Multiscale patterns of rarity in fungi, inferred from fruiting records

Running title: Rarity in European fungi

Abstract

Aim: Characterising the distribution and abundance of organisms is a fundamental part of understanding their population dynamics and development of conservation policies for rare species. It is unknown whether fungi show similar trends to other organisms in their macroecological patterns of abundance and spatial distribution. Here, we investigated fungal abundance-occupancy relationships to determine whether fungi that are common at a local scale tend to be more widely distributed.

Location: UK and Switzerland

Time period: 1950 - 2014

Major taxa studied: Fungi

Methods: We used a local dataset of fruiting records of 2,319 species in the UK, accumulated over 65 years, and one from Switzerland of 319 species, spanning 32 years. Using record number and occurrence as proxies for abundance, in each case we examined the form of species and rank abundance distributions, and compared these with distributions of records in the national databases over the same time. We plotted relationships of local number of records and regional occupancy, and calculated multi-scale indices of rarity for all fungal species.

Results: There was a remarkable congruence in the patterns found in the UK and Switzerland. Regional assemblages are characterised by many rare species, while few are common (fitting the lognormal distribution). However, at local scales, distributions best fitted a power law, suggesting that habitat availability or dispersal processes may play important roles. Fungi with high local record number are densely distributed nationally, but unlike other organisms, locally rare fungi may also be densely distributed at a wider scale.

Main conclusions: Fungal fruiting records can be used to infer patterns in fungal distributions. Abundances in local assemblages may be determined by the position of the assemblage in the overall geographic range of each species, dispersal ability and environmental filtering. We advocate the use of multiscale approaches to rarity in future fungal sampling programmes, to provide more reliable information for future conservation policy decisions and fungal biogeography.

KEYWORDS

abundance-occupancy, conservation, lognormal, models, mushrooms, rank abundance, fruit bodies

1 | INTRODUCTION

Understanding why some species are rarer than others is a fundamental part of community ecology with ramifications in conservation biology, including the management of habitats and natural resources. However, 'rarity' itself is a relative concept, in which the abundance or extent of occurrence of a species is defined in relation to that of others (Gaston, 1994). Furthermore, the rarity of a species depends upon the ecological scale at which the taxon is recorded; species may be considered rare at one scale, but common at another (Hartley &

Kunin, 2003). Thus, rare species should never be considered in isolation, but as important components of assemblages and 'hotspots' of species diversity (Heegaard, Gjerde, & Saetersdal, 2013).

The species abundance distribution (SAD) is one of the simplest ways of describing the pattern of relative abundance across the species detected in an assemblage. Fisher, Corbet, & Williams (1943) realised that histograms depicting the frequencies of species abundance show a hollow curve, in which many species consist of a few individuals, while only a few species are abundant. This pattern appears to be universal and thus, in alternative parlance, most species are rare, while only a few are common (McGill et al., 2007). A useful complementary method of describing community assemblies is the rank abundance distribution (RAD), in which species' abundance is plotted against their rank in abundance (Foster & Dunstan, 2010). RADs can be informative, as they display all the data rather than grouping abundance into 'bins', resulting in the masking of some information (McGill et al., 2007).

A large body of work exists on fitting models to the hollow curve. However, few models are ever rejected since their prediction ends with stating the nature of the curve, and little attempt has been made to go beyond this and provide explanations for it (McGill et al., 2007). Nevertheless, SADs remain one of the most important tools for describing and understanding community assembly and its management. In particular, they can be useful in informing conservation decisions and determining extinction risk (Matthews & Whittaker, 2015).

It is evident that while SADs have been produced for virtually all groups of organisms, their use in fungal ecology is extremely restricted. In a meta-analysis of SADs, only two (of 558 distributions) were of fungi, both involving lichens (Ulrich, Ollik, & Ugland, 2010). Lichenised fungi, which are macroscopic organisms, are often treated like plants in ecological studies, but non-lichenised fungi are often studied completely separately. This is at least

partly because non-lichenised fungi are invisible for most of their lives as mycelium within soil, wood or some other solid substrate, making enumeration almost impossible (Watkinson, Boddy, & Money, 2015). However, Ascomycetes and Basidiomycetes periodically produce macroscopic fruit bodies which can be enumerated.

The development of molecular techniques to detect hidden mycelia is revolutionizing the study of fungal communities, and has provided indications of patterns in global fungal biogeography (Tedersoo et al., 2014). However, SADs and RADs depend on recording the numbers of individuals of each species, which is still not practicable on a large scale using molecular approaches.

Based on the meta-analysis of macro-organisms other than fungi, Ulrich et al. (2010) concluded that fully-censused assemblages tend to show SADs that are best described by a lognormal distribution, while assemblages that are incompletely sampled tend to show distributions that are best described by the log series model or a type of power law. These latter distributions still show extreme skew (very many rare species), even when plotted on a log scale. More recently, Dumbrell, Nelson, Helgason, Dytham, & Fitter (2010a) examined the abundance of arbuscular mycorrhizal fungi (AMF) in 33 different communities, testing three different models: the lognormal fitted in 73% of cases, while 27% were described by the broken stick model and none by the geometric series. Unterseher et al. (2011) also found that the lognormal model best described AMF abundance, while Dumbrell et al. (2010b) showed that the lognormal also described AMF abundance well, but the best model fit was a neutral model, the zero sum multinomial. This led to the conclusion that niche differentiation processes are important in structuring the community, as well as neutral processes such as dispersal limitation. These findings contrast with small-scale studies of fungi on leaves, where log series models (indicating incomplete sampling) predominate (Thomas & Shattock,

1986; Unterseher et al., 2011), though neutral models have also provided a good fit (Feinstein & Blackwood, 2012).

While the majority of fungal studies have taken place at localized scales, those that used broader scales also showed variation in best model fits, either with lognormal or log series (Nielsen, Kjoller, Bruun, Schnoor, & Rosendahl, 2016) or neutral models (Gumiere, Durrer, Bohannan, & Andreote, 2016). Thus, it is unclear whether fungi do or do not show similar patterns of abundance to other organisms, beyond the fact that most species seem to be rare and few are common (Nemergut et al., 2013). In particular, as rarity is scale-dependent, a true depiction can only be achieved by multiscale comparisons (Leroy, Canard, & Ysnel, 2013), yet such an approach has never been applied to fungi.

The interrelationship of rarity and scale is formalized in another long established pattern in macroecology: the abundance-occupancy relation (i.e. the relation between the local abundance of species and the size of their ranges within a region). A large body of literature, both theoretical and empirical, has shown that this is another universal and positive relation; species that are locally abundant tend to occupy wider ranges, i.e. they are more widespread (Gaston et al., 2000; Borregaard & Rahbek, 2010). However, while a number of comprehensive reviews list the wide variety of taxonomic groups that show such relationships (e.g. Holt, Gaston, & He, 2002), fungi are absent from all such analyses. It is intriguing that the closest approach is that of Roney, Kuparinen & Hutchings (2015), in which lichens were the only taxonomic group in Canada not to show a positive relation, though sample size (n=15 species) was small.

Abundance-occupancy relationships are not just important in understanding the structuring forces in local communities, but also for their role in species conservation and habitat management (McGeoch & Latombe, 2016). These relationships, in addition to analysis of SADs and RADs, could provide essential tools for characterization of rare fungi and their

conservation, but to date, such an approach is lacking. In general, for the very same reasons of crypsis and sampling outlined above, fungi have lagged behind most taxonomic groups in assessments of rarity and the construction of Red Lists for their protection (Dahlberg, Genney, & Heilmann-Clausen, 2010). However, many species of fungi produce fruiting structures (sporocarps) that can be counted, thereby providing a good proxy for individual abundance, and from which designations of 'common' or 'rare' can be inferred (Dahlberg & Mueller, 2011). While assigning fruit bodies to different individuals may be problematic at very small scales (< 10 m, Dahlberg & Mueller, 2011), records of occurrence across geographic ranges, calculated as the 'area of occupancy' (Gaston, 1994), can provide data that are of similar quality to other taxonomic groups (Truong et al., 2017). The limiting factor is then the distribution and knowledge of recorders, but coordinated large scale surveys have enormous untapped potential to provide information on fungal species abundance and distributions which we currently lack (Molina, Horton, Trappe, & Marcot, 2011; Andrew et al., 2017). Indeed, surveys of fruit bodies are an accepted method for biodiversity assessments, and often reveal species which are undetected by sequencing methods (Runnel, Tamm, & Lohmus, 2015). Furthermore, while offering great promise for the future, molecular methods cannot currently be used to perform macroecological studies of the types reported here. This is because of the problems that exist within sequence databases, due to the high number of unnamed and incorrectly named species, plus primer and other methodological biases which are particularly acute for soil-dwelling species (Khomich et al., 2018).

Coordinated databases of the occurrence of fungal fruit bodies have been used successfully to document recent changes in the phenology and spatial distributions of fungi, in response to changing climate (Boddy et al., 2014; Gange et al., 2018). Similar such databases and museum collections have been used in a wide variety of plant and animal studies to examine

distributions of species abundances and ranges, to show changes over time, and ultimately to inform conservation policy (Pyke & Ehrlich, 2010). However, with the exception of a couple of notable animal and plant pathogens, fungi are again absent from such analyses.

Here, we use two databases of fungal fruiting records, including lichenised fungi, assembled in the UK over the last 65 years: (1) a local data set comprising haphazard collections, with at least weekly frequency from 1950 to 2014, covering an area of approximately 3 000 km^2, part of which was originally used to document phenological changes (Gange, Gange, Sparks, & Boddy, 2007); and (2) data for the whole of the UK, taken from The Fungal Records Database of Britain and Ireland (FRDBI; www.fieldmycology.net). We also use two data sets from Switzerland; a local study in five plots, each of 300 m^2 (three 10 x 10 m) plots at the La Chanéaz Forest Reserve, comprising weekly fruit body counts from May to December from 1975-2006 (described in Andrew et al. 2018) and data for the whole of Switzerland over the same period (www.swissfungi.ch). A part (28 y) of the local data set was used in a general analysis of varying bin sizes and species abundance distributions (Straatsma & Egli, 2012). To our knowledge, no other local data sets in the world are as comprehensive in their extent and time span as these (Andrew et al. 2017).

Our first objective was to examine the SAD and RAD from each of these datasets, using fungal records to calculate abundance on the basis of both the number of records and the occupancy. Our hypothesis was that national scale data would show the classic lognormal distribution, indicating 'complete sampling', while the local sets may show different (log series or power law) patterns, suggesting dispersal limitation or niche-related processes (Ulrich et al., 2010). Our second objective was to examine the abundance-occupancy relationships for these fungi, and we hypothesised that these would be positive, given that other microbial abundance patterns such as species-area relationships seem to mirror those of other organisms (Nemergut et al., 2013). Finally, we examined the multiscale patterns of

rarity in fungi in the UK and Switzerland, using the approach of Leroy et al. (2013). In general, species that are rare at a local scale also tend to be rare at a wider, regional scale (Freckleton, Gill, Noble & Watkinson, 2005). If the long-established assertion that 'everything is everywhere, the environment selects' (O'Malley, 2008) is correct, then fungi should follow a similar pattern. However, fungi are often dispersal-limited (Molina et al., 2011; Peay, Kennedy & Talbot, 2016), so the relation may be far less obvious.

2 | METHODS

2.1 | Composition of the data sets

The UK local data set consists of 62,087 occurrence records of 2,319 fungal species, spanning the years 1950 – 2014 (inclusive). A total of 310 observers contributed records from 1,558 different localities, all within a 30 km radius of Salisbury, Wiltshire, UK (51.068° N, 1.795° W), covering an area of 2,828 km^2. All records and identifications were confirmed by the late E.G. Gange, with problematic species being confirmed by Royal Botanic Gardens, Kew. Localities were visited on a haphazard basis, but each was visited at least once per year. Each record was referenced by a six figure Ordnance Survey grid reference (https://www.ordnancesurvey.co.uk/), allowing occupancy to be calculated at a resolution of 1 km x 1 km squares (out of a total of 614). Further details on record assembly are provided in Gange et al. (2007). 'Abundance' was defined as the total number of records of occurrence (i.e. not the total number of fruit bodies) for each species, and area of occupancy as the total number of 1 km x 1 km squares in which each species was recorded, so as to be comparable with similar previous analyses (Gaston et al., 2000).

The full UK national data set spans a wider time scale and also contains records for the island of Ireland. These data are from multiple sources, contributed by individuals, foray

lists, scientific societies, herbaria records, and publications of the British Mycological Society. We excluded records collected: (1) before 1950, (2) from outside mainland Britain, and (3) which were missing location data, leaving 1,361,069 separate data points for the 2,319 species from 55,882 localities over an area of approximately 209,330 km^2. These records do not include the local data (above), which have since been incorporated into the national set. Each record was referenced at the resolution of 10 km x 10 km; the standard grid system in the UK. As above, 'abundance' was measured as the total number of records for each species, while occupancy was the number of 10 km x 10 km squares in which each species was found. A complete list of all species used is given in Supplementary Table S1.

Sampling for the Swiss local data set is described in full in Heegaard et al. (2017) and Andrew et al. (2018), and full species lists are given in the supplementary material of Andrew et al. (2018) and Table S2. Weekly fruit body counts took place from 1975 – 2006, but the 10 x 10m plots were only divided into 1 x 1 m contiguous sub plots in 1992. Thus, the description of occupancy is not relevant in this data set, as the scale is too small and the data consists of the total number of records of 319 separate species. A subset of the complete Swiss national dataset was used, to include the same 319 species over the same time span as the local data, producing 97,358 separate records covering an area of 41,285 km^2. Occupancy at the 10 km x 10 km scale was defined in the same way, using grid references as above.

2.1 | Data analyses

2.1.1 | Local dataset species accumulation curves

We first examined the nature of the local data sets by calculating species accumulation curves and estimating the species pool which may exist if all possible species were found. The latter

was examined with three methods: Chao 2, first order jackknife, and Bootstrap. These analyses were performed with the package 'vegan' in R 3.4.1 (Oksanen et al., 2017; R Core Team, 2017).

2.1.2 | Species abundance distributions

All species abundance distributions were fitted using the R package 'sads' (Prado, Miranda, & Chalom, 2016) which uses maximum likelihood methods to fit and compare different models. These were the gamma, lognormal, and Weibull (the three most commonly used continuous distributions), plus the geometric and the negative binomial models. These were fitted with zero truncation, since species with zero records were unknown. We also fitted Fisher's log series, and three associated power law functions, Pareto, power, and power bend (implementation of the latter two not including zeroes); the log series being a special case of the power bend. We also fitted MacArthur's broken stick model and the Poisson lognormal model; the latter describes species' abundances in a Poisson sample from an underlying log normal assemblage. Finally, we examined the fit of two neutral models, the metacommunity Zero-sum multinomial distribution, which is thought to describe a community under random drift, and the Volkov model, thought to describe a community under neutral drift, with immigration. References to the use of all models are provided in Prado et al. (2016).

2.1.3 | Rank abundance distributions

Rank abundance distributions were fitted using the 'radfit' command in the R package 'vegan' in a similar manner. In this case, we used the niche preemption model (also termed the Geometric Series), lognormal, broken stick, and two discrete power law distributions: the Zipf and Zipf-Mandelbrot. In all cases, Akaike Information Criteria (AIC) values were

computed to determine which model(s) provided the best fit to the data (Burnham & Anderson, 2002). Those produced for each model were compared using the delta AIC (Δ_i). A Δ_i value < 2 indicates interaction between models, values $3 < \Delta_i < 9$ indicate little interaction and $\Delta_i > 10$ no interaction (Burnham & Anderson, 2004).

2.1.4 | Relationships between abundance at local and national scales

Relationships between the number of records at local and national scales were examined with a Generalised Additive Model (GAM) procedure, using the 'mgcv' package in R. To examine abundance-occupancy relationships, we followed Holt & Gaston (2003) and Zuckerberg, Porter & Corwin (2009) in using the logit transformation for occupancy data and the log transformation for the number of records, expressed as the total number for each species over the 65 and 32 year periods. As Zuckerberg et al. (2009) comment, phylogenetic approaches are rarely required in abundance occupancy analyses, since closely related species can vary greatly in their distributions and population sizes. As a check, we examined some of the larger genera represented in the UK databases, *Cortinarius* (88 species), *Russula* (72 species), *Mycena* (59 species), *Lactarius* (44 species), and *Entoloma* (44 species). For these genera, the record data at the local scale showed huge variation, with a ratio between the most and least numerous species of 34, 100, 104, 64, and 36 times respectively. Thus, even at the local scale, the variation in the number of records of species within genera is so great that controlling for phylogenetic relatedness is unwarranted, and we conducted an ordinary least squares regression procedure, with occupancy as the dependent variable (Holt & Gaston, 2003).

2.1.5 | Multiscale rarity

If non-linear relationships between abundance at different scales are found, then a multiscale approach is justified (Leroy et al., 2013). As this was so, we calculated two-scale (local and national) rarity weights for all species in the UK and Switzerland, using the R package 'rarity', (Leroy et al., 2013). These were scaled between 0 and 1, with a greater degree of rarity being indicated by a higher value of the index. Calculation of these weights involves an appropriate weighting method and the use of a rarity cut-off value. To achieve this, we used Gaston's quartile definition - that rare species are those 25% with the lowest number of records or occurrence (Gaston, 1994; Leroy et al., 2013).

3 | RESULTS

3.1 | Characteristics of the local data sets

There was no trend over time in the number of collections, or forays per year in the UK (Figure 1a, $F_{1,63} = 3.51$, $P > 0.05$). It should be noted that databases of this type do not record forays when no species were found. Low numbers in years such as 1976, 1990 and 2011 represent poor years for fruiting, caused by lack of rainfall.

The total number of species (the 'species pool') estimated from the UK species accumulation curve (Figure 1b) varied depending on the method, with the Chao estimating 3,526 ± 96.9, jackknife 3,313 ± 141.4, and bootstrap 2,852 ± 80.8. Therefore, these values suggested that between 68% and 84% of the total 'available' species were detected in the 65 years of recording.

The total species pool estimates for the Swiss local data were more consistent, with the Chao estimating 388.75 ± 21.8, jackknife 388.75 ± 17.4 and bootstrap 351.19 ± 10.7. These

values suggested that 82 – 90% of the total species were recorded in the 32 years of sampling. The species accumulation curve is shown in Figure 1c.

3.2 | Species and rank abundance distributions

The species abundance distribution for UK national scale records was best fitted by the lognormal distribution (AIC = 33 305.1) (Figure 2a). No other models provided a good fit to the data (Supplementary Table S3), with the next best fit provided by the Poisson lognormal ($\Delta_i = 18.0$, $P < 0.001$). There was no interaction between models ($18 < \Delta_i < 3592$). The SAD for national scale occupancy data was also fitted best by the lognormal (AIC = 29 093.6) (Figure 2b), this being better than the Weibull model ($\Delta_i = 9.2$, $P < 0.01$). The rank abundance distribution for national record number was also best fitted by the lognormal (AIC = 84 952) (Figure 2c), but that for occupancy data was best fitted by the Preemption model (Geometric series) (AIC = 24 202) (Figure 2d). With both RADs, fitting of the Zipf-Mandelbrot failed, as its estimation is difficult (Oksanen et al., 2017).

The Swiss national record number data was also best fitted by the lognormal distribution (AIC = 3997.6) though the Weibull and Broken stick also provided a good fit (Table S3, Figure S1). The SAD for Swiss national scale occupancy data was also best fitted by the lognormal (AIC = 3248.4). The rank abundance distribution for Swiss national record data was best fitted by the Broken stick, while occupancy data were best fitted by the Geometric series (Table S3).

The species abundance distribution for UK local record numbers was best fitted by the Pareto distribution (AIC = 1 5594.8) (Figure 3a), as was that for the Swiss local record numbers (Table S3, Figure S1). Meanwhile, the abundance distribution for UK local occupancy was also best fitted by the Pareto distribution (AIC = 13367.4) (Figure 3b) (Table

S3). In both cases, all other models differed from the Pareto ($P < 0.001$). Rank abundance fits for UK local data followed an identical pattern to national data (Table S3), fitting a lognormal and Geometric series respectively (Figure 3c,d). Swiss local record data differed from the national data, wherein the lognormal provided the best fit (Table S3).

3.3 | Abundance-occupancy relationships

Species with the greatest number of records at the UK national scale also had the greatest number at the local scale (Figure 4a). These data were best fitted by a non-linear model (R^2 = 58.8%, $P < 0.001$), rather than a linear relation (R^2 = 47%), because species with very few records (i.e. were 'rare') locally may have few or very many records nationally, illustrated by the flat bottom to the graph. However, there appeared to be a tipping point, with very common species (more than 1,000 records nationally) showing a linear relation with the local number of records. A similar relation was seen for occupancy data; species that are most densely distributed at the national scale are also so at the local scale (Figure 4b), but locally sparely distributed species may be sparsely or densely distributed nationally. A non-linear relation (R^2 = 57%, $P < 0.001$) was also seen in these data, rather than a linear one (R^2 = 44.4%), with a tipping point of occurrence in about 200 of the national 10 km x 10 km squares.

Swiss record data followed a very similar pattern (Figure S2) and were best fitted by a non-linear model (R^2 = 21.1%, $P < 0.001$), rather than a linear relation (R^2 = 15.1%). There again appeared to be a tipping pint, with very common species (more than 350 records nationally) showing a linear relation with local record number (Figure S2).

The abundance-occupancy relationships showed a remarkable similarity in the two countries (Figure 5). Although both relationships are significant, they are relatively weak (UK: R^2 = 43.9%; Swiss: R^2 = 13.8%), as species that are rare (least abundant) on a local

scale can be sparsely or densely distributed on a national scale. In contrast, species with high local record numbers tend to be densely distributed nationally. Species with high local record numbers but sparse distributions nationally are absent in both data sets.

3.3 | Multiscale indices of rarity

In the UK, most, but not all, species that are rare on a national scale are also rare on a local scale (R^2 = 65.2%, $P < 0.001$) (Figure 6a), and the significant relation is clearly driven by the preponderance of data with high rarity indices. Likewise, those which are sparsely distributed nationally also tend to be sparsely distributed on a local scale (Figure 6b), though the relation is considerably weaker (R^2 = 49.8%, $P < 0.001$) and the pattern more diffuse. The pattern is even more accentuated in Swiss record data (Figure S3) (R^2 = 12.3%, $P < 0.001$), with the majority of species being rare at the local scale. In these data, there were no species that were locally common but nationally rare.

The proportions of species falling into the four possible categories of rarity generated by the two scale approach are given in Table 1. For both data sets, the vast majority of species can be considered rare at both spatial scales. Only between 1% (based on number of records in UK and Switzerland) and 6% (based on occupancy in UK) of species could be considered common at both spatial scales (Table 1).

Discussion

This is the first macroecological study of rarity patterns in fungi. By using four comprehensive data sets, we have shown that while some similarities exist in patterns of abundance between fungi and other organisms, there are also noticeable differences. Both UK and Swiss data showed the classic hollow curve of species abundance, but while the

national data were best fitted by a lognormal model, the local data sets were uniquely fitted by a Pareto distribution (with very many rare species). Abundance-occupancy relationships of fungi were positive, and similar in the UK and Switzerland, but showed a different pattern to those of other organisms.

Perhaps the most obvious conclusion from these data is that irrespective of the approach taken, most species of fungi are rare, while only a few can be considered common. Both number of records and occupancy at the national scales were best described by the lognormal distribution, as with marine and soil bacteria (Fuhrman, 2009; Ferrenberg et al., 2013; Nemergut et al., 2013) and most macroorganisms (Ulrich et al., 2010). There has been much debate on whether lognormal SADs are the product of sampling artefacts, model fitting, the influence of environmental variables, or the apportionment of niches between species (Williamson and Gaston, 2005; McGill et al., 2007). Furthermore, we must not forget that the lognormal is a purely statistical distribution. However, despite the potential for artefacts, the finding that lognormal distributions tend to arise in assemblages that are completely sampled (Ulrich et al., 2010), strongly suggests that there are good biological reasons for such patterns, including niche processes, competition and dispersal.

The dictum for microbes that 'everything is everywhere, but the environment selects', (reviewed by O'Malley (2008)), has been challenged in many microbial studies (Martiny et al., 2007). Fungal species certainly exhibit biogeographical patterns at continental or smaller scales (Taylor et al. 2006; Tedersoo 2017). In general, everything is not everywhere, but environmental filtering certainly plays a role in determining fungal distributions, with dispersal limitation being proposed as one of the main drivers (Peay et al., 2016). We found variation in the occupancy within the geographic range of fungi of two or three magnitudes at both national scales and at the local scale in both countries, clearly supporting the fact that not all species occur everywhere within their range. Furthermore, relatively low amounts of

variation were explained by our analyses of local vs. national record number and occupancy, and also with the multiscale analysis of rarity indices, suggesting that environmental filtering, most likely manifest as habitat availability, plays an important role. This was particularly true in Switzerland, where landscape structure is more heterogeneous than the UK (Hofer, Wagner, Herzog & Edwards, 2008).

A recent meta-analysis suggests that few fungi may be habitat generalists (Meiser, Bálint & Schmitt, 2014) and so the availability of habitats in the local environment determines species occurrence (Kivlin, Winston, Goulden, & Treseder, 2014). This fact is further supported by the two local data sets displaying a fit to a power law, rather than the lognormal, upholding our first hypothesis and suggestive of niche-related processes (i.e. habitat availability) playing a role (Ulrich et al., 2010). Both these data sets are free from many forms of bias that influence such analyses (Gange, Gange, Mohammad, & Boddy, 2012; Lavoie, 2013), particularly as they were coordinated regular surveys over long time periods, that were not influenced by citizen scientists recording certain species (e.g. edible fungi) or searching in known localities (Geldmann et al., 2016). However, such model fits may still be indicative of incomplete or imperfect sampling (McGill, 2003; Ulrich et al., 2010), particularly as neither species accumulation curve was asymptotic. A further complication is that spatial distributions of saprotrophic and ectomycorrhizal fungi in the UK have changed in recent years, correlated with changes in temperature and rainfall (Gange et al., 2018).

This is the first time that a Pareto distribution has been fitted to fungal data sets, though previous authors generally examined a limited range of models (e.g. Dumbrell et al., 2010a; Unterseher et al., 2011; Gumiere et al., 2016). Pareto distributions are characterised by the presence of many species of low abundance (often singletons) and far fewer of high abundance, producing a long ‘thin’ tail to the SAD. Such distributions are widely reported in physics, computer science, economics and social sciences as well as biology (Newman,

412 2005). Our data are remarkably similar to those of many invertebrate distributions, with 28%
413 singletons in the UK local fungal data, and 9% in the Swiss data, compared with 29-32% for
414 tropical arthropods (Coddington, Agnarsson, Miller, Kuntner, & Hormiga, 2009) and 17% for
415 temperate spiders (Leroy et al., 2013). However, this is considerably less than the 53%
416 singletons recorded in a short term (1 year) survey of fruit body abundance of temperate
417 forest fungi in northern Spain (Abrego & Salcedo, 2014).

418 It is most likely that dispersal ability and niche availability influences the numbers of very
419 rare fungal species (Unterseher et al., 2011). In British lichens, species with high
420 colonization ability (dispersal) occupy larger geographic ranges (Leger & Forister, 2009) and
421 this may be true for fungi generally (Cox, Newsham, Bol, Dungait, & Robinson, 2016), so
422 limited dispersal ability may explain why many species are rare (Molina et al., 2011).
423 Meanwhile, since the number of fungi in an assemblage may be functionally related to the
424 number of plants (Hawksworth (1991), (though see also Tedersoo et al. (2014) for a
425 contradiction with soil fungi) and assemblages of plants, even when completely censused,
426 appear to follow power law distributions (Ulrich et al., 2010), the availability of plant
427 substrates (niches) may be a major factor influencing fungal distributions.

428 Fungal species that were rare (measured as either records or occupancy) on a national
429 scale were also rare on a local scale. The national number of records explained about 47-
430 58% of the variation in local record number, similar to the 31% for phytoplankton and 58%
431 for aquatic bacteria (Ostman et al., 2010). This conclusion was also reinforced by the
432 multiscale analyses; here the majority of species were rare at both scales. However, this
433 analysis showed that it is quite possible for all parts of the graphical spectrum to be occupied,
434 further refuting the 'everything is everywhere…' idea and upholding our original hypothesis.
435 Calculation of the rarity weights for each species is an important aspect of our analysis, as it
436 gives a numerical index for each species, which is far more informative than simple

437 categories (Leroy et al., 2013). In future, such indices could help with the construction of
438 Red Lists, provided that the quantitative information can be related to IUCN criteria adapted
439 for fungi (Dahlberg & Mueller, 2011).

440 Our study is also the first to find good evidence for a positive abundance-occupancy
441 relation for fungi, upholding our second hypothesis. Comparison with previous studies is
442 hampered by authors using different measures of occupancy and abundance or by treating
443 abundance as the dependent variable. However, the form of the fungal relation is different to
444 that of other analyses which have used the same approach (logit and log, with occupancy on
445 the y axis) (e.g. Holt & Gaston, 2003; Zuckerberg et al., 2009), which show clear linear
446 relationships, with R^2 values between 60 and 90%. The fungal relationships, although very
447 similar in the two countries, were much more diffuse and bear some similarity to that of
448 marine bacteria (Amend et al., 2013), but not to intestinal bacteria (Green, Fisher, McLellan,
449 Sogin, & Shanks, 2016). Our data are similar to all others in that there were no locally
450 abundant species with sparse national distributions, but the critical difference is that there
451 were many locally rare species which are densely distributed at a wider scale.

452 Eight possible mechanisms which might account for a positive abundance-occupancy
453 relation have been proposed (Gaston, Blackburn, & Lawton, 1997; Gaston et al., 2000). The
454 first pertains to sampling bias, which may result from low sampling intensity at small spatial
455 scales. We do not believe that poor sampling in the local data sets has contributed to the
456 observed relation, as there was no trend in 'foray effort' over time in the UK and
457 standardized weekly counts were conducted in Switzerland. Furthermore, the UK local data
458 comprised 6,868 separate forays and each involved the collection and identification of every
459 fungus seen, while the Swiss data comprised 992 separate sampling occasions. Citizen
460 science data, while not without its faults, can be used for macroecological analyses, if
461 collated properly, and many previous analyses of this type have used such data (Dickinson,

462 Zuckerberg & Bontner, 2010). Indeed, patterns of phenology in these national and local data
463 sets are remarkably similar (Andrew et al., 2018), suggesting that the local data sets were not
464 biased towards or against certain species. It is possible that model fits might change if all of
465 the local species estimated to be in the pool were found. However, given that all of the
466 'missing' species must be represented by very low numbers of records, the most likely
467 outcome would be that the model fit will remain the same, while the thin tail of the SAD
468 would be extended.

469 Phylogenetic relatedness has been suggested as a second possible, but unlikely, influence
470 on the relation (Gaston et al., 1997) and is also unlikely in our study due to the enormous
471 variation in abundance and range within almost all genera. A third proposal is that the
472 position in the overall geographic range of a species is important in determining its local
473 abundance; species at the edge of their overall range generally have lower abundance. It is
474 interesting that a prediction arising from this hypothesis is that widespread species may show
475 high or low local density, while species with restricted geographic ranges only have low
476 density (Gaston et al., 1997). This would give a triangular abundance-occupancy relation, as
477 found in this study. Given the differences in UK climate from N-S and W-E, and the
478 sensitivity of fungi to climate (Boddy et al., 2014; Gange et al., 2018), it is plausible that
479 locally rare species might vary greatly in their geographic range, depending on what part of
480 the overall range the local area occupies. The other five hypotheses, based on resource use,
481 resource availability, habitat selection, metapopulation dynamics or vital rates seem far less
482 likely to apply to fungi.

483 Overall, using four extensive data sets, we have shown that fungi exhibit some markedly
484 different macroecological patterns to other organisms. In particular, the abundance-
485 occupancy relationships for fungi are very different, and suggest that the forces that
486 determine commonness and rarity in other organisms are different for fungi. It is clear that

after either 32 or 65 y of intensive sampling in the two localities, many fungal species remained undetected and that the vast majority of species could be considered as rare.

AUTHOR CONTRIBUTIONS

ACG and EGG designed the study. EGG collected the local data in the UK, which was analysed by ACG, LPA and AN. SE collected and collated the local data in Switzerland, B S-I coordinated and georeferenced the Swiss national data, CA harmonised, formatted and prepared all the Swiss data, which were analysed by ACG. ACG, LPA, CA, and LB wrote the paper, with contributions from all other authors.

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684 **Table 1** Percentage of species in different categories of rarity, as measured by the number of
685 records and occupancy (in parenthesis for UK data only).
686

UK, n= 2,319		National	
		Rare	Not rare
Local	Rare	96.2 (85.3)	1.6 (7.5)
	Not rare	0.6 (1.1)	1.6 (6.1)

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Switzerland, n=319		National	
		Rare	Not rare
Local	Rare	87.3	10.9
	Not rare	0	1.8

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694 **Figure 1** Temporal characteristics of the local datasets. (a) The number of annual forays in
695 the UK, (b) the accumulated total number of species observed over 65 years in the UK and
696 (c) the accumulated total number of species observed over 32 years in Switzerland.

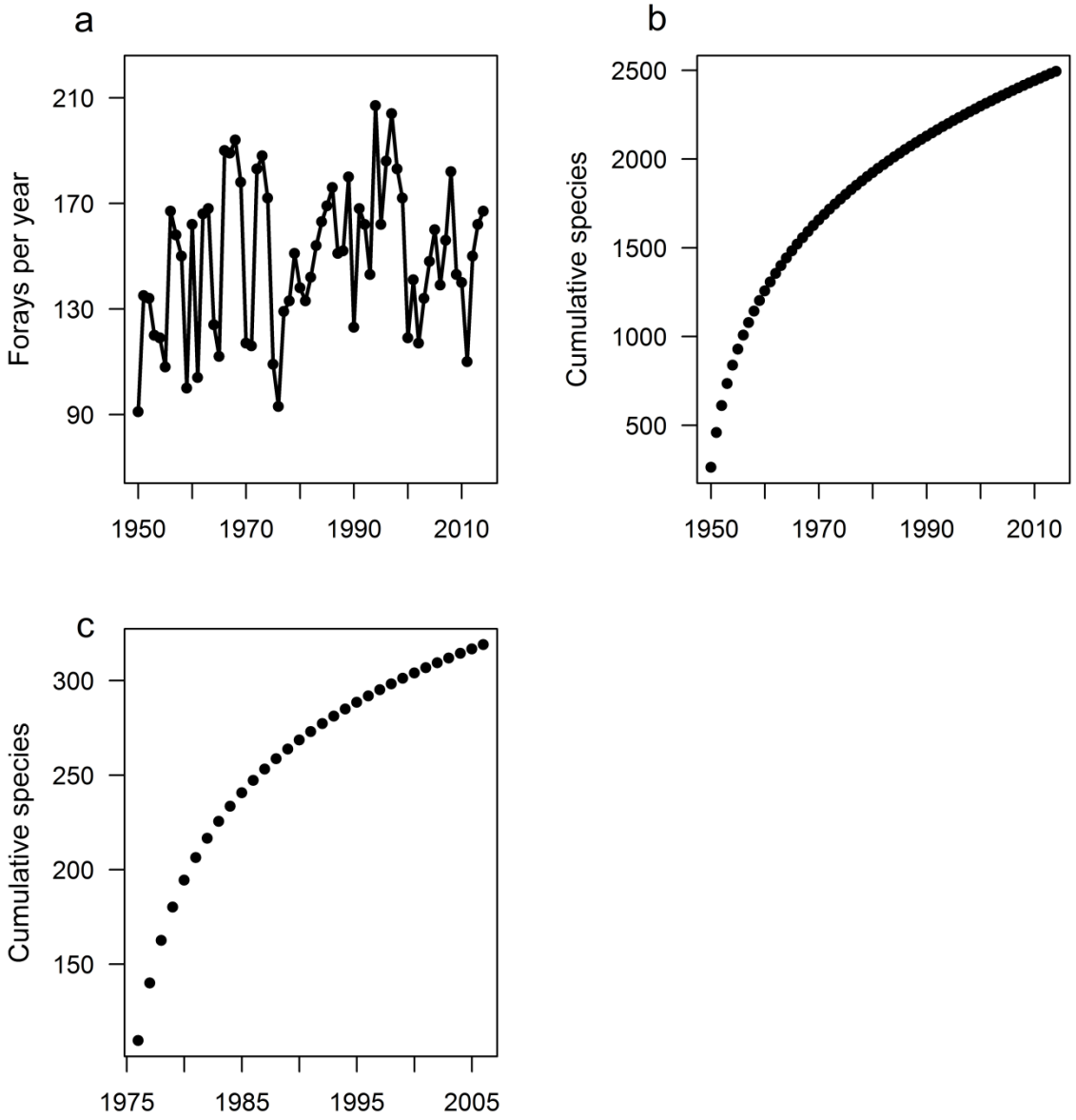

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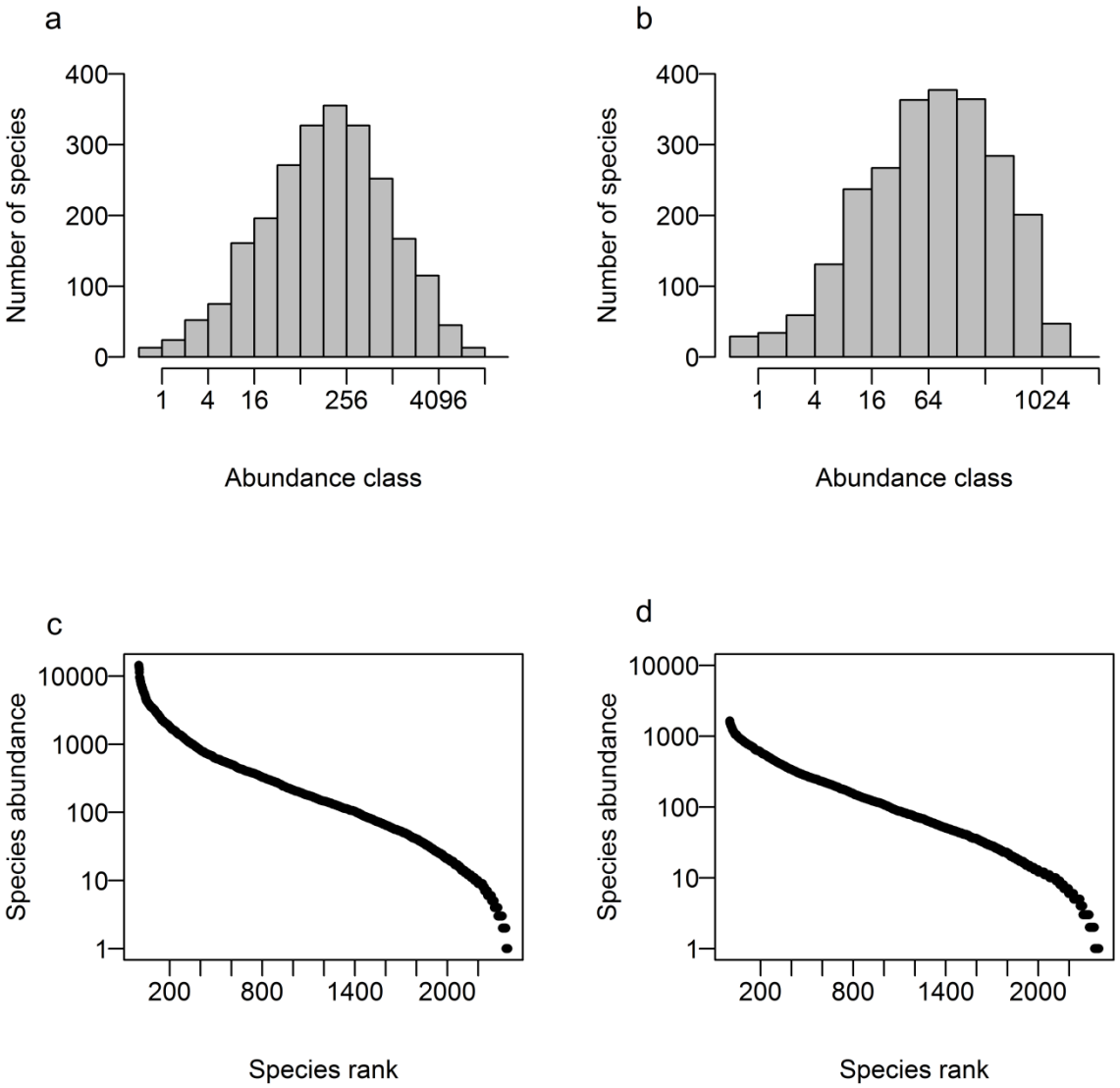
Figure 2 Frequency distributions for species abundance (SAD) and rank abundance (RAD) of the UK national data set based on (a,c) number of records and (b,d) occupancy.



710 **Figure 3** . Frequency distributions for species abundance (SAD) and rank abundance

711 (RAD) of the UK local data set based on (a,c) number of records and (b,d) occupancy.

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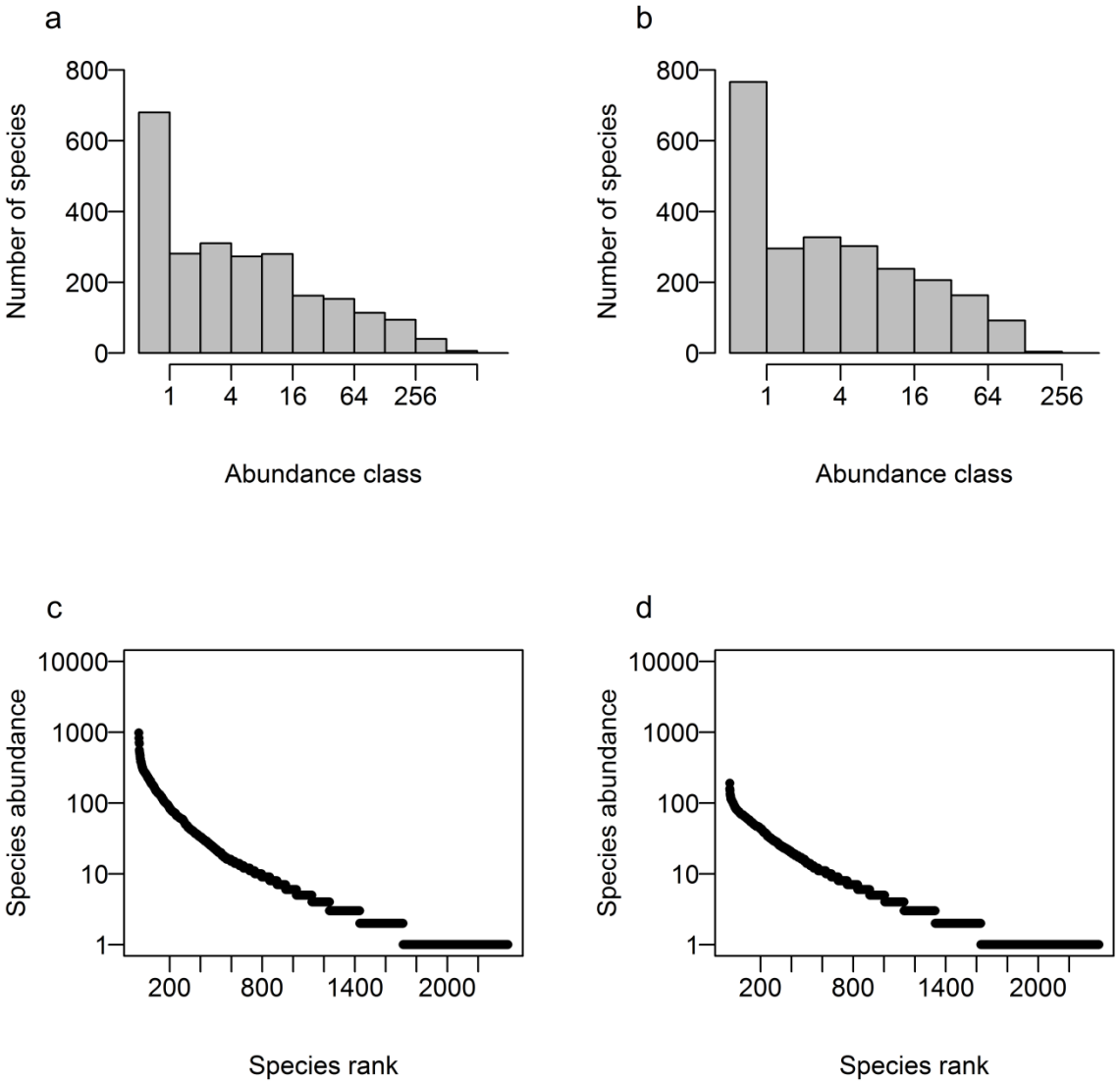

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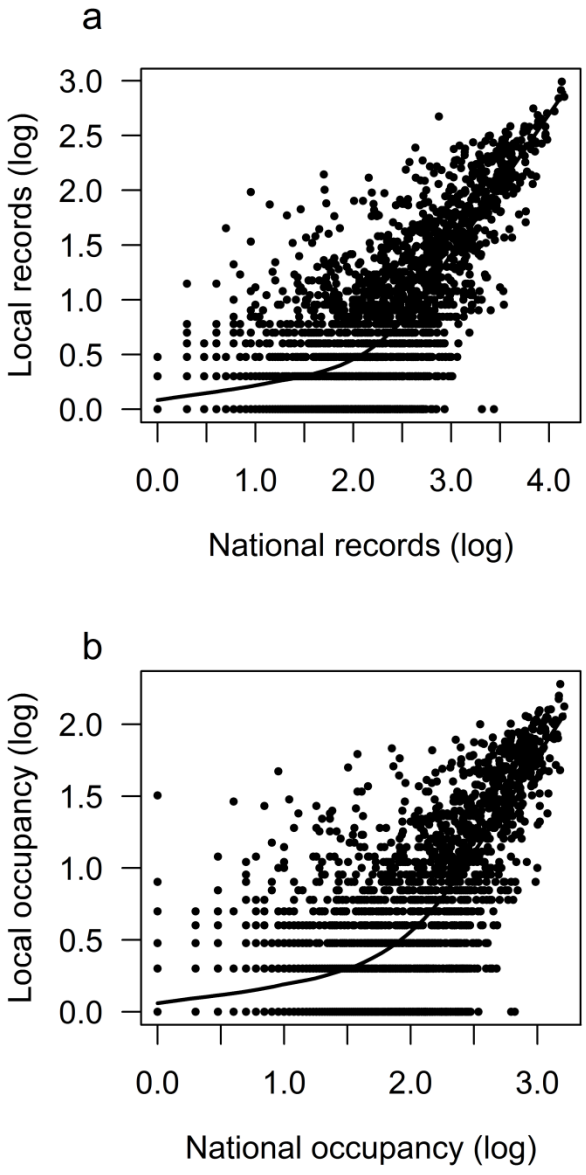
717 **Figure 4** Relations between UK local and national scale data. (a) Relationship between
718 number of local and national records. (b) Relationship between local and national occupancy.
719 Species with the most records nationally also have most records at a local scale (a), while
720 those which are most densely distributed nationally are also so at a local scale, measured by
721 counts in 10 km and 1 km grids respectively (b).The fitted lines are from a locally weighted
722 regression (loess) procedure.



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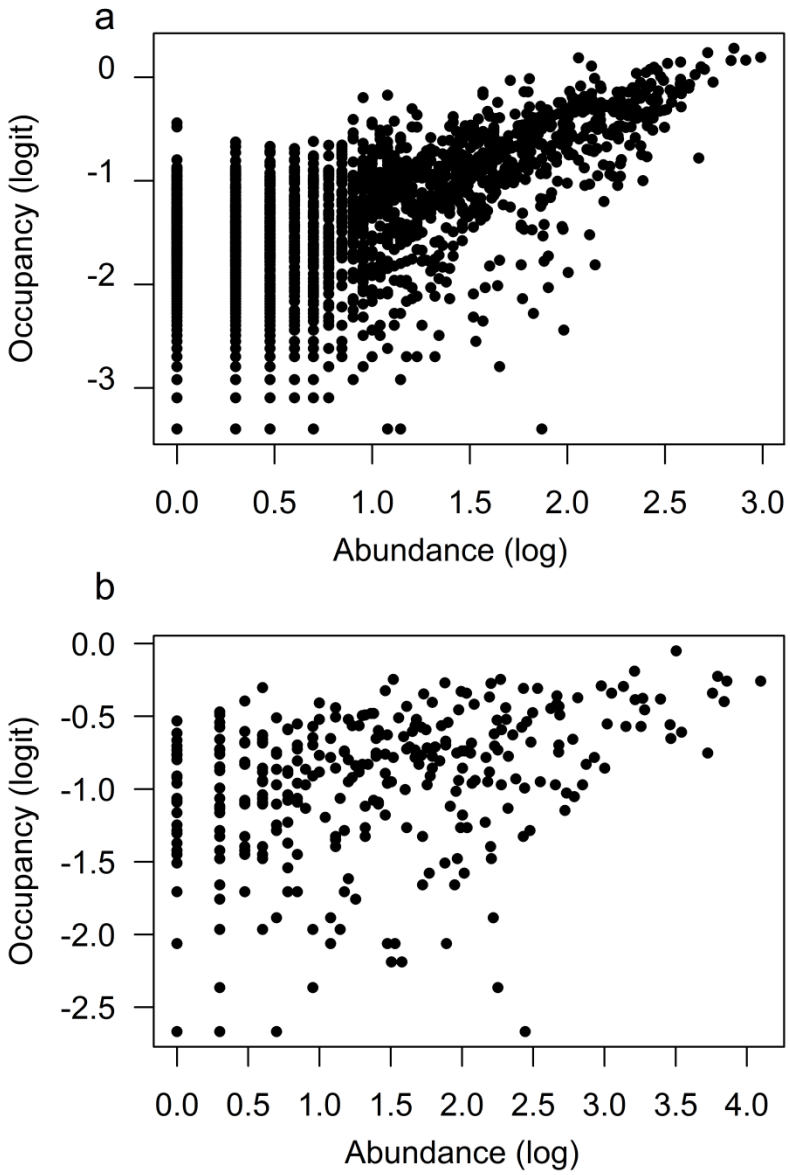
726 **Figure 5** The abundance-occupancy relations for (a) British and (b) Swiss fungi. Species
727 with high numbers of records locally tend to be densely distributed at a wider scale.
728 However, species with low local record number may be sparsely or densely distributed at a
729 wider scale.

730



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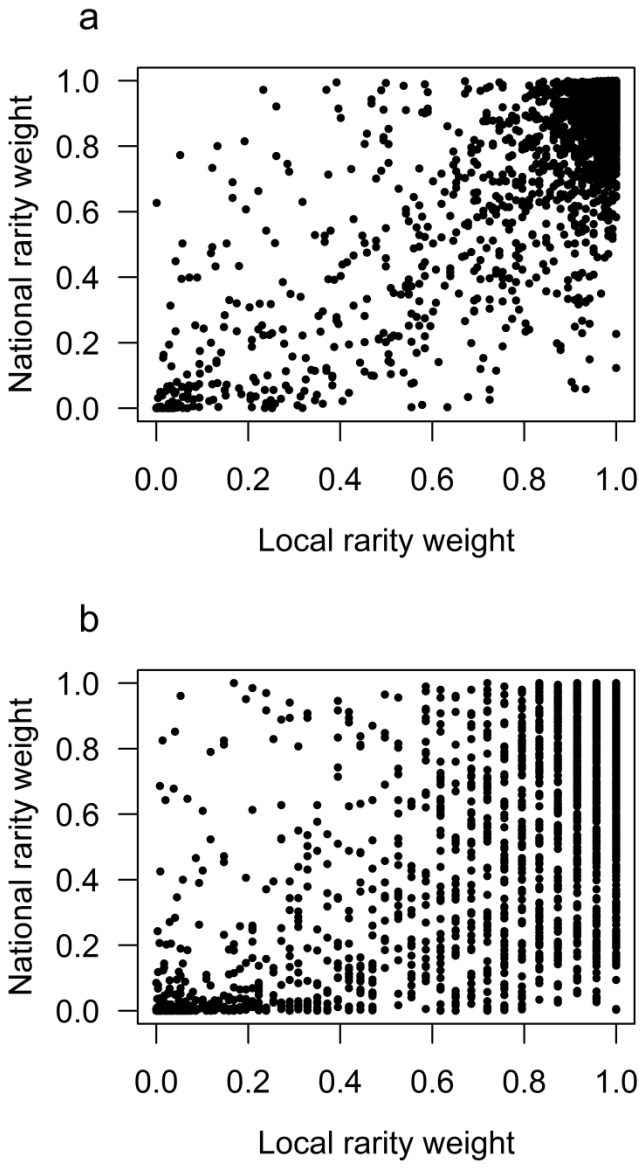
734 **Figure 6** Multiscale patterns of rarity in British fungi. Using (a) number of records or (b)
735 occupancy, species can be rare at one scale, but common at another and *vice versa*. The
736 majority of species are rare at both scales, using data of the number of records, but the pattern
737 for occupancy is different, suggesting that species with low occupancy locally may be
738 sparsely or densely distributed at a larger scale.



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743 **Figure S1**. SAD and RAD for Swiss national data

744 **Figure S2.** Relation between Swiss local and national scale data

745 **Figure S3**. Multiscale patterns of rarity in Swiss fungi

746 **Table S1**. Complete species list for the UK

747 **Table S2**. Complete species list for Switzerland

748 **Table S3**. Results of model fits

749