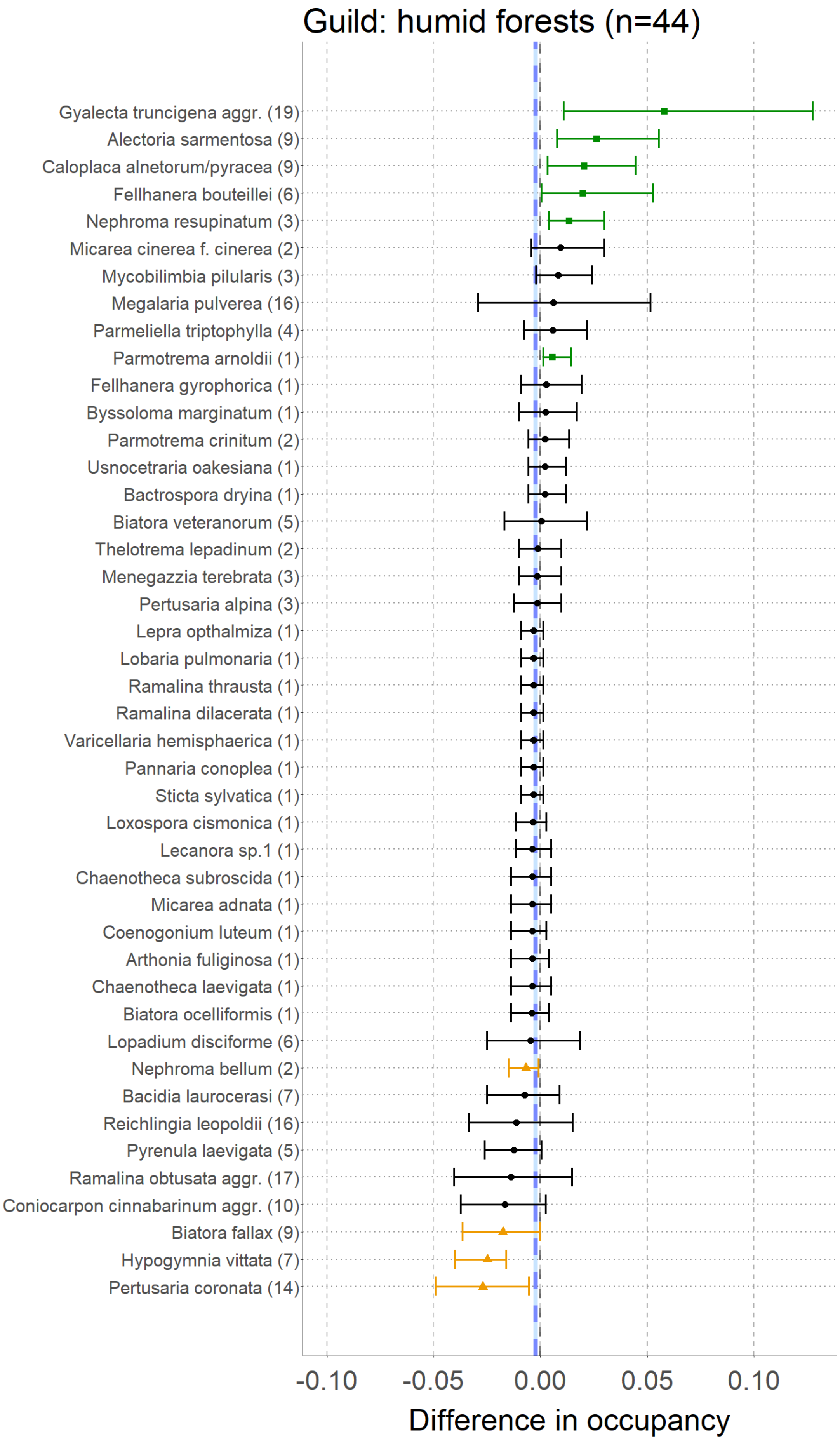
Fig. S2 Comparison of the posterior distributions of the 30 main parameters. The grey boxplot was obtained from the model as reported in the main manuscript, the beige boxplot uses an alternative, wider prior for regression coefficients (SD=100 instead of SD=10), and the purple boxplot uses a wider Cauchy prior for the standard deviation term of the species random effects (SD=25 instead of SD=1).

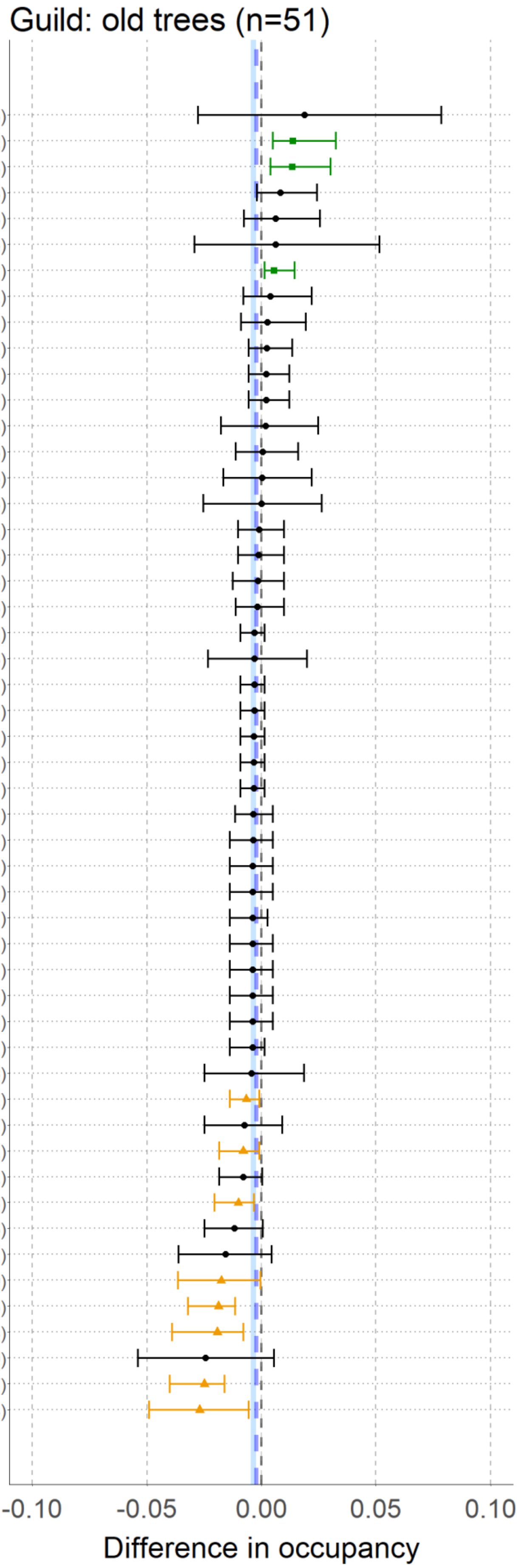
Appendix 4 – Plots of estimated species-specific changes across Switzerland for all guilds

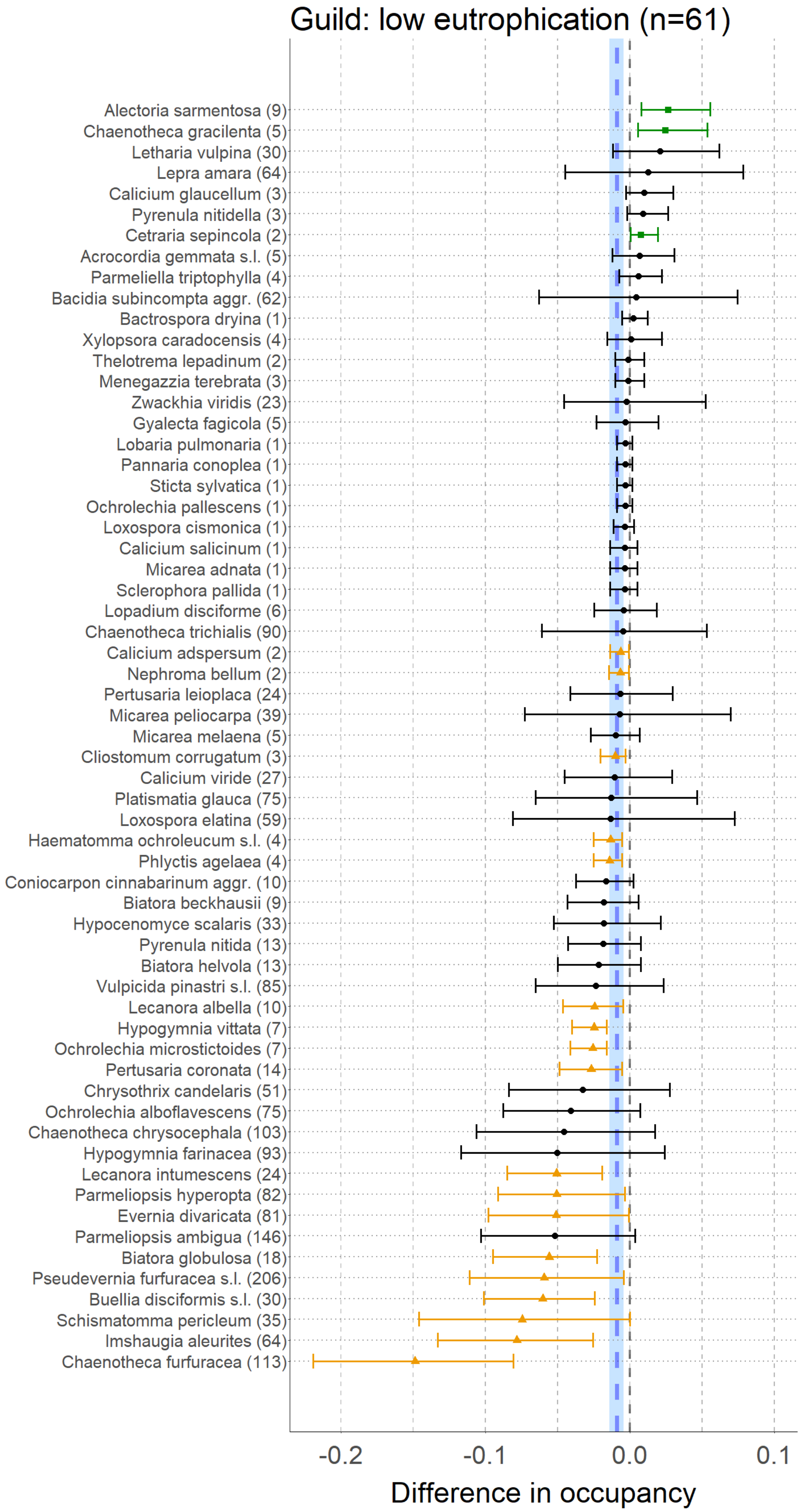



Guild: cyano (n=10)
Nephroma resupinatum (3)
Parmeliella triptophylla (4)
Collema flaccidum (9)
Collema nigrescens aggr. (5)
Pannaria conoplea (1)
Sticta sylvatica (1)
Peltigera collina (4)
Nephroma bellum (2)
Nephroma parile (5)
Leptogium saturninum (9)
-0.10
-0.05
0.00
0.05
0.10
Difference in occupancy


Guild: free-standing trees (n=27)
Melanohalea elegantula (10)
Lecanora hagenii aggr. (125)
Lecanora barkmaniana (20)
Rinodina polysporoides (12)
Phaeophyscia ciliata (6)
Melanelixia subargentifera (21)
Myriolecis sambuci (34)
Caloplaca obscurella (6)
Xanthomendoza ulophyllodes (10)
Flavopunctelia flaventior (5)
Ramalina fastigiata (6)
Physcia vitii (1)
Phaeophyscia insignis (1)
Candelariella antennaria/viae-lacteae (2)
Phaeophyscia hirsuta (2)
Phaeophyscia poeltii (2)
Ramalina fraxinea (8)
Physconia grisea s.l. (9)
Xanthomendoza fallax aggr. (15)
Caloplaca chrysophthalma (1)
Physconia enteroxantha (3)
Arthrosporum populorum (3)
Anaptychia ciliaris (11)
Ochrolechia turneri (14)
Xanthomendoza fulva (8)
Lecanora allophana s.l. (29)
Polycauliona polycarpa (53)
-0.10
-0.05
0.00
0.05
0.10
0.15
Difference in occupancy


Guild: humid forests (n=44)
Gyalecta truncigena aggr. (19)
Alectoria sarmentosa (9)
Caloplaca alnetorum/pyracea (9)
Fellhanera bouteillei (6)
Nephroma resupinatum (3)
Micarea cinerea f. cinerea (2)
Mycobilimbia pilularis (3)
Megalaria pulverea (16)
Parmeliella triptophylla (4)
Parmotrema arnoldii (1)
Fellhanera gyrophorica (1)
Byssoloma marginatum (1)
Parmotrema crinitum (2)
Usnocetraria oakesiana (1)
Bactrospora dryina (1)
Biatora veteranorum (5)
Thelotrema lepadinum (2)
Menegazzia terebrata (3)
Pertusaria alpina (3)
Lepra opthalmiza (1)
Lobaria pulmonaria (1)
Ramalina thrausta (1)
Ramalina dilacerata (1)
Varicellaria hemisphaerica (1)
Pannaria conoplea (1)
Sticta sylvatica (1)
Loxospora cismonica (1)
Lecanora sp.1 (1)
Chaenotheca subroscida (1)
Micarea adnata (1)
Coenogonium luteum (1)
Arthonia fuliginosa (1)
Chaenotheca laevigata (1)
Biatora ocelliformis (1)
Lopadium disciforme (6)
Nephroma bellum (2)
Bacidia laurocerasi (7)
Reichlingia leopoldii (16)
Pyrenula laevigata (5)
Ramalina obtusata aggr. (17)
Coniocarpon cinnabarinum aggr. (10)
Biatora fallax (9)
Hypogymnia vittata (7)
Pertusaria coronata (14)
-0.10
-0.05
0.00
0.05
0.10
Difference in occupancy


Guild: old trees (n=51)
Alyxoria varia aggr. (23)
Calicium pinastri (2)
Nephroma resupinatum (3)
Mycobilimbia pilularis (3)
Ramalina fastigiata (6)
Megalaria pulverea (16)
Chaenotheca chlorella (1)
Candelariella antennaria/viae-lacteae (2)
Fellhanera gyrophorica (1)
Parmotrema crinitum (2)
Usnocetraria oakesiana (1)
Bactrospora dryina (1)
Ramalina fraxinea (8)
Collema nigrescens aggr. (5)
Biatora veteranorum (5)
Calicium montanum (13)
Thelotrema lepadinum (2)
Menegazzia terebrata (3)
Pertusaria alpina (3)
Nephromopsis laureri (3)
Lepra opthalmiza (1)
Gyalecta fagicola (5)
Lobaria pulmonaria (1)
Ramalina thrausta (1)
Varicellaria hemisphaerica (1)
Pannaria conoplea (1)
Sticta sylvatica (1)
Thelopsis rubella (1)
Calicium salicinum (1)
Chaenotheca subroscida (1)
Micarea adnata (1)
Coenogonium luteum (1)
Sclerophora pallida (1)
Gyalecta flotowii (1)
Strangospora pinicola (1)
Chaenotheca laevigata (1)
Biatora rufidula (1)
Lopadium disciforme (6)
Calicium adspersum (2)
Bacidia laurocerasi (7)
Calicium lenticulare (2)
Caloplaca lucifuga (2)
Cliostomum corrugatum (3)
Chaenotheca phaeocephala (5)
Anaptychia ciliaris (11)
Biatora fallax (9)
Acolium karelicum (5)
Rinodina efflorescens (4)
Pertusaria coccodes (19)
Hypogymnia vittata (7)
Pertusaria coronata (14)
-0.10
-0.05
0.00
0.05
0.10
Difference in occupancy


Guild: low eutrophication (n=61)
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Chaenotheca gracilenta (5)
Letharia vulpina (30)
Lepra amara (64)
Calicium glaucellum (3)
Pyrenula nitidella (3)
Cetraria sepincola (2)
Acrocordia gemmata s.l. (5)
Parmeliella triptophylla (4)
Bacidia subincompta aggr. (62)
Bactrospora dryina (1)
Xylopsora caradocensis (4)
Thelotrema lepadinum (2)
Menegazzia terebrata (3)
Zwackhia viridis (23)
Gyalecta fagicola (5)
Lobaria pulmonaria (1)
Pannaria conoplea (1)
Sticta sylvatica (1)
Ochrolechia pallescens (1)
Loxospora cismonica (1)
Calicium salicinum (1)
Micarea adnata (1)
Sclerophora pallida (1)
Lopadium disciforme (6)
Chaenotheca trichialis (90)
Calicium adspersum (2)
Nephroma bellum (2)
Pertusaria leioplaca (24)
Micarea peliocarpa (39)
Micarea melaena (5)
Cliostomum corrugatum (3)
Calicium viride (27)
Platismatia glauca (75)
Loxospora elatina (59)
Haematomma ochroleucum s.l. (4)
Phlyctis agelaea (4)
Coniocarpon cinnabarinum aggr. (10)
Biatora beckhausii (9)
Hypocenomyce scalaris (33)
Pyrenula nitida (13)
Biatora helvola (13)
Vulpicida pinastri s.l. (85)
Lecanora albella (10)
Hypogymnia vittata (7)
Ochrolechia microstictoides (7)
Pertusaria coronata (14)
Chrysothrix candelaris (51)
Ochrolechia alboflavescens (75)
Chaenotheca chrysocephala (103)
Hypogymnia farinacea (93)
Lecanora intumescens (24)
Parmeliopsis hyperopta (82)
Evernia divaricata (81)
Parmeliopsis ambigua (146)
Biatora globulosa (18)
Pseudevernia furfuracea s.l. (206)
Buellia disciformis s.l. (30)
Schismatomma pericleum (35)
Imshaugia aleurites (64)
Chaenotheca furfuracea (113)
-0.2
-0.1
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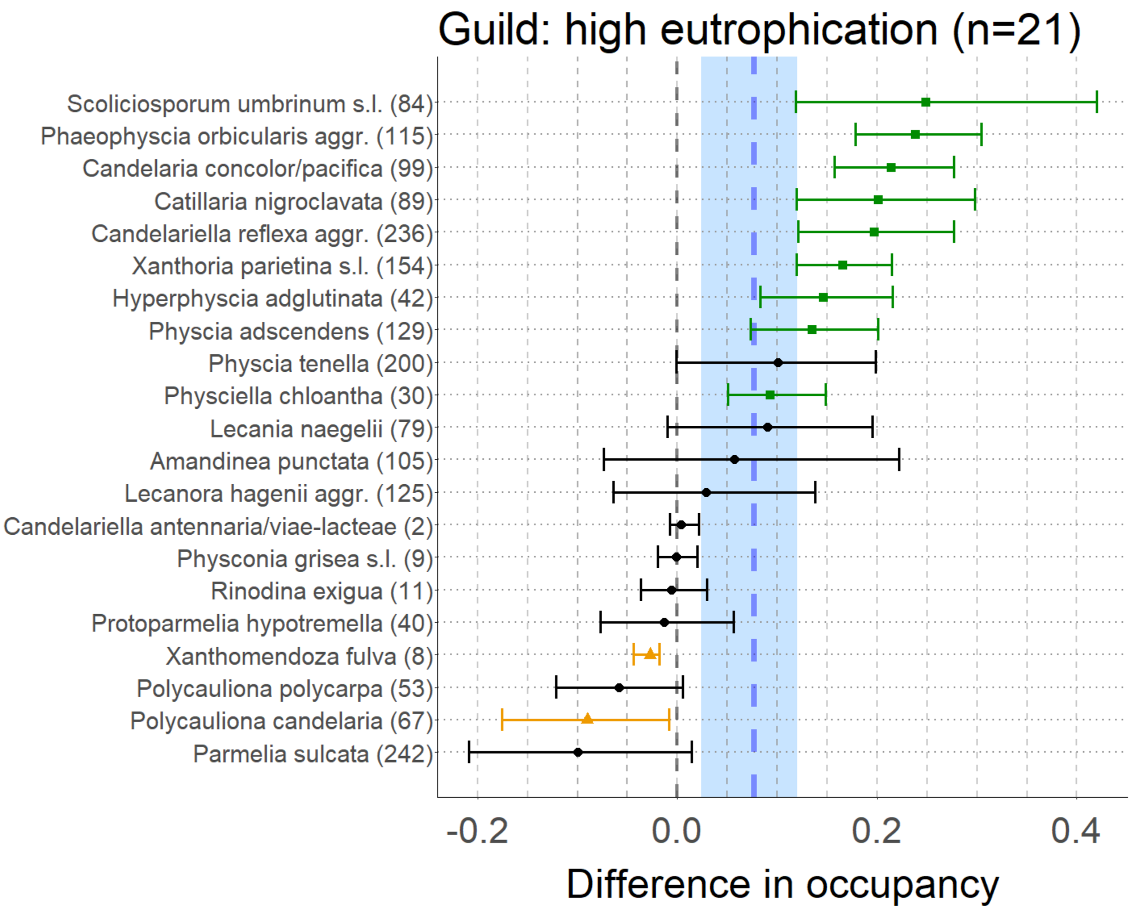
0.1
Difference in occupancy


Guild: high eutrophication (n=21)
Scoliciosporum umbrinum s.l. (84)
Phaeophyscia orbicularis aggr. (115)
Candelaria concolor/pacifica (99)
Catillaria nigroclavata (89)
Candelariella reflexa aggr. (236)
Xanthoria parietina s.l. (154)
Hyperphyscia adglutinata (42)
Physcia adscendens (129)
Physcia tenella (200)
Physciella chloantha (30)
Lecania naegelii (79)
Amandinea punctata (105)
Lecanora hagenii aggr. (125)
Candelariella antennaria/viae-lacteae (2)
Physconia grisea s.l. (9)
Rinodina exigua (11)
Protoparmelia hypotremella (40)
Xanthomendoza fulva (8)
Polycauliona polycarpa (53)
Polycauliona candelaria (67)
Parmelia sulcata (242)
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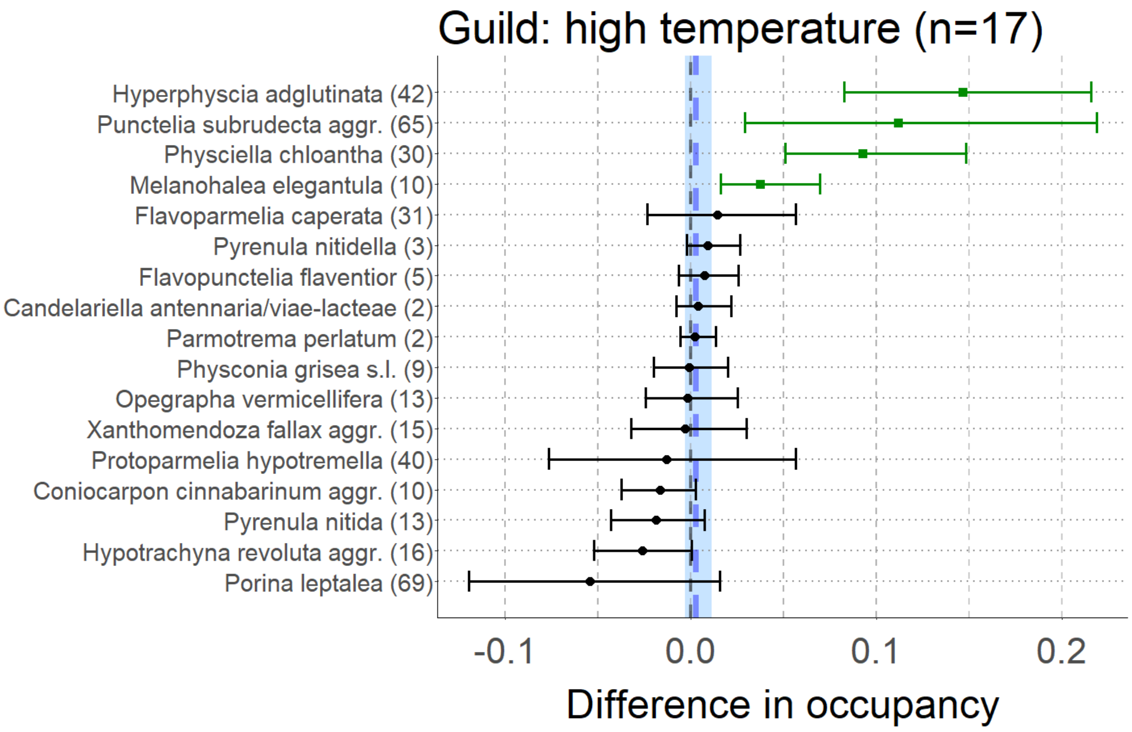
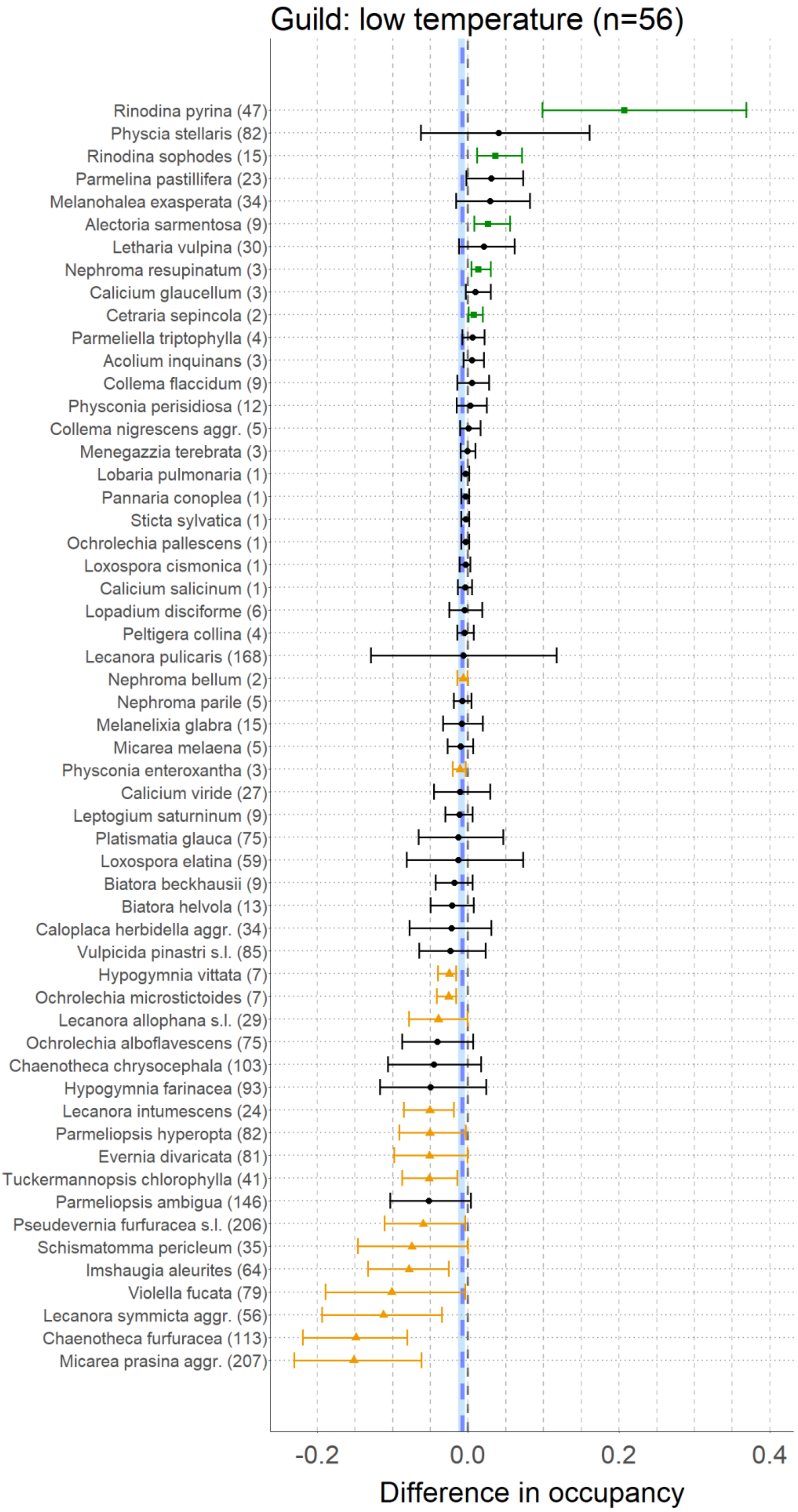
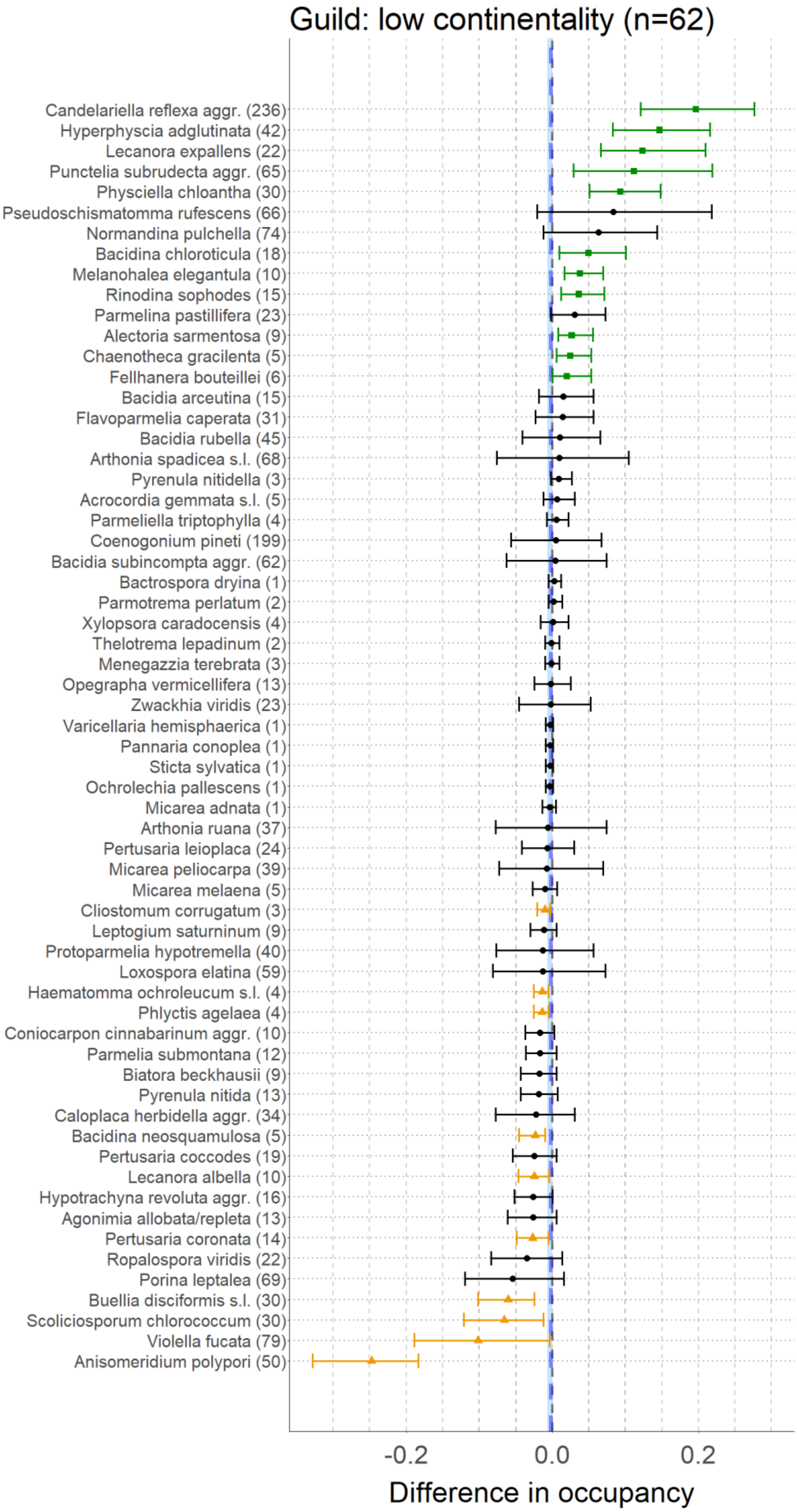
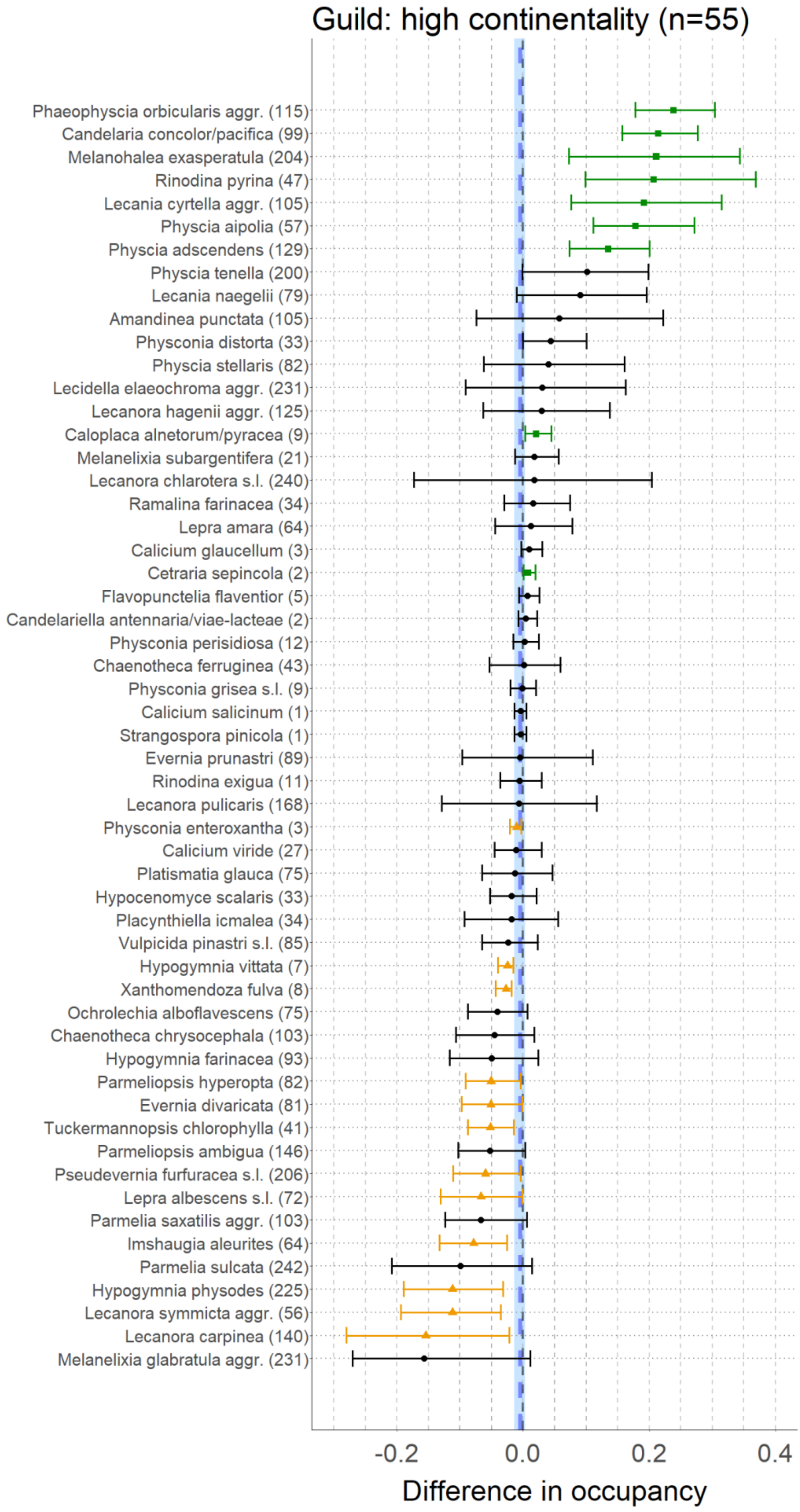
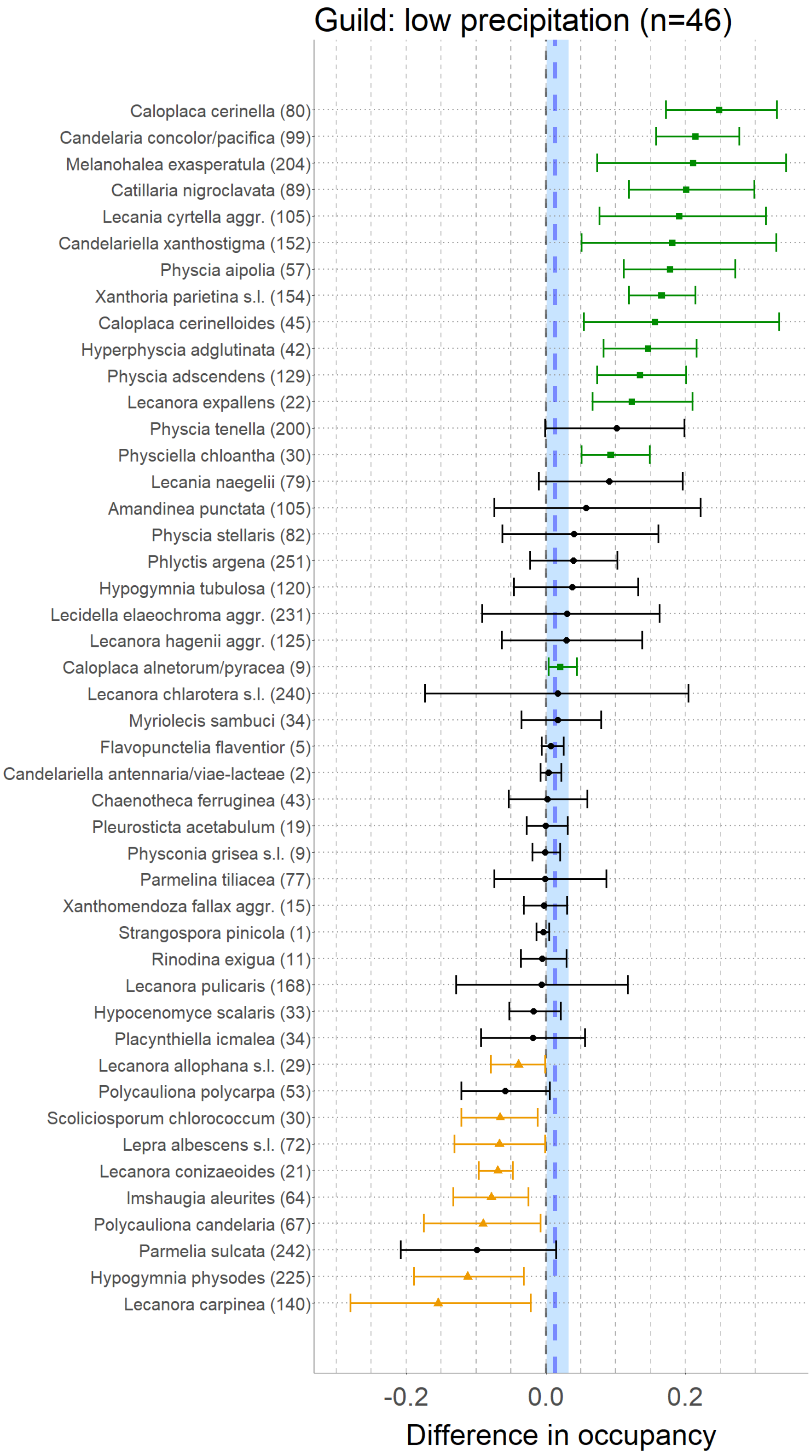
Difference in occupancy

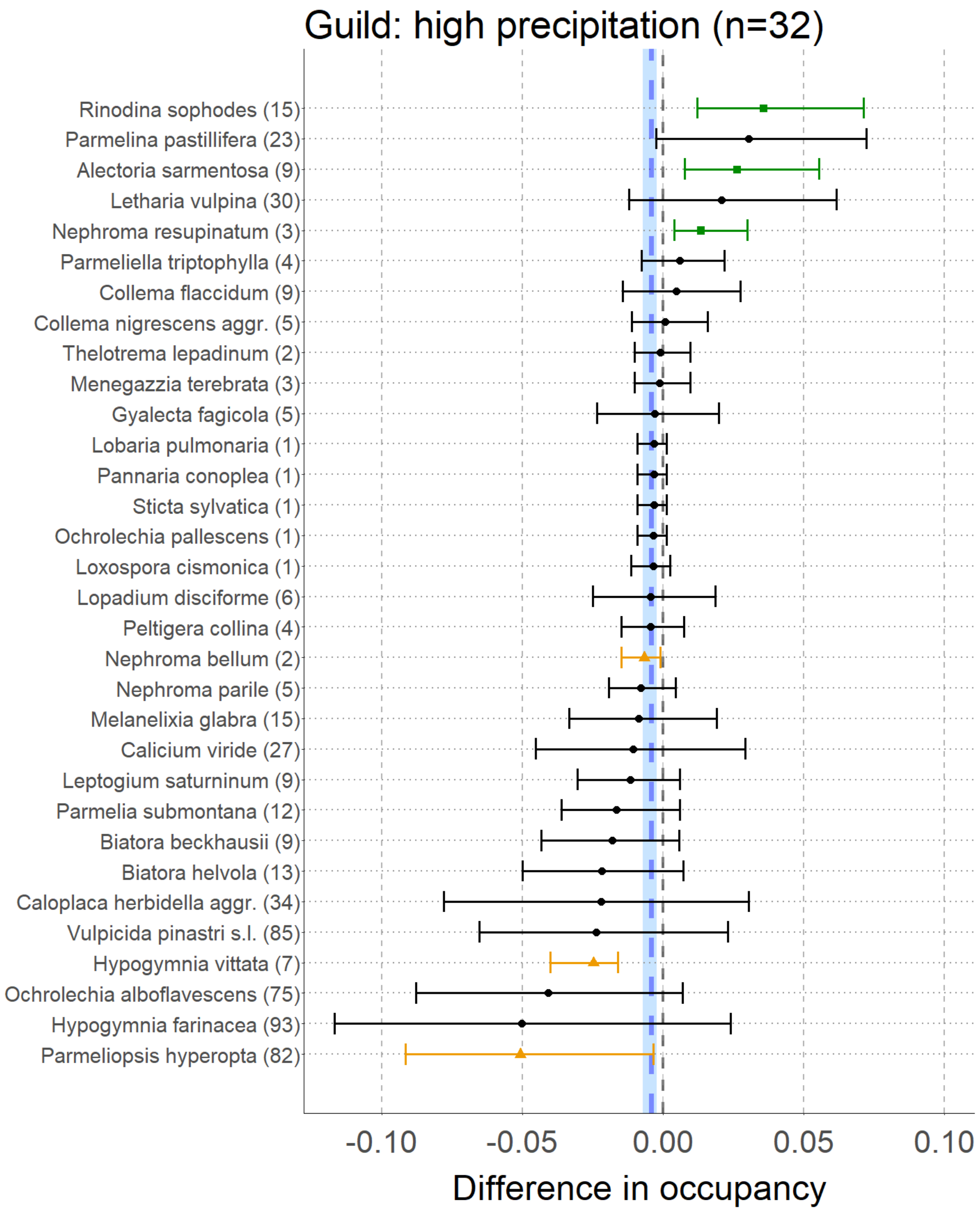

Guild: high temperature (n=17)
Hyperphyscia adglutinata (42)
Punctelia subrudecta aggr. (65)
Physciella chloantha (30)
Melanohalea elegantula (10)
Flavoparmelia caperata (31)
Pyrenula nitidella (3)
Flavopunctelia flaventior (5)
Candelariella antennaria/viae-lacteae (2)
Parmotrema perlatum (2)
Physconia grisea s.l. (9)
Opegrapha vermicellifera (13)
Xanthomendoza fallax aggr. (15)
Protoparmelia hypotremella (40)
Coniocarpon cinnabarinum aggr. (10)
Pyrenula nitida (13)
Hypotrachyna revoluta aggr. (16)
Porina leptalea (69)
-0.1
0.0
0.1
0.2
Difference in occupancy

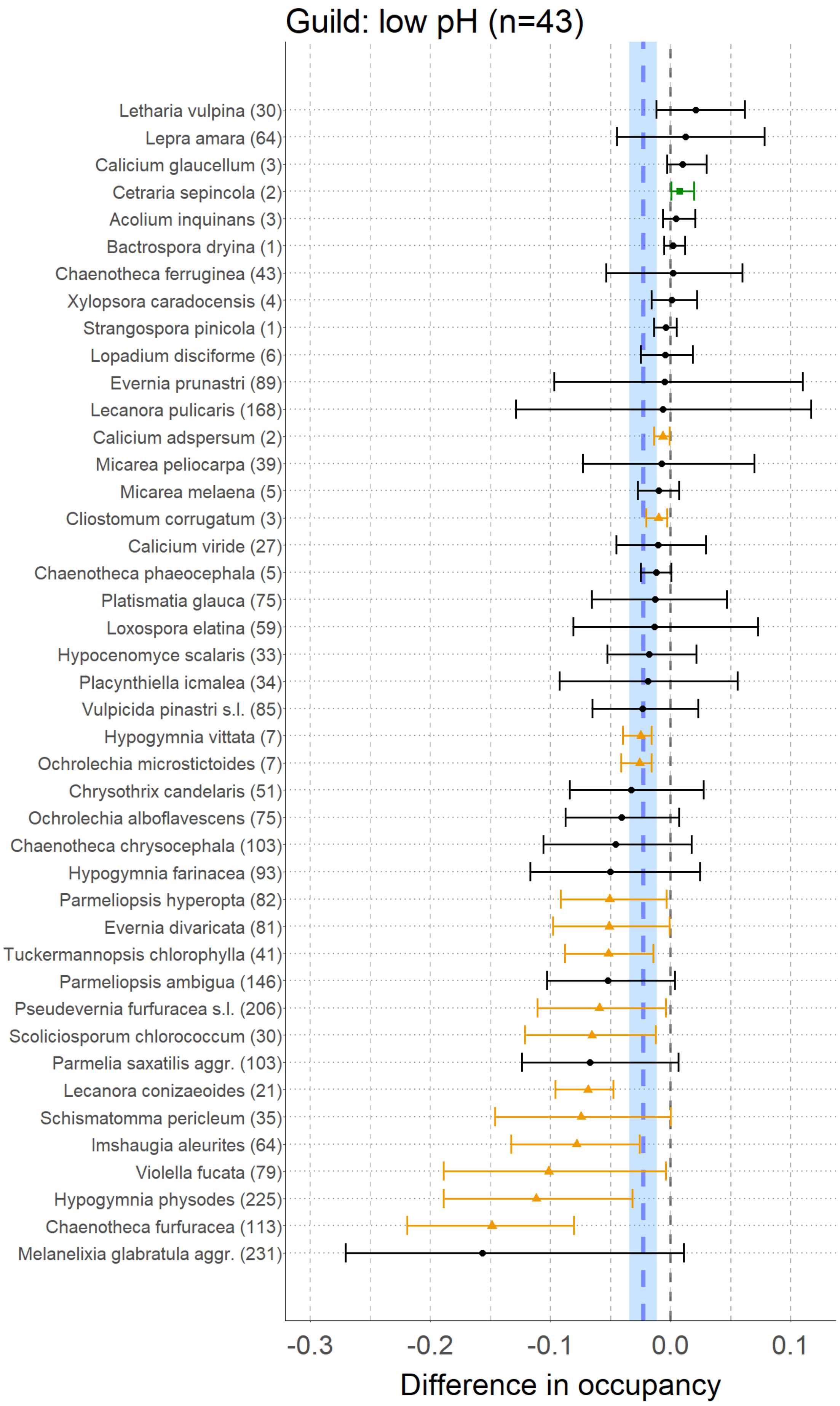

Guild: low temperature (n=56)
Rinodina pyrina (47)
Physcia stellaris (82)
Rinodina sophodes (15)
Parmelina pastillifera (23)
Melanohalea exasperata (34)
Alectoria sarmentosa (9)
Letharia vulpina (30)
Nephroma resupinatum (3)
Calicium glaucellum (3)
Cetraria sepincola (2)
Parmeliella triptophylla (4)
Acolium inquinans (3)
Collema flaccidum (9)
Physconia perisidiosa (12)
Collema nigrescens aggr. (5)
Menegazzia terebrata (3)
Lobaria pulmonaria (1)
Pannaria conoplea (1)
Sticta sylvatica (1)
Ochrolechia pallescens (1)
Loxospora cismonica (1)
Calicium salicinum (1)
Lopadium disciforme (6)
Peltigera collina (4)
Lecanora pulicaris (168)
Nephroma bellum (2)
Nephroma parile (5)
Melanelixia glabra (15)
Micarea melaena (5)
Physconia enteroxantha (3)
Calicium viride (27)
Leptogium saturninum (9)
Platismatia glauca (75)
Loxospora elatina (59)
Biatora beckhausii (9)
Biatora helvola (13)
Caloplaca herbidella aggr. (34)
Vulpicida pinastri s.l. (85)
Hypogymnia vittata (7)
Ochrolechia microstictoides (7)
Lecanora allophana s.l. (29)
Ochrolechia alboflavescens (75)
Chaenotheca chrysocephala (103)
Hypogymnia farinacea (93)
Lecanora intumescens (24)
Parmeliopsis hyperopta (82)
Evernia divaricata (81)
Tuckermannopsis chlorophylla (41)
Parmeliopsis ambigua (146)
Pseudevernia furfuracea s.l. (206)
Schismatomma pericleum (35)
Imshaugia aleurites (64)
Violella fucata (79)
Lecanora symmicta aggr. (56)
Chaenotheca furfuracea (113)
Micarea prasina aggr. (207)
-0.2
0.0
0.2
0.4
Difference in occupancy

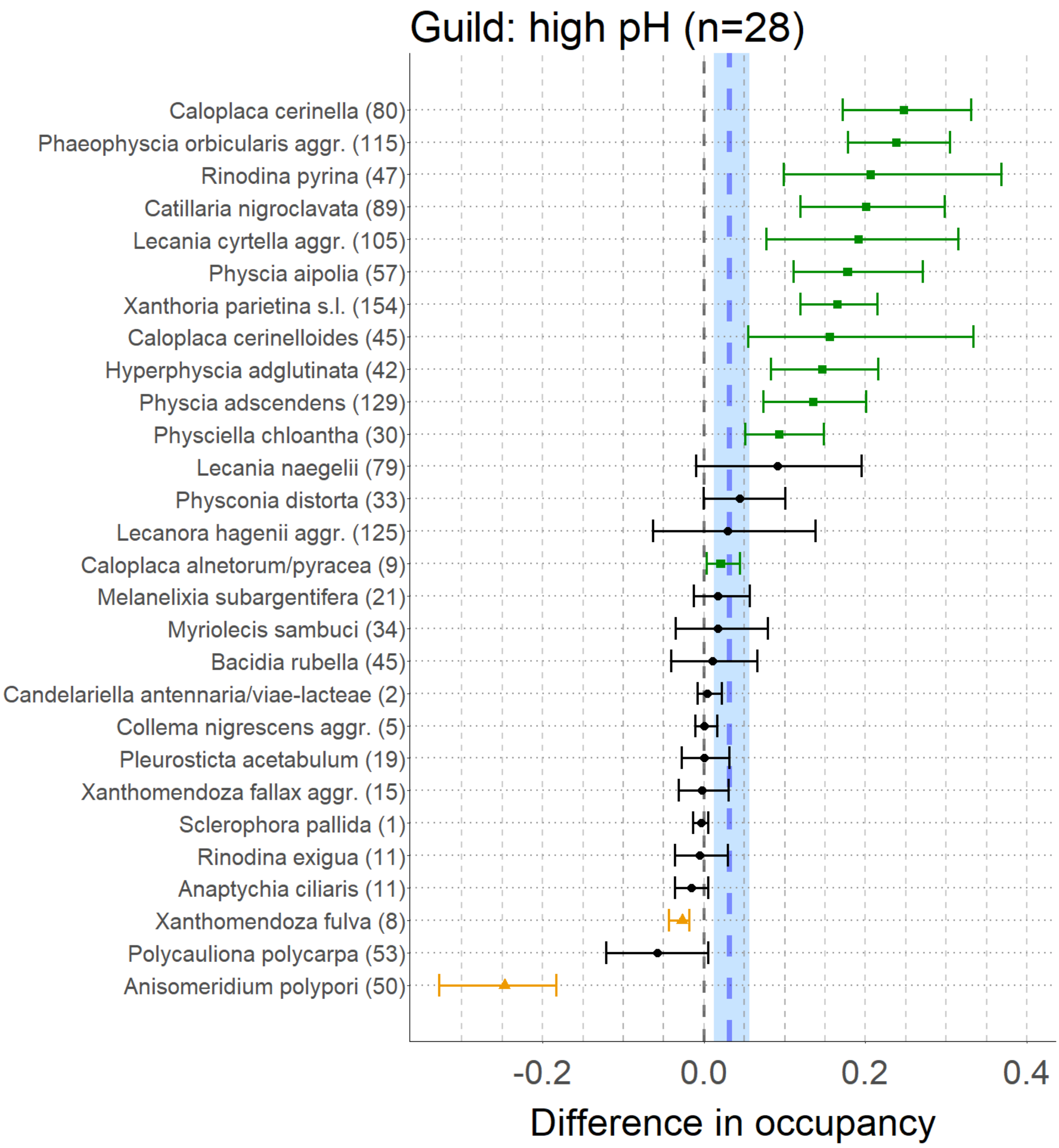

Guild: low continentality (n=62)
Candelariella reflexa aggr. (236)
Hyperphyscia adglutinata (42)
Lecanora expallens (22)
Punctelia subrudecta aggr. (65)
Physciella chloantha (30)
Pseudoschismatomma rufescens (66)
Normandina pulchella (74)
Bacidina chloroticula (18)
Melanohalea elegantula (10)
Rinodina sophodes (15)
Parmelina pastillifera (23)
Alectoria sarmentosa (9)
Chaenotheca gracilenta (5)
Fellhanera bouteillei (6)
Bacidia arceutina (15)
Flavoparmelia caperata (31)
Bacidia rubella (45)
Arthonia spadicea s.l. (68)
Pyrenula nitidella (3)
Acrocordia gemmata s.l. (5)
Parmeliella triptophylla (4)
Coenogonium pineti (199)
Bacidia subincompta aggr. (62)
Bactrospora dryina (1)
Parmotrema perlatum (2)
Xylopsora caradocensis (4)
Thelotrema lepadinum (2)
Menegazzia terebrata (3)
Opegrapha vermicellifera (13)
Zwackhia viridis (23)
Varicellaria hemisphaerica (1)
Pannaria conoplea (1)
Sticta sylvatica (1)
Ochrolechia pallescens (1)
Micarea adnata (1)
Arthonia ruana (37)
Pertusaria leioplaca (24)
Micarea peliocarpa (39)
Micarea melaena (5)
Cliostomum corrugatum (3)
Leptogium saturninum (9)
Protoparmelia hypotremella (40)
Loxospora elatina (59)
Haematomma ochroleucum s.l. (4)
Phlyctis agelaea (4)
Coniocarpon cinnabarinum aggr. (10)
Parmelia submontana (12)
Biatora beckhausii (9)
Pyrenula nitida (13)
Caloplaca herbidella aggr. (34)
Bacidina neosquamulosa (5)
Pertusaria coccodes (19)
Lecanora albella (10)
Hypotrachyna revoluta aggr. (16)
Agonimia allobata/repleta (13)
Pertusaria coronata (14)
Ropalospora viridis (22)
Porina leptalea (69)
Buellia disciformis s.l. (30)
Scoliciosporum chlorococcum (30)
Violella fucata (79)
Anisomeridium polypori (50)
-0.2
0.0
0.2
Difference in occupancy

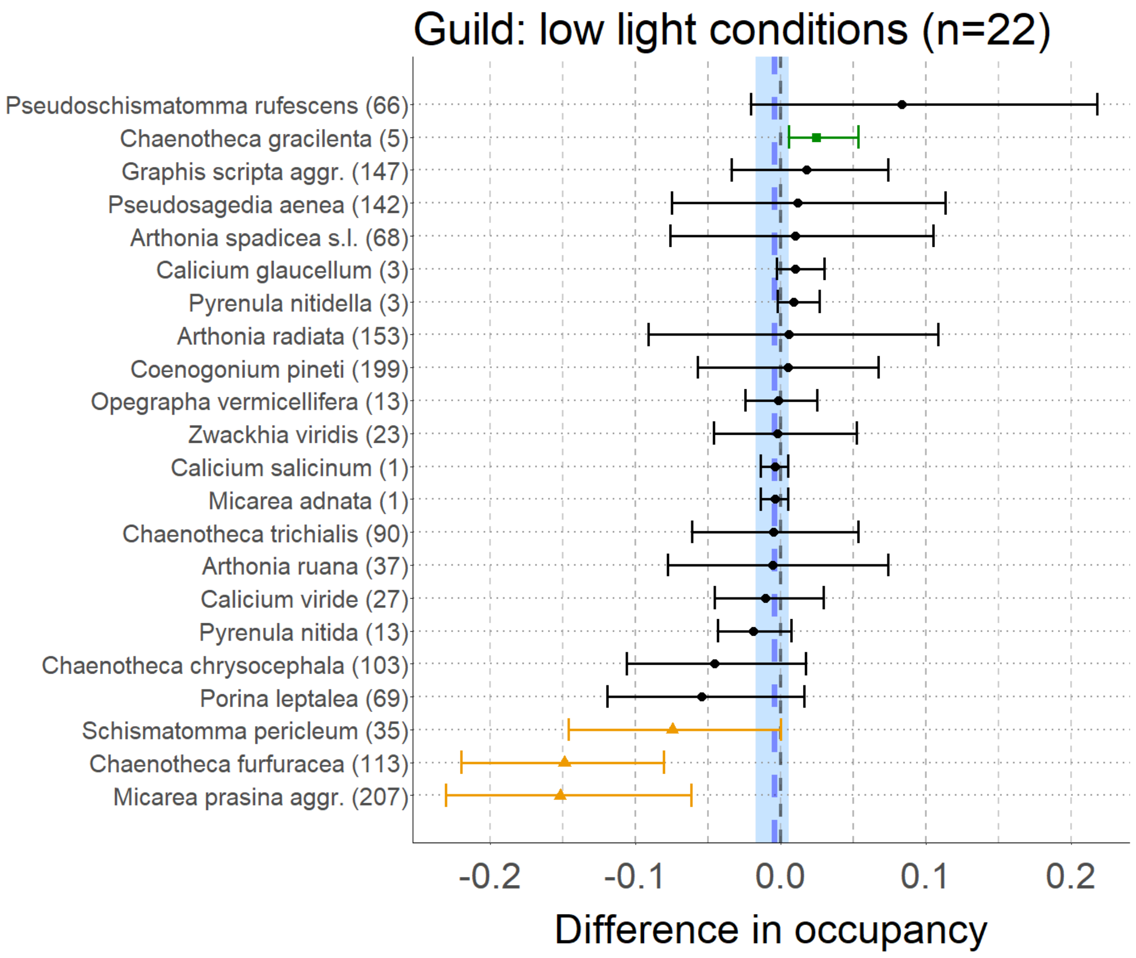

Guild: high continentality (n=55)
Phaeophyscia orbicularis aggr. (115)
Candelaria concolor/pacifica (99)
Melanohalea exasperatula (204)
Rinodina pyrina (47)
Lecania cyrtella aggr. (105)
Physcia aipolia (57)
Physcia adscendens (129)
Physcia tenella (200)
Lecania naegelii (79)
Amandinea punctata (105)
Physconia distorta (33)
Physcia stellaris (82)
Lecidella elaeochroma aggr. (231)
Lecanora hagenii aggr. (125)
Caloplaca alnetorum/pyracea (9)
Melanelixia subargentifera (21)
Lecanora chlarotera s.l. (240)
Ramalina farinacea (34)
Lepra amara (64)
Calicium glaucellum (3)
Cetraria sepincola (2)
Flavopunctelia flaventior (5)
Candelariella antennaria/viae-lacteae (2)
Physconia perisidiosa (12)
Chaenotheca ferruginea (43)
Physconia grisea s.l. (9)
Calicium salicinum (1)
Strangospora pinicola (1)
Evernia prunastri (89)
Rinodina exigua (11)
Lecanora pulicaris (168)
Physconia enteroxantha (3)
Calicium viride (27)
Platismatia glauca (75)
Hypocenomyce scalaris (33)
Placynthiella icmalea (34)
Vulpicida pinastri s.l. (85)
Hypogymnia vittata (7)
Xanthomendoza fulva (8)
Ochrolechia alboflavescens (75)
Chaenotheca chrysocephala (103)
Hypogymnia farinacea (93)
Parmeliopsis hyperopta (82)
Evernia divaricata (81)
Tuckermannopsis chlorophylla (41)
Parmeliopsis ambigua (146)
Pseudevernia furfuracea s.l. (206)
Lepra albescens s.l. (72)
Parmelia saxatilis aggr. (103)
Imshaugia aleurites (64)
Parmelia sulcata (242)
Hypogymnia physodes (225)
Lecanora symmicta aggr. (56)
Lecanora carpinea (140)
Melanelixia glabratula aggr. (231)
-0.2
0.0
0.2
0.4
Difference in occupancy

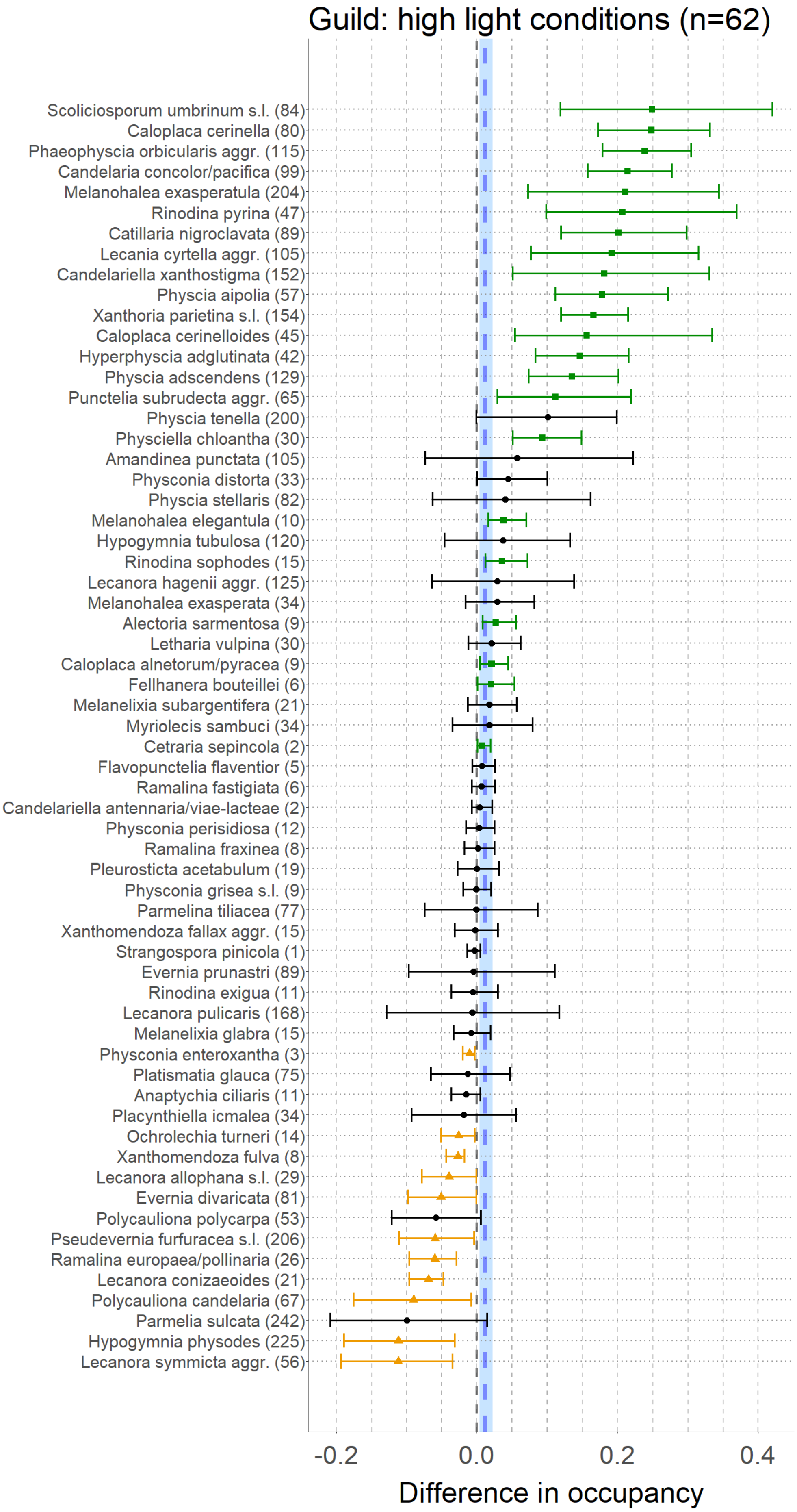

Guild: low precipitation (n=46)
Caloplaca cerinella (80)
Candelaria concolor/pacifica (99)
Melanohalea exasperatula (204)
Catillaria nigroclavata (89)
Lecania cyrtella aggr. (105)
Candelariella xanthostigma (152)
Physcia aipolia (57)
Xanthoria parietina s.l. (154)
Caloplaca cerinelloides (45)
Hyperphyscia adglutinata (42)
Physcia adscendens (129)
Lecanora expallens (22)
Physcia tenella (200)
Physciella chloantha (30)
Lecania naegelii (79)
Amandinea punctata (105)
Physcia stellaris (82)
Phlyctis argena (251)
Hypogymnia tubulosa (120)
Lecidella elaeochroma aggr. (231)
Lecanora hagenii aggr. (125)
Caloplaca alnetorum/pyracea (9)
Lecanora chlarotera s.l. (240)
Myriolecis sambuci (34)
Flavopunctelia flaventior (5)
Candelariella antennaria/viae-lacteae (2)
Chaenotheca ferruginea (43)
Pleurosticta acetabulum (19)
Physconia grisea s.l. (9)
Parmelina tiliacea (77)
Xanthomendoza fallax aggr. (15)
Strangospora pinicola (1)
Rinodina exigua (11)
Lecanora pulicaris (168)
Hypocenomyce scalaris (33)
Placynthiella icmalea (34)
Lecanora allophana s.l. (29)
Polycauliona polycarpa (53)
Scoliciosporum chlorococcum (30)
Lepra albescens s.l. (72)
Lecanora conizaeoides (21)
Imshaugia aleurites (64)
Polycauliona candelaria (67)
Parmelia sulcata (242)
Hypogymnia physodes (225)
Lecanora carpinea (140)
-0.2
0.0
0.2
Difference in occupancy


Guild: high precipitation (n=32)
Rinodina sophodes (15)
Parmelina pastillifera (23)
Alectoria sarmentosa (9)
Letharia vulpina (30)
Nephroma resupinatum (3)
Parmeliella triptophylla (4)
Collema flaccidum (9)
Collema nigrescens aggr. (5)
Thelotrema lepadinum (2)
Menegazzia terebrata (3)
Gyalecta fagicola (5)
Lobaria pulmonaria (1)
Pannaria conoplea (1)
Sticta sylvatica (1)
Ochrolechia pallescens (1)
Loxospora cismonica (1)
Lopadium disciforme (6)
Peltigera collina (4)
Nephroma bellum (2)
Nephroma parile (5)
Melanelixia glabra (15)
Calicium viride (27)
Leptogium saturninum (9)
Parmelia submontana (12)
Biatora beckhausii (9)
Biatora helvola (13)
Caloplaca herbidella aggr. (34)
Vulpicida pinastri s.l. (85)
Hypogymnia vittata (7)
Ochrolechia alboflavescens (75)
Hypogymnia farinacea (93)
Parmeliopsis hyperopta (82)
-0.10
-0.05
0.00
0.05
0.10
Difference in occupancy


Guild: low pH (n=43)
Letharia vulpina (30)
Lepra amara (64)
Calicium glaucellum (3)
Cetraria sepincola (2)
Acolium inquinans (3)
Bactrospora dryina (1)
Chaenotheca ferruginea (43)
Xylopsora caradocensis (4)
Strangospora pinicola (1)
Lopadium disciforme (6)
Evernia prunastri (89)
Lecanora pulicaris (168)
Calicium adspersum (2)
Micarea peliocarpa (39)
Micarea melaena (5)
Cliostomum corrugatum (3)
Calicium viride (27)
Chaenotheca phaeocephala (5)
Platismatia glauca (75)
Loxospora elatina (59)
Hypocenomyce scalaris (33)
Placynthiella icmalea (34)
Vulpicida pinastri s.l. (85)
Hypogymnia vittata (7)
Ochrolechia microstictoides (7)
Chrysothrix candelaris (51)
Ochrolechia alboflavescens (75)
Chaenotheca chrysocephala (103)
Hypogymnia farinacea (93)
Parmeliopsis hyperopta (82)
Evernia divaricata (81)
Tuckermannopsis chlorophylla (41)
Parmeliopsis ambigua (146)
Pseudevernia furfuracea s.l. (206)
Scoliciosporum chlorococcum (30)
Parmelia saxatilis aggr. (103)
Lecanora conizaeoides (21)
Schismatomma pericleum (35)
Imshaugia aleurites (64)
Violella fucata (79)
Hypogymnia physodes (225)
Chaenotheca furfuracea (113)
Melanelixia glabratula aggr. (231)
-0.3
-0.2
-0.1
0.0
0.1
Difference in occupancy


Guild: high pH (n=28)
Caloplaca cerinella (80)
Phaeophyscia orbicularis aggr. (115)
Rinodina pyrina (47)
Catillaria nigroclavata (89)
Lecania cyrtella aggr. (105)
Physcia aipolia (57)
Xanthoria parietina s.l. (154)
Caloplaca cerinelloides (45)
Hyperphyscia adglutinata (42)
Physcia adscendens (129)
Physciella chloantha (30)
Lecania naegelii (79)
Physconia distorta (33)
Lecanora hagenii aggr. (125)
Caloplaca alnetorum/pyracea (9)
Melanelixia subargentifera (21)
Myriolecis sambuci (34)
Bacidia rubella (45)
Candelariella antennaria/viae-lacteae (2)
Collema nigrescens aggr. (5)
Pleurosticta acetabulum (19)
Xanthomendoza fallax aggr. (15)
Sclerophora pallida (1)
Rinodina exigua (11)
Anaptychia ciliaris (11)
Xanthomendoza fulva (8)
Polycauliona polycarpa (53)
Anisomeridium polypori (50)
-0.2
0.0
0.2
0.4
Difference in occupancy


Guild: low light conditions (n=22)
Pseudoschismatomma rufescens (66)
Chaenotheca gracilenta (5)
Graphis scripta aggr. (147)
Pseudosagedia aenea (142)
Arthonia spadicea s.l. (68)
Calicium glaucellum (3)
Pyrenula nitidella (3)
Arthonia radiata (153)
Coenogonium pineti (199)
Opegrapha vermicellifera (13)
Zwackhia viridis (23)
Calicium salicinum (1)
Micarea adnata (1)
Chaenotheca trichialis (90)
Arthonia ruana (37)
Calicium viride (27)
Pyrenula nitida (13)
Chaenotheca chrysocephala (103)
Porina leptalea (69)
Schismatomma pericleum (35)
Chaenotheca furfuracea (113)
Micarea prasina aggr. (207)
-0.2
-0.1
0.0
0.1
0.2
Difference in occupancy


Guild: high light conditions (n=62)

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DISCUSSION

In this dissertation, I studied the detection probability and occurrence of epiphytic lichens in a large dataset that has been collected for the Swiss national Red List. I found in **Chapter 1** that the *mixed* nature of the data, with a subset of the sites visited twice and the rest visited only once, was suitable for occupancy models and that single-visit sites contribute information to the estimation of occupancy and detection probability. In **Chapter 2**, I found that average detection probability of epiphytic lichens on these standardised sampling plots was around 50% for the sampling period 1995–2000, with considerable variation between observers and species. In **Chapter 3**, I corrected for this considerable detection error while comparing the occupancy of epiphytic lichens in that period to a more recent dataset sampled over the period 2018–2022. I found that these changes correlated well with forest management practices as well as environmental pollution and climate change.

This Discussion has several objectives. First, I will present additional analyses on detection probability not reported in **Chapter 3** to emphasize the importance of accounting for it. Second, I will compare occupancy models to pseudo-turnover, a metric often used in plant surveys to estimate reproducibility of results. Third, I will point out weaknesses in my analyses that are due to violations of crucial model assumptions. Fourth, I will give recommendations on how the Swiss Red List sampling of lichens could be improved. I then venture to extend to more general recommendations for surveys of plants and fungi. Fifth, I describe how the ecological findings from this thesis will be useful when applying IUCN criteria for the upcoming national Red List assessment. And sixth and last, I will shortly outline possible lines of research for the future.

Imperfect detection of lichens

In the analysis of the dataset from the first Red List (sampling period 1995–2000) in **Chapter 2**, we found an average detection probability across all species and observers of 49%. The same dataset was also analysed in **Chapter 3**, with a slightly adjusted species list that would match the taxa recorded during the sampling period for the second Red List (2018–2022). Although the two-season model from **Chapter 3** was slightly more complex and did not share all covariates with the single-season model in **Chapter 2**, the resulting estimates of detection probability were generally similar. There were, however, a few noteworthy differences and additional aspects which I will shortly present here.

Multiple observers

The first difference is that 57 surveys during the recent sampling period were conducted by two or sometimes more observers simultaneously. Expecting a positive effect from the presence of additional observers, I included a covariate in the detectability part of the occupancy model in **Chapter 3** that indicated the presence (1) or absence (0) of multiple observers. Fig. 1 describes the effect of three detection covariates — observer experience, presence of multiple observers, and species conspicuousness — on detection probability, contrasted with the intercept. The regression coefficient of multiple observers was similar to the coefficient for conspicuousness and much stronger than the experience of the main observer. The effect of experience was smaller than what we had found in **Chapter 2**, while the effect of conspicuousness was largely unaltered.

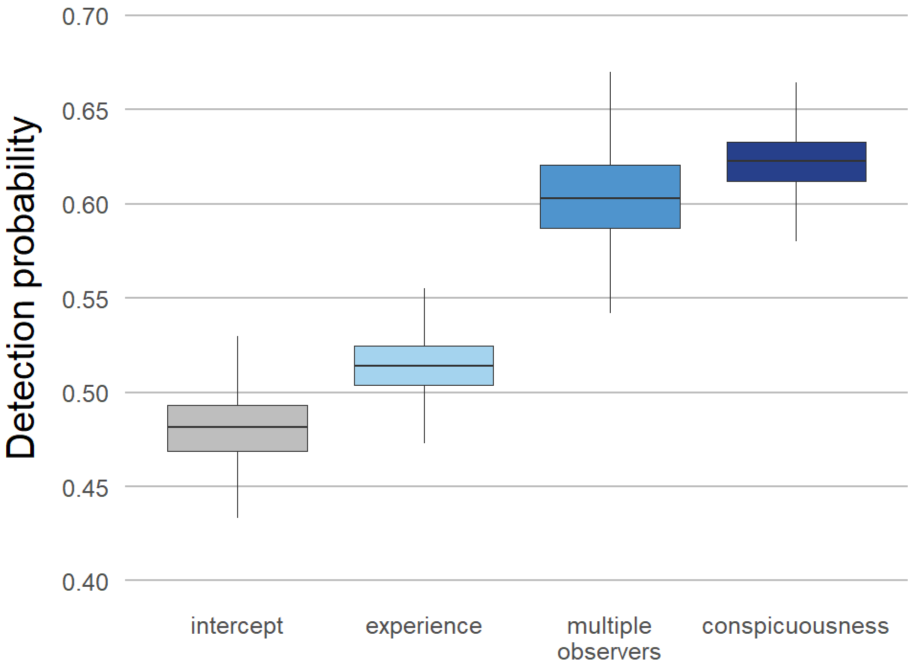

Fig. 1 Detectability-related parameters as estimated on the probability scale. The intercept represents the case when a survey is conducted by one person alone who has no previous experience and when the species is inconspicuous. The intercept is averaged across all observers. The three other boxplots are calculated as the intercept + the regression coefficient of the respective covariate.

Differences between observers

In **Chapter 2**, posterior point estimates suggested that observer-specific detectabilities varied between 0.33 and 0.72, a difference of a factor of two. The observer-specific detectabilities estimated in **Chapter 3** (see its Supplementary materials) suggest a range between 0.20 and 0.78, a difference of nearly a factor of four (Fig. 2). The difference appears even greater when considering that these estimates are corrected for variation in the number of species people had already recorded (what we called *experience*) and that no observer began the fieldwork without any prior lichen surveys.

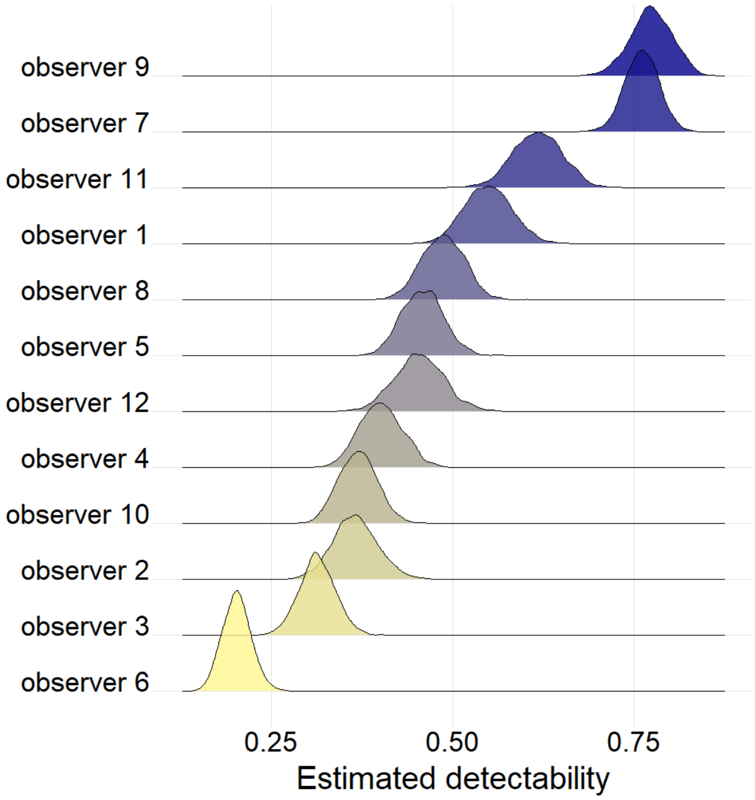

Fig. 2 Posterior densities of observer-specific detection probabilities as estimated in **Chapter 3**. These estimates are intercepts, i.e., they represent the basic detectability of a single observer for an inconspicuous species (conspicuousness = 0) that they have not encountered before (experience = 0).

The variable experience, which we found to be an important covariate in **Chapter 2** and **Chapter 3**, was modelled as observer- and species-specific indicator (0 if the observer had never recorded the species prior to the survey, 1 if they had). That means that its positive effect represents the increased chance that an observer will find those species again which they have previously reported. Accumulated experience with other lichen species, on the other hand, was not explicitly accounted for in any model. It is possible, or even likely, that more experienced observers (i.e., who have seen more species overall) may generally have a higher detection probability. With twelve observers, our sample size is rather small to test for such an effect statistically, but I can explore the results qualitatively. Fig. 3 shows the observer-specific detectability estimates (identical to those in Fig. 2) plotted against the number of species the observer had recorded until the middle of the sampling period in which they participated. The positive slope of the added regression line suggests that experience could indeed have positive effects on detection probability which are not accounted for by the covariate. It is highly probable that people who have surveyed lichens for longer — and who are therefore likely to have seen many more species — may have "developed an eye" for lichens in general, allowing them to more easily detect all species, even those they have never seen before.

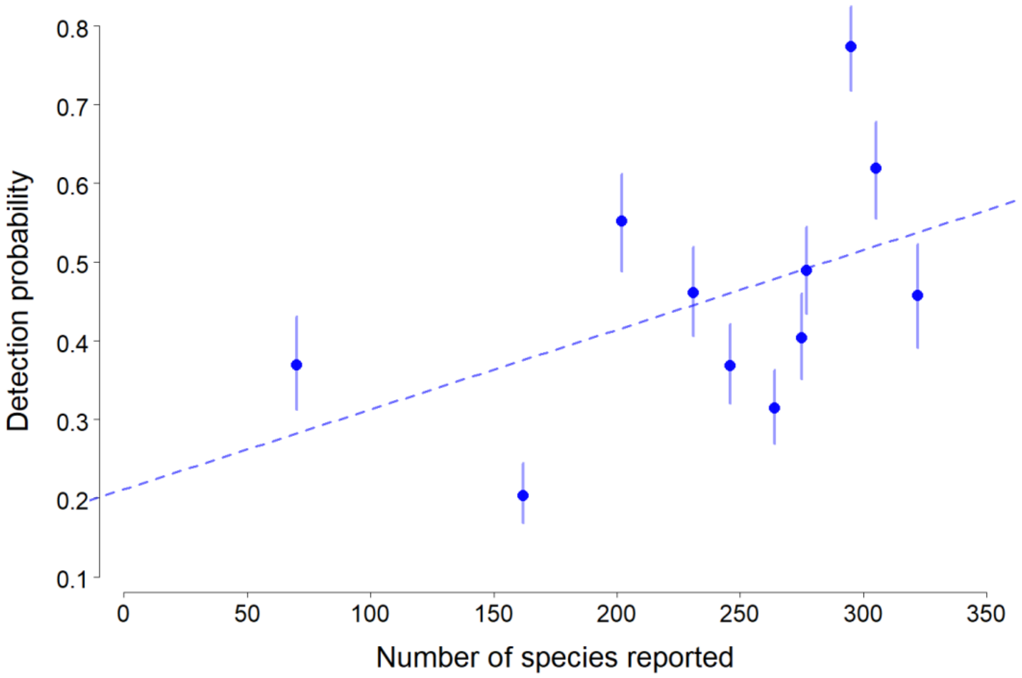

Fig. 3 Observer-specific detection probabilities in relation to their experience. Experience is here measured as the number of species the person had reported to the database prior to the third year of the respective survey, i.e., the cut-off is 1997 for observers participating in the first sampling period, and 2020 for observers participating in the second sampling period. Vertical bars represent the 95% credible interval of the detection estimate. The dashed line describes the slope of a linear regression line fitted through the points.

It is also evident from this figure that experience (at least when measured as the number of species previously recorded) not nearly explains all variation in detection probability. Observers of abundant experience and observers of little experience can have a detectability that may lie either above or below what would be predicted based on their experience. Collecting habits, diligence of surveying, allocation of time, or even vision could be factors that determine an observer's detection probability. As these variables and potential interactions among them are difficult to measure accurately, it will hardly be possible to avoid the necessity to account for observer identity in the form of a random or fixed effect. By doing so, I believe that indirect effects of experience are adequately modelled.

Variation over time

In the Introduction, I enumerated the consequences of ignoring imperfect detection in static species distribution models. An additional problem arises when dealing with monitoring data over time. If detection probability changes over time, its effects may blur potential changes in the population (Archaux et al., 2012; Kendall et al., 1996), at least if the two are not estimated separately. Changes in detection probability may be caused my many factors, such as a different set of observers, a different sampling strategy, changes in vegetation structure that may make it more difficult to detect species, or changes in abundance of a species. Due to the limited number of repeated visits in the lichen datasets, I was not able to account for spatial heterogeneity in detection probability that may be due to vegetation structure or local abundance. It was a fact, however, that the set of observers differed between the two sampling periods and that the sampling strategy was not identical. Six people were involved in the sampling for the first Red List (1995–2000), five people in the sampling for the current Red List (2018–2022). Only two people participated in both. During the first Red List, observers collected a list of lichen species *per substrate* — normally resulting in several species lists per plot — while there was only a species list *per plot* during the second Red List. Fig. 4 illustrates the difference in detection probability between the two Red List teams, considering their accumulated experience at the end of the respective sampling period. The first Red List team had an average detectability of 50%, the second Red List team an average detectability of 45%. Although their posterior distributions overlap, the posterior distribution of their difference leaves little doubt that detection probability was

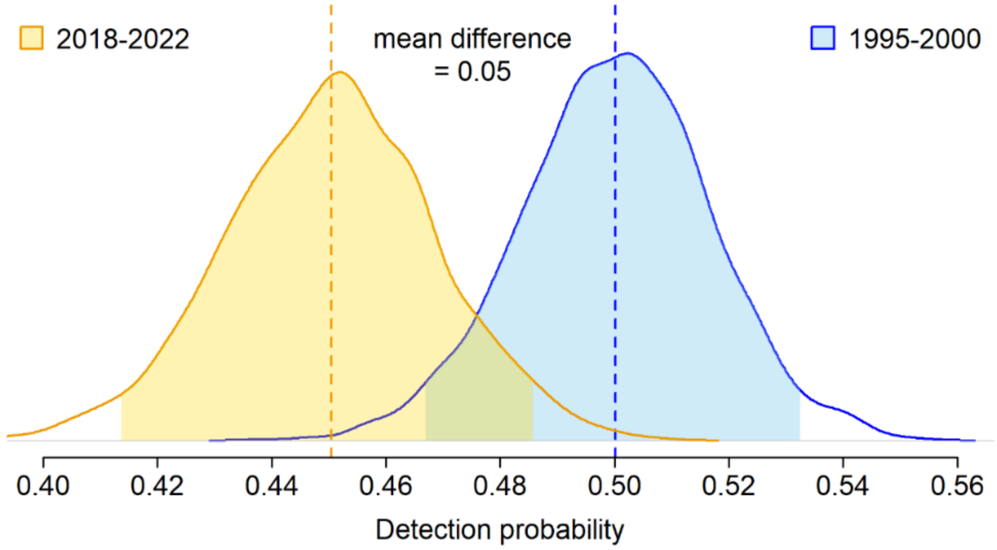

Fig. 4 Average detection probability for the two Red List teams. The team for the sampling period 2018–2022 consisted of five observers who conducted regular and repeated visits with the same protocol (orange). For the sampling period 1995–2000 only the six observers who conducted the regular first visits are included for their team average (blue), because the repeated visits in that period were conducted with a different sampling protocol.

different between the two sampling teams: the probability that the first team had a higher detectability than the second is 99.9%. It is likely that the difference was primarily caused by the change in sampling strategy, but I cannot rule out any effect of the set of observers.

Consequences of ignoring imperfect detection

It is difficult to know the magnitude of the bias caused by imperfect detection until it is accounted for and estimates can be compared to observations. In **Chapter 2**, I described the consequences of imperfect detection on estimates of species frequency by contrasting the estimated with the observed number of occupied sites. I now want to shortly compare the estimates from the dynamic context in **Chapter 3** with *summaries* of the observed data that ignore detection probability. We were interested in the dynamics of occupancy and had to estimate detection probability separately for each sampling period to account for potential changes in detectability. As described above, there was indeed a difference between the two sampling periods. The difference was not large (5%), but Archaux et al. (2012) found that even differences like these would greatly increase the risk of drawing erroneous conclusions about population changes. Fig. 5 illustrates where summaries of guild-specific occupancy

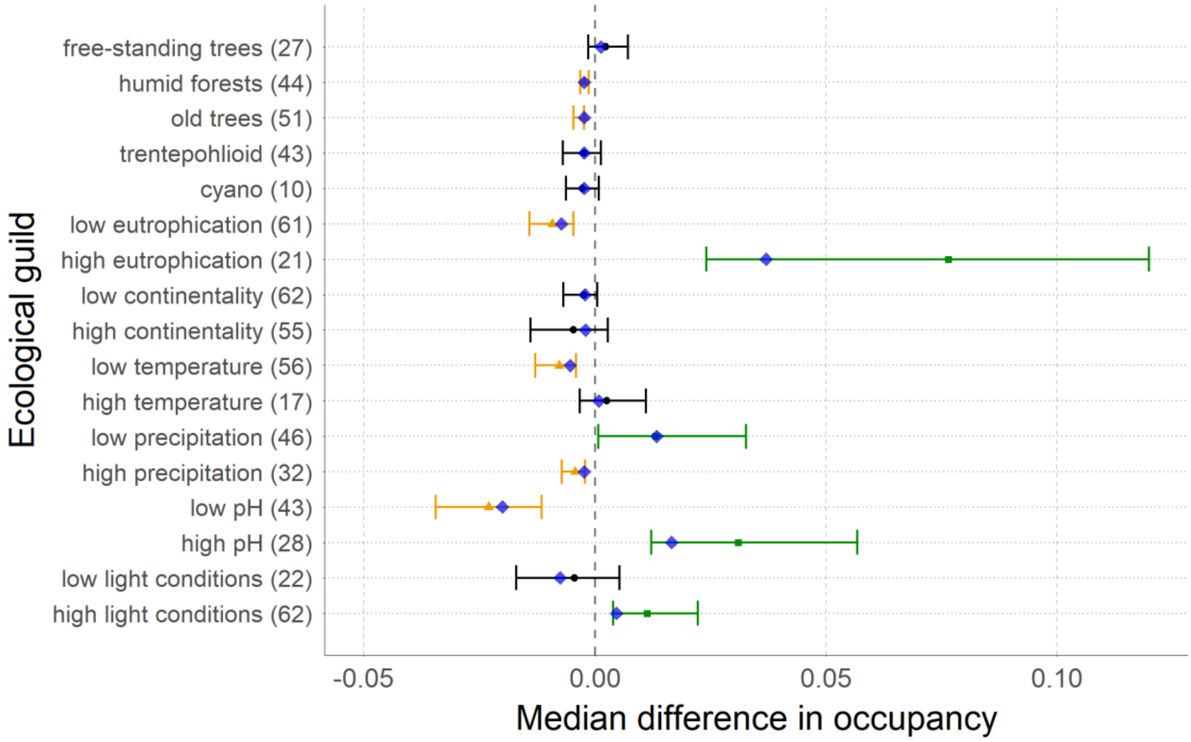

Fig. 5 Estimated and observed population trends over time. This figure is a copy of Fig. 2 in **Chapter 3** with guild-specific estimates and 95% credible intervals (CRI). It here includes the observed changes as given by the summary of the raw “presence/absence” data from the first visits (blue diamonds). As these values are directly taken from the observed data without correcting for detection probability, there is no uncertainty around them. All observed values fall within the CRI of the estimated changes.

changes are when detection probability is ignored. As detection-ignorant values do not have any observational uncertainty, there are no credible intervals around these. The background figure is identical with figure 2 of **Chapter 3** to provide a comparison with detection-corrected estimates. The general pattern is the same as in the detection-corrected figure in **Chapter 3**: the same guilds show strong changes, and the minor differences are found mostly in the guilds with weak changes. From an ecological standpoint, the conclusions I drew in **Chapter 3** would therefore qualitatively have been the same even if I had not accounted for imperfect detection. It would, however, have been impossible to know the degree of certainty with which these changes were estimated.

Estimates of change over time at the species level were less robust to ignoring imperfect detection than guild-based estimates. For 10 % of all species (n=32), the observed change fell outside the 95% credible interval of the estimated change (Fig. 6 A). Although detection probability alone cannot explain all the difference between estimated and observed change, the direction and magnitude of the difference is at least correlated with differences in detection probability between the two sampling periods for these 32 cases (Fig. 6 B). For the species *Rinodina pyrina* and *Anisomeridium polypori*, for

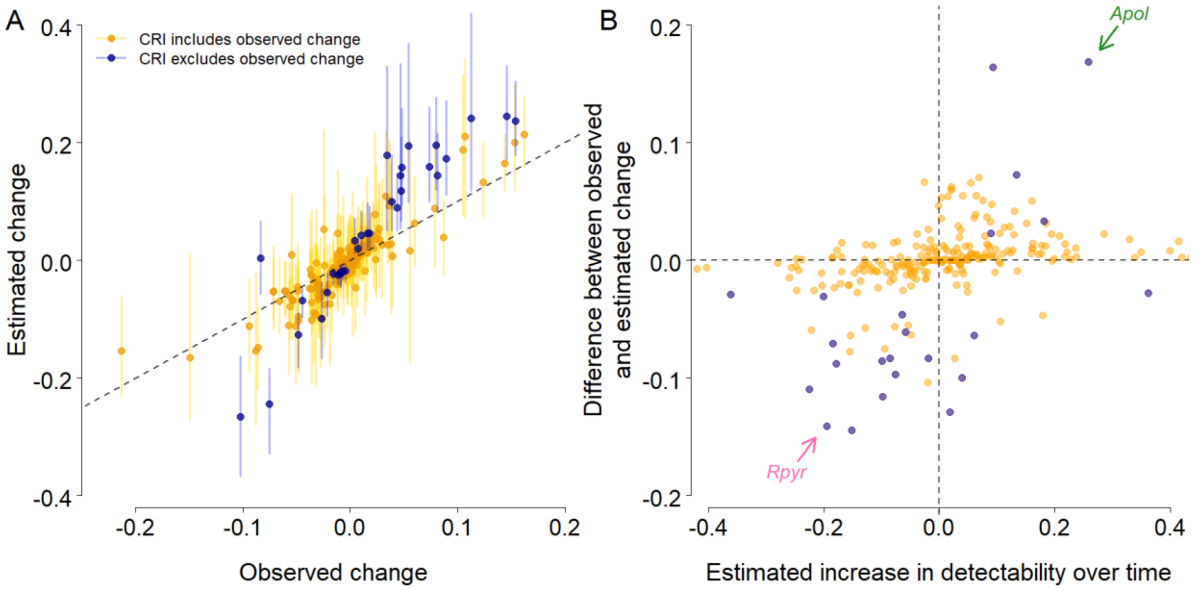

Fig. 6 Differences between estimated and observed changes in species-specific occupancy over time and their relation to detectability. The estimated change in occupancy between 1995–2000 and 2018–2022 is illustrated with its 95% credible interval (CRI) and plotted against the observed change, i.e., the raw "presence/absence" of the first visits (A). Orange indicates that the observed change falls into the CRI of the estimated change, blue indicates that it falls outside the CRI. The difference between observed and estimated change is then plotted against the change in detection probability estimated by the model (B). Arrows indicate the position of two example species: *Rinodina pyrina* (pink) and *Anisomeridium polypori* (green). For these 32 extreme cases where the estimated change varies significantly from the observed change, the difference tends to be correlated to changes in detectability.

example, ignoring the remarkable change in their detection probability over time would have led to different conclusions regarding their population change.

Pseudo-turnover vs. occupancy models

Pseudo-turnover

Turnover describes a change in species composition over time (or across space). For example, a site has experienced a turnover of 20% from one point in time to the next when 80% of the community has remained the same. *Pseudo-turnover* then describes a difference in species lists obtained from the same community which looks like a turnover, but which is due to sampling error and not actual changes in species composition. The error is also called *observer error*, because the species lists often come from surveys of the same community by different people, so close in time that the community cannot have changed between the surveys. The concept of pseudo-turnover was first suggested by Nilsson and Nilsson (1985). The formula to calculate pseudo-turnover *PT* for two surveys is:

$$PT = \frac{b + c}{2a + b + c}$$

where *a* is the number of species that were detected by both observers, *b* is the number of species detected only by the first observer, and *c* is the number of species detected only by the second observer. In other words, pseudo-turnover describes the proportion of species that were overlooked by either of the two observers in relation to all detected species. This definition already points at one weakness of pseudo-turnover: it is estimated with respect to *all detected species* and thus ignores the fact that some species may be missed by both observers.

Pseudo-turnover has been used a lot in plant sureys and monitoring programs of vegetation to assess sampling error and reproducibility of results (e.g., Boch et al., 2022; Burg et al., 2015; Futschik et al., 2020; Kapfer et al., 2016; Morrison, 2016; Traub & Wüest, 2020). The use of pseudo-turnover may have its justification for general comparisons between observers or sampling conditions. However, when compared to the flexibility of occupancy models and their ability to not only estimate but actually *account for* sampling errors, I find the usefulness of pseudo-turnover to be rather limited.

An occupancy model can estimate anything from site-specific occupancy per species, effects of environmental covariates on the occurrence of different species, species richness per site to ecological indicator values averaged per site. And all these estimates are corrected for detection probability and have an associated uncertainty. The model can equally output estimates of detection probability per observer, per species, or with respect to different sampling conditions (date, local abundance, etc.).

Detectability-corrected estimates can also be made for sites without repeated visit and, as I showed in **Chapter 1**, these sites even provide additional information to the estimation of detection probability, in contrast to analyses of pseudo-turnover. The following questions can therefore easily and directly be answered with one analysis:

- How many occurrences are there of each species? (corrected for imperfect detection)
- What is the average species richness per site? (corrected for imperfect detection)
- Have average ecological indicator values changed over time? (corrected for imperfect detection)
- Does detection probability vary with ecological indicator values?
- In which month is a species most easily detected?
- Which species are missed most often?
- Has average detection probability changed over time?
- Which observers could benefit from further training?

When abundance of species is collected in some form or other, there are even more ways to account for detection probability. Counts of individuals (independent of the definition of an individual) can be analysed with binomial *N*-mixture models (Royle, 2004; Royle & Nichols, 2003) and cover estimates in ordinal cover classes can be analysed with a recently proposed ordinal zero-augmented beta model (Irvine et al., 2019). These models sound complicated, but they follow the same hierarchical logic as occupancy models do.

My last argument in favour of occupancy models is perhaps a little anecdotal. A vegetation ecologist once told me that they were unhappy about a few individual observers, because these were so incredibly thorough and would find many more species than the others. Such exceptionally good observers represented outliers compared to the average and caused noise in parameter estimates, because they did not have the same sampling error. It struck me as absurd that it should be a disadvantage to have such diligent people *because they committed fewer errors than the average person*. This “problem” could be avoided with an adequately parameterised occupancy model. By describing differences between observers with a fixed effect, an occupancy model allows observer detectabilities to vary independently of other observers. An exceptionally good observer would then be estimated to have a higher detection probability than the others, and there would be no problem with this “outlier” — quite the opposite in fact. As the presence of a species in an occupancy model can also only be 100% unambiguous where it was actually observed, an exceptionally good observer contributes comparatively more information to parameter estimation than a less gifted observer.

Any dataset that is suitable for analysis of pseudo-turnover is also perfectly suitable to be analysed with a multi-species occupancy model (Dorazio & Royle, 2005). When the goal is to compare community changes over time, a dynamic multi-species occupancy model (Dorazio et al., 2010) would be an elegant option compared to estimating pseudo-turnover for each time point separately. It would be interesting to repeat one of the pseudo-turnover assessments with an occupancy model and see 1) whether the conclusions with respect to sampling error would be the same, 2) what additional insights could be gained from an occupancy model on detectability differences between observers, species or sampling conditions, and 3) whether the ecological conclusions (trends over time, ecological indicator values, etc.) would be the same.

A (conditional) ode to multi-species occupancy models

As the name suggests, multi-species occupancy models (MSOMs) are occupancy models that are fitted to data from multiple species (Dorazio & Royle, 2005; Chapter 11 in Kéry & Royle, 2016; Chapter 15 in MacKenzie et al., 2018). These powerful models can be used to estimate species richness of different communities, infer habitat effects on the organism group assessed, or estimate species-specific distribution patterns, all while accounting for imperfect detection. In **Chapter 2**, I used an MSOM to estimate the effect of sampling covariates (observer experience, species conspicuousness, etc.) on epiphytic lichens in general, and to find out how much the detection probability of single species can vary between different observers. This analysis would have been impossible without an MSOM. In **Chapter 3**, I used an MSOM to assess changes over time as they were experienced by different ecological guilds of species. While such an analysis could have been done with a generalized linear model, I believe it would have been less accurate, more precise than it should be (because it would have ignored observational uncertainty), and, admittedly, less fun.

There are two approaches to including multiple species in an MSOM. The first approach models species with a fixed factor for each model parameter, so that species-specific parameters are independent of each other (p. 662–667 in Kéry & Royle, 2016). The resulting model is equivalent to stacking multiple single-species models on top of each other. Independence between species implies a large number of parameters, which means that the model is rather *data-hungry* and requires a minimum number of observations per species to inform parameter estimates, as is the case for single-species models. The second approach is to model species-specific parameters as coming from a distribution that is shared among species but with a random effect for the individual species (p. 667–682 in Kéry & Royle, 2016). With this approach, the estimates for one species are no longer independent of the estimates for other species. The advantage is that species with very few (or even zero) observations can be included, and the model is still able to make species-specific estimates with reasonable certainty by *borrowing* *strength* from other species (Dorazio & Royle, 2005; MacKenzie et al., 2005; Ovaskainen & Soininen, 2011). The downside is that their estimates — and all species' estimates to some extent — are drawn towards the mean across all species rather than being informed by the (very scarce) information that was available for the rare species themselves, making species more similar to each other than they really are, an effect called *shrinkage* (Royle & Link, 2002; Xu et al., 2012).

In **Chapter 2** and **Chapter 3**, I used the second approach to describe variation between species. Fitting a random effect for species enabled me to include all species in the data for which there was at least one detection from a sampling site. Had I defined fixed effects for the different species, I would probably have had to exclude species with less than ten, or maybe even twenty detections. In community data like these, where most species are rare, that would have meant the exclusion of up to 60% of the species (Fig. 7), a considerable loss especially to the analysis in **Chapter 3**. Estimates of occupancy dynamics for extremely rare species (one or two detections) could not be made with great certainty and were likely shrunk towards the common mean. Nevertheless, the model's estimates of population change for species with three and more observations generally agreed well with the perception of some of my Red List colleagues, who have twenty years of experience with lichen surveys in Switzerland. I also tried to reduce shrinkage in **Chapter 3** by defining the random effect with a *t*-distribution with 4 degrees of freedom instead of a normal distribution. This *t*-distribution has longer tails than a normal distribution and therefore allows a greater number of species to have extreme values in comparison to the rest.

As I found in **Chapter 1**, the occupancy model (multi-species or not) also allowed the inclusion and use of all sampling sites, even if the majority only had a single visit for each sampling period. Instead of the 416 sites I analysed in **Chapter 2**, the sample size would otherwise have been 46, and much less representative of the full sample. The sample size in **Chapter 3** would have been reduced from 446 to 63 (see Table 1 in **Chapter 3**).

Writing and fitting MSOMs in JAGS (Plummer, 2003) and nimble (de Valpine et al., 2017) offered additional freedom in the specification of parameters. Although this freedom is not limited to MSOMs or even occupancy models, JAGS and nimble allowed the specification of a random species effect with independent means and standard deviation per observer in **Chapter 2**, which would not have been possible with software with pre-defined functions like the R packages unmarked (Fiske & Chandler, 2011), ubms (Kellner et al., 2022), or spOccupancy (Doser et al., 2022a).

Throughout this thesis, I have also stumbled across some caveats of MSOMs. The first is my impression that the models in **Chapter 2** and **Chapter 3** slightly overestimated the species richness for sites with few detected species. As I discussed in the Supplementary Materials of **Chapter 2** (Appendix 3), I believe that this potential bias can be attributed to the limited number of covariates in the occupancy part of the model. The general scarcity of data — only around 40% of species had more than 20 occurrences (Fig. 7) — did not allow the inclusion of all the environmental variables that would have been desirable and important as covariates to occupancy. I had to be particularly restrictive with categorical covariates, because any additional parameter required a random effect for species, and every additional random effect substantially slowed down the model.

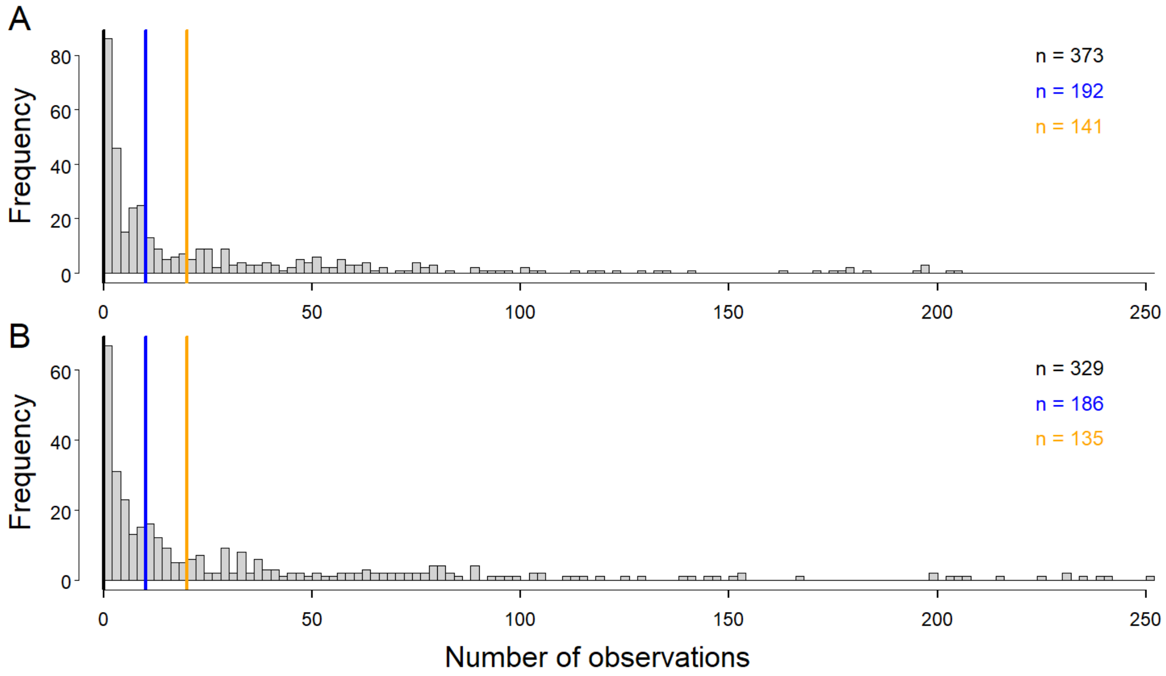

Fig. 7 Frequency distribution of the number of observations per species. An observation is here defined as a site with at least one detection of the species for the dataset presented in **Chapter 2** (A) and the dataset presented in **Chapter 3** (B). The legend counts the number of species that would be included for different thresholds in the minimum number of observations would be used. The use of a multi-species occupancy model with random species effects allowed the use of a threshold of ≥ 1 (black). To fit a model with fixed species effects, a much higher threshold would have been necessary to guarantee the identifiability of species-specific parameters. With the realistic thresholds of ≥ 10 (blue) or ≥ 20 (orange), the sample sizes would have been considerably smaller.

The second major problem I was not able to solve and that is inherent to MSOMs was how to deal with sampling effort. Species richness being constant, detection probability is likely to increase with sampling effort (Chen et al., 2009; Garrard et al., 2008; Moore et al., 2014). The only proxy for sampling effort in the lichen data was the time spent on each survey. However, as there was neither a minimum nor a maximum time restriction per survey, the time spent at a site seemed rather the *result* of the detected species richness than the *cause* of it. To know how sampling effort could be incorporated into an MSOM, an extensive simulation study would be necessary, which unfortunately exceeded the scope of this dissertation. I did, however, attempt a small-scale simulation study to find an indication of the correct treatment. The results were rather sobering: If longer survey time indeed increased detection probability per species, model estimates would be biased, whether survey time was added as a covariate to detection probability or not. When survey time was included as a covariate, its effect would seem highly significant, because detection success (i.e., number of detected species) obviously correlated strongly with survey time. The model then estimated that it was the short survey time that had led to some sites having very few detected species, while in reality, these sites may just have been extremely poor in substrate and lichens. In fact, the observer may even have been able to search the available substrate very thoroughly in the short time. In other words, including survey time as covariate would have aggravated the bias I described in the previous section, i.e., overestimate species richness on sites with few detected species. On the other hand, ignoring survey time when it did affect detection probability also resulted in a bias, but in the opposite direction. The few repeated visits did not indicate how the direction of the relationship between survey time and detection probability may change under different levels of species richness. As my simulations suggested a much greater bias when I included survey time than when I did not, I chose the latter option. One day there will hopefully be a fully-fledged simulation (or empiric) study that finds a solution to this problem.

To summarize my praise, I see the greatest value of (multi-species) occupancy models in their ability to 1) directly account for imperfect detection in estimates of species frequency and species richness, 2) output parameter estimates at any level of interest such as species, observer, site, habitat type, or survey, 3) use data of all species, incl. rare ones, and 4) harness the information from data in a mixed format where only a subset of all sites contains repeated visits. Some challenges remain for future statisticians and/or ecologists to solve, namely, how to include sampling effort (e.g., survey time) into the model, or how to counteract the model's tendency to overestimate the number of species on sites where very few species were observed and, supposedly, very few species were present.

Potentially violated assumptions

Assumptions are unavoidable when fitting statistical models to data and, often, additional assumptions are made when interpreting the results. In the previous section, I already mentioned the potentially violated assumption that detection probability per species was independent of survey time and that it was constant across sites of different levels of species richness. I also described the possible consequences of its violation and that the resulting bias depended on the direction of the ignored correlation. There are three other assumptions I suspect, or even know, to have been violated to some extent: Population closure between the first and the repeated visit, availability of all species for detection, and the absence of false-positive sampling errors.

Population closure

Population closure is one of the most important assumptions of occupancy models (MacKenzie et al., 2002; Tyre et al., 2003). Closure means that the population at a site does not change between what Pollock (1982) terms the *secondary sampling occasions* (i.e., repeated visits) that occur within the same *primary sampling period* (in **Chapter 3**, the two primary sampling periods were 1995–2000 and 2018–2022). When occupancy Ψ is the variable of interest, there are two ways in which a violation of this assumption can affect the estimates. The first one occurs if the occupancy status changes between visits. For example, when the first observer detects a species and the species then disappears from the site before the second visit is made, the second observer has nothing to detect, and the detection history will be [1 0]. The occupancy model infers the presence of the species from the first detection and concludes that the second observer missed it. This false attribution of the zero in the detection history to detection error leads to an underestimation of the true detection probability and thus an overestimation of occupancy (Rota et al., 2009).

The second way in which a violation of the closure assumption can affect estimates is more subtle and relates to changes in abundance and not the occupancy status *per se*. The status of an occupied site is unchanged as long as there is at least one individual of the species present. Unfortunately, however, detection probability is not. The probability of detecting a site as occupied p is related to abundance in the following way:

$$p = 1 - (1 - \theta)^N,$$

where θ is the detection probability *per individual* and N is the number of individuals (Bayley & Peterson, 2001). The term $(1 - \theta)^N$ describes the probability of not finding a single one of the N individuals present, which is equivalent to a failure to detect the occupied status of the site. One minus this term is then the opposite, i.e., the probability of correctly detecting a site as occupied. It is clear from this relationship that p not only depends on θ but also on N. Fig. 8 illustrates this relationship for three levels of θ. For any given θ, p is most sensitive to changes in abundance when abundance is low. If the closure assumption is violated and the number of individuals (but not the occupancy status of the site) varies between repeated visits, detection probability is going to vary accordingly. This relationship holds, independent of the definition of an individual. Whether an individual is considered

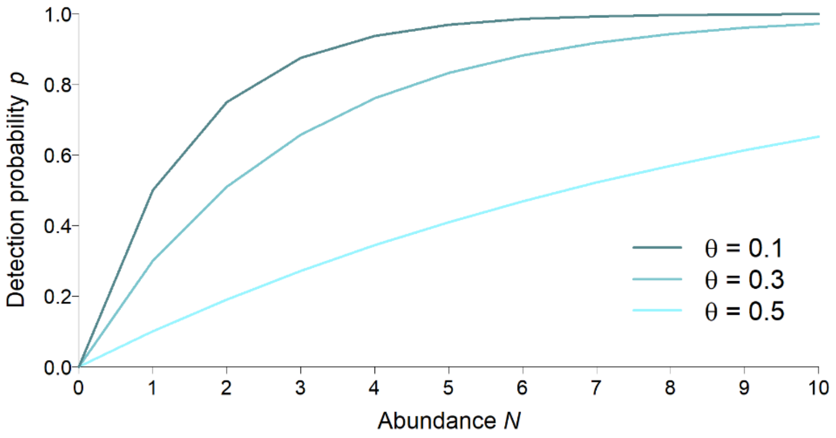

Fig. 8 Relationship between detection probability *p* and abundance *N*. When *θ* is the per-individual detection probability of a species at a site, the site-specific detection probability *p* will depend on the number of individuals *N* at the site. A change in *N* between repeated visits will therefore affect the sampling conditions.

a genetically unique unit, a functional unit (Scheidegger & Goward, 2002), or some measure of spatial cover: when there is more of a species at a site, it is more likely that its presence will be noticed.

I assumed population closure in all chapters for this thesis and it is likely that this assumption was not always fulfilled in the two lichenological studies. In **Chapter 2**, the time that elapsed between the first and the repeated visit never exceeded one year. In **Chapter 3**, however, the time gap ranged from a few weeks to four years. It was impossible to do otherwise, because many sites had already been surveyed for 2–3 years when we obtained the money to conduct repeated surveys. At the time, we believed that populations (or at least occupancy) were very unlikely to change, even over a period of four years. There are now several reasons for being less convinced of this stability. When going out to conduct the repeated visits for the recent sampling period (2018–2022), we realized that many alterations can happen to a site which are not due to the “natural lichenological speed” of colonizing, growing, or going locally extinct.

Tree harvest

There were seven sites (of 46) on which at least one, and sometimes several, trees had been cut and carried away by foresters between the first and the repeated visit. Any lichen species that sat exclusively on these trees must necessarily have changed occupancy status between the visits. If a species grew on both the removed trees and others at the site, the removal of some thalli must at least have reduced the local abundance of the species, lowering the chance to detect it in the way described above. My possibilities to account for such changes without discarding all data from the repeated visit were limited. Luckily, I knew which tree/s had been removed by forest management and I also knew which lichen species had been detected on which trees in the first visit. Given that forestry-related changes always reduce the chances and never increase them, I manipulated the observed data from the second survey as follows: If a species was detected *only* in the first visit — detection history [1 0] — and *only on trees that were removed*, I replaced the 0 in the data from the second visit with NA to represent the uncertainty that the observer *may* have detected the species if it had still be present on the site. If, however, a species was detected only during the second visit, I kept the detection history [0 1], assuming that the species was present already during the first visit and was simply missed. I also did not change anything if a species was detected in both visits, independent of the tree, assuming that the species (also) grew on trees that were not removed. By introducing these NAs, I hoped to avoid the negative bias in the second observer's detection estimate that would be due to a change in occupancy.

Branches on the ground

The pure chance of a recently fallen branch with readily identifiable lichens may also have altered the conditions between the first and the repeated survey. In contrast to forestry-related removal of trees, which always disadvantaged the second observer, a recent branch fall may have been to the advantage of either observer. Unfortunately, I could not account for such chance events. At least in the recent sampling period (2018–2022), we freely searched all substrate available, incl. branches that had fallen to the ground, and noted the species on the first substrate we found it on. In fact, fallen branches were particularly yielding, because they often offered more nicely developed thalli of species like *Physcia* sp. and *Phaeophyscia* sp. than could be found on the trunks of trees. Excluding or replacing these numerous detections from fallen branches was not a promising approach here, because the number of excluded or replaced detections/non-detections would have been very large in comparison to the effect of fallen branches.

Natural colonization and extinction processes

We assumed that no lichen species would colonize a site and grow to identifiable size between repeated visits, and that no species disappeared of a natural cause (not due to forestry or chance). This assumption may be correct for some species and sites in stable environmental conditions — e.g., in the middle of a forest — but I suspect that it may be violated in forest gaps and open areas and particularly by species that grow on young trees, like *Arthonia radiata* or *Graphis scripta* aggr., or by species colonizing new branches like *Physcia* sp., *Caloplaca cerinella/cerinelloides*, or *Candelaria concolor*. Sillett *et al.* (2000) found that 17 lichen genera had colonized previously sterilized branches after four years in a fir stand in Northwestern USA, and Caruso *et al.* (2010) observed numerous colonization events of lignicolous lichens in a boreal forest in Sweden after three years. There is no reason why colonization rates should be smaller here.

Collecting for identification

The last but possibly not least alteration of the local community may have been caused by ourselves. Many lichen species cannot be identified in the field and were therefore collected for later identification. Not collecting specimens would have meant that we would have to work with parataxonomic units instead of species (e.g., Casanovas et al., 2014), but parataxonomic units have little value for national Red Lists. Although we never purposefully collected large specimens where little was available, our sampling must have deprived the site of some thalli, thus reducing their local abundance. I even believe that we may unknowingly have collected the last thallus of some species that were growing at some site, actually altering their occupancy state.

It is impossible to know the exact extent of each of these effects on occupancy. Rota et al. (2009) and Kendall et al. (2013) have developed methods to test whether the closure assumption is fulfilled. Unfortunately, however, their methods were designed for single-species occupancy models and have greatest power when colonization and extinction rates are large, detection probability high, and there are more than two repeated visits, which is not the case here. I can therefore only draw a qualitative conclusion: any unwanted changes in occupancy and local abundance between our repeated visits may have resulted in an underestimation of detection probability and thus an overestimation of occupancy. I did not find a pervasive difference in detectability between the first and the repeated visits, which gives me reason to hope that the bias introduced by the violation of the closure assumption is of limited magnitude.

Entire community available for detection

When the standardised data from the sampling period 1995–2000 were interpreted for the first national Red List assessment, perfect detection was assumed, i.e., a species was considered present on a site where it was detected and absent from sites where it was not detected (Scheidegger et al., 2002). Although we no longer make this assumption and instead correct for missed detections, we now assume that all species are available for detection during the field survey. It is evident from earlier studies, however, that some lichens grow higher up in the tree than two meters from the ground (Boch et al., 2013; Fritz, 2009; Kiebacher et al., 2016; Marmor et al., 2013). These species will consequently be missed with our standard sampling method. The proportion of individuals that is unavailable for detection depends on the lichen species, the tree species and the habitat type, which governs the quantity of light that is available to the stem and crown. Some lichens show a clear preference for positions higher in the tree (Fritz, 2009; Kiebacher et al., 2016; Marmor et al., 2013), making these species particularly prone to be missed during our survey. Others just occasionally occur above two meters and the unavailability of some individuals would simply reduce their probability of detection by a reduced number of detectable individuals (Johansson et al., 2010).

The occupancy model I fitted to the data in **Chapter 2** and **Chapter 3** does not distinguish between species that are present but unavailable for detection and species that are truly absent from the site. The resulting occupancy estimate will therefore be biased low (DiRenzo et al., 2022; Kéry & Schmidt, 2008; Nichols et al., 2008), and the magnitude of the bias depends on how often the respective species is "hidden" at heights above two meters. Estimates exist for some species (Boch et al., 2013; Fritz, 2009; Kiebacher et al., 2016; Marmor et al., 2013) but not nearly for all, and whether the crown preference found in these previous studies is transferrable to the size and placement of sampling sites in the lichen Red List data remains to be tested. Extensions to occupancy models have been suggested to estimate availability separately from detectability, but the heightened model complexity requires additional sources of information to distinguish between the two parameters, e.g., in the form of abundance or sampling at different scales (Kendall & White, 2009; Kéry & Schmidt, 2008; Nichols et al., 2008, 2009). With the current sampling strategy, the necessary information was not available in the lichen data.

No false positives

False positives arise when a species is recorded at a site where it does not occur. Such an error can occur either through misidentification or through accidental errors at later data-handling stages, i.e., typing errors, use of ambiguous abbreviations, or mistakes while entering or restructuring data. The standard occupancy model and many of its derivatives assume the absence of false positives (Dorazio et al., 2010; Dorazio & Royle, 2005; MacKenzie et al., 2002; Tyre et al., 2003). Under this assumption, any detection history with at least one detection will translate into a certainty of 100% that the site is occupied. If some of these detections are false, the number of occupied sites will be estimated higher than it actually is (Royle & Link, 2006). The bias can be surprisingly large, even when the error rate is relatively small, and it increases with the number of repeated visits (Miller et al., 2011, 2015).

I assumed the absence of false-positive sampling errors in all chapters in this thesis despite being aware that it could hardly always be fulfilled in the lichen data. None of my colleagues would claim their identifications are always infallible, and cursory mistakes have likely happened to everyone at some point. The justification for making this assumption anyway came from the efforts that were undertaken to avoid or at least reduce false-positive errors as much as possible. First, everybody employed for fieldwork and identification had prior experience with systematic field surveys of lichens that lasted at least several months. Second, species that require microscopy or chemistry for identification were systematically collected in the field. In case of doubt, also species that can normally be identified in the field were collected and confirmed in the lab. Third, most species with decisive chemistry were analysed with thin layer chromatography to remove doubts about their identification. And fourth, when people identified very rare species, found species new to Switzerland, or where they remained doubtful of their identification, an exchange within the team allowed other people to confirm or correct the identification. Exchange was particularly strong between the less and the more experienced people on the team.

Any false positives that do exist in our data are not likely to be evenly distributed across species. I believe that collections of rare species were more often confirmed by other people than common species, and rare species should thus have fewer false positives. I also believe that some species or species groups are more prone to misidentification or disagreements about their taxonomic concept between lichenologists than others. For example, many of my specimens belonging to the genus *Candelariella* were given different names by different experts, while I have not seen anybody disagree on a sample of *Pseudevernia furfuracea*. If my impression is correct, false-positive error among these difficult groups could be considerable, while it may be non-existent or negligible for others.

There are extensions to occupancy models that incorporate false-positive sampling error (Bailey et al., 2013; Ferguson et al., 2015; Guillera-Arroita et al., 2017; Louvrier et al., 2018; Miller et al., 2011, 2013, 2015; Royle & Link, 2006). As a 0 in a detection history can now represent either an unoccupied site or an occupied site (imperfect-detection error), and a 1 can also represent either an unoccupied site (false-positive error) or an occupied site, the parameters in this model are no longer identifiable without additional information. I find two approaches particularly promising for a potential application to lichen data similar to ours.

The first approach sorts detections into two levels of certainty (Miller et al., 2011). The model still assumes no false positives among *certain* detections, but by allowing false positives among the *uncertain* detections, it realistically relaxes this assumption for the portion of the data that is most likely to be faulty. To apply their method to lichen data, one could for example define a detection as certain when several lichenologists have agreed on its identity. Detections would be uncertain if a specimen was seen by no other than the observer/identifier themselves and certain if it was seen by several people. For chemically distinct species, certainty could alternatively describe whether the morphological identification was confirmed by thin layer chromatography (certain) or not (uncertain). Genetic confirmation by DNA sequencing would be yet another alternative way, though rather expensive and limited to species groups that have been taxonomically well investigated, of obtaining certain identifications. A reasonable number of certain and uncertain detections are a prerequisite for the model to estimate both detection probability and false-positive error. With many species having only a few detections in our data, the model can either be applied only to species with enough data, or the species-specific estimates must be informed via random effects.

The second approach is more technical and does not require additional information on the certainty of detections. Instead, the trick here is to use informative priors to constrain parameters in such a way that they become identifiable (Cruickshank et al., 2019). One could for example believe that the false-positive rate, as defined by Royle and Link (2006), lies between 0 and 0.1, which could be represented by a uniform prior over that interval. Or that the rate is more likely to be closer to 0 rather than to 1 but without setting an upper limit. In this case, a beta prior with parameters 1 and 10 may be more appropriate. An even more informative prior could be obtained by systematically estimating the false-positive rate from other (but similar) data and using this estimate as a prior, either in the form of a constant or a distribution. By checking, e.g., every 10th or 20th collection of a species with DNA or some other trustworthy method (common consensus among lichenologists may be enough), it would quickly become obvious which species are more often misidentified or mixed up when entering data.

Recommendations for lichen sampling in the Swiss Red List

I have shown that detection probability is far from perfect in the standardised surveys conducted for the national Red List of lichens. Consequently, I consider it of great importance to continue conducting repeated visits in all large-scale lichen surveys, so that estimates of occupancy and changes therein can be corrected for imperfect detection.

During my analyses, I discovered some limitations of the data and saw potential that just a few adjustments to the sampling design could expand the limits of possible inference and improve our understanding in a future Red List assessment: the assignment of observers to sampling sites, the number and timing of the repeated visits, the creation of an index of detectability, and the calibration and confirmation of taxonomic concepts.

Distribution of observers in space and time

Repeated visits by each observer allow the estimation of observer-specific detection probabilities. With only 46 repeated visits, five to six observers, and a non-random distribution of observers across Switzerland, the sample size per person is however so small that there are likely to be several observer-specific differences that cannot be estimated accurately and are thus not accounted for. The simplest way to avoid the undesirable effects of geographic or elevational clustering of observers would be to assign sites (incl. repeated visits) to observers in a random or strategically stratified way — considering possible restrictions of mobility. The resulting data would likely be more homogeneous and thus statistically sounder. As an additional benefit, it would also be easier to keep the first and second observers of repeated-visit sites anonymous.

Number and timing of repeated visits

The lichen data consisted of detections and non-detections from 46 sites visited twice and several hundreds of sites visited once. Although such data are suitable for occupancy models and, as I showed throughout this thesis, can produce reasonably precise estimates of detection probability and occupancy, they only just fulfill the minimum requirements for a separate estimation of occupancy and detection (MacKenzie et al., 2002; Tyre et al., 2003). Using an extraordinary experimental dataset, Bhatti (2020) showed how imprecise and sometimes even inaccurate estimates can be when relying on only two repeated visits. This suggests that increasing the number of repeated visits would yield more precise and accurate estimates of detection probability, especially for species with low detection probability (Bhatti, 2020; MacKenzie & Royle, 2005). As I showed in **Chapter 1**, having more than two repeated visits also improves the contribution of single-visit data to parameter estimation. I would therefore recommend conducting a third visit to some of the sites that were already visited two times. However, as I consider the effect of repeated collecting on abundance and/or occurrence of species as non-negligible, I would not increase the number of visits to more than three, and even the third visit should be conducted with particular care in order to not deprive the site of many more individuals and species. The chance of obtaining a complete species list with as few collections as possible could be maximized by conducting the third survey with several (at least three but ideally all) observers. The combination of multiple people with possibly complementary detectabilities for species has been shown to be beneficial to overall detection probability (**Chapter 3**; Bhatti, 2020; Vondrák et al., 2016). Collections could be further minimized if the team had a list of all the species detected during the first two visits, and the goal would simply be to complete that list with yet-undetected species. As this procedure would be entirely different from the procedure of the first two visits, it should be modelled as independent of the regular surveys.

In addition to improved precision in parameter estimates, conducting a few such thorough surveys with the entire team of observers would also be a good occasion to 1) calibrate survey procedure between observers or 2) discover potential differences in taxonomic concepts, which could further be confirmed by microscopic, chemical, or genetic analyses to estimate misidentification rates (see below).

When it comes to timing, I would highly recommend conducting the repeated visits within a few months after the first visit, in any future lichen study that includes repeated visits. As I described in a previous section on population closure, weather events (e.g., storms that make trees or branches fall) or forestry interventions (i.e., removal of trees) could otherwise easily alter occupancy or abundance of species between the visits. The colonization of the site by a new species or the extinction of a species may be improbable within one year, but being on the safe side with respect to such dynamics would be an additional advantage of not spacing repeated visits further apart than a year.

Detectability-related index

In **Chapter 2** and **Chapter 3** I found that some variation in detection probability can be predicted by covariates such as observer experience, observer identity, species conspicuousness, and identifiability. Other variables are also likely to affect detectability in some way, such as habitat and substrate heterogeneity or, as mentioned in an earlier section, sampling effort. I cannot find literature that suggests it, but I think it would be worth an attempt to let the observers themselves set an index value for their detectability during a survey. For example, an estimate of the structural heterogeneity of the site (e.g., number of lichen-suitable microhabitats) as judged by the observer at the end of the survey could be used as a covariate to detection probability. I would expect detection probability to decline with increased structural complexity of the site.

Alternatively, observers could rate their own sampling effort in relation to the encountered species richness and substrate availability. Such an index would surely be subjective and thus observer-specific, but it could roughly describe the gradient I (and others) have experienced in the field which spans from "I have really thoroughly searched the little available substrate and am certain to have found everything" to "I keep finding new species everywhere I look, and I could easily spend two more hours here, but the sun is going down and I still have an hour's hike before I am back".

Although these indices may seem vague and difficult to reproduce, they may describe some of the variation in detection probability that I have not been able to account for, due to a combination of scarcity of data and inability to include sampling effort (survey time) as a covariate in a satisfactory way.

Calibration of taxonomic concepts and confirmed identifications

In a previous section on false-positive sampling errors, I described the consequences of misidentifications on parameter estimates. To avoid biases of this kind, it would be easy to systematically check a handful of all identified specimens for each species-observer pair. Most concepts can probably be agreed upon with standard identification tools (macromorphology, dissecting or light microscope, chemistry). In case of disagreements, or as objective confirmation, an additional genetic analysis of a few specimens could give clarity. When such comparisons between the identifications of different observers are consistently done from the beginning of the study, false-positive sampling errors due to misidentification could be avoided, or at least minimized. When comparisons are made *post-hoc*, they could instead be used to estimate the occurred false-positive sampling error.

Recommendations for plant and fungal surveys

Although this thesis focusses on lichens, the conclusions I have drawn with respect to detection probability are likely to extend to other sessile organisms. In most plant surveys, for example, detection probability is not accounted for (Kellner & Swihart, 2014; Perret et al., 2023). Yet, it has repeatedly been shown to be far from perfect (Al-Chokhachy et al., 2013; Chen et al., 2009, 2013; Garrard et al., 2008, 2013; Gregg & Kéry, 2006; Middleton & Vining, 2022; Perret et al., 2023). Because most plants and fungi show seasonal variation in morphology and availability, detectability is likely to be even lower and therefore lead to stronger biases than what I found in the lichen data. Very recently, Perret (2023) wrote a PhD thesis on the subject of detectability of plants and its effects on population estimates, providing an excellent overview of the plant-related detectability literature. The mycological literature, though more scarce, also suggests that detectability can be a real issue in fungal surveys (Lõhmus, 2009; Mair et al., 2017; Moor et al., 2020; Saine et al., 2020) and that imperfect detection is among the great challenges of modelling species distributions of fungi (Hao et al., 2020). I agree with the general conclusion of these studies: imperfect detection is ubiquitous in surveys of sessile organisms, and many analyses could benefit from the inclusion of detection probability as a source of error.

I have shown in this thesis that a relatively small number of repeated-visit sites is enough to estimate and account for detection probability, especially when combined with all the single-visit data. I have also shown how limited detectability is likely to be in such a standardised survey and that parameter estimates are biased accordingly. It is rather common practice in studies of plants and fungi to collect data of the same mixed structure as our lichen data. While plant monitoring programs often use the repeated-visit data to evaluate reproducibility of species lists but without accounting for the estimated error (Burg et al., 2015; Futschik et al., 2020; Plattner et al., 2004; Traub & Wüest, 2020; Vittoz et al., 2010), the goal of repeated visits in fungal surveys is rather to increase the chance of detecting species at least once when visits are spaced over different seasons and weather conditions (A. Gross, personal communication). I would warmly recommend botanists and mycologists alike to make the small step of building a suitable occupancy model for their data and exploring its possibilities.

Translating results into IUCN criteria

Unfortunately, the species-specific estimates of population changes obtained in **Chapter 3** cannot directly be used for the Red List assessment of these species. This is first, because the estimated variable, i.e., difference in proportion of occupied sites (absolute change), is not a criterion proposed by the IUCN. The IUCN criterion that estimates the past change in occupancy of a species, criterion A2c, uses the *relative* change and not the *absolute* change (IUCN, 2012, 2022). The second reason is that this criterion refers to a change over a period of three generations and not the fixed 20 years between the two surveys. Generation lengths vary between species, depending for example on the longevity of their substrate, and further calculations are therefore necessary to upscale or downscale the estimated change to the desired period.

The results from **Chapter 3** are nevertheless useful for the national assessment in several ways. If desired, the output can easily be adapted to estimate *relative* change, instead of absolute change. By a simple cross-multiplication, the estimate can then be scaled to the necessary stretch of time (three generation lengths) required by the criterion. But above all, the guild-specific changes give us an idea how environmental changes in the past decades have already affected lichens sensitive to certain stressors, and this knowledge can even be applied to species not represented in the data. Among them are at least 200 other epiphytic lichens that were never found on any of the sampling sites, and all terricolous and lignicolous species not assessed here at all. Many of them have similar ecological indicator values and, in the absence of more detailed species-specific information on past or ongoing population changes, it may be reasonable to infer that the rate of change is similar to the change experienced by the guild they best fit into. Alternatively, the guild-specific estimate could be used to infer a change in the habitat quality of the species (still criterion A2c) or, in case of nitrogen-sensitive species, the effect of environmental pollutants (criterion A2e). When projecting changes into the future (criteria A3 and A4), the present results can be used as a yard stick/benchmark to know the magnitude of change that is realistically possible.

At an international scale, the systematic community changes in Switzerland may indicate which threats could be affecting the species at a broader, international or even global, scale. Assessors of global Red List assessment often refer to regional assessments of occupancy and population changes to understand and estimate population status and threats globally. It would therefore be very valuable if more countries, regions, or continents conducted similar analyses of their lichen communities.

Outlook

Modelling the occupancy, distribution, and population changes of lichens for conservation is a large field with, I believe, much untapped potential. In addition to some suggestions I made earlier, I primarily see potential for future research in the identification of crucial covariates for lichen occupancy, and the application of recently developed models that integrate data from multiple datasets of different origin and structure.

Choice of covariates for distribution modelling of lichens

Species distribution models are crucial for Red List assessments and species conservation in general (Guisan et al., 2013). These models, incl. occupancy models, use environmental variables to predict observed occurrences (Elith & Leathwick, 2009). Though completeness can never be achieved, the right choice of variables determines the precision and accuracy of the model's predictions. The number of studies that evaluate distribution models for lichens is small compared to the number of studies on other organism groups, and I find that there are countless approaches but little consensus on the most essential variables.

Many studies on lichen distribution include climatic variables in one form or another. Temperature and precipitation are the most common, but some studies also modelled solar radiation (Ellis et al., 2017; Giordani et al., 2014) or continentality of the climate (Bolliger et al., 2007). Temperature and precipitation variables come in different shapes, from yearly to seasonal to monthly averages, summed rainfall, or number of days above a certain threshold (Allen & Lendemer, 2016; Bolliger et al., 2007; Dymytrova et al., 2016; Ellis et al., 2014; Ellis & Coppins, 2010; Giordani, 2006; Henrys et al., 2015; Hurtado et al., 2020; Janssen et al., 2019; Nascimbene et al., 2016; Phinney et al., 2022). When data are abundant in relation to the complexity of the model, it is possible to test for the best-fitting version of a variable. Through such a test, Ellis et al. (2007) found that species varied in which aspect of a climate variable performed best. While occurrences of some species were best predicted by the yearly range of temperatures, others were best predicted by the temperature of the warmest month, with similar differences for precipitation. This suggests that there is no one-size-fits-all solution. Nevertheless, some variables seem to work for more species than others, and physiological studies may provide answers to why some aspect of the climate may be more limiting than the other.

Habitat-related covariates are even more difficult to choose, measure (or otherwise obtain), and model because of the abundance of factors, potential correlations among them, and the vastly different spatial scales at which they operate. In a country like Switzerland, for example, the topographic heterogeneity leads to strong correlations between elevation, yearly mean temperature, and land-use type (and consequently also nitrogen deposition). Including all these variables in the same model then reduces the power of drawing inference at the covariate level. Small-scale variables like bark pH or crevice depth, air humidity, or light exposure are important predictors of lichen occurrence (Jüriado et al., 2009; Mežaka et al., 2012; Moning et al., 2009; Phinney et al., 2019; Stanton, 2015), but such data are cumbersome to collect and therefore not usually available at larger scales (Eaton et al., 2018). Epiphytic, lignicolous, terricolous, and saxicolous lichens must also necessarily vary in their set of important variables. While availability of suitable bark substrate is indispensable for epiphytic lichens, soil pH or the proportion of grass cover are probably more decisive for the presence of terricolous species. More differences are likely to exist also within these groups, and, again, no set of variables will probably work for all. Yet, within a given group of species (an ecological guild for example), it may be possible to identify a set with the most relevant predictors.

Larger-scale categorical variables like types of land use, habitat, or forest are also undoubtedly crucial explanatory variables of lichen occurrence (Bolliger et al., 2007; McCune et al., 2003; Nascimbene et al., 2014; Stofer et al., 2006; Wolseley et al., 2006; Yahr et al., 2014). However, they can on the one hand affect lichen occurrences beyond their boundaries, e.g., agriculture can influence the degree of eutrophication in neighbouring habitats. And on the other hand, the number of model parameters to estimate increases rapidly with categorical covariates, augmenting the necessity for large amounts of data which may not always be available.

Beyond single-dataset analyses

Standardised data, such as detection/non-detection data, from strategically distributed sampling sites are very valuable. In contrast to opportunistic sampling, where species are searched freely without following a system, a randomized or stratified-randomized design can avoid uneven spatial sampling and thereby reduce the risk of estimator biases (Guillera-Arroita et al., 2015; Isaac & Pocock, 2015; Yackulic et al., 2013). It has even been shown that inconspicuous and difficult-to-identify lichens had a greater chance of being detected on sites sampled strategically than by free search (Cáceres et al., 2008). However, standardised surveys require more resources, and their number and spatial resolution is seldom large enough to detect all species that inhabit the area for which inference is wanted. We know, for example, that there are around 200 additional species of epiphytic lichens in Switzerland that were never detected during any of our standardised surveys. Opportunistic sampling usually yields more records per unit time and can locate and survey biodiversity hotspots quicker than static sampling plots (Ellis & Coppins, 2017). Consequently, the number of opportunistic or presence-only records is often greater than the number of records coming from standardised surveys (Miller et al., 2019). Countless models have been developed to model data of either presence-only data (Dorazio, 2012; Kéry et al., 2010; Pearce & Boyce, 2006; Phillips et al., 2006; Renner et al., 2015; Ward et al., 2009), or structured presence/absence or detection/non-detection data (Bayley & Peterson, 2001; Hanski, 1994; MacKenzie et al., 2002; Moilanen, 1999; Tyre et al., 2003). Integrating multiple data types in the same model, on the other hand, is a rather novel approach.

Data-integrating methods explicitly model the dependencies between species detections in different data sources while accounting for the different sampling processes that have produced them (Ahmad Suhaimi et al., 2021; Fletcher et al., 2016; Isaac et al., 2020; Koshkina et al., 2017; Miller et al., 2019; Pacifici et al., 2017). In comparison to single-dataset analyses, parameter estimates can be substantially improved in accuracy and precision (Fletcher et al., 2016; Koshkina et al., 2017; Pacifici et al., 2017; Schaub et al., 2007). It is certainly challenging to integrate data from various sources and the usefulness of the effort should be carefully assessed (Simmonds et al., 2020). And where datasets differ in spatial resolution, a common unit must be found to avoid biases (Isaac et al., 2020; Pacifici et al., 2019). In general, however, data-integrating methods promise great potential for modelling for conservation, both for individual species (Malchow et al., 2022; Zipkin & Saunders, 2018) and entire communities (Doser et al., 2022b). The huge effort done by citizen scientists — who report millions of observations to databases like GBIF (www.gbif.org) every year — could thus be rewarded by making their data informative to species distribution models. It would be interesting to compare the results of this thesis to those obtained by an integrated-data model which uses all data points from the database.

I believe there is great potential to establish a more standardised approach to lichen distribution modelling. The approach should be scalable to the desired geographic extent, be applicable to many species of similar ecological requirements, include data from different sources, and, ideally, consider sources of error and sampling bias. A list of readily available environmental variables would make the workflow accessible to more than just the developers. I see the establishment of pan-national or global Red List assessments as the principal area of application for this modelling approach, but its usefulness extends to studies of species ecology, lichen response to global change, or even macroecology and macroevolution.

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Supervisor: Christoph Scheidegger
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