Article (refereed) - postprint

Jarvis, Susan G.; Holden, Elizabeth M.; Taylor, Andy F.S. 2017. **Rainfall and temperature effects on fruit body production by stipitate hydnoid fungi in Inverey Wood, Scotland**.

Rainfall and temperature effects on fruit body production by stipitate hydnoid fungi in Inverey Wood, Scotland

Susan G. Jarvis[1]*, Elizabeth M. Holden[2] and Andy F. S. Taylor[3,4]

[1] Centre for Ecology and Hydrology, Lancaster Environment Centre, Bailrigg, LA1 4AP, UK

[2] Caslum, Isle of Canna, PH44 4RS, UK

[3] The James Hutton Institute, Craigiebuckler, Aberdeen, AB15 8QH, UK

[4] School of Biological Sciences, University of Aberdeen, Aberdeen, AB24 3UU, UK

*Corresponding author. Email: susjar@ceh.ac.uk

Abstract

Stipitate hydnoid fungi are considered to be rare in the United Kingdom based on infrequent and localised observations of fruit bodies. Here, we investigate whether the production of stipitate hydnoid fruit bodies is related to weather conditions using a 14 year standardised survey of 11 species associated with Scots pine. Fruit body production was highly variable over time and asynchronous between species. Relationships with climatic predictors were variable between species, however both overall abundance and species richness of stipitate hydnoid fruit bodies were related to rainfall. These results suggest that climatic conditions in the preceding months can influence the likelihood of observing stipitate hydnoid fruit bodies, but that a large part of variation in fruiting of these taxa remains unexplained.

Main text

The occurrence and abundance of fungal fruit bodies are variable under natural conditions. Where surveys have been conducted in the same area over multiple years, many species are not observed in all years (Sato *et al.*, 2012) and there is often large variation in the number of fruit bodies produced when fruiting does occur (Straatsma *et al.*, 2001; Pilz *et al.*, 2006). It is important to understand the drivers of fruit body production because the presence or absence of fruit bodies is the primary measure used to determine the conservation status of fungi. Stipitate hydnoid fungi are ectomycorrhizal fungi which are considered to be rare in the United Kingdom based on infrequent observation of fruit bodies and evidence of declining occurrence across Europe (Newton *et al.*, 2002). It has been noted that these fungi produce fruit bodies sporadically, with sometimes several years between fruit body records (van der Linde *et al.*, 2012).

Using molecular identification techniques it has been shown that stipitate hydnoid fungi can be present and active belowground and not fruit for several years (van der Linde *et al.*, 2009, 2012; Gordon & Van Norman, 2014). This suggests that, for stipitate hydnoids, the sporadic fruiting patterns may be explained by variation in fruit body production between years, rather than rapid turnover of populations.

One potential driver of interannual variation in fruit body production is weather. Both the timing and production of fruit bodies have been linked to yearly variation in temperature and rainfall (Krebs *et al.*, 2008; Boddy *et al.*, 2014). There is evidence from previous studies that lagged weather influences on fungal fruiting can be important, for example temperature in previous months or years (Krebs *et al.*, 2008; Ágreda *et al.*, 2016). To narrow down the large possible range of weather related variables to a set of testable models, three hypotheses were derived regarding the timing of weather conditions and occurrence of stipitate hydnoid fruit bodies:

1. Fruiting is triggered by decreasing temperatures as autumn sets in and would be best predicted by the minimum temperature in the preceding month.

3

2. Fruiting occurs once photosynthate accumulation by the ectomycorrhizal host plant has reached a certain level and carbon begins to be moved belowground in higher quantities (Högberg et al., 2010), and is therefore related to accumulated growing degree days.

3. Fruiting is regulated by water availability and can only occur under sufficiently moist conditions (Wilkins & Harris, 1946), determined by total rainfall in preceding months.

To test these hypotheses requires a consistent survey of fungal fruiting across a relatively long period. The data used here are from a survey of stipitate hydnoid fruit bodies from a single Scots pine stand in Scotland over 14 years. The study site is located along a 150 metre transect approximately 8 metres wide in Inverey Wood, Scotland (56°59'N, 03°31'W) and is described in detail in van der Linde *et al*. (2012). The transect was surveyed three times a year (in August, September and October) between 2001 and 2014 by a single surveyor (EH) and all new stipitate hydnoid fruit bodies were recorded.

Long term fruiting surveys are relatively rare, and difficulties in maintaining survey effort over time mean it is sometimes necessary to adjust for potential biases in data collection reducing the power to detect patterns (e.g. Sato *et al.* 2012). The stipitate hydnoid survey used here is unusual in that data were collected by a single highly experienced surveyor from a small well defined area in a standardised manner. Combined with the focus on a single taxon and the relative longevity of stipitate hydnoid fruit bodies mean we have very high confidence that the survey recorded all fruit bodies present and error in identification was extremely low. This means that although the dataset is small, the power to detect true patterns in fruiting should be high.

Over 14 years of survey, 11 species of stipitate hydnoid fungi were recorded along the transect. Of these, three species only fruited in a single year (*Phellodon niger*, *P. tomentosus* and *Sarcodon squamosus*) and only one species fruited in every year (*Hydnellum ferrugineum*).

The number of fruit bodies recorded was highly variable between species and years (Figure 1). Most species appeared to show some degree of periodicity in fruiting whereby one or two years of high

4

production were followed by a year or more when few or no fruit bodies were produced. However, there was no evidence of synchronicity between the species i.e. peak fruit body production for different species occurred in different years.

To test the three hypotheses of how fruiting might link to weather, daily climate data from nearby weather stations were summarised to calculate minimum monthly temperature, accumulated growing degree days and total rainfall. Weather data were taken from the Braemar station (57°0'N, 03°23'W; 8.3 km distant) for all months except December 2002, January 2003, May, June and July 2005 and April 2008 when data were taken from observations at the Balmoral station (57°02'N, 03°13'W, 19 km distant) to replace missing data. All indices were calculated for, or up to, the month prior to the survey. Growing degree days were summed over all days from 1st January to the end of the month prior to survey. Rainfall was summed over three periods to test which was most important: the previous month, previous three months and previous six months. The final dataset is provided as Supplementary Data.

The three hypotheses were tested by fitting generalised linear mixed models with all three climatic terms as fixed effects. Firstly, to choose which temporal period to average rainfall over, three models with each aggregation period (previous month, previous 3 months, previous 6 months) plus the other two fixed effects were fitted to each species. Models were then compared using Deviance Information Criterion (DIC) and the model with the lowest DIC chosen. Secondly, the significance of each parameter in the best model was assessed by whether or not the 95% credible intervals of the estimate overlap zero.

For each species, fruit body counts on each sampling occasion were modelled as both abundance and presence-absence. Although abundance may be expected to be more sensitive to weather variation, it may also be more likely to be affected by non-climatic variables and, therefore, it may be harder to detect weather related patterns using this data. Occurrence of fruit bodies was modelled with a binomial distribution and abundance was modelled with an overdispersed Poisson

distribution by including individual level random effects (Hadfield, 2010). The total number of fruit bodies produced and the species richness observed were modelled as Poisson distributed variables. A random term for year was included in all models. All models were fitted using the MCMCglmm package with 1,000,000 iterations, 100,000 of which were treated as a burn-in period and discarded. Three chains were run for each model and the Gelman-Rubin diagnostic from the coda package (Gelman *et al.*, 2004; Plummer *et al.*, 2006) was used to check for convergence. Predictors were scaled and centred prior to analysis to improve convergence. All analysis was conducted in R version 3.0.3 (R Core Team, 2015).

Results of the models showed that there were no consistent relationships across taxa between either occurrence or abundance of fruit bodies and climatic variables, as might be expected given the lack of synchronicity in fruiting between species. Some species (*Hydnellum peckii*, *H. aurantiacum*) were more likely to occur after mild autumns while others (*Bankera fuligineoalba*, *H. ferrugineum*) were more abundant after high rainfall (Table 1). There was no evidence that growing degree days affected fruiting (hypothesis 2) nor that low temperatures in the preceding month were linked to fruiting (hypothesis 1). Therefore, patterns of fruiting and relationships with weather variables for individual species were highly variable. However across all species, high rainfall in the preceding months was linked to both higher species richness and total fruit body count, in accordance with hypothesis 3 and supporting previous findings (Boddy *et al*. 2014). The lack of consistent relationships between individual species likely reflects the influence of unmeasured drivers of fruiting. In particular, disturbance has been hypothesised to be a determinant of fruiting for these taxa (Newton *et al.*, 2002).

Our findings suggest that, although interannual climatic variation is linked to overall patterns in fruit body production of stipitate hydnoid fungi, variation in fruiting between species at this site is largely unexplained despite the fact that observer and detection biases were minimal. The small scale of this study, both spatially and temporally, limit the analysis and conclusions that can be drawn, and

longer term surveys replicated in multiple areas would add greatly to our understanding. However, maintaining such high quality surveys is challenging; the transect studied here has not been monitored since 2014. To monitor the conservation status of these fungi it would appear that multiple years of survey are required to fully census the species richness at any one site. Rare fruiters will be easily missed during field recording and, as our current assessments of species for inclusion on red lists is based on the appearance of fruit bodies, a better understanding of the factors that influence their fruiting patterns is important. Integration of molecular methods into long term surveys could help to achieve this and to identify whether aboveground declines in occurrence are also apparent belowground (Newton *et al.*, 2002).

7

References

Ágreda T, Águeda B, Fernández-Toirán M, Vicente-Serrano SM, Òlano JM. 2016. Long-term monitoring reveals a highly structured interspecific variability in climatic control of sporocarp production. *Agricultural and Forest Meteorology* **223**: 39–47.

Boddy L, Büntgen U, Egli S, Gange AC, Heegaard E, Kirk PM, Mohammad A, Kauserud H. 2014. Climate variation effects on fungal fruiting. *Fungal Ecology* **10**: 20–33.

Gelman A, Carlin JB, Stern HS, Rubin DB. 2004. *Bayesian Data Analysis*. Boca Raton, FL: Chapman and Hall/CRC.

Gordon M, Van Norman K. 2014. Molecular monitoring of protected fungi: mycelium persistence in soil after timber harvest. *Fungal Ecology* **9**: 34–42.

Hadfield JD. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* **33**: 1–22.

Högberg MN, Briones MJI, Keel SG, Metcalfe DB, Campbell C, Midwood AJ, Thornton B, Hurry V, Linder S, Näsholm T, *et al.* 2010. Quantification of effects of season and nitrogen supply on tree below-ground carbon transfer to ectomycorrhizal fungi and other soil organisms in a boreal pine forest. *New Phytologist* **187**: 485–493.

Krebs CJ, Carrier P, Boutin S, Boonstra R, Hofer E. 2008. Mushroom crops in relation to weather in the southwestern Yukon. *Botany* **86**: 1497–1502.

van der Linde S, Alexander IJ, Anderson IC. 2009. Spatial distribution of sporocarps of stipitate hydnoid fungi and their belowground mycelium. *FEMS Microbiology Ecology* **69**: 344–352.

van der Linde S, Holden E, Parkin PI, Alexander IJ, Anderson IC. 2012. Now you see it, now you don't: The challenge of detecting, monitoring and conserving ectomycorrhizal fungi. *Fungal Ecology* **5**: 633–640.

Newton AC, Watling R, Davy LM, Holden E, Ward SD. 2002. Progress towards implementing the Biodiversity Action Plan for stipitate hydnoid fungi in Scotland. *Botanical Journal of Scotland* **54**: 89–110.

Pilz D, Molina R, Mayo J. 2006. Effects of thinning young forests on chanterelle mushroom production. *Journal of Forestry* **104**: 9–14.

Plummer M, Best N, Cowles K, Vines K. 2006. CODA: Convergence Diagnosis and Output Analysis for MCMC. *R News* **6**: 7–11.

R Core Team. 2015. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing.

Sato H, Morimoto S, Hattori T. 2012. A thirty-year survey reveals that ecosystem function of fungi predicts phenology of mushroom fruiting. *PloS One* **7**: e49777–e49777.

Straatsma G, Ayer F, Egli S. 2001. Species richness, abundance, and phenology of fungal fruit bodies over 21 years in a Swiss forest plot. *Mycological Research* **105**: 515–523.

Wilkins WH, Harris GCM. **1946**. The ecology of the larger fungi V. An investigation into the influence of rainfall and temperature on seasonal production of fungi in a beechwood and a pinewood. *Annals of Applied Biology* **33**: 179–188.

Figure legends

Figure 1. Trends in total fruit body production (A) and species richness (B) of stipitate hydnoid fungi at Inverey over 14 y. For each plot the total number of fruit bodies across each of three survey dates is combined within each year. C) to J) show the pattern in fruiting for each species individually to demonstrate the irregularity of fruiting in these taxa (three species which only fruited in one year each are not shown). Note the scale of the y axis is variable between panels.

Table 1. Model information and coefficients from generalised linear mixed models of fruit body occurrence and abundance against climatic parameters. 95% credible intervals are shown in brackets. Only significant terms (where 95% credible intervals do not overlap zero) are shown, non-significant terms shown as NS.

Species[a]	No. occurrences (maximum 42 over 14 years)	Occurrence models		Abundance models	
		Minimum temperature in previous month	Aggregated rainfall	Minimum temperature in previous month	Aggregated rainfall
Bankera fuligineoalba	14	NS	2.52 (0.85, 4.20)*	NS	1.31 (0.27, 2.83)*
Hydnellum aurantiacum	8	3.49 (0.49, 8.42)	NS	NS	NS
Hydnellum ferrugineum	26	NS	1.67 (0.58, 2.96)‡	NS	1.00 (0.31, 1.77)‡
Hydnellum peckii	9	3.84 (0.86, 8.76)	NS	3.18 (0.57, 7.95)	NS
Hydnellum scrobiculatum agg.[b]	9	NS	NS	NS	4.08 (0.29, 11.20)†
Phellodon melaleucus	8	NS	NS	NS	NS
Sarcodon glaucopus	9	NS	NS	NS	NS
Total species richness	-	0.23 (0.03, 0.62)	0.40 (0.22, 0.55)*	-	-
Total fruit body number	-	-	-	NS	0.96 (0.39, 1.58)†

[a] Three species with one occurrence were not modelled (*Phellodon niger*, *P. tomentosus* and *Sarcodon squamosus*) along with one species with three occurrences (*Hydnellum caeruleum*)

[b] Model for *Hydnellum scrobiculatum* agg. showed poor convergence

*Rainfall aggregated over past month; † rainfall aggregated over past three months; ‡ rainfall aggregated over past six months. DIC used to select best model in each case