


Herpomyces ectoparasitic fungi (Ascomycota, Laboulbeniales) are globally distributed by their invasive cockroach hosts and through the pet trade industry

Walter P. Pfliegler, Ferenc Báthori, Tristan W. Wang, András Tartally & Danny Haelewaters


To cite this article: Walter P. Pfliegler, Ferenc Báthori, Tristan W. Wang, András Tartally & Danny Haelewaters (2018) Herpomyces ectoparasitic fungi (Ascomycota, Laboulbeniales) are globally distributed by their invasive cockroach hosts and through the pet trade industry, Mycologia, 110:1, 39-46

To link to this article: <https://doi.org/10.1080/00275514.2017.1418567>

 View supplementary material 

 Published online: 04 Jun 2018.





 Submit your article to this journal 

 View related articles 

 View Crossmark data 



Herpomyces ectoparasitic fungi (Ascomycota, Laboulbeniales) are globally distributed by their invasive cockroach hosts and through the pet trade industry

Walter P. Pfliegler ^a, Ferenc Báthori ^b, Tristan W. Wang ^c, András Tartály ^b, and Danny Haelewaters ^{d,e}

^aDepartment of Biotechnology and Microbiology, University of Debrecen, Debrecen, Hungary; ^bDepartment of Evolutionary Zoology and Human Biology, University of Debrecen, Debrecen, Hungary; ^cHarvard College, Cambridge, Massachusetts 02138; ^dDepartment of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts 02138; ^eFarlow Reference Library and Herbarium of Cryptogamic Botany, Harvard University, Cambridge, Massachusetts 02138

ABSTRACT

The introduction of non-native animals occasionally results in the co-introduction of their microbial symbionts or parasites. The trade of exotic pets and zoo animals has inadvertently introduced several parasitic species to countries where they are non-native. Both the presence of suitable native hosts and opportunity for dispersal determine whether these non-native species become naturalized. During our studies dealing with species of *Herpomyces* (Ascomycota, Laboulbeniomyces), fungi that are exclusively ectoparasitic on cockroaches (Hexapoda, Blattodea), we make use of artificial colonies. Most of our specimens originate from pet stores and laboratory populations. Although they were originally intended for transmission studies, we discovered that some cockroaches from artificial colonies carried fruiting bodies of *Herpomyces*. We screened a total 292 cockroaches from 11 populations that we maintained after purchase. Sources were different pet stores, a toxicological laboratory, and a biological supply company. In eight populations, we found at least some *Herpomyces*-infected cockroaches. Parasite prevalence varied between 8.77% and 86.33%. Host associations were *Blatta orientalis* with *Herpomyces stylopygae*, *Blattella germanica* with *H. ectobiae*, *Periplaneta americana* with *H. periplanetae*, *Phoetalia pallida* with *H. leurolestis*, and *Shelfordella lateralis* with an undescribed species of *Herpomyces*. Apart from the new reports, host associations, and consequences for taxonomy (a new species based on morphological and molecular characters), we started to think about the geographic distributions of these fungi and how we, humans, shape them through spreading hosts and through international pet trade. We reviewed the currently known records of *Herpomyces*-associated cockroaches and host-parasite relationships. Based on the available data, on a global scale, at least half of the currently known species of *Herpomyces* are spread by globally invasive host species and through international pet trade. This indicates that the distribution and host range of these obscure and often unnoticed fungi are affected by human activities.

ARTICLE HISTORY

Received 23 February 2017
Accepted 14 December 2017

KEYWORDS

Fungal parasite; distribution; invasive species; laboratory animals; pet trade

INTRODUCTION

The study of microbial invasions is a relatively new and challenging field. The complexity of microbial communities, and difficulty of detecting invasive species, has prevented research into the biology and distribution of alien microbes (Litchman 2010; Kinnunen et al. 2016; Roy et al. 2017). Invasive microbes may be directly introduced by human activities (Litchman 2010) or indirectly co-introduced with other invasive multicellular species (e.g., Roy et al. 2011; Dunn and Hatcher 2015). Any of these natural enemies may be able to mediate invasion success of their host.


Introduced species may carry novel natural enemies to native hosts in the newly occupied range, the so-

called novel weapons hypothesis (Roy et al. 2011; Dunn and Hatcher 2015; Blackburn and Ewen 2016). Alternatively, introduction may result in loss of their natural enemies; this is the enemy release hypothesis (Jeffries and Lawton 1984; Colautti et al. 2004; Roy and Lawson Handley 2012). Often, these effects on invasion success are hard to evaluate, as seen in the case of microsporidia of the invasive *Harmonia axyridis*¹ supposedly killing native competitors (Vilcinskis et al. 2013; but see Solter et al. 2013; Gegner et al. 2015). Furthermore, the role of enemy release may differ between the different phases of an invasion (introduction, establishment, spread) (Drake 2003; Haelewaters et al. 2017).

CONTACT Walter P. Pfliegler; Danny Haelewaters  walterpfliegler@gmail.com (W.P.P.); dhaelewaters@fas.harvard.edu (D.H.)

The current address of Tristan W. Wang is Plant Pathology and Plant-Microbe Biology Section, School of Integrative Plant Science, Cornell University, Ithaca, New York 14850.

¹Taxonomic authorities for all fungal and insect taxa are provided in SUPPLEMENTARY TABLE 2.

 Supplemental data for this article can be accessed on the publisher's Web site.

© 2018 The Mycological Society of America

Successful co-introduction of a natural enemy is an important event, even if it does not influence the spread of its host. Any co-introduction represents the inadvertent appearance of an additional invasive species in the new range. If the natural enemy is able to shift to new host species and permanently associate with these hosts, its invasion history becomes independent from its original host (Lymbery et al. 2014). Theoretically, new exotic natural enemies may further negatively impact biodiversity by displacing native natural enemies that share a coevolutionary history with local hosts (sensu Heath and Whitaker 2015).

Fungi as introduced/invasive species.—Expanding world trade and climate change have raised concerns about the spread of invasive fungi and non-native plant diseases (Rossman 2009). Pimentel et al. (2005) estimated that over 20,000 species of microbes and plant diseases have invaded the USA, leading up to \$25.8 billion per year in economic losses and damages and control costs. Among introduced/invasive fungi, the focus has been on plant diseases, mainly because of their economic impacts. Reports on vertebrate-infecting species (e.g., chytridiomycosis in amphibians or mammalian lobomycosis) or on invasive macrofungi (e.g., *Clathrus archeri*, native to Australia and New Zealand) provide additional insight into how different fungi may rapidly spread to new geographic regions as a consequence of human activities. However, the range expansions of saprophytes and invertebrate-associated species, such as the enigmatic Laboulbeniales, remain poorly understood.

Laboulbeniales.—The order Laboulbeniales comprises 2100 species of microscopic, ectoparasitic fungi (Ascomycota, Laboulbeniomycetes). Hosts belong to three subphyla of Arthropoda: Chelicerata (subclass Acari, mites; and order Opiliones, harvestmen), Myriapoda (class Diplopoda, millipedes), and Hexapoda (class Insecta, true insects). Most Laboulbeniales occur on species in the orders Coleoptera (beetles, 80% of described species) and Diptera (flies, 10%), but they also parasitize Dermaptera (earwigs), Hemiptera (true bugs), Hymenoptera (Formicidae, ants), Mallophaga (bird lice), Orthoptera (crickets and allies), Thysanoptera (thrips), and Blattodea (cockroaches and termites) (Santamaria et al. 2017).

Laboulbeniales form microscopic fruiting bodies (thalli) on the external surfaces of host arthropods, enabling a relatively easy screening of living and preserved host specimens using a stereomicroscope. This

allows researchers to assess host-parasite associations over periods of time, especially when insects were collected in the context of all-taxa biodiversity inventories (e.g., Haelewaters et al. 2015). Both the taxonomy and species diversity of Laboulbeniales are actively studied. New discoveries such as county records and newly reported species are continuously expanding not only geographical ranges but also host spectra of the order. Thus far, however, few studies have focused on distributional range expansions or invasiveness of Laboulbeniales/Laboulbeniomycetes. In the following paragraphs, we review host associations and geographic spread of three species of Laboulbeniales that are non-native in North America (*Hesperomyces virescens*, *Ilyomyces mairei*) or Europe (*Laboulbenia formicarum*).

Hesperomyces virescens is currently under intensive investigation because its “main host” is the invasive multicolored Asian ladybird *Harmonia axyridis*, amongst around 30 other host species of ladybirds (Haelewaters et al. 2017). *Hesperomyces virescens* is spreading around the world, seemingly following its main host, although only after a certain time lag ranging between 2 and 16 y. *Harmonia axyridis* acquired the parasite after one or multiple host shifts from European and/or North American native ladybirds, after which *H. axyridis* quickly became the dominant host. This was possible because of several features that promote efficient transmission of *H. virescens* on this host species. These features include long life span as an adult, multivoltinism, promiscuity, and overwintering in dense aggregations.

Another example is the fungus *Ilyomyces mairei*, known from *Stenus* beetles (Coleoptera, Staphylinidae). *Ilyomyces mairei* was recently reported in Massachusetts, on a specimen of *Stenus clavicornis*, collected in 2007 (Haelewaters et al. 2015). Before this record, *I. mairei* was only known on *Stenus* spp. in France and Spain. *Stenus clavicornis*, the North American host species, is a European native that was introduced into North America in the 20th century, with the first record from Quebec in 1968 (Majka and Klimaszewski 2008). The report of *I. mairei* on this host from Massachusetts probably represents a co-colonization event through which both the host beetle and its ectoparasite somehow expanded their distributional range from Europe to North America. Possibly, there was a time lag between the expansion of the host’s range and the parasite’s.

The ant-associated species *Laboulbenia formicarum* is thought to have spread from North America (Espadaler et al. 2011) by an unknown host ant and became associated with at least two ant species native to Europe: *Lasius grandis* in Portugal (Madeira) and *L.*

niger in France (Espadaler and Santamaria 2003; Gómez et al. 2016). Recently, it was also discovered on the ant *Lasius neglectus*, which is an invasive species in Europe and probably originated from Asia Minor (Seifert 2000). Apparently, *L. formicarum* shifted to this new host in France and Spain. Although *L. formicarum* has probably infected *L. grandis* after a host shift from a non-native ant of North American origin (Espadaler and Santamaria 2003), the infection of *L. niger* in France may have happened because of co-occurrence with infected populations of *L. neglectus*.

Laboulbeniales on cockroaches.—*Herpomyces* Thaxt. is a genus of Laboulbeniales specialized on cockroaches (Hexapoda, Blattodea). It includes 25 species, some of which are associated with globally invasive hosts. Examples are *Herpomyces ectobiae* on *Blattella germanica*, *H. stylopygae* on *Blatta orientalis*, and *H. periplanetae* on *Periplaneta americana* (Thaxter 1908, 1931; Beccaloni et al. 2016). Unfortunately, in many cases, *Herpomyces* species have been reported on unidentified cockroaches. Because cockroaches are present all over the world and the distribution of many host species is relatively well known, *Herpomyces* may be an ideal target among Laboulbeniales to study biogeography over time on a global scale.

For our studies dealing with Laboulbeniales in general and *Herpomyces* in particular, we developed an interest in host specificity. How strict is the specificity of a given fungus to its host? Is there a one-on-one relationship, i.e., one host species for each fungal species, or is there a wider host range, and do environmental conditions affect this specificity (sensu De Kesel 1996; Cottrell and Riddick 2012)? For this purpose, our teams purchased cockroaches from pet stores and laboratory colonies. Because these specimens were intended to serve as targets, i.e., to be infected with ascospores of *Herpomyces* spp., we screened them to make sure they would be clean from infection. However, surprisingly, some cockroaches already carried *Herpomyces* thalli. This led us to the purchase of more cockroaches from artificial colonies and questions about the geographic distributions of these fungi and the role international trade may play.

In this paper, we present the results of screening 11 artificial populations of cockroaches from biological supply companies and pet stores for the presence of fungal infection. In addition, we review the entomological and mycological literature to identify the native area versus invasive ranges for all known *Herpomyces* hosts and verify their availability in the pet trade. We

aimed to assess the potential of insect trade in distributing fungal parasites of insects and, more generally, the potential of invasive cockroaches in distributing these parasites worldwide.

MATERIALS AND METHODS

Living *Blaptica dubia*, *Phoetalia pallida*, and *Shelfordella lateralis* were obtained from pet stores in Budapest and Debrecen, Hungary. Two populations of *Periplaneta americana* cockroaches were purchased from a North American biological supply company, and a third population was obtained from an online pet store in California, USA. The cockroaches were held in escape-proof terrariums in environmental chambers (25 ± 1 C and 14:10 [light:dark] h), each terrarium containing 20–50 specimens. Artificial colonies of *Blattella germanica* and *Blatta orientalis* cockroaches were maintained in a toxicological laboratory in Budapest, Hungary. Specimens for these colonies originated from free-living cockroaches, which were collected years ago in Budapest. Nomenclature of cockroaches follows Beccaloni et al. (2016).

Cockroaches were screened for *Herpomyces* infection using a stereomicroscope at 20–50× magnification. Screening happened upon arrival unless noted in TABLE 1. Parasite prevalence was assessed for the cockroaches in each artificial colony. Infected hosts were killed either in ethanol or by freezing and subsequently stored in 90–100% ethanol. We removed individual thalli from the host using Minuten Pins (BioQuip catalog no. 1208SA; Rancho Dominguez, California) inserted into wooden rods. Permanent slides were made in Amann solution following the procedures of Benjamin (1971) with modifications (Haelewaters et al. 2015). We viewed mounted specimens at 400–1000× magnification for identification using Thaxter's descriptions (1908, 1931). Microscope slides are deposited at Farlow Herbarium, Harvard University (FH).

In addition, we reviewed the available literature for the host species and distributional records of all described species of *Herpomyces*. Native and non-native distributions of each host species were surveyed from various literature sources. Availability in the pet trade industry for each host species was surveyed based on an Internet search using Google with each species name, their common synonyms, and the words “sale,” “pet,” and “colony” conducted on 21 Nov 2016.

Photographs were made using a Motic B1 compound microscope with USB Moticam 2500 camera and Motic Images Plus 2.0 software (Motic, Richmond, British Columbia, Canada).

Table 1. Host species, numbers of examined hosts, the prevalence of the infection, and the species of *Herpomyces* reported in this study.

Host species	Colony	Date obtained	Date screened	Prevalence (number of adult roaches screened)	Fungal species
<i>Blaptica dubia</i>	Pet store 1, Debrecen, Hungary	Nov 2013	Nov 2014	0% (<i>n</i> = 10)	—
<i>Blatta orientalis</i>	Toxicology laboratory, Budapest, Hungary	May 2015	Same date	36% (<i>n</i> = 25)	<i>Herpomyces stylopygae</i> Speg.
<i>Blattella germanica</i>	Toxicology laboratory, Budapest, Hungary	May 2015	Same date	8.77% (<i>n</i> = 57)	<i>Herpomyces ectobiae</i> Thaxt.
<i>Periplaneta americana</i>	Biological supplies company, North Carolina, USA	Mar 2015	Same date	66.67% (<i>n</i> = 27)	<i>Herpomyces periplanetae</i> Thaxt.
<i>Periplaneta americana</i>	Biological supplies company, North Carolina, USA	Feb 2016	Same date	86.36% (<i>n</i> = 22)	<i>Herpomyces periplanetae</i> Thaxt.
<i>Periplaneta americana</i>	Pet store, California, USA	Feb 2016	Same date	68.29% (<i>n</i> = 41)	<i>Herpomyces periplanetae</i> Thaxt.
<i>Phoetalia pallida</i>	Pet store 1, Debrecen, Hungary	Nov 2013	Nov 2014	40% (<i>n</i> = 15)	<i>Herpomyces leurolestis</i> Thaxt.
<i>Phoetalia pallida</i>	Pet store 2, Debrecen, Hungary	Feb 2015	Same date	0% (<i>n</i> = 20)	—
<i>Shelfordella lateralis</i>	Pet store 1, Debrecen, Hungary	Nov 2013	Nov 2014	80% (<i>n</i> = 40)	<i>Herpomyces</i> , sp. nov.
<i>Shelfordella lateralis</i>	Pet store 2, Debrecen, Hungary	Feb 2015	Same date	0% (<i>n</i> = 15)	—
<i>Shelfordella lateralis</i>	Pet store 3, Budapest, Hungary	Mar 2015	Same date	75% (<i>n</i> = 20)	<i>Herpomyces</i> , sp. nov.

RESULTS

We surveyed 11 populations of cockroach species obtained from pet stores as well as from a biological supply company and laboratory colonies. The number of examined hosts, their origin, the prevalence of infection, and the reported species of *Herpomyces* are given in TABLE 1. Cockroaches in eight colonies bore thalli of *Herpomyces*. *Herpomyces stylopygae* was found in the single colony of *Blatta orientalis* from the Hungarian toxicology laboratory. *Herpomyces ectobiae* was recorded in the one colony of *Blattella germanica* cockroaches from the same laboratory. An undescribed species of *Herpomyces* was present in two of the three colonies of *Shelfordella lateralis* obtained from different pet stores. *Herpomyces periplanetae* thalli were detected on *P. americana* specimens of all three colonies from the North American biological supply company and from the pet store in California, USA. Finally, *H. leurolestis* was found in one of two populations of *Phoetalia pallida*. All fungi were reported from the host species they were originally described from. Microphotographs for *H. stylopygae* and the undescribed *Herpomyces* from *S. lateralis* are given in FIG. 1.

DISCUSSION

New records and species of *Herpomyces*.—The records of *H. ectobiae*, *H. leurolestis*, and *H. stylopygae* are new for Hungary (Santamaria et al. 1991). *Herpomyces ectobiae* is known in all continents except Oceania. Thus far, European reports were from Belgium, France, Poland, and Spain (Santamaria 2003). *Herpomyces leurolestis* was described by Thaxter (1931) on *Phoetalia pallidus* (as *Leurolestes pallidus*) from Guyana and Trinidad and was not reported since. To date, *H. stylopygae* is only reported

from Belgium, Italy, France, Poland, and Spain in Europe (Santamaria 2003).

We discovered an undescribed species of *Herpomyces* on *Shelfordella lateralis*. The host was described as *Periplaneta lateralis* and then transferred to *Blatta (Shelfordella) lateralis* (Princis 1966). Later, Bohn (1985) raised *Shelfordella* to the genus level. The phylogenetic relationships between the genera *Blatta* and *Shelfordella* are still unresolved (Djernaes et al. 2012). Initially, we thought that the fungus was *H. stylopygae*, but after careful morphological examination, it was clear that it represented a new species. Among other characteristics separating it from *H. stylopygae*, the most striking is its secondary axis forming a completely hyaline shield; in *H. stylopygae*, the base of the shield is blackened (Spegazzini 1917; Thaxter 1931; FIG. 1). Also *H. periplanetae* has a hyaline shield but female thalli of this species carry a higher number of perithecia (generally five; Thaxter 1908). In addition to morphology, the new species is supported by sequence data of the internal transcribed spacer (ITS) region (ITS1-5.8S-ITS2 = ITS rDNA, to be exact) (unpubl. data). A formal description of the new species from *S. lateralis* will be presented along with sequence data in a subsequent publication (Haelewaters et al. in review).

***Herpomyces* in artificial cockroach colonies and insect trade.**—Artificial colonies of insects provide optimal environmental conditions for contact parasites such as Laboulbeniales, because these ectoparasites usually thrive best in dense host populations in damp and moist places (Wang et al. 2016). Such conditions allow for intra- and intergenerational transmission of ascospores. Since *Herpomyces* thalli are microscopic, measuring up to 225 μm long, infections mostly go unnoticed by the owners of the colonies. Laboratory cockroaches, which are often



Figure 1. Photographs of two female *Herpomyces* thalli. A. *Herpomyces stylopygae*. B. *Herpomyces*, sp. nov. The most striking differences between the two species are visible in the shield of the secondary axis of the female thalli. First, the length of the shield differs, being 51–80 μm in *H. stylopygae* and 26–56 μm in the undescribed species. Second, in *H. stylopygae*, the base of the shield is consistently blackened, whereas in the new species the shield is entirely hyaline. The arrowhead in B points at two antheridial necks, which are part of the much smaller male thallus (located behind the shield). Scale bar = 50 μm .

used as model organisms (e.g., Peterson et al. 2008), are apparently also hosts for these fungal parasites. Given that some Laboulbeniales are known to have certain effects on their hosts—data are available for *Hesperomyces virescens* (Nalepa and Weir 2007), *Laboulbenia formicarum* (Konrad et al. 2015), and *Rickia wasmannii* (Csata et al. 2014; Báthori et al. 2015)—the presence and abundance of *Herpomyces* in laboratory cockroaches used as model animals may have caused unrecognized, unwanted impacts on the outcome of toxicological and other studies.

Invasive routes of *Herpomyces* spp.—The cockroaches *B. orientalis*, *B. germanica*, and *P. americana* all have an almost worldwide distribution and reached Europe and North America hundreds of years ago, whereas *P. pallida* may have arrived to both continents more recently (Rehn 1945; Princis 1954; Kramer and Brenner 2009; Roques et al. 2009;

Beccaloni et al. 2016). Our literature review highlights inconsistencies between the native areas of the hosts and the geographic distribution of host-*Herpomyces* associations. Details for all 26 *Herpomyces* species are given in SUPPLEMENTARY TABLE 1, including their known distribution and host species, along with the native and invasive ranges of the hosts and availability in the pet trade.

Blatta orientalis is thought to have originated in southern Russia between the Black Sea and the Caspian Sea—Crimea has been mentioned as the westernmost border of its native range—and *H. stylopygae* was reported on this host from Europe, Africa, North and South America, and Asia (FIG. 2A). *Blattella germanica* probably originates from Asia and *H. ectobiae* was reported on specimens from Europe, Africa, Asia, and North and South America (FIG. 2B). *Periplaneta americana* originates from Africa, *H. chaetophilus* Thaxt. was reported on specimens from Africa, Asia, and North through South America, and *H. periplanetae* on specimens from Africa, Asia, Europe, and North through South America (FIG. 2C). *Phoetalia pallida* is native in Asia, and its parasite *H. leurolestis* was recorded from it in the West Indies and in Central and South America (FIG. 2D).

Based on these reports, *H. ectobiae*, *H. periplanetae*, and *H. stylopygae*, three fungal species so far never collected on European native cockroaches, are likely to be invasive in Europe and North America, much like their respective host species. *Herpomyces leurolestis*, on the other hand, represents an unintentional introduction by the pet trade industry in Europe, without having been reported in nature thus far in Europe.

Globally distributed *Herpomyces* spp.—To date, at least seven *Herpomyces* species have not been reported in their hosts' native range, only on continents where the host cockroach is an invasive species: *H. chaetophilus*, *H. diplopterae*, *H. leurolestis*, *H. nyctoborae*, *H. platyzosteriae*, *H. supellae*, and *H. tricuspoidatus*. In many parts of the world, the majority of reported *Herpomyces* species are associated with invasive hosts. This raises three scenarios for species of *Herpomyces* extending their range, and each of the widely distributed species may fall in one of these: (i) the fungi are introduced together with their hosts into new geographic areas; (ii) they follow their hosts into new ranges after a certain time lag (host pursuit), like *H. virescens* “lags” behind its main host, *H. axyridis*; or (iii) they shift between ecologically similar host species, from local hosts to the invasive hosts, or vice versa.

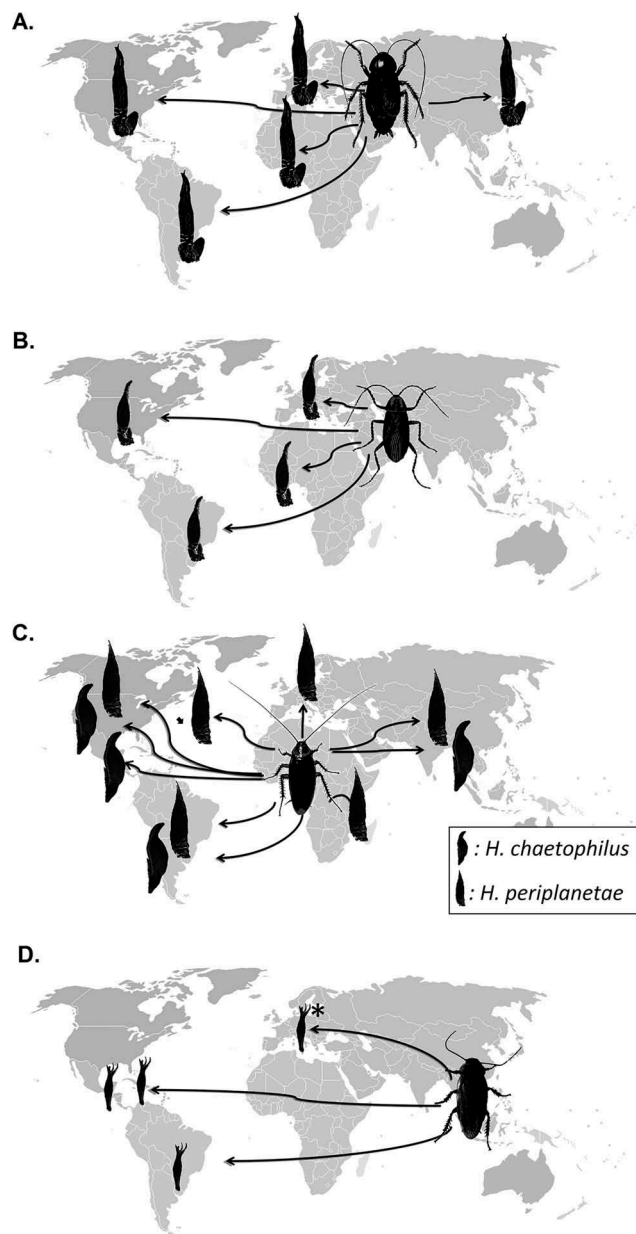


Figure 2. Records of *Herpomyces* spp. on some non-native cockroach hosts in different regions of the world, along with the hosts' native ranges. Silhouettes of hosts and fungal thalli represent records from individual continents or oceanic islands (with arrowhead representing the island of Bermuda). A. *Blatta orientalis* with *H. stylopygae*. B. *Blattella germanica* with *H. ectobiae*. C. *Periplaneta americana* with *H. chaetophilus* and *H. periplanetae*. D. *Phoetalia pallida* with *H. leurolestis*. An asterisk (*) represents occurrence of the fungus exclusively in captive populations. Images of fungi and host cockroaches not to scale.

If host shifts take place from local hosts to invasive ones, the fungi themselves are not considered invasive. In this case, the microevolutionary process of divergent natural selection between such populations experiencing different environmental conditions would have ultimately led to reproductive isolation

and even (incipient) speciation (Schluter 2000). Thus, deep divergence between fungal populations of a given species in different geographic areas could be expected, analogous to the recently described endemic lineages of the amphibian pathogen *Batrachochytrium dendrobatidis* (Rosenblum et al. 2013). Only detailed genetic data coupled with extensive collecting efforts from local and invasive cockroaches for each of these species will provide insights into their evolutionary history and their historic and current distribution patterns.

Herpomyces chaetophilus was recently reported on *P. americana* from Massachusetts, USA (Wang et al. 2016). The presence of this fungus in North America may be the result of host pursuit. The fungus was probably introduced into North America after Roland Thaxter's years of research, 1891–1932. Although Thaxter (1902) described *H. chaetophilus* himself, from Mauritius and Zanzibar, and although much of his fieldwork took place in eastern coastal North America (Pfister 1982), he never recorded it from this continent.

Interestingly, three species, *H. periplanetae*, *H. stylopygae*, and *H. tricuspidatus*, were reported from at least two different continents from multiple host species. This distribution pattern may be a consequence of invasive host-related dissemination or independent shifts by widely distributed fungal parasites to new hosts introduced to their range. Possible host shifts and widely disseminated hosts may hinder backtracking the original host and geographic range of many *Herpomyces* species, especially when these fungi have not been collected from wild native host populations. Several hosts of *Herpomyces* are available worldwide in the insect pet trade, and further screening may reveal additional species of these fungi disseminated with their hosts. We assume that the industry of exotic arthropod trade and the unintentional introduction of arthropods potentially account for other cases of exotic Laboulbeniales dissemination worldwide.

The histories of exotic hosts and fungal ectoparasites may vary from species to species. More collections and genetic comparisons of fungal populations internationally would help reveal how different fungi have become globally distributed or colonized newly arrived hosts in their native range. The data and scenarios presented here are parts of a more complex story, one we are only starting to unravel. We call for highly collaborative efforts, including focused field collections and generation of molecular data, to shed light on Laboulbeniales gaining advantage from insect invasions related to human activities.

ACKNOWLEDGMENTS

The authors thank József Schmidt for providing *B. germanica* and *B. orientalis* samples. The authors are grateful for Heidi Hopkins (Species File Group, University of Illinois Urbana-Champaign) for her excellent input with cockroach nomenclature and taxonomy and for commenting on a previous version of the manuscript.

D.H. wants to take the opportunity to specifically acknowledge Dr. Meredith Blackwell for being an inspiration for young, aspiring mycologists. Several years ago, in 2009, I contacted her and while I was just a simple, starting bachelor student at the time, she went far and wide to provide me with the answers I needed. She is a prime example of a researcher who is not shy to help or share data and, because of this, sets the bar high for other PIs, professors, and senior researchers.

Funding

W.P.P. was supported through the ÚNKP-16-4-IV New National Excellence Program of the Ministry of Human Capacities of Hungary. A.T. and F.B. were supported by the “AntLab” Marie Curie Career Integration Grant, part the 7th European Community Framework Programme. T.W.W. acknowledges the Harvard College Research Program, for supporting his senior thesis work on *Herpomyces* (2015–2016).

ORCID

Walter P. Pfliegler  <http://orcid.org/0000-0001-6723-4416>
 Ferenc Báthori  <http://orcid.org/0000-0001-5452-5257>
 Tristan W. Wang  <http://orcid.org/0000-0001-6889-2453>
 András Tartally  <http://orcid.org/0000-0002-3284-8239>
 Danny Haelewaters  <http://orcid.org/0000-0002-6424-0834>

LITERATURE CITED

- Báthori F, Csata E, Tartally A. 2015. *Rickia wasmannii* increases the need for water in *Myrmica scabrinodis* (Ascomycota: Laboulbeniales; Hymenoptera: Formicidae). *Journal of Invertebrate Pathology* 126:78–82, doi:10.1016/j.jip.2015.01.005
- Beccaloni G, Eades DC, Hopkins H. 2016. Cockroach Species File Online. Version 5.0/5.0. [cited 2017 Dec 09]. Available from: <http://cockroach.speciesfile.org/HomePage/Cockroach/HomePage.aspx>
- Benjamin R. 1971. Introduction and supplement to Roland Thaxter’s contribution towards a monograph of the Laboulbeniaceae. *Bibliotheca Mycologica* 30:1–155.
- Blackburn TM, Ewen JG. 2016. Parasites as drivers and passengers of human-mediated biological invasions. *Ecohealth* 14:S61–S73, doi:10.1007/s10393-015-1092-6
- Bohn H. 1985. *Blatta furcata* (Karny), the nearest relative of the Oriental cockroach (*Blatta orientalis* L.) (Insecta: Blattodea: Blattidae). *Israel Journal of Zoology* 33:39–50.
- Colautti RI, Ricciardi A, Grigorovich IA, Macisaac HJ. 2004. Is invasion success explained by the enemy release hypothesis? *Ecology Letters* 7:721–733, doi:10.1111/j.1461-0248.2004.00616.x
- Csata E, Erős K, Markó B. 2014. Effects of the ectoparasitic fungus *Rickia wasmannii* on its ant host *Myrmica scabrinodis*: changes in host mortality and behavior. *Insectes Sociaux* 61:247–252, doi:10.1007/s00040-014-0349-3
- Cottrell TE, EW Riddick. 2012. Limited transmission of the ectoparasitic fungus *Hesperomyces virescens* between lady beetles. *Psyche* 2012:814378, doi:10.1155/2012/814378
- De Kesel A. 1996. Host specificity and habitat preference of *Laboulbenia slackensis*. *Mycologia* 88:565–573, doi:10.2307/3761150
- Djernaes M, Klass K-D, Picker MD, Damgaard J. 2012. Phylogeny of cockroaches (Insecta, Dictyoptera, Blattodea), with placement of aberrant taxa and exploration of out-group sampling. *Systematic Entomology* 37:65–83, doi:10.1111/j.1365-3113.2011.00598.x
- Drake JM. 2003. The paradox of the parasites: implications for biological invasion. *Proceedings of the Royal Society B: Biological Sciences (Supplement)* 270:S133–S135, doi:10.1098/rsbl.2003.0056
- Dunn AM, Hatcher MJ. 2015. Parasites and biological invasions: parallels, interactions, and control. *Trends in Parasitology* 31:189–199, doi:10.1016/j.pt.2014.12.003
- Espadaler X, Lebas C, Wagenknecht J, Tragust S. 2011. *Laboulbenia formicarum* (Ascomycota, Laboulbeniales), an exotic parasitic fungus, on an exotic ant in France. *Vie Milieu* 61:41–44.
- Espadaler X, Santamaria S. 2003. *Laboulbenia formicarum* Thaxt. (Ascomycota, Laboulbeniales) crosses the Atlantic. *Orsis* 18:97–101.
- Gegner T, Otti O, Tragust S, Feldhaar H. 2015. Do microsporidia function as “biological weapon” for *Harmonia axyridis* under natural conditions? *Insect Science* 22:353–359, doi:10.1111/1744-7917.12224
- Gómez K, Espadaler X, Santamaria S. 2016. Ant-fungus Interactions: *Laboulbenia camponoti* Batra in Italy and a New Host for *L. formicarum* Thaxter (Fungi: Ascomycota, Laboulbeniales). *Sociobiology* 63:950, doi:10.13102/sociobiology.v63i3.1057
- Haelewaters D, Pfliegler WP, Gorczak M, Pfister DH. In review. Birth of an order: comprehensive phylogenetic study excludes *Herpomyces* (Fungi, Laboulbeniomycetes) from Laboulbeniales. *Molecular Phylogenetics and Evolution*.
- Haelewaters D, Zhao SY, Clusella-Trullas S, Cottrell TE, De Kesel A, Fiedler L, Herz A, Hesketh H, Hui C, Kleespies RG, Losey JE, Minnaar IA, Murray KM, Nedvĕd O, Pfliegler WP, Raak-van den Berg CL, Riddick EW, Shapiro-Ilan DI, Smyth RR, Steenberg T, van Wielink PS, Viglášová S, Zhao Z, Ceryngier P, Roy HE. 2017. Parasites of *Harmonia axyridis*: current research and perspectives. *BioControl* 62:355–371, doi:10.1007/s10526-016-9766-8
- Haelewaters D, Zhao SY, De Kesel A, Handlin RE, Royer IR, Farrell BD, Pfister DH. 2015. Laboulbeniales (Ascomycota) of the Boston Harbor islands I: species parasitizing Coccinellidae and Staphylinidae, with comments on typification. *Northeastern Naturalist* 22:459–477, doi:10.1656/045.022.0304
- Heath A, Whitaker AH. 2015. Mites (Acari: Pterygosomatidae, Macronyssidae) taken from lizards intercepted at the New Zealand border. *Systematic and Applied Acarology* 20:739, doi:10.11158/saa.20.7.3

- Jeffries MJ, Lawton JH. 1984. Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society* 23:269–286, doi:10.1111/j.1095-8312.1984.tb00145.x
- Kinnunen M, Dechesne A, Proctor C, Hammes F, Johnson D, Quintela-Baluja M, Graham D, Daffonchio D, Fodelianakis S, Hahn N, Boon N, Smets BF. 2016. A conceptual framework for invasion in microbial communities. *The ISME Journal: Multidisciplinary Journal of Microbial Ecology* 10:2773–2775, doi:10.1038/ismej.2016.75
- Konrad M, Grasse A V, Tragust S, Cremer S. 2015. Anti-pathogen protection versus survival costs mediated by an ectosymbiont in an ant host. *Proceedings of the Royal Society B* 282:20141976, doi:10.1098/rspb.2014.1976
- Kramer RD, Brenner RJ. 2009. Cockroaches (Blattaria). In: Mullen GR, Durden LA, eds. *Medical and veterinary entomology*. 2nd ed. New York: Academic Press. p. 43–58.
- Litchman E. 2010. Invisible invaders: non-pathogenic invasive microbes in aquatic and terrestrial ecosystems. *Ecological Letters* 13:1560–1572, doi:10.1111/j.1461-0248.2010.01544.x
- Lymbery AJ, Morine M, Kanani HG, Beatty SJ, Morgan DL. 2014. Co-invaders: the effects of alien parasites on native hosts. *International Journal for Parasitology: Parasites and Wildlife* 3:171–177, doi:10.1016/j.ijppaw.2014.04.002
- Majka CG, Klimaszewski J. 2008. Introduced Staphylinidae (Coleoptera) in the Maritime provinces of Canada. *Canadian Entomologist* 140:48–172, doi:10.4039/n06-099
- Pfister DH. 1982. A note on Roland Thaxter's collection localities. *Mycotaxon* 15:341–344.
- Pimentel D, Zuniga R, Morrison D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the U.S. *Ecological Economics* 52:273–288, doi:10.1016/j.ecolecon.2004.10.002
- Princis K. 1954. Wo ist die Urheimat von *Blatta orientalis* L. zu suchen? *Opuscula Entomologica* 19:202–204.
- Princis K. 1966. Blattariae: Suborbo Blattoidea. Fam.: Blattidae, Nocticolidae. *Orthopterorum Catalogus* 8:402–614.
- Rehn JAG. 1945. Three new species of the *Reticulosa* group of the Blattid genus *Cariblatia* (Orthopter, Blattinae, Pseudomopinae). *Notulae Naturae* 149:1–15.
- Rosenblum EB, James TY, Zamudio KR, Poorten TJ, Ilut D, Rodriguez D, Eastman JM, Richards-Hrdlicka K, Joneson S, Jenkinson TS, Longcore JE, Parra Olea G, Toledo LF, Arellano ML, Medina EM, Restrepo S, Flechas SV, Berger L, Briggs CJ, Stajich JE. 2013. Complex history of the amphibian-killing chytrid fungus revealed with genome resequencing data. *Proceedings of the National Academy of Sciences of the United States of America* 110:9385–9390, doi:10.1073/pnas.1300130110
- Rossmann AY. 2009. The impact of invasive fungi on agricultural ecosystems in the United States. *Biol Invasions* 11:97–107, doi:10.1007/s10530-008-9322-2
- Roy HE, Hesketh H, Purse BV, Eilenberg J, Santini A, Scalera R, Stentford GD, Adriaens T, Bacela-Spychalska K, Bass D, Beckmann KM, Bessell P, Bojko J, Booy O, Cardoso AC, Essl F, Groom Q, Harrower C, Kleespies R, Martinou AF, van Oers MM, Peeler EJ, Pergl J, Rabitsch W, Roques A, Schaffner F, Schindler S, Schmidt BR, Schönrogge K, Smith J, Solarz W, Stewart A, Stroz A, Tricarico E, Turvey KMA, Vannini A, Vilà M, Woodward S, Wynns AA, Dunn AM. 2017. Alien pathogens on the horizon: opportunities for predicting their threat to wildlife. *Conservation Letters* 10:477–484, doi:10.1111/conl.12297
- Roy HE, Lawson Handley L-J. 2012. Networking: a community approach to invaders and their parasites. *Functional Ecology* 26:1238–1248, doi:10.1111/j.1365-2435.2012.02032.x
- Roy HE, Rhule E, Harding S, Lawson Handley L-J, Poland RL, Riddick EW, Steenberg T. 2011. Living with the enemy: parasites and pathogens of the ladybird *Harmonia axyridis*. *BioControl* 56:663–679, doi:10.1007/s10526-011-9387-1
- Santamaria S. 2003. Laboulbeniales, II. *Acompsomyces-Ilyomyces*. *Flora Mycologica Iberica* 5:1–344.
- Santamaria S, Balazuc J, Tavares II. 1991. Distribution of the European Laboulbeniales (Fungi, Ascomycotina) an annotated list of species. *Treballs de l'Institut Botànic de Barcelona* 14:1–113.
- Santamaria S, Enghoff H, Gruber J, Reboleira ASP. 2017. First Laboulbeniales from harvestmen: the new genus *Opilionomyces*. *Phytotaxa* 305:285–292, doi:10.11646/phytotaxa.305.4.4
- Seifert B. 2000. Rapid range extension in *Lasius neglectus* (Hymenoptera, Formicidae)—an Asian invader swamps Europe. *Mitteilungen Museum Naturkunde Berlin, Deutsche Entomologische Zeitschrift* 47:173–179.
- Solter LF, Kyei-Poku GK, Johnny S. 2013. Comment on “Invasive harlequin ladybird carries biological weapons against native competitors”. *Science* 341:1342-c, doi:10.1126/science.1241600
- Schluter D. 2000. *The ecology of adaptive radiation*. Oxford, UK: Oxford University Press. 288 p.
- Spegazzini C. 1917. Revisión de las Laboulbeniales Argentinas. *Anales del Museo Nacional de Historia natural de Buenos Aires* 29:445–688.
- Thaxter R. 1902. Preliminary Diagnoses of New Species of Laboulbeniaceae. V. *Proceedings of the American Academy of Arts and Sciences* 38:9–57, doi:10.2307/20021736
- Thaxter R. 1908. Contribution towards a monograph of the Laboulbeniaceae. Part II. *Memoirs of the American Academy of Arts and Sciences* 13:217–469, doi:10.2307/25058090
- Thaxter R. 1931. Contribution towards a monograph of the Laboulbeniaceae. Part V. *Memoirs of the American Academy of Arts and Sciences* 16:1–435, doi:10.2307/25058136
- Vilcinskis A, Stoecker K, Schmidtberg H, Röhrich CR, Vogel H. 2013. Invasive harlequin ladybird carries biological weapons against native competitors. *Science* 340:862–863, doi:10.1126/science.1234032
- Wang TW, De Kesel A, Haelewaters D, Pfister DH. 2016. Farlow Herbarium cockroach hosts new record of Laboulbeniales for North America. *Rhodora* 118:26–31, doi:10.3119/15-20