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Commentary

On species richness estimates, climate change and host shifts in wood-inhabiting fungi

S U M M A R Y

In a recent paper in *Fungal Ecology*, Gange *et al.* (2011) concluded that the wood-inhabiting basidiomycote *Auricularia auricula-judae* has widened its host range and changed its phenology since 1980 in the study area in southern England, most likely as a response to global warming. At the same time the authors report, that the number of macrofungi fruiting on *Sambucus nigra*, the most common host of *A. auricula-judae*, has tripled, while another fungus preferring *S. nigra*, *Hyphodontia sambuci*, has remained constant. We challenge these conclusions and point out that the reported changes may just as well reflect a change in foraging quality over time. To support this statement we present an analysis of data from an ongoing mapping project in Denmark. We show that species accumulation curves and species richness estimators are highly context specific, and that random sampling by amateurs and specialists provide very different representations of actual patterns in nature. We show that the three species analysed by Gange *et al.* (2011) behave very differently in this context, and are hence not straight forward to compare over time based on data from amateur forays. We conclude that more rigorous standardising procedures are needed to reach sound scientific conclusion based on analyses of foray data over time.

In *Fungal Ecology* 4, Gange *et al.* (2011), used a long term dataset to analyse for changes in fruiting time and host selection patterns among two wood-inhabiting basidiomycote species-*Auricularia auricula-judae* and *Hyphodontia sambuci*, both commonly associated with *Sambucus nigra*. In addition, the overall species pool of wood-inhabiting fungi on this host was assessed over time. The authors concluded that *A. auricula-judae* has widened its host range and changed its phenology since 1950, with earlier appearance of fruitbodies and a longer fruiting period, consistent with observed climate warming and changing rainfall patterns.

Analyses utilising long term datasets for fungi have a substantial scientific potential and are becoming more and more feasible to conduct with the development of databases holding records of sightings and collections of fungi. Indeed, recent papers utilising such data have been published in the most prestigious scientific journals, including *Science* and *PNAS* (Gange *et al.* 2007; Kausserud *et al.* 2008, 2010). However,

the utilisation of data recorded over decades is not straightforward. Sampling is not necessarily comparable over time, as already discussed extensively by Arnolds (1988), and also acknowledged by Gange *et al.* (2011). One challenge is that sampling effort is rarely constant over time. This may be corrected for, by standardising the relative frequency of each species in the dataset relative to the total number of records in each year (Arnolds 1988; Nauta & Vellinga 1993; Kery *et al.* 2010), as also done by Gange *et al.* (2011). A far more tricky challenge is to compensate for the fact that the way sampling has been conducted, i.e. the sampling quality, may change over time. So far no standard approaches have been developed to address this issue, but Gange *et al.* (2011) provided three strong arguments supporting that the reported change in host selection in *A. auricula-judae* is reflecting real biological phenomena, rather than sampling bias. First, they state that the shape of the host species accumulation curve over time is so deviant, that it cannot reflect an effect of sampling effort. Secondly, they argue that the exact coincidence in the expansion of host range with a change in fruiting phenology and increasing species diversity on *S. nigra* support that these changes have a biological background. Finally, they use *H. sambuci* as a kind of standard species on which to evaluate the changes reported for *A. auricula-judae*. The argument is that because *H. sambuci* has shown no change in host selection and phenology over time, this points to a consistent sampling quality over time of fungi related to the common host *S. nigra*.

While we welcome these approaches to data validation, we do not feel convinced that they are sufficient to rule out sampling bias. The aim of the current commentary is to provide a constructive critique to the approach applied by Gange *et al.* (2011) and to point out future directions to control for changes in data quality over time when analysing large datasets from unstructured samplings of species in nature. Our critique is based on four steps. First we evaluate species richness estimators as a general tool for analysis of richness patterns in fungal datasets. Secondly, we apply the approach to a Danish dataset, in order to explore the sensitivity of species richness estimators to sampling quality. Thirdly, we compare our results with those presented by Gange *et al.* (2011) to evaluate possible shortcomings in their data validation. Finally, we provide some directions for future

development of the research field. It is important to note that we use the term sampling quality in a non-normative way. We are not so much interested in discussing, which sampling strategies have the highest quality, but more in evaluating how different approaches to data sampling, i.e. variation in sampling quality over time or space, influence data and derived measures of diversity.

On species accumulation curves and richness estimators

Gange *et al.* (2011) used species accumulation curves and the species richness estimator Chao2 to investigate host selection patterns among their study organisms. These methods are very useful for assessing if the sampling effort is sufficient to detect the total species pool in a study area (e.g. Scharff *et al.* 2003), for detecting differences among sampled subcommunities in a standardised way (e.g. Colwell *et al.* 2004; Heilmann-Clausen & Christensen 2004) and for extrapolating the expected total species pool within a specific sampling regime (e.g. Colwell & Coddington 1994; Unterseher *et al.* 2008).

Using the Chao2 estimator Gange *et al.* (2011) estimated the total number of wood-decay fungi on *S. nigra* in their study area as 22, based on 238 actual foray records of 12 species from the period 1950 to 2008. In the same way, the numbers of hosts for *A. auricula-judae* was estimated as 33, based on 308 actual records on 16 hosts. Four hosts were recorded for *H. sambuci* with *S. nigra* holding 70 % of the records, *Fagus sylvatica* holding 28 %, and *Ilex aquifolium* and *Clematis vitalba* each holding 1 %. The Chao2 estimator of total number of predicted hosts was not indicated for this species.

The question now is whether these figures reflect what is actually going on in nature. We think they actually do, but suspect that they tell more about the behaviour of fungal recorders than about the fungi themselves. First of all, it is important to acknowledge that species accumulation curves and richness estimators are only reliable within a specific and consistent sampling regime. They are addressing how many species will be recorded if this sampling regime is followed in perpetuity or extended to cover all available habitat, but do not tell how representative a sampling regime is for unravelling real patterns in nature. In other words, they do not tell the size of the total species pool, unless the input data is representative of the total species (and substratum) pool.

Fungal foraging is not a standardised method and hence the application of richness estimators on foray data is tricky. The question of host selection is a delicate issue here for two reasons. Firstly, foraging effort is likely to be unbalanced in relation to the real host substratum frequencies in the landscape. Secondly, foraging activity does not have the intention of uncovering the total species pool occurring on a given host. Most forayers will concentrate efforts on species that can be easily spotted and identified in the field, leaving the more inconspicuous or difficult species behind. However the size of the pool of easily spotted and identified species is not constant, neither among forayers, nor for the individual forayer over time. It depends both on the skills of the individual forayer, and on

the total available taxonomic knowledge and awareness in the bigger society of mycologists.

A comparable analysis of Danish atlas data

To address how sampling quality can impact the quality of collected data, we have analysed data extracted from the Danish Basidiomycote Atlas (www.svampeatlas.dk) using the Chao2 species richness estimator as applied by Gange *et al.* (2011). EstimateS vers. 8.2.0 (Colwell 2009) was used for the calculations, treating each individual record as a sample (Hortal *et al.* 2006). For reasons of comparability, the bias corrected option for calculation of Chao2 was used throughout, even though the classic calculation was suggested by the software in a few of the conducted analyses.

The Danish climate is slightly cooler than the climate in Salisbury (annual mean temp 7.7° versus c. 9.5 °C) with about equal precipitation (712 versus c. 850 mm), based on www.dmi.dk and www.metoffice.gov.uk, respectively. The Danish Basidiomycete Atlas has operated an online platform for reporting fungal sightings and collections since Mar. 2009, and is planned to run until the end of 2013. In total, the project has generated about 100,000 unique fungal records in the first 2 yr. These records have been submitted by more than 200 voluntary reporters, primarily interested amateur mycologists (Læssøe *et al.* 2011). The projects involve a validation procedure for all species considered to be critical or difficult to determine by amateurs. As part of the validation procedure volunteers are encouraged to upload photographs documenting their records.

To date (12th Aug. 2011) 654 records of wood-inhabiting macrofungi have been reported on *S. nigra*, while the numbers of records with a host genus indicated amounts to 683 and 95 for *A. auricula-judae* and *H. sambuci*, respectively. The latter species requires validation, based either on microscopical examination of a physical specimen, or a convincing field photograph, showing the typical appearance of the species on its most common host, *S. nigra*.

In Fig 1, the performance of the Chao2 estimator is illustrated for host diversity in *A. auricula-judae* and *H. sambuci* and in Fig 2 for macrofungal species richness on *S. nigra* in all cases based on the full dataset. Only for *A. auricula-judae*, has the curve reached a stabilising level, with a narrowing 95 % confidence interval. This indicates that the current amount of sampling is still insufficient to give a reliable estimate of the total number of species or hosts for the two other species in Denmark.

To explore the impact of sampling quality on data we divided the Danish dataset in two subsets: (1) A Copenhagen subset, comprising records stemming from a ca. 2100 km² large area in the Greater Copenhagen area, i.e. roughly corresponding in size to the Salisbury sample area in England. Data are provided by voluntary reporters, with varied sampling strategies, but with a general emphasis on species identifiable in the field. The area is by far the most intensively surveyed part of Denmark within the Basidiomycote Atlas. (2) A specialist subset based on records from intensive forays and excursions conducted as part of the Atlas project, involving experts and a strong emphasis on

microscopical examination of difficult specimens. It is important to note that also the specialist sampling is derived from unstructured sampling with no intention to uncover real patterns in nature.

In Table 1, basal data for these two subsets are compared to the Salisbury dataset, and in addition data are given for the full Danish dataset and for a combined subset made by merging subsets 1 and 2. The latter combination was made in order to explore the relative nature and contributions of subsets 1 and 2 to the total dataset. The values of subset 1 (Copenhagen) correspond quite well with those from Salisbury. The most striking difference is that the number of species recorded on *S. nigra* is somewhat higher in Copenhagen (20) compared to Salisbury (12). Subset 2 (specialist) is much smaller and more species poor than the Salisbury and Copenhagen datasets, except in *H. sambuci*. In this species the specialist data are excessively species rich with 12 hosts recorded in a total sample of only 20 records, i.e. more than four times the number of hosts reported in the Salisbury and Copenhagen datasets, despite a much lower number of total records. The contribution of the specialist data to the total

number of species in the combined dataset (subsets 1 & 2) increases markedly from one species in *A. auricula-judae* over six in *S. nigra* and nine in *H. sambuci*.

We interpret these trends to be general, and reflective of the complexity of sampling fungal biodiversity. Thus, *A. auricula-judae* is an easily observed species. Voluntary fungal recorders will easily spot it, and will typically be able to identify the woody hosts on which it occurs, due to its preference for recently dead, often still attached dead wood. Sampling the fungal community on *S. nigra* is a more demanding task, because many macrofungi occurring on this host are not readily identified in the field. For this reason, even the modest, but more specialised sampling effort in the specialist subset contributes with a substantial number of unique species to the combined subset. Finally, *H. sambuci* is the trickiest species to explore using only random records from volunteers, which, in the Danish case, have strongly underestimated the real diversity of hosts utilised by this species. As already indicated this is because the species is only readily spotted and identifiable in the field, when it occurs on *S. nigra*. Records from other hosts are only reliable after microscopical examination of sampled specimens.

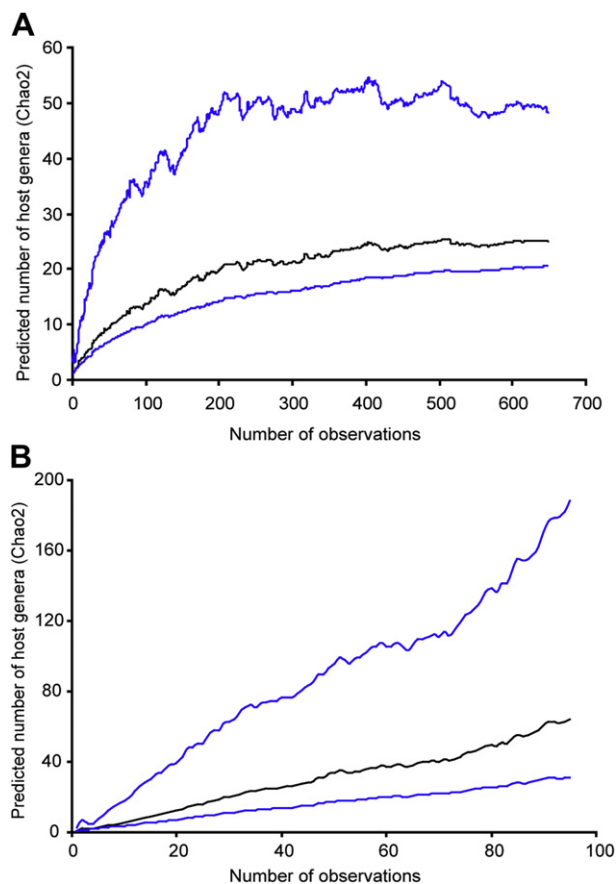


Fig 1 – The performance of the Chao2 estimator of total species richness of host genera utilised by *A. auricula-judae* (A) and *H. sambuci* (B) in Denmark, in relation to number of observations. Thin lines are 95 % confidence limits. Observations were added to the analysis in the same order as entered into the database by voluntary reporters. Note that x and y axes are scaled differently in A and B.

Changes in host selection and phenology in Salisbury – a critique

Now, one may ask why the Danish results are relevant in relation to Gange *et al.* (2011). They compare patterns of species richness and host selection over time, while we compare sampling quality between foray types. The comparison is relevant because it is unlikely that sampling quality has remained constant over the 59 yr covered by the Salisbury dataset. The fungal taxonomic knowledge has increased immensely in this period (e.g. Blackwell 2011), and the focus of curiosity most likely has changed over time. Possibly, it has become more and more common to look for other species than the standard records on various hosts, and we suggest that the changes in host selection of *A. auricula-judae* and the increasing number of fungal species recorded on *S. nigra* over time reported by Gange *et al.* (2011) may, at least partly, reflect changes in sampling quality, rather than biological changes.

Gange *et al.* (2011) also reported that *A. auricula-judae* has shifted its phenology in the study area over time, towards earlier fruiting, probably as a response to climate warming. Thus, the first fruiting date was statistically related to the preceding Mar. temperature, with higher temperatures resulting in earlier first fruiting dates in the fungus. Even though we certainly believe that climate change has had a strong impact on fruiting phenology in fungi (cf. Gange *et al.* 2007; Kausrud *et al.* 2010) we are puzzled by this result. *A. auricula-judae* is a fungus with tough and resistant fruit bodies and perhaps not the best candidate for a study on changes in fruiting phenology. In another study from southern England, Reid & Thomas (1985) reported that fruit bodies of the species can survive as spore producing for more than a full year and possibly longer despite being frozen solid at intervals and at other times becoming desiccated. The fruit bodies simply regain their flexible, fresh, spore producing

Table 1 – Number of records and species, and estimated total species richness for wood-inhabiting fungi on *Sambucus nigra* and hosts for *Auricularia auricula-judae* and *Hyphodontia sambuci* in Salisbury and Denmark. For the Danish dataset values are given both for the full dataset, and for two subsets, separate and combined. Numbers in brackets in the columns for the two subsets, marks the unique contribution of each subset to the combined dataset

Species		UK, Salisbury	Denmark, subset 1, Copenhagen	Denmark, subset 2, specialist	Denmark, subsets 1 & 2 combined	Denmark, full data set
<i>S. nigra</i>	Number of records	238	240	39	279	649
	Number of recorded species	12	20(18)	8(6)	26	41
	Predicted number of species (Chao2)	22	72	23	131	165
<i>A. auricula-judae</i>	Number of records	308	243	31	274	683
	Number of recorded species	16	15(11)	5(1)	16	20
	Predicted number of species (Chao2)	33	22	6	30	24
<i>H. sambuci</i>	Number of records	50 ^a	34	20	54	95
	Number of recorded species	4	5(2)	12(9)	14	19
	Predicted number of species (Chao2)	n.i.	11	29	29	64

n.i.: not indicated.

a A minimum based on Fig 5 in Gange et al. (2011).

stage in mild, wet periods. This observation is supported to be general, based on observations from other parts of Europe. For instance, Kriegelsteiner (2000) reported the species from all calendar months in an intensive mapping project in Southern Germany. The same pattern is evident in the Danish basidiomycote atlas. In this, 36 photos of fresh fruit bodies have been uploaded to document recordings. These are distributed over all calendar months, except Apr. and Sep., and with a peak in Mar. According to Kriegelsteiner (2000), new fruit bodies of the species are formed between Sep. and early Apr. In line with this, Reid & Thomas (1985) noted new fruit bodies in late Nov., while Lind (1913), based on observations from Denmark, stated that the fungus appears between Feb. and Jun.

Gange et al. (2011) do not exactly state how the distinction was made between fresh and old fruit bodies. According to their Fig 2 fresh fruit bodies were recorded between mid May and late Dec., but never in Jan. through Apr. which, as indicated above, is part of the main fruiting season in other parts of Europe. It is not possible for us to judge if this reflects nobody looking for the species during this period in Salisbury, but we predict that fresh fruit bodies of *A. auricula-judae* can be found through mild and humid winter and spring periods also in that area. Thus, we suggest that the reported change in fruiting phenology may reflect a shift in recording effort over the year, which in itself may have been influenced by climate change.

Finally, we are critical of the use of *H. sambuci* as a kind of standard species on which to evaluate the changes reported in *A. auricula-judae*. As already mentioned, *H. sambuci* is not easily identified in the field, except when found on *S. nigra*. The species is widespread and very common in temperate Europe, and according to Eriksson & Ryvarde (1976) it occurs “on deciduous wood of all sorts but most often in hedges, garden bushes, thickets etc. Even if it not restricted to *Sambucus (nigra)* as the epithet could suggest, it occurs with a striking regularity on this substrate”. From southern Germany, Kriegelsteiner (2000) enumerated 30 host genera,

while Bernicchia & Gorjón (2010) reported 26 different hosts, including conifers, dwarf scrubs and ferns from Italy. In the Danish atlas 19 host genera are recorded so far, including grasses, sedges and herbs. Of these the majority were recorded only in the specialist dataset, while only five hosts were recorded in the Copenhagen dataset. In this light, we suggest that the four hosts recorded from Salisbury represent only a superficial sneak preview into the actual host selection of *H. sambuci* in that area. More hosts are likely if sampling is extended to a broader selection of potential plant hosts, paired with microscopical examination of samples. The very strong predominance of records on *S. nigra* may be at least partly circular, reflecting that this host is where you expect to find the species, and also where it develops large, very conspicuous fruit bodies.

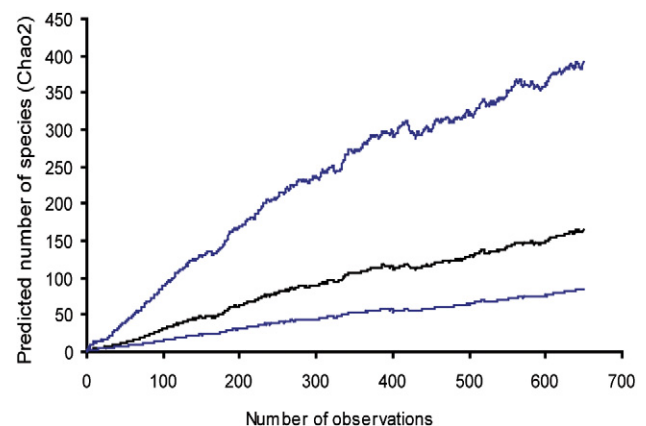


Fig 2 – The performance of the Chao2 estimator of total species richness for wood-inhabiting fungi predicted to occur on *S. nigra* in Denmark, in relation to number of observations. Thin lines are 95 % confidence limits. Observations were added to the analysis in the same order as entered into the database by voluntary reporters.

Judging from the analysis of the Danish data, there is the basis for even more curiosity in respect to exploring macrofungi fruiting on *S. nigra*. We see no reasons not to believe that the true diversity of macrofungi fruiting on this host in the Salisbury area is closer to, or indeed exceeding the Copenhagen estimate of 72 species rather than corresponding to the local estimate of 22 species.

In summary, we suggest that the changes in host selectivity and phenology over time reported from Salisbury could reflect a change in sampling quality just as well as biological changes. The statistical correlation between Mar. temperatures and first fruiting date in *A. auricula-judae* does at first sight support that biological changes have occurred, but as long as eventual changes in foray timing over the period are not indicated or controlled for, it is impossible for the reader to judge if this correlation is causal or incidental.

On the other hand it is worth mentioning that Gange *et al.* (2011) are not the first to discuss changes in the occurrence of *A. auricula-judae*. Thus, Knudsen & Pedersen (1980) reported the species to be expanding its range in Denmark, and being, at least in Southern Scandinavia, limited to zones with an average Jan. temperature exceeding 0 °C. As an alternative factor explaining the distribution of the species, Knudsen & Pedersen (1980) mentioned nutrient availability. Already Lange (1974) and van der Laan (1976) hypothesised that a high nutrient status was important in explaining the distribution of *A. auricula-judae* in Belgium, Denmark and the Netherlands. Thus, increased nitrogen levels and dust deposition may have made *F. sylvatica*, which naturally has a moderately acidic and nutrient poor bark (Barkman 1958), more suitable for *A. auricula-judae*.

Recommendations

In conclusion, we find it critical to appreciate time series data from fungal forays as very interesting, but tricky data sources with a substantial scientific potential. The knowledge of fungal taxonomy and ecology has increased immensely since the 1950's, fuelling curiosity and changing the behaviour of fungal forayers. Further, the appreciation of different habitat types has changed over time, in recent years reflecting an increasing focus on fungal conservation (Barron 2011). These shifts call for more sophisticated approaches to standardise data, not only considering sampling effort, but also sampling quality. Otherwise, it remains unclear whether changes in data reflect biological changes or changes in sampling quality.

As a minimum, standardising should involve attempt to control for changes in foray timing, habitat and substratum type representation over time, and account for the fact that different fungi vary considerably in detectability (Löhmus 2009). Gange *et al.* (2011) indicate that more analyses on host shifts based on the Salisbury dataset are under way. It will be very interesting to see the results of these analyses and the way that the data standardising challenge has been solved.

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