



## Climatic effects on the distribution of ant- and bat fly-associated fungal ectoparasites (Ascomycota, Laboulbeniales)

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### ABSTRACT

Laboulbeniales (Ascomycota: Laboulbeniomycetes) are obligate ectoparasitic fungi of arthropods with a worldwide distribution. Their effects on host physiology and behaviour as well as their ecology have recently gained wider attention. One aspect that is virtually unknown regarding Laboulbeniales and arthropod-associated fungi in general, is how abiotic factors shape the distribution of these parasites. We used ant- and bat fly-associated Laboulbeniales to study whether climatic elements play a role in the distribution of fungal species. We collected uninfected and Laboulbeniales-infected insects belonging to three species: bat flies *Nycteribia schmidlii* and *Penicillidia conspicua* (Diptera: Nycteribiidae) and the ant *Myrmica scabrinodis* (Hymenoptera: Formicidae). We used climatic variables and performed statistical analyses to explain the distribution of Laboulbeniales infection. Our results show a higher likelihood of Laboulbeniales presence in habitats with low annual mean temperature and humidity, suggesting that climatic elements can considerably shape the distribution of Laboulbeniales species.

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### 1. Introduction

What is the distribution of any given species? What are the environmental factors and biological mechanisms underlying species distributions? These are among the fundamental questions for studies in ecology, evolution, and conservation (Ferrier, 2002; Rushton et al., 2004; Parmesan, 2006). Species distributions are shaped by abiotic and biotic factors. Abiotic climatic factors, such as

temperature and precipitation, presumably play a significant role in species occurrence and diversity (Duke et al., 1998; Whittaker et al., 2001; Araújo et al., 2008).

The distribution of parasites depends on the distribution of their potential host(s), although both do not necessarily overlap (Strona, 2015). The abundance, ecology, sex, and diversity of their hosts all have a modulating effect on parasite distribution (Anderson and Gordon, 1982; Christe et al., 2000; Stanko et al., 2006), with additional effects of abiotic factors, such as humidity, precipitation and/or temperature (Morgan et al., 2009; Froeschke et al., 2010). The increase in latitudinal parasite diversity in certain host taxa, such as micro- and macro-parasites of humans (Guernier et al., 2004) and vector-borne parasites in primates (Nunn et al., 2005), is explained

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in part by the climatic differences along the latitudes.

In contrast to certain animal taxa associated with vertebrates (e.g., bird lice, bat flies), studying the ecology and distribution of parasitic microbes and microfungi is often hindered by methodological constraints. The presence or absence of these microscopic organisms is often hard to observe on a sufficiently large number of hosts, as it may require living hosts, culturing methods, host dissection, etc. Furthermore, the number of individual parasites on a host is often hard to define or to determine, especially when dealing with filamentous species or unicellular microbes.

Several lineages of Fungi are obligate or opportunistic biotrophs, living in or on a wide range of host species. Members of the order Laboulbeniales (Ascomycota: Laboulbeniomycetes) are unique in that they form non-hyphal, multicellular fruit bodies or *thalli*, which are the result of determinate growth. Laboulbeniales complete their entire life cycle on the integument of a living arthropod and their thalli persist on host individuals (Haelewaters et al., 2015c; Báthori et al., 2018). Thus Laboulbeniales thalli can be easily recorded from and individually counted on any preserved host, providing an opportunity to study parasite prevalence, geographic spread, and thallus distribution over the host body.

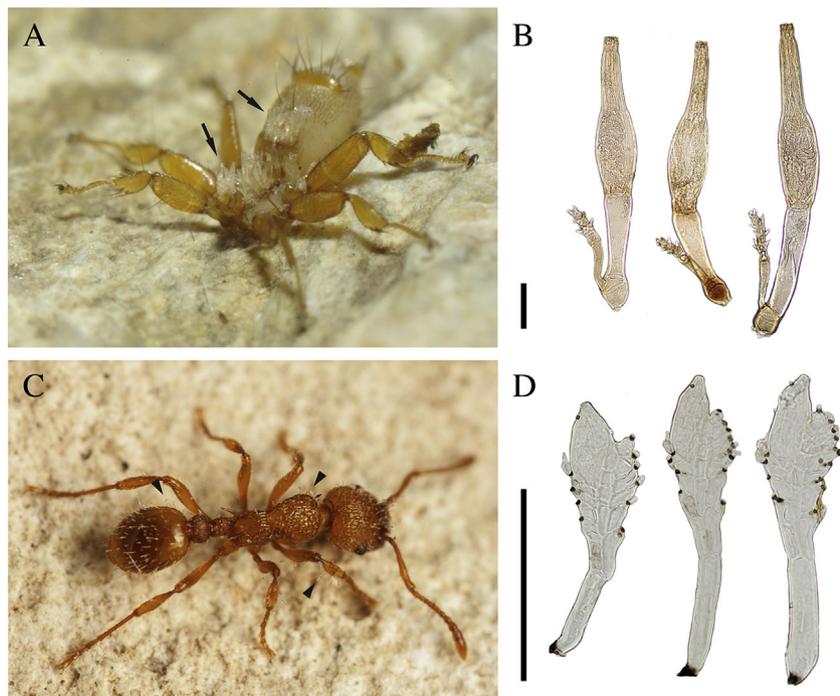
Climatic factors may contribute to the geographic spread and prevalence of Laboulbeniales (*sensu* Haelewaters et al., 2018). In this study, we address this question by exploring two parasite-host systems. These are well-documented examples that have yielded valuable insights into the biology of these fungi. *Arthrorhynchus eucampsipodae* and *Arthrorhynchus nycteribiae* are associated with Eastern Hemisphere bat flies (Fig. 1A–B) (Diptera: Nycteribiidae), whereas *Rickia wasmannii* is associated with *Myrmica* ants (Hymenoptera: Formicidae) in Europe (Fig. 1C–D).

Bat flies (Diptera: Nycteribiidae and Streblidae) are highly specialized, blood-sucking obligate ectoparasites of bats. These parasites are known or suspected vectors of several pathogens in bats (Dick and Patterson, 2006; Witsenburg et al., 2015). Bat flies show specialized morphological and physiological adaptations,

making them one of the most unique dipteran groups. They all have reduced eyes (ocelli) and highly modified body shapes, with a strongly chitinised integument. Females give birth to a single, third instar larva (instead of laying eggs, as most dipteran species). During the development, the larva feeds on the extraction of intra-uterine milk glands. When the third-instar larval stage is reached, females leave their bat hosts to larviposit the offspring on the host's roost wall (e.g., cave walls). The larvae immediately pupate and develop for a few weeks until emergence. The newly emerged adult flies immediately try to locate a new bat host (Theodor, 1967; Dick and Patterson, 2006).

Bat flies are divided into two cosmopolitan families, Nycteribiidae and Streblidae, but these groups are subject to phylogenetic revision (Dittmar et al., 2006). Nycteribiids show a predominantly Eastern Hemisphere distribution, and they are dorsoventrally flattened and wingless. Streblids, on the other hand, are more diverse in the Neotropical region, and the body plans and wings in this family are highly diverse. Streblid species range from laterally to dorsoventrally flattened. Most streblids have wings, although not always functional, while a minority (3%) is wingless (Dick and Patterson, 2006). In Europe, 16 nycteribiid and one streblid species have been reported so far (Szentiványi et al., 2016).

Thus far, four genera of Laboulbeniales have been found associated with bat flies (Haelewaters et al., 2018; Doggoniuck et al., 2019). These are *Arthrorhynchus*, *Dimeromyces*, *Gloeandromyces*, and *Nycteromyces*. *Gloeandromyces* (four species, three *formae*) and *Nycteromyces* (two species) occur on streblid bat flies. Species of *Gloeandromyces* are currently restricted to Central and northern South America, although the number of records is limited (Thaxter, 1917, 1931; Haelewaters and Pfister, 2019). *Nycteromyces streblidinus* is known from Central and South America, whereas the second species in the genus, *Nycteromyces orientalis*, is known from Tanzania, India, and Australia (Doggoniuck et al., 2019). *Dimeromyces* is a large genus with a wide host range encompassing 115 species, two of which were very recently described from bat flies



**Fig. 1.** Study systems discussed in this paper. (A) *Nycteribia schmidlii*, female bat fly infected by *Arthrorhynchus* sp. (groups of thalli indicated by arrows). (B) Three thalli of *Arthrorhynchus nycteribiae*. (C) *Myrmica scabrinodis* covered with *Rickia wasmannii* thalli (indicated by arrowheads). (D) Three thalli of *Rickia wasmannii*. Scale bars = 100 µm.

**Table 1**All bat fly species from *Miniopterus schreibersii*, with indication of association with Laboulbeniales fungi. When available, prevalence data is given.

Bat fly species	Laboulbeniales species	Prevalence	Reference(s)
<i>Nycteribia kolenatii</i>	No infection		Haelewaters et al. (2017)
<i>N. latreillii</i>	No infection		Szentiványi et al. (2018)
<i>N. parvula</i>	<i>Arthrorhynchus eucampsipodae</i>		Blackwell (1980)
<i>N. pedicularia</i>	No infection		Blackwell (1980), Szentiványi et al. (2018)
<i>N. schmidlii</i>	<i>A. eucampsipodae</i>	2.7%	Haelewaters et al. (2017)
	<i>A. eucampsipodae</i>	4.9%	Szentiványi et al. (2018)
	<i>A. nycteribiae</i>	0.4%	Blackwell (1980)
	<i>A. nycteribiae</i>	0.4%	Haelewaters et al. (2017)
<i>Penicillidia conspicua</i>	<i>A. nycteribiae</i>		Blackwell (1980)
	<i>A. nycteribiae</i>	23.1%	Haelewaters et al. (2017)
	<i>A. nycteribiae</i>	22.9%	Szentiványi et al. (2018)
<i>P. dufourii</i>	No infection		Haelewaters et al. (2017)
	<i>A. nycteribiae</i>		Blackwell (1980)
	<i>A. nycteribiae</i>	7.7%	Szentiványi et al. (2018)
<i>P. indica</i>	<i>A. nycteribiae</i>		Blackwell (1980)
<i>P. jenynsii</i>	<i>A. nycteribiae</i>		Blackwell (1980)
<i>P. oceanica oceanica</i>	<i>A. nycteribiae</i>		Blackwell (1980)
<i>Phthiridium biarticulatum</i>	No infection		Blackwell (1980)

(Rossi et al., 2015, 2016; Dogonniuck et al., 2019). *Arthrorhynchus* is specific to nycteribiid bat flies in the Eastern Hemisphere. Three species are recognised, of which *A. eucampsipodae* and especially *A. nycteribiae* (Fig. 1B) are the most common ones (Blackwell, 1980; Haelewaters et al., 2017). The third species, *Arthrorhynchus cyclopodiae* is only known from the type material in Papua New Guinea (Speiser, 1901). Additionally, Merola (1952) described a fourth species from Italy, *Arthrorhynchus acrandros*, which likely represents a synonym of *A. nycteribiae*. In Europe, *Nycteribia schmidlii*, *Penicillidia conspicua*, and *Penicillidia dufourii* appear to be the main hosts for *Arthrorhynchus* spp. (Haelewaters et al., 2017). Under extensive sampling, the observed parasite prevalence is 3.1–4.9% on *N. schmidlii*, 22.9–25.0% on *P. conspicua*, and 2.0–7.7% on *P. dufourii* (Haelewaters et al., 2017; Szentiványi et al., 2018). In addition, parasite prevalences seem to vary geographically (Szentiványi et al., 2018). A tripartite overview of *Miniopterus schreibersii* with its bat fly hosts and their associated Laboulbeniales fungi is given in Table 1.

Ants (Hymenoptera: Formicidae) play a significant role in many terrestrial ecosystems. They are often locally abundant and form symbiotic relationships with microbes, fungi, plants, and other animals (Hölldobler and Wilson, 1990). *Myrmica* is a widespread genus consisting of 188 extant and 11 fossil species (Bolton, 2016) and usually takes part in any temperate ant community (Jansen et al., 2010 and references therein). These ants can be found in several different environments across the temperate Holarctic region (Elmes et al., 1998). Habitats include forests, steppes, bogs, meadows, mountains, and human-altered landscapes (Jansen et al., 2010; Radchenko and Elmes, 2010). This variation over habitats may have an effect on diet, behaviour, and symbiotic relationships (Witek et al., 2014; Markó et al., 2016). In addition, Elmes et al. (1998) described disparate ecological preferences of European *Myrmica* species (to soil moisture and soil temperature).

Ants are the only known hymenopterans known to host Laboulbeniales. Of the six species of Laboulbeniales described on ants, *R. wasmannii* (Fig. 1D) is the most widespread. Reports of *R. wasmannii* are known from Austria, Belgium, Bulgaria, Czech Republic, France, Germany, Greece, Hungary, Italy, Luxembourg, the Netherlands, Poland, Romania, Slovakia, Slovenia, Spain, Switzerland, and the United Kingdom (Haelewaters et al., 2015b; De Kesel et al., 2016; Báthori et al., 2017). *Rickia wasmannii* can be found on ten *Myrmica* species (Báthori et al., 2017), but most published reports are from *Myrmica scabrinodis*. Nevertheless, host choice plasticity has been suggested based on data from the Netherlands, where Haelewaters et al. (2015b) found *R. wasmannii*

on *Myrmica sabuleti* (38%,  $n = 3876$ ), *M. scabrinodis* (11%,  $n = 643$ ), and *Myrmica ruginodis* (0.55%,  $n = 182$ ). Thallus density and parasite prevalence were calculated based on year-round pitfall capture data. Later, De Kesel et al. (2016), who collected directly from nests from the same site, found an infection prevalence of 100% on *M. scabrinodis* ( $n = 50$ ).

*Rickia wasmannii* and its most-often reported host, *M. scabrinodis*, have been increasingly studied to understand how Laboulbeniales affect their hosts at the individual level (Csata et al., 2014, 2017a; Báthori et al., 2015) and at society-level (Csata et al., 2017b). Moreover, this system has also been used to assess how infection varies across host colonies, host individuals, host age, body parts of hosts, habitats, and time of year (Haelewaters et al., 2015a; Markó et al., 2016; Báthori et al., 2018).

In this study, we investigated the effect of climatic factors on the distribution of Laboulbeniales using two distantly related insect groups. Employing both bat fly associates and ant associates allows us to account for a wide range of conditions. These phylogenetically unrelated insect groups are infected by closely related species of Laboulbeniales. Given the dissimilar biology and life histories of these insects, finding similar patterns of geographic distribution and prevalence of their ectoparasites related to climatic factors could lead to the formulation of general principles related to these interactions. Ecology may have more impact than host when considering patterns of geographical range and frequency of occurrence of these ectoparasites.

## 2. Material and Methods

### 2.1. Study systems

First, we chose *M. schreibersii* and its highly specialized bat flies *N. schmidlii* and *P. conspicua* to reveal the distribution of associated Laboulbeniales. *Miniopterus schreibersii* is a cave-dwelling bat species and the only European representative of the Miniopteridae family. *Miniopterus schreibersii* occurs mostly in the Mediterranean region, showing its northernmost distribution in Slovakia. It is a migratory species and often changes its roosting sites during the year, although consistent in using caves and underground places as roost sites. Females form nursery colonies during the summer where the colony size can reach up to thousands of individuals (Kunz, 1982). Two fungal species are found on the bat flies of *M. schreibersii*: *A. eucampsipodae* was during our recent surveys only associated with *N. schmidlii*, whereas *A. nycteribiae* parasitizes mostly *P. conspicua* but can also be found on *N. schmidlii*

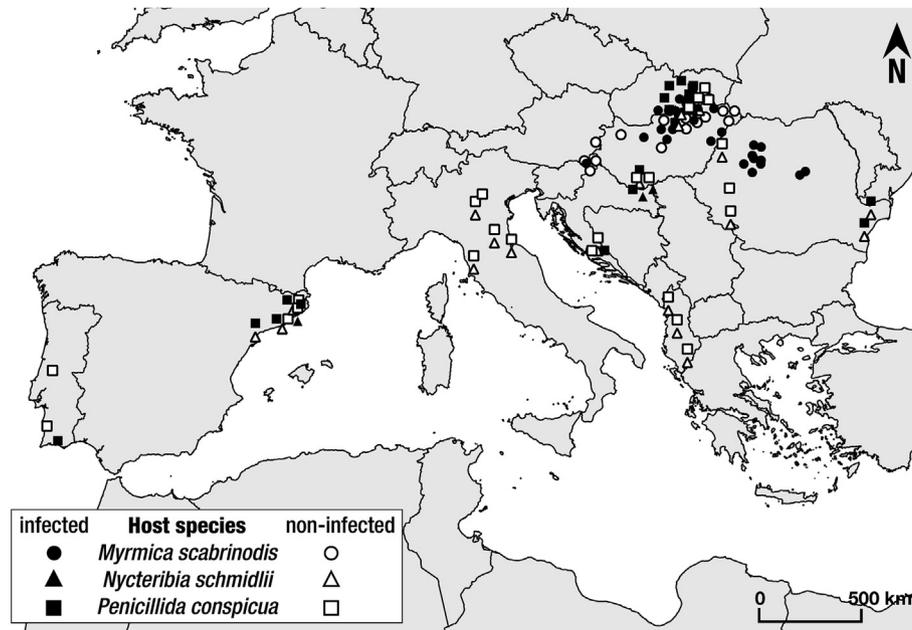


Fig. 2. Geographic coverage and sampling of the study. Some locations are displaced to show overlapping samples.

(Haelewaters et al., 2017; Szentiványi et al., 2018, Table 1).

In addition, we selected the ant *M. scabrinodis* and *R. wasmannii* as a second study system. We consider individual ant nests as colonies that can be either infected or uninfected. As a result, we do not present prevalence data about individual ants, but only at the level of the colony.

## 2.2. Material collection and identification

### 2.2.1. Bat flies and *Arthrurhynchus* spp.

Data from bat flies removed from *M. schreibersii* bats were taken from Haelewaters et al. (2017) and Szentiványi et al. (2018). This includes presence versus absence data of Laboulbeniales per screened bat fly specimen and prevalence information over bat fly species. Voucher bat fly specimens are deposited at the Museum of Zoology, Lausanne (Switzerland), under the access number: 2873-17CH02.

### 2.2.2. Ants and *Rickia wasmannii*

*Myrmica scabrinodis* ant nests were opened during the vegetation period in Hungary and Romania (Fig. 2) between 2001 and 2017. Five to ten workers per nest were stored in 67.5% ethanol for identification following Seifert (1988) and Radchenko and Elmes (2010). Voucher samples are deposited at the private collection of AT at the Department of Evolutionary Zoology and Human Biology, University of Debrecen and in the Hymenoptera Collection of the Hungarian Natural History Museum (Budapest). Additional data were collected from the literature from Hungary, Romania, and Slovakia (Tartally et al., 2007, 2008; Bezděčková and Bezděčka, 2011; Csata et al., 2013) and the Hymenoptera Collection of the Hungarian Natural History Museum. Identification of Laboulbeniales thalli was based on species descriptions in Thaxter (1908) and De Kesel et al. (2016).

## 2.3. Statistical analysis

### 2.3.1. Presence of Laboulbeniales fungi at the surveyed locations

Our table of presence data consisted of 114 observations on the presence or absence of thalli from 87 surveyed locations in 10

European countries, including all presence or absence data from three species of Laboulbeniales (*A. eucampsipodae*, *A. nycteribiae*, *R. wasmannii*). Raw data were grouped by locations, so in each observation (i.e. row), the location of survey, the host species present in the given location, and, when present, the species of the fungus were recorded. Therefore, we had records of presence of a given fungus species on a given host species in the surveyed locations. When no fungi were found, the absence of Laboulbeniales fungi was recorded for the given location.

For the analyses, bioclimatic variables were selected which were expected to explain infection patterns. Bioclimatic variables ( $n = 19$ , Table 2) are derived from monthly minimum temperature, maximum temperature and precipitation data (Busby, 1991). Climatic data were obtained from the MERRAclim database (Vega et al., 2017), using bioclimatic variables from the 2000s decade at 5 arcminutes resolution.

During preliminary analyses, we used Mann-Whitney's U tests to compare values of the different bioclimatic variables between infected and uninfected locations to assess which variables have considerable effect on Laboulbeniales presence. Holm's *post hoc* P-value adjustment (Holm, 1979) was then used to select the 11 significant variables (out of 19) for further analyses, namely: annual mean temperature (bio1), mean diurnal range (bio2), mean temperature of driest quarter (bio9), mean temperature of coldest

Table 2  
Bioclimatic variables used in the study (data source: Vega et al., 2017).

Variable	Description
bio1	Annual Mean Temperature
bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
bio9	Mean Temperature of Driest Quarter
bio11	Mean Temperature of Coldest Quarter
bio12	Mean Annual Humidity
bio13	Humidity of Wettest Month
bio14	Humidity of Driest Month
bio16	Humidity of Wettest Quarter
bio17	Humidity of Driest Quarter
bio18	Humidity of Warmest Quarter
bio19	Humidity of Coldest Quarter

quarter (bio11), mean annual humidity (bio12 as kg of water per kg of air; see Vega et al., 2017), humidity of the wettest month (bio13), humidity of driest month (bio14), humidity of the wettest quarter (bio16), humidity of the driest quarter (bio17), humidity of the warmest quarter (bio18), and humidity of the coldest quarter (bio19).

Variables were re-scaled (by dividing the variable by its standard deviation) and centred at zero (by subtracting the mean of the given variable from all values in the variable) before performing a principal component analysis (*stats* package, R Core Team, 2014). Prior to the estimation of principal components (PCs), all based on Kaiser (1960) criterion, we retained only principal components with eigenvalues of 1 or higher.

To evaluate the degree of association between fungus presence-absence and climatic predictors, we fitted a binomial generalized linear mixed-effects model (GLMM), using the *lme4* package in R (Bates et al., 2014), where presence-absence data was used as the binary response variable, while the principal components of bioclimatic variables were included as fixed explanatory variables. Host species was included in the model as a random factor to control for the non-independence of observations in these categories. We refer to this model as GLMM-A in the results.

### 3.2.3. Prevalence of *Arthrorynchus* fungi at the surveyed locations

Our table of prevalence data consisted of 69 observations on the prevalence of Laboulbeniales infection. Data were grouped by locations, therefore in each observation (i.e. row), the location of survey, the host species present in the given location, and, when present, the species of the fungus were recorded, together with the prevalence of infection with the given fungus species (i.e. proportion of infected hosts in all the surveyed individuals at the given location). Presence or absence data of *R. wasmannii* on *M. scabrinodis* were only collected on the scale of geographical locations; no data were available on the number of infected ants within a site. Consequently, prevalence of fungi was only analysed on the bat flies *P. conspicua* and *N. schmidlii*.

We used the same bioclimatic variables as described in the analysis of presence of Laboulbeniales fungi (Table 2). Similarly, we carried out a principal component analysis on the bioclimatic variables of the prevalence data to decrease the number of predictor variables and to eliminate linear correlation between predictors. A new principal component analysis was necessary because different climatic values were included in the prevalence-data table.

To assess whether there was an association between climatic factors and *Arthrorynchus* prevalence we fitted a binomial GLMM, in which prevalence was the response variable, while the calculated PCs were fixed predictors. We also included host species as a random factor. We refer to this model as GLMM-B in the results.

## 3. Results

### 3.1. Presence of Laboulbeniales at the surveyed locations

Of the 114 observations, 26 were from *N. schmidlii* ( $n = 615$  surveyed hosts), 46 from *P. conspicua* ( $n = 285$  surveyed hosts), and 42 from *M. scabrinodis* (infection was surveyed at colony-level; see Material and Methods). At least one species of Laboulbeniales was found at 47 (out of the 87) surveyed locations (Fig. 2).

Infection of the bat fly species with the different *Arthrorynchus* species was principally host-specific, as the recorded host-fungus pairs were almost exclusive: *N. schmidlii* infected by *A. eucampsipodae* and *P. conspicua* infected by *A. nycteribiae*. There were two exceptions: in one of the locations, *A. nycteribiae* was found on *N. schmidlii* ( $n = 3$ ), and in another location *A. eucampsipodae* was found on *P. conspicua* ( $n = 2$ ).

Regarding our ant–Laboulbeniales system, our dataset only included the host *M. scabrinodis*.

The principal component analysis yielded two components with eigenvalues higher than 1: PC1-A and PC2-A. The two components represented ca. 78% and 16% of the variance in the bioclimatic data, respectively, cumulatively explaining ca. 94% of the total variance (for the correlation of bioclimatic variables and calculated PCs of presence-absence data, see Fig. S1).

Based on the model GLMM-A, the first principal component (PC1-A) had a significant negative effect on the presence of Laboulbeniales fungi at the surveyed locations ( $z = -3.73$ ,  $P < 0.001$ ), whereas the second principal component (PC2-A) did not show a significant effect ( $z = -1.43$ ,  $P = 0.152$ ; see Fig. 3), indicating higher likelihood of Laboulbeniales presence in habitats of low annual mean temperature and humidity (Fig. 3).

### 3.2. Prevalence of *Arthrorynchus* fungi at the surveyed locations

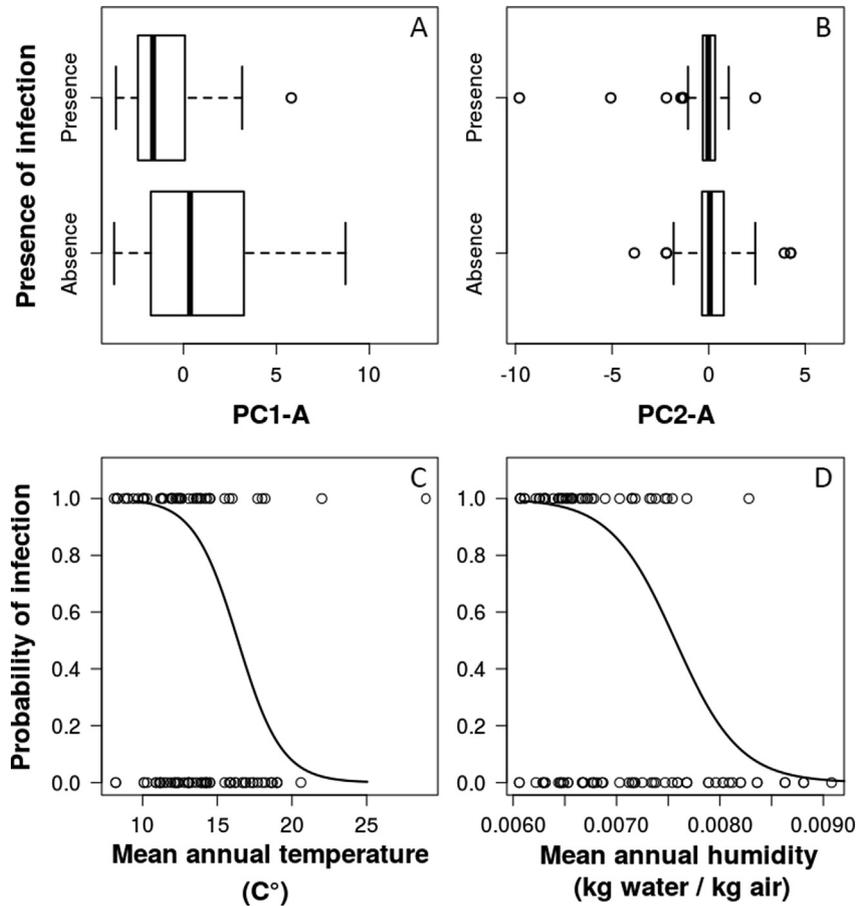
Of the 69 observations, 26 were on *N. schmidlii* bat flies and 43 on *P. conspicua* bat flies. In the habitats where *Arthrorynchus* was present, the average prevalence of *A. eucampsipodae* was  $19.9 \pm 12\%$  (mean  $\pm$  standard deviation), while prevalence of *A. nycteribiae* was  $47 \pm 29\%$  (total number of surveyed hosts: 615 and 285 of *N. schmidlii* and *P. conspicua*, respectively). Based on Kaiser (1960) criterion, we retained two principal components after principal component analysis, with the cumulative proportion of variance being ca. 94% (the individual proportion of variance explained were ca. 76% and 18% for PC1-B and PC2-B, respectively; for the correlation of bioclimatic variables and calculated PCs of prevalence data, see Fig. S2).

The results of the model GLMM-B showed that the first principal (PC1-B) component of bioclimatic variables significantly influenced the prevalence of *Arthrorynchus* fungi, showing a negative relationship between the principal component and prevalence ( $z = -2.15$ ,  $P = 0.032$ ; see Fig. 4). The second principal component (PC2-B) did not show a significant effect on prevalence ( $z = 0.34$ ,  $P = 0.735$ ). Based on these results, prevalence seems to be negatively affected by annual mean temperature and humidity (Fig. 4).

## 4. Discussion

The presence and intensity of Laboulbeniales infection can vary within and between populations due to biotic effects, such as host age and sex as well as aggregation behaviour (Nalepa and Weir, 2007; Báthori et al., 2018). Little is known about how abiotic factors influence the temporal and spatial distribution of these fungi. No research on this topic has been done regarding Laboulbeniales. For other fungal groups, studies have mostly focused on plant-microfungus systems, where (changing) climate conditions were shown to greatly affect plant pathogen distribution, host-fungus interactions (e.g., plant immunity, fungal virulence), and pathogen survival and reproduction, both in experimental and observational studies (Garrett et al., 2006; Velásquez et al., 2018). Particularly well-documented are systems involving *Fusarium* head blight (Sordariomycetes: Hypocreales), powdery mildews (Leotiomycetes: Erysiphales), and rusts (Pucciniomycetes: Pucciniales) of important crops, where field studies have been augmented by laboratory infection experiments and statistical modelling (e.g., Amsalem et al., 2006; Glawe, 2008; Del Ponte et al., 2009; Bebbler et al., 2016; de Valavieille-Pope et al., 2018).

In the present study on Laboulbeniales and ant or bat fly hosts (the latter as members of a tripartite relationship), the occurrence and prevalence of the infection at the sampled locations ( $n = 87$ ) is mostly affected by temperature and humidity, showing higher likelihood of fungal presence in habitats with low annual mean



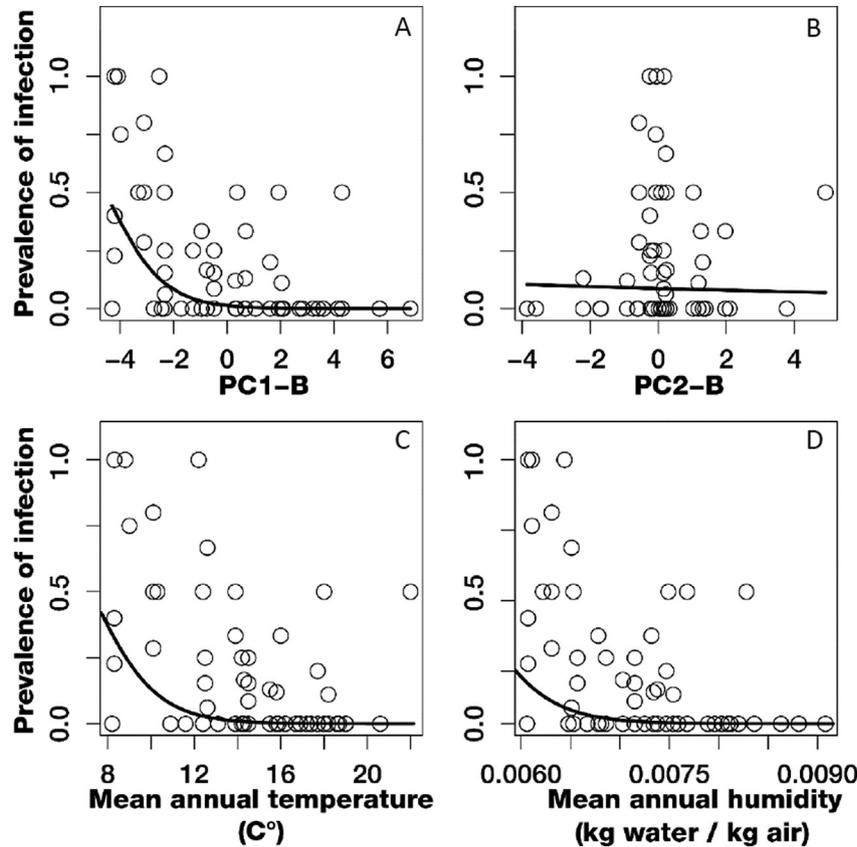
**Fig. 3.** Distributions of the values of first (PC1-A) and second principal components (PC2-A) calculated from 11 bioclimatic variables (A and B, respectively) in the absence and presence of Laboulbeniales fungi. Relationship of mean annual temperature (bio1, C) and presence of Laboulbeniales infection, and of mean annual humidity (bio12, D) with the presence of Laboulbeniales infections. Circles represent observed data, and curves show the probability of the presence of infection at a given value of mean annual temperature and mean annual humidity, predicted by GLMM-A ( $n = 114$ ).

temperature and humidity. Our data are the first to show the importance of abiotic factors in the distribution of Laboulbeniales on a large geographical scale, and to our knowledge, the first on hyperparasitic fungi.

It has been shown for numerous arthropod species that their immune response is temperature-dependent. For instance, the immune response is stronger at higher temperatures in crickets (Adamo and Lovett, 2011), termites (Fuller et al., 2011), and tenebrionid larvae (Catalán et al., 2012). These results suggest that higher temperatures contribute to disease resistance in insects. In areas with increased annual mean temperatures, bat flies and ants are less infected by Laboulbeniales, implying that these host populations might indeed be more resistant. Two notes should be made in this regard. First, it is impossible to assess the effect of temperature in germination or virulence of Laboulbeniales ascospores, because of the lack of physiological data. Second, the presence of immune-regulating bacteria can also alter pathogen development in their insect hosts (Kambris et al., 2009; Hughes et al., 2011; Wong et al., 2011). For example, *Wolbachia* intracellular bacteria are known to provide resistance to a range of pathogens and parasites, e.g., in mosquitoes (Moreira et al., 2009; Yixin et al., 2013) and flies (Gupta et al., 2017). Recent reports of *Wolbachia* symbionts in both ants and bat flies (Wilkinson et al., 2016; Treanor, 2017) underline the need for future investigations concentrating on the distribution of these bacteria and their possible immune-altering capabilities.

Cave-dwelling bats, including *M. schreibersii*, spend up to 62% of their time in caves (Codd et al., 2003), where climatic conditions are stable. This may play a role in the decreased reproductive activity of bat flies during winter months (Lourenço and Palmeirim, 2008). De Kesel (1997) showed that the presence of Laboulbeniales was significantly linked to the life cycle of their carabid hosts. We, therefore, hypothesize that the frequency of occurrence of Laboulbeniales on bat flies of cave-dwelling bats is lower during winter. The density of bat flies is higher during their reproductive period (Marshall, 1982), which increases opportunity for spore transmission because of the higher number of possible encounters between bat fly individuals.

*Miniopterus schreibersii* spends a considerable time (6 h per night) outside the cave actively foraging (Vincent et al., 2011). This means that associated bat flies are exposed to outside climatic parameters, which in turn may affect the biology and occurrence of their parasitic fungi. Outside climatic parameters and cave microclimate conditions may influence the distribution and reproductive success of ectoparasitic bat flies as well as their parasitic fungi. Additionally, *M. schreibersii* is a thermophilous species with a mainly Mediterranean distribution, suggesting that occurrence of fungi is actually more related to climatic effects, since host availability is not a limiting factor in warmer areas. Some factors may modulate climatic effects in the insect hosts' microhabitat: bat activity can modify the microclimate in caves, through heat



**Fig. 4.** Relationship of first (PC1-B) and second principal components (PC2-B) with prevalence of Laboulbeniales fungi (A and B, respectively). Relationship between mean annual temperature (bio1) and prevalence of *Arthrorhynchus* infection (C), and between mean annual humidity (bio12) and prevalence of *Arthrorhynchus* infection (D). Circles represent observed data, and curves show the predicted prevalence of infection at a given value of mean annual temperature and mean annual humidity, based on GLMM-B ( $n = 69$ ).

production and guano deposition (Baudinette et al., 1994). Similarly, ants are capable of thermoregulation of their nests (Banschbach et al., 1997) and worker individuals may frequently leave their nest for long periods of times (Jones and Oldroyd, 2006 and references therein), during which they are exposed to outside climatic conditions.

When the distribution of Laboulbeniales infection is examined on ants in different microhabitats, such as dry and moist sampling areas, fungal infection is dominantly present on ants preferring moister habitats (Markó et al., 2016), which suggests an interaction between infection and humidity. Our findings suggest that this interaction is negative on a larger geographical scale on the same host. In addition, Haelewaters et al. (2015b) found that *M. sabuleti*, which prefers drier habitats (Elmes et al., 1998), can be more heavily infected compared to *M. scabrinodis*, pointing to host choice plasticity and geographic variation in infection rates of *R. wasmannii*.

In general, studies on the influence of humidity on the presence and development of parasitic and pathogenic fungi on their hosts are contradictory (Roberts and Campbell, 1977 and references therein). This seems to be the result of contrasting ecological requirements in the development of different species. For instance, the occurrence of the entomopathogenic fungus *Beauveria bassiana* (Sordariomycetes: Hypocreales) does not seem to be affected by humidity on its beetle host *Acanthoscelides obtectus* (Coleoptera: Chrysomelidae) (Ferron, 1977). Nevertheless, both the transmission and development of some entomopathogenic fungi in the order Entomophthorales (Zoopagomycota: Entomophthoromycotina) seem to be influenced by humidity (Roberts and Campbell, 1977;

Pell et al., 2001). In addition, the psychrophilic fungus *Pseudogymnoascus destructans* (Leotiomycetes, *incertae sedis*), the causal agent of white-nose syndrome in cave bats throughout Europe and North-America, causing high mortality in populations at several places, is also known to prefer cold and highly humid environments (Langwig et al., 2012). In Laboulbeniales, it is generally suggested that higher humidity and temperature help the development and occurrence of the fungi (Meijer, 1975; Arndt and Desender, 2002; Riddick and Schaefer, 2005; Santamaria et al., 2014). De Kesel (1996) provided evidence that the development of Laboulbeniales is dependent on favourable environmental conditions but also a suitable host. In addition, our knowledge on how climatic elements might alter host behaviour is limited. Behavioural differences might also contribute to differences in symbiont transmission, presence, and prevalence.

In conclusion, our results confirm the importance of climatic elements – humidity and temperature – on fungal occurrence. We used two distant insect groups to test the climatic effect on ectoparasitic fungal infections. While these host groups show and occupy strongly different ecological needs and habitats, our results are consistent in both groups, highlighting the fact that these fungi have complex ecological relationships with their hosts, and in the case of bat fly-associated species, probably with the bat hosts of their hosts. Our results show that higher temperatures may be a limiting factor in the development of these fungi, either through their own ecological needs or, indirectly, through regulating the immune response of their hosts. We suggest concentrating future research on different taxonomic host groups where presence-absence infection data are available to reveal how parasitic and

pathogenic fungi are distributed not only on a geographical but also on a temporal scale to better understand disease dynamics in invertebrates.

### Ethics approval

Animal capture was conducted according to the Swiss Animal Legislation (legislation number 2964).

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### Competing interests

The authors declare that they have no competing interests.

### Availability of data and materials

Datasets supporting the conclusions of this article are included in [Supplementary Table 1](#) as well as [Supplementary Figure 1–2](#).

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### Supplementary data

Supplementary data related to this article can be found at <https://doi.org/10.1016/j.funeco.2019.03.003>.

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