Fungal Ecology 22 (2016) 17–25

Contents lists available at ScienceDirect

Fungal Ecology

journal homepage: www.elsevier.com/locate/funeco

Climate impacts on fungal community and trait dynamics

Carrie Andrew [a,*], Einar Heegaard [b], Rune Halvorsen [c], Fernando Martinez-Peña [d,e], Simon Egli [f], Paul M. Kirk [g], Claus Bässler [h], Ulf Büntgen [f,i,j], Jorge Aldea [k], Klaus Høiland [a], Lynne Boddy [l], Håvard Kauserud [a]

[a] Section for Genetics and Evolutionary Biology (EVOGENE), University of Oslo, Blindernveien 31, 0316, Oslo, Norway
[b] Norwegian Institute of Bioeconomy Research, Fanaflaten 4, N-5244, Fana, Norway
[c] Department of Research and Collections, Natural History Museum, University of Oslo, NO-0318, Oslo, Norway
[d] Center for Agro-Food Research and Technology of Aragon (CITA), 50059, Zaragoza, Spain
[e] Cesefor Foundation, 42005, Soria, Spain
[f] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, CH-8903, Birmensdorf, Switzerland
[g] Mycology Section, Jodrell Laboratory, Royal Botanic Garden, Kew, Surrey, TW9 3DS, UK
[h] Bavarian Forest National Park, Freyunger Str. 2, D-94481, Grafenau, Germany
[i] Oeschger Centre for Climate Change Research (OCCR), Bern, 3012, Switzerland
[j] Global Change Research Centre AS CR, v.v.i., Belidla 986/4a, Brno, CZ, 60300, Czech Republic
[k] Sustainable Forest Management Research Institute, University of Valladolid-INIA, 34004, Palencia, Spain
[l] Organisms and Environment, Cardiff School of Biosciences, Biomedical Building, Museum Avenue, Cardiff, CF10 3AX, UK

A R T I C L E I N F O

Article history:
Received 23 October 2015
Received in revised form
5 March 2016
Accepted 14 March 2016

Corresponding editor: Jacob Heilmann-Clausen

Keywords:
Community structure
Fungi-forest-climate interactions
Life-history traits
Long-term data
Successional models

A B S T R A C T

Although climate change and variability can impact fungal phenology, the effects on community composition are less understood. Additionally, climatic variability might modify trait selection in fungi, including spore size and dispersal characteristics. Compositional and trait modifications of fungal communities would have important consequences for fungal biogeography, interactions with plant communities, and ecosystem functions. In this study, we analysed long-term fungal sporocarp community structure and dynamics in response to climate change and variability. We tested whether observed changes in the fungal sporocarp community related to climate, temporal or spatial differences among plots. Fungal trait associations with climatic variables were tested. Climate and endogenous patterns of succession each significantly affected composition, with regional variance in the affecting climate variables. Evidence for climate-driven reproductive trait selection related to spore dimensions, spore-bearing surfaces, and mode of fungal nutrition. Future research should then prioritize examining the impacts of climate on spore production and dispersal, plus other fungal traits.

1. Introduction

Global change and climate variability are both directly and indirectly impacting fungal ecology, including fruiting phenology, sporocarp production, and composition of communities based on presence of sporocarps (Gange et al., 2007; Kauserud et al., 2008a; Moore et al., 2008; Andrew and Lilleskov, 2009; Kauserud et al., 2010, 2011, 2012; Büntgen et al., 2013a; Diez et al., 2013; Andrew and Lilleskov, 2014; Boddy et al., 2014; Büntgen et al., 2015). Along with changes in phenology and production, traits such as spore and sporocarp characteristics are correlated with environmental variables (Kauserud et al., 2008b, 2011), suggesting a potential for cascading effects of phenological alterations on dispersal dynamics of fungal communities. Not only does climate affect fruiting and dispersal, but also inter-specific fungal interactions, interactions with hosts and other organisms, and trophic interactions (Gange et al., 2011, 2013; Boddy et al., 2014).

Given the unprecedented rate of change in environmental conditions exacerbated by anthropogenically induced climate change and variability (WMO, 2014), it is imperative to understand if, and how, it might alter fungal community composition (Lilleskov and Parrent, 2007). At the core of a community response to climate change are the species-specific responses, which vary in the magnitude of effect (e.g., Andrew and Lilleskov, 2009; Gange et al.,

* Corresponding author.
E-mail address: c.j.andrew@ibv.uio.no (C. Andrew).

http://dx.doi.org/10.1016/j.funeco.2016.03.005
1754-5048/

2011; Büntgen et al., 2012). While species often respond to climate at the individual-level (Crowther and Bradford, 2013), certain traits are shared across a species that can provide a more uniform measure of response to climate variability. These traits may be key to understanding how temporal changes in fungal communities are influenced by abiotic factors. For example, phenological processes at a national scale relate to climate (Kauserud et al., 2011). With respect to climate change and variability, other ecological traits such as nutrient modes (saprotrophic, ectomycorrhizal) and spore dimensions have likewise been implicated as important (Kauserud et al., 2011, 2012; Diez et al., 2013). Trait-mediated selection processes, then, may be of the utmost importance to future community composition.

To understand the impact of climate change and variability on fungal community change with time, we analysed two unique datasets from Spain and Switzerland consisting of 18 and 32 years of sporocarp surveys respectively. Previous research at both sites has established the importance of climate for sporocarp phenology and production: at the Swiss site, autumnal sporocarp appearances in August were delayed with warmer temperatures, and growing season precipitation positively impacted both sporocarp diversity and productivity from 1975 to 1999 (Straatsma et al., 2001). Additionally, selective thinning of the forest in 1986 resulted in understory tree release from canopy dominants with increased ectomycorrhizal sporocarp production two years later (Egli et al., 2010). At Pinar Grande, Spain, the total biomass of four commercially valuable edible taxa was highly influenced by autumnal weather patterns, with marked increases in productivity during warm and rainy years (Martínez-Peña et al., 2012a). Phenological responses by fungi to drought have also been documented at Pinar Grande (Büntgen et al., 2015). These results indicate a potential for climate to affect fungal community composition and dynamics over time, but this idea has not been tested.

Here, we used the Swiss and Spanish datasets to test whether climate change and variability are affecting fungal community dynamics. We specifically aimed to use these long-term datasets to tease apart the effects of climate variation, natural successional dynamics, and spatial variability on fungal community composition. We hypothesized that a combination of endogenous succession, climate forcing, and spatial variability would influence changes in the fungal community, but that the relative importance of these factors may vary between these datasets due to different climate and ecosystem contexts (e.g., the Spanish site is more generally precipitation-limited while the Swiss site more equally affected by precipitation and temperature). Finally we used these datasets to test how fungal traits relating to nutrient acquisition and dispersal (e.g., hymenial layer type and spore dimensions) may also be affected by climate and successional patterns.

2. Materials and methods

2.1. Site descriptions

Two datasets of high-resolution sporocarp count records, collected over 18–32 years from two different regions, Spain and Switzerland, were analysed in relation to climatic, temporal and trait-based changes. The datasets' timespan and intra-annual monitoring periods differed, but for both sites monitoring was comprehensive during the main fungal fruiting seasons of each region. However, these differences prevented direct statistical comparisons.

One data set was from the La Chanéaz Fungus Reserve near Payerne, Switzerland (Swiss Federal Institute for Forest, Snow and Landscape Research WSL; 46°47′55″ to 46°48′10″ N and 6°59′52″ to 7°00′30″ E) within a mixed forest dominated by European beech (*Fagus sylvatica*) and Norway spruce (*Picea abies*). La Chanéaz is situated at an altitude of ca. 585 m with a continental climate where temperature and precipitation are both limiting factors (Straatsma et al., 2001). Mean annual temperature, by monthly means, between 1975 and 2006 ranged from 7.8–10.5 °C (with an overall mean of 9.2 °C and standard deviation of 0.7 °C), and precipitation, again by monthly means, was 52.4–94.3 mm (overall mean of 73.7 mm and standard deviation of 11.5 mm). Please refer to the ‘Climate data’ section below for more information on the meteorological data.

Sporocarp count surveys at La Chanéaz took place from 1975 to 2006 at weekly intervals throughout the growing season of May to November (calendar weeks 20–50). Surveys were conducted within five 300 m^2 plots divided into 100 m^2 subplots, with a finer-detail sub-subplot sampling resolution of 1 m^2 implemented from 1992 onwards. Management history varied among the five plots within the site (i.e., there was within-site heterogeneity), but was consistent within each plot both before and during surveys. Periodic small-area (patch-wise) interventions were occasionally made to reduce canopy closure and ensure natural regeneration by native tree species.

The second dataset was from a Scots pine (*Pinus sylvestris*) forest in the Parque Micológico de Pinar Grande (ca. 41°52′04″ N, 02°56′10″ W) near Soria, Spain. There were eighteen 150 m^2 plots which differed in stand age and management history, with at least three plots per class (Büntgen et al., 2013b); ≤15 years, 16–30 years, 31–50 years, 51–70 years, > 70 years. Altitude at Pinar Grande ranged from ca. 1097–1543 m.

Summer precipitation was considered the main limiting climatic element at Pinar Grande. During the study period, mean annual temperature, by monthly means, ranged from 5.8 to 10.0 °C (with an overall mean of 8.1 °C and standard deviation of 1.2 °C) and precipitation, again by monthly means, from 37.6 to 132.1 mm (overall mean of 67.7 and standard deviation of 21.7 mm). Further details regarding the climate data are provided below.

Weekly sporocarp collections across the 150 m^2 plots were conducted at the 1 m^2 resolution between the calendar weeks of 35–50 from 1995 to 2012. A comprehensive analysis of production and composition with respect to site variability and management can be found in Martínez Peña (2008).

2.2. Fungal taxonomies and traits

Taxonomies between site datasets were synonymized based on Index Fungorum and Species Fungorum (Cannon and Kirk, 2007; Kirk et al., 2008; http://www.indexfungorum.org; www.speciesfungorum.org). Synonymies and nomenclatural changes across time were also accounted for during this process.

Taxa were removed from the final analyses if cap diameter measures were not available from published literature and also if they were biased by limited ability of collectors to notice them. The discarded taxa comprised 1.8% of all sporocarp records. Following taxonomic parsing, agaricoid sporocarps, i.e., pored and gilled taxa with stems and circular caps (sporocarps of the Agaricomycetes; see Supplementary material 1), remained.

Fungal traits for all taxa were compiled from Knudsen and Vesterholt (2008) and Breitenbach and Kränzlin (1991, 1994, 2000, 2005), as in Kauserud et al. (2008b, 2011). The following sporocarp traits were extracted from the texts: nutritional group (i.e., saprotroph or ectomycorrhizal) and habitat type, sporocarp durability, mean cap diameter, hymenial layer type, mean spore length, breadth and spore colour. Mean cap area was calculated from the mean diameter and was used for biomass estimates. Spore volume was estimated from spore length and breadth, assuming an ellipsoidal spore shape. Taxonomic categorizations (genus, family