



Tropical Occurrence and Agricultural Importance of *Beauveria bassiana* and *Metarhizium anisopliae*

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Specialty section:

This article was submitted to
Agroecology and Ecosystem Services,
a section of the journal
Frontiers in Sustainable Food Systems

Received: 11 October 2019

Accepted: 09 January 2020

Published: 29 January 2020

Citation:

McGuire AV and Northfield TD (2020)
Tropical Occurrence and Agricultural
Importance of *Beauveria bassiana* and
Metarhizium anisopliae.
Front. Sustain. Food Syst. 4:6.
doi: 10.3389/fsufs.2020.00006

Entomopathogenic fungi are often relied on as important components of integrated pest management in tropical agriculture, either as biopesticides or as naturally occurring microbes conserved in the environment. Tropical abiotic conditions are often well-suited for microbial growth, and tropical habitats can be teeming with microbial biodiversity. However, competitive interactions with other fungi and the need to overcome defenses of hosts adapted to high fungal loads may inhibit the ability of insect pathogens to control tropical pests. Here, we review the current literature on *Beauveria bassiana* and *Metarhizium anisopliae* inhabiting tropical environments and their potential use as biological control agents. In some cases there is not a clear distinction between temperate and tropical agroecosystems, such as in the level of organic matter or soil texture in agricultural soils. Therefore, the effects of these soil characteristics in temperate agroecosystems are likely applicable to tropical systems as well. In contrast, factors such as microbial biodiversity and seasonal fluctuation in environmental conditions can differ dramatically between temperate and tropical systems. Therefore, we discuss literature that can be generalized to tropical systems. Where temperate and tropical systems are likely to differ we synthesize the literature specifically for tropical agroecosystems. We also provide hypotheses to stimulate future work on latitudinal gradients and the relative importance of biotic and abiotic factors in governing entomopathogen prevalence and community composition. These hypotheses provide a path forward to developing theory guiding the conservation and augmentation of entomopathogenic fungi to prevent pest outbreaks.

Keywords: *Beauveria bassiana*, *Metarhizium anisopliae*, biological control, biopesticide, IPM, entomopathogenic fungi

INTRODUCTION

Growing insecticide resistance and impacts on human and environmental health have encouraged entomopathogenic fungi (EPF) use for biocontrol (Inglis et al., 2001). Tropical environments support impressive microbial biodiversity (Thompson et al., 2017), including many parasites of arthropods (Mahe et al., 2017). However, by far the most common commercially available EPF in tropical and subtropical agroecosystems belong to two genera: *Beauveria* and *Metarhizium* (Ascomycota: Hypocreales) (Faria and Wraight, 2007; Li et al., 2010; Kumar et al., 2018; Mascarin et al., 2019). Here, we review literature focused on controlling arthropod pests with entomopathogens, with particular emphasis on these two genera.

Metarhizium and *Beauveria* have pan-global distributions revealing significant genetic diversification, with a wide insect host range and vast ecological niches (Driver et al., 2000; Rehner and Buckley, 2005; Zimmermann, 2007). Thus, many aspects of using these EPF to control pests span latitudinal gradients, and we discuss these generally. Environmental conditions and species compositions, however, can differ greatly between tropical and temperate regions, so we discuss these factors with specific reference to tropical studies and use general theory resulting from model systems to bridge gaps in the current literature and stimulate further studies.

EPF are generally formulated as biopesticides and applied in response to outbreaks. However, if the habitat is well-suited for the particular fungal strain to the environment it may be possible for fungal applications to serve as inoculative releases, where the EPF remain in the soil and prevent insect outbreaks. Here, we describe entomopathogenic fungal niche preferences to help inform EPF use to prevent pest outbreaks. We focus on two species *Beauveria bassiana* and *Metarhizium anisopliae*, but each most likely represents a broader range of species and strains that were previously grouped together. Therefore, the majority of cited papers regarding these fungal species refer to *Beauveria bassiana* and *Metarhizium anisopliae sensu lato*, due to recent taxonomic revisions (e.g., Driver et al., 2000; Bidochka et al., 2001; Inglis et al., 2019).

BEAUVERIA AND METARHIZIUM

Entomopathogenic fungal species, *B. bassiana* and *M. anisopliae* control a wide range of pests (Kassa et al., 2004; Castrillo et al., 2010; Migiro et al., 2010; Singha et al., 2010; Skinner et al., 2012; Akmal et al., 2013; Wraight et al., 2016). These fungi can also inhabit the leaf surface of variety of plant species and environments (Meyling and Eilenberg, 2006a; Garrido-Jurado et al., 2015), inhabit soil as saprophytes (Evans, 1982), or grow endophytically (Greenfield et al., 2016). The apparently wide distribution and diversity of pathogen hosts attacked by these fungi, and persistence in the environment when hosts are rare suggest potential value in integrated pest management programs across diverse locations and conditions (Lacey et al., 2015).

Fungal propagule persistence and efficacy on plants is directly influenced by temperature, humidity, sunlight, and microbial activity on the phylloplane (Jaronski, 2010). Much of our knowledge comes from *in vitro* studies (Fargues et al., 1997; Luz and Fargues, 1997; Fargues and Luz, 2000; Devi et al., 2005; Shin et al., 2017). However, it is unclear whether *in vitro* data be extrapolated to field conditions (Keyser et al., 2017), due to environmental influence on processes such as infection potential, conidial persistence and complex abiotic and biotic interactions that are rarely duplicated in laboratory environments (Inglis et al., 2001; Lacey et al., 2015).

Metarhizium and *Beauveria* readily colonize plant rhizospheres, forming endophytic associations (Vega et al., 2009; Behie et al., 2015). *Beauveria* species associate with several tropical or subtropical plant species, including cocoa (Posada and Vega, 2005), banana (Akello et al., 2008), and coffee (Vega, 2008). Post-endophytic colonization, *Metarhizium robertsii* can

even transfer insect-derived nitrogen to plants (Behie et al., 2012). *Beauveria* and *Metarhizium's* plant host affiliations in agriculture and ecosystem services (i.e., beneficial symbiosis in plants and control of insect pest populations) make them promising candidates for their application as biopesticides in tropical agriculture. The use of EPF as biopesticides in a variety of agroecosystems provides exciting and sustainable farm management opportunities, but in depth knowledge of endemic fungal species is crucial to identifying scenarios and environments when the insect pathogen will be most effective (Meyling and Eilenberg, 2007; Meyling et al., 2009; Perez-Gonzalez et al., 2014).

LIFE IN THE SOIL

Soil can act as a reservoir for fungal inoculates (Castrillo et al., 2010), dispersing above-ground by wind, rain-splash and insect activity, or via infection of soil-dwelling insects and radial hyphal growth (Meyling and Eilenberg, 2007). Hypocreaean fungi efficacy and persistence is influenced by soil type, moisture levels, and microbial interactions (Inglis et al., 2001). While tropical soils may contain very high organic matter and microbial diversity, the agricultural levels for each depend primarily on farm management practices (Moeskops et al., 2010; Bai et al., 2018), and texture varies widely amongst tropical soils without clear distinctions from temperate systems (Pulla et al., 2016). Therefore, temperate studies describing soil physical characteristics effects on EPF persistence and efficacy are likely directly applicable to tropical systems.

Soils high in organic matter often teem with microbes, potentially allowing antagonistic interactions between microbes (Inglis et al., 1998; Pal and Gardener, 2006). In temperate studies, antagonistic effects of increased microbial activity in the soil contributed to the inhibition of *B. bassiana* (Studdert and Kaya, 1990; Kessler et al., 2003; Quesada-Moraga et al., 2007), *B. brongniartii* (Kessler et al., 2004), and *M. anisopliae* (Jabbour and Barbercheck, 2009). For example, high soil moisture content promoted occurrence of antagonistic organisms, suggesting soil moisture could either directly or indirectly reduce conidia survival (Lingg and Donaldson, 1981; Jabbour and Barbercheck, 2009). However, this has been refuted by other studies in temperate regions finding little or no relationship between soil moisture and EPF occurrence, potentially due to limited variation in sampled soil moisture levels or oxygen deficiency (Griffin, 1963; Ali-Shtayeh et al., 2003; Kessler et al., 2003).

Soil oxygen levels during infection can promote mycelial growth, thermal tolerance, germination, and virulence against insects (Garza-López et al., 2012; Miranda-Hernández et al., 2014; Garcia-Ortiz et al., 2015; García-Ortiz et al., 2018; Oliveira and Rangel, 2018). *In vitro* studies reveal a positive correlation between enriched oxygen concentrations (26 and 30% O₂) and conidial quality when compared to normal atmospheric oxygen levels (21% O₂) (Miranda-Hernández et al., 2014; Garcia-Ortiz et al., 2015; García-Ortiz et al., 2018). Similarly, at deprived oxygen levels, the same contrast in conidia growth and virulence applies, reducing under ambient oxygen concentrations (Garza-López et al., 2012; Oliveira and Rangel, 2018). Germination

under hypoxic conditions is lower than at normal atmospheric levels (Garza-López et al., 2012), increasing as oxygen conditions become enriched (Miranda-Hernández et al., 2014). Thus, aerating soil during mycelial growth may facilitate optimal entomopathogenic fungal development and pest control.

Soil texture influences fungal propagule transmission and retention. Increasing clay content can promote entomopathogenic fungal persistence, likely due to smaller pore size and/or the adsorption of conidia to clay and organic particles (Ignoffo et al., 1977; Storey and Gardner, 1988; Quesada-Moraga et al., 2007). However, high clay content can also inhibit the ability of a potential host to encounter another, due to reduced porosity for conidial penetration to deeper soil layers and potential transmission (Vänninen et al., 2000; Fuxa and Richter, 2004). Therefore, mechanical filtration of the soil structure can be a major determinant of entomopathogenic fungal persistence and effectiveness when applied to soil (Storey and Gardner, 1988). For example, the efficacy of *B. bassiana* against the red fire ants *Solenopsis invicta* improved when applied to wetter soils, promoting conidia transmission and infection rates (Fuxa and Richter, 2004).

NICHE PREFERENCE

The Habitat Selection Hypothesis

Biotic interactions may alter tropical EPF persistence (Jaronski, 2010), particularly The habitat selection hypothesis for *Metarhizium* species suggests this is a key difference between temperate and tropical regions (Bidochka et al., 2002). Bidochka and Small (2005) suggested *Metarhizium* genotypes are associated with habitat types in temperate and polar regions and are more likely associated with certain host insects in (sub)tropical regions. The authors also suggested *M. anisopliae* originated in Southeast Asia but now comprises an assemblage of cryptic species, many of which traverse large geographical barriers. Temperate studies regarding *Beauveria* and *Metarhizium* have highlighted their preference for habitat selection over associations with insect hosts (Meyling and Eilenberg, 2006b; Meyling et al., 2009; Ormond et al., 2010). Any insect host associations of *M. anisopliae* at higher latitudes were attributed to the insect's habitat, suggesting that abiotic factors could potentially be driving the population genetic structure (Bidochka et al., 2001).

Takatsuka (2007) characterized *Beauveria* isolates from Japan using ISSR-PCR and found no evidence for long-term coevolution between the fungus and insect hosts, supporting the Bidochka et al. (2002) hypothesis that variation in persistence of the free-living, saprophytic stage of a facultative insect pathogen drives population genetic structure. In contrast, Bridge et al. (1997) suggested coevolution between tropical *M. flavoviride* var. *minus* isolates of a single genotype and those insects belonging to the superfamily *Acridoidea*. Tropical isolates of *M. flavoviride* var. *minus* with host-preference traits differed from those with a European derivation. Interestingly, the majority of isolates in the publications supporting the Bidochka and Small (2005) hypothesis regarding the association of *Metarhizium* spp. with insect host species have a tropical origin (Rombach et al., 1986; St. Leger et al., 1992; Bridge et al., 1993, 1997; Leal et al., 1994;

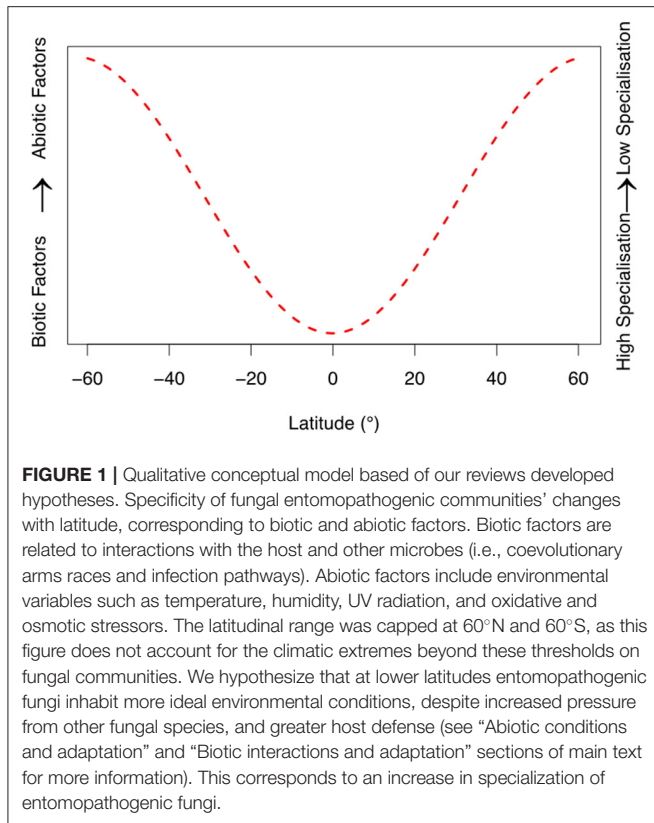
Tigano-Milani et al., 1995). However, future analyses are needed to define these relationships.

Metarhizium strains have adapted to particular environments, supporting versatile life-history strategies (Lovett and St. Leger, 2015). Adjustments in environmental stress responses can arise from adaptation to environmental abiotic (e.g., temperature, UV radiation, and humidity) and biotic factors relating to infection of a host (e.g., antimicrobial and behavioral stressors) (Lovett and St. Leger, 2015; Ortiz-Urquiza and Keyhani, 2015). Conidia produced under abiotic and biotic stress can withstand a broader environmental range, and improve virulence against insects (Li et al., 2015; Rangel et al., 2015). For example, overcoming acridid host behavioral fevers during infection can produce more thermotolerant entomopathogenic fungal isolates (Fargues et al., 1997; Blanford and Thomas, 2000; Rangel et al., 2005). Behavioral defensive traits in grasshoppers can result in discrepancies between entomopathogenic fungal species and their effectiveness in controlling pest populations at different temperatures (Inglis et al., 1999). Grasshopper nymphs infected with *B. bassiana* and *M. acridum* experienced reduced levels of mortality when temperature was increased, and *M. acridum* substantially outcompeted *B. bassiana* in nymphal mortality at higher temperatures (Inglis et al., 1999).

From the evidence primarily presented for *Metarhizium* we propose two general hypotheses for EPF: (i) Abiotic factors are primary determinants of population genetic structure at higher latitudes, due to the insect pathogen's requirement to adapt seasonality and extreme environmental conditions. (ii) Conversely, biotic factors (interactions with other species and fungal-host associated infection pathways) are the primary regulators of EPF population genetic structure in lower latitudes. We evaluate these hypotheses in light of recent research below. To visually present our hypotheses, we constructed a conceptual model (Figure 1). This is meant to qualitatively describe our hypotheses to stimulate future research, rather than stand alone as a mathematical model.

Abiotic Conditions and Adaptation

Fungi inhabiting higher latitudes experience a wider range of temperatures due to seasonality (Wielgolaski and Inouye, 2003). Thus, abiotic stressors (particularly temperature) at higher latitudes may predominantly drive population genetics and adaptability of EPF. In temperate regions, EPF must adapt to a broad range and greater levels of climatic intensities (Maggi et al., 2013; Wang et al., 2017), whereby abiotic factors primarily influence generalist pathogen's survival (Bidochka et al., 2001; Lennon et al., 2012). In contrast, we hypothesize that low latitude biotic factors such as species richness and pathogen-insect associations that drive coevolutionary arms races predominately influence EPF life history. Phylogenetic *B. bassiana* cluster by habitat type more at seasonally variable high latitudes (Ormond et al., 2010), although one study found no seasonal effect in regions of sub-tropical climates (Garrido-Jurado et al., 2015). Phylogenetically structured investigations suggest *B. bassiana* adapts gene regulation to environmental conditions, with habitat adaptation driving population dynamics (Bidochka et al., 2002; Xiao et al., 2012). Thus, differences in the magnitude of seasonal environmental conditions at different latitudes may contribute to



the observed temporal dissimilarities in *B. bassiana* population dynamics between the studies.

Environmental conditions near entomopathogenic fungal survival limits can drive local adaptation when these limits are regularly experienced (Doberski, 1981; Vidal et al., 1997). The optimal temperature for growth and virulence against insect hosts of *Metarhizium* and *Beauveria* species is generally between 25 and 30°C (Luz and Fargues, 1997; Ekesi et al., 1999; Devi et al., 2005; Bugeme et al., 2009). However, significant variation exists in a fungal pathogen species' thermal preference and their effects on potential hosts, due to the environment in which the pathogens evolved (Fargues et al., 1997; Bugeme et al., 2009; Alali et al., 2019), and individual strains can differ in their thermal optima (Doberski, 1981; Thomas and Jenkins, 1997; Alali et al., 2019). *M. acridum* isolates obtained from a hot environment exhibited greater performance at higher temperatures than those derived from a much cooler climate (Thomas and Jenkins, 1997). Similarly, sub-tropical *B. bassiana* strains collected from hotter areas of Syria demonstrated greater thermotolerant ability than the outlier collected from a site experiencing lower temperatures (Alali et al., 2019). Regarding virulence against insects, temperate isolates of *B. bassiana* were significantly more effective against the elm bark beetle (*Scolytus scolytus* F.) at low temperatures (2 to 6°C) than isolates of *M. anisopliae* originating from tropical and sub-tropical latitudes (Doberski, 1981), although it is impossible to separate fungal species differences from differences arising from the geographical sources of the two fungal strains. *B. bassiana* and *M. anisopliae* are also sensitive to

ultraviolet radiation, prompting UV protectant use in oil-based field sprays (Inglis et al., 1995; Shin et al., 2017; Kumar et al., 2018). UV tolerance often varies among isolates from different latitudes (Braga et al., 2001; Fernandes et al., 2008), and habitat types (Bidochka et al., 2001). Isolates of *B. bassiana* and *M. anisopliae* closer to the equator exhibit higher UV tolerance, and cold-adapted populations from higher latitudes generally experience optimal conditions in colder temperatures (Fernandes et al., 2008). In Canada *Metarhizium* isolates encountered in forested habitats are less tolerant to UV radiation and are more cold-active compared to agricultural landscapes (Bidochka et al., 2001). Thus, abiotic selection at high latitudes (e.g., UV exposure in a given habitat type) for specific genetic groups of fungal entomopathogens could influence their effectiveness in agriculture, particularly if isolates are sourced from forested or hedgerow habitats.

Biotic Interactions and Adaptation

Tropical forests support high entomopathogenic mycotaxa diversity, where the teleomorphs (sexual stages) of hypocrealean fungi are mostly found and are often more specialized in their host range than asexual morphotypes (Evans, 1982; Vega et al., 2012; Hu et al., 2014). In contrast, asexually developing EPF (anamorphs) inhabit both tropical and temperate climates (Vega et al., 2012). Lab studies in model systems that increased biodiversity observed corresponding intensification of evolutionary arms races between hosts and parasites (Betts et al., 2018). Similarly, genetic diversity and host specificity of some fungal species suggests that host insects can exert strong selective pressures on pathogens through a cascade of defense and counter-defense mechanisms (Maurer et al., 1997; Evans et al., 2011; Mukherjee and Vilcinskis, 2018). For example, *Metarhizium* often evolved from specialist to generalist insect pathogens; an expansion in host range coinciding with fungal occupation of an expanding latitudinal range (Bidochka and Small, 2005; Hu et al., 2014). However, in high species-density rainforest areas, high fungal tropical diversity may experience stronger pressure from hosts and competitors that can favor the occurrence of pathogens such as the teleomorph genus *Cordyceps* (Evans, 1982; Sung et al., 2007; Aung et al., 2008), and specialist fungal entomopathogens of the genus *Ophiocordyceps* (Aung et al., 2008; Evans et al., 2011; Araújo et al., 2015). Phylogenomic analyses suggest *Beauveria* spp. is the asexual life stage of the *Cordyceps* lineage (Xiao et al., 2012). Despite *Beauveria* having direct genetic links to *Cordyceps*, generalist *Beauveria* and *Metarhizium* are less common within tropical rainforest habitats, and are more frequently encountered in agriculture (Rehner, 2005; Aung et al., 2008). The contrast in life-histories between these specialists and generalist fungi could be attributed to the loss of the repeat-induced point mutations in *B. bassiana* and *Metarhizium* spp. (infers the sexual cycle to be rare in both fungi), which was a prerequisite of these fungal pathogens for the expansion of gene families (Xiao et al., 2012; Lovett and St. Leger, 2017).

Given the probable southeast Asian origin of *Metarhizium* (the continent with the highest genotypic diversity) (Bidochka and Small, 2005; Lovett and St. Leger, 2017), and the

subsequent evolutionary changes in specificity (Hu et al., 2014), a geographical range expansion to temperate regions may have corresponded to a more generalist host range. We hypothesize that this could be due in part to lower host species richness in temperate regions (Thompson et al., 2017), and a need to adapt to greater variation in climatic conditions focusing adaptation on abiotic conditions. A remaining question is how greater potential host diversity in tropical environments alters these selection pressures. Future research into how insect-pathogen arms races alter community composition with changes in latitude would improve management of entomopathogens in different latitudes. Additionally, empirical evaluations of fungi collected at different latitudes and laboratory experiments will improve our knowledge of endemic fungal species and their relevance within a particular system, alongside their appropriate use in biocontrol regimes.

IMPROVING FUNGAL PERSISTENCE AND INSECT OUTBREAK PREVENTION

The ability of some fungal species to cross large geographical barriers (i.e., cosmopolitan in nature) does not imply that the

application of fungal pathogens as an agricultural biopesticide will ensure fungal persistence. Rather, researching the appropriateness of a fungal pathogen specific to the target environment is required, including interactive effects of individual biotic/abiotic factors. Efforts should be directed toward focusing on endemic fungal communities and applied within its derived system. Regional differences between suitable fungal application type, host range (i.e., generalist vs. specialist) and the dominant environmental factors (biotic/abiotic) on pathogen performance can better predict the long-term success of entomopathogenic biocontrol and help prevent insect outbreaks.

AUTHOR CONTRIBUTIONS

AM wrote the first draft. AM and TN contributed significantly to subsequent drafts.

FUNDING

AM was supported by a AusIndustry Innovations Connections grant to TN.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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