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Bee response to fire regimes in Mediterranean pine forests: The role of nesting preference, trophic specialization, and body size

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Abstract

Fire is an important and frequent disturbance in Mediterranean-type ecosystems affecting the structure and dynamics of bee communities. We explored the effect of fire history on taxonomic and functional composition of wild bees on Rhodes Island, Greece, using UV-bright pan trap sampling. We carried out a fourth-corner analysis based on Generalized Linear Models to identify significant interactions between functional traits (nesting preferences, trophic specialization, and body size) and fire history, defined by fire frequency and post-fire age of sites. Our analysis showed that species diversity and abundance at various taxonomic levels did not display significant differences among different fire history regimes (twice-burnt, recently-burnt, old-burnt, and unburnt). The effect of fire was detected when focusing on functional traits rather than species. Ground nesting bees were positively associated with recently-burnt sites, which provide bare soil and therefore nesting sites for this group of bees. Polylectic bees were positively associated with twice-burnt sites, indicating the dominance of generalist bee species. Larger bees were positively associated with post-fire age, probably due to the larger foraging range of larger bees that enables a more efficient exploitation of aggregated resources. Our results show that responses of wild bee species to fire are driven by nesting preference, trophic specialization, and body size.

Zusammenfassung

Brände sind eine wichtige und häufige Störung in Ökosystemen mit mediterranem Klima, die die Struktur und Dynamik von Bienengemeinschaften beeinflussen. Wir untersuchten die Wirkung von Bränden auf die taxonomische und funktionelle Zusammensetzung von Wildbienen auf Rhodos, Griechenland, indem wir die Artenvielfalt der Bienen und deren Artzusammensetzung mit Hilfe von Farbschalen erfassten. Wir verwendeten ein Generalisiertes Lineares Modell basierend auf einer

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Fourth-corner-Analyse, um Wechselwirkungen zwischen funktionalen Merkmalen (Nistplatzvorlieben, trophische Spezialisierung und Körpergröße) und der Brandgeschichte (definiert nach Brandfrequenz und Zeit seit dem letztem Brand; im Einzelnen beinhaltete dies folgende Gruppen: vier Jahre zuvor gebrannt, einschließlich Gebieten, die in den letzten Jahren einmal bzw. zweimal gebrannt hatten, vor mindestens 20 Jahren gebrannt und unverbrannt seit mindestens 50 Jahren) zu erforschen. Unsere Analyse zeigte, dass die Artenvielfalt und Abundanz auf Gemeinschafts- und Familienebene keine signifikanten Unterschiede zwischen den verschiedenen Brandgeschichten aufweisen. Jedoch hatten Brände Einfluss auf funktionale Merkmale. Im Einzelnen waren bodennistende Bienen positiv mit unverbrannten Gebieten assoziiert, was vielleicht die dort vorherrschende Vielfalt der verfügbaren Nistplätze widerspiegelt. Polylektische Bienen waren positiv mit zweimal verbrannten Gebieten assoziiert, was die Dominanz der Generalisten unter den Bienenarten anzeigt. Größere Bienen waren positiv mit der Zeit seit dem letzten Brand assoziiert, wahrscheinlich aufgrund deren größeren Reichweite bei der Nahrungssuche, die eine effizientere Nutzung der Ressourcen ermöglicht. Unsere Ergebnisse zeigten, dass der Einfluss von Bränden auf Wildbienen hauptsächlich von Nistplatzvorlieben, trophischer Spezialisierung und Körpergröße abhängig ist.

Keywords: Wild bees; Fire history; Post-fire age; Fire frequency; Mediterranean-type ecosystems; Beta diversity; Functional traits; Fourth-corner analysis

Introduction

The majority of crops and wild plants rely on animal-mediated pollination for reproduction (Klein et al., 2007; Ollerton, Winfree, & Tarrant, 2011). Therefore, pollination is an invaluable ecosystem service for the maintenance of diversity (Ashman et al., 2004) and has a considerable economic value for food production (Kremen et al., 2007). Bees (Hymenoptera: Apoidea) constitute the most prominent group of animal pollinators for both natural and agricultural ecosystems. However, bees are threatened by a series of human disturbances, resulting in a worldwide bee decline (Biesmeijer et al., 2006; Potts et al., 2010). Among the most important disturbances affecting bee diversity is land use change (including habitat loss, fragmentation, urbanization, and wild fires), pesticide use, invasion of pathogens, alien species, and climate change (for a review see Potts et al., 2010).

In Mediterranean-type ecosystems, fire is one of the most frequent and important disturbances, which shapes the abundance and structure of post-fire wild bee communities both directly and indirectly through changes in soil and vegetation (Moretti, Duelli, & Obrist, 2006). As an immediate effect, wild bee diversity decreases due to direct mortality by fire, food resources decline, while the immediate recolonization of burnt areas is hindered by the limited foraging range of bees (Ne'eman, Dafni, & Potts, 2000). In fact, recolonization progresses gradually with time passed since the fire event and also depends on fire frequency. During the first post-fire years, bee diversity is driven by a higher availability of bare ground (Campbell, Hanula, & Waldrop, 2007; Potts et al., 2005) and the wider range of floral resources due to increased abundance and diversity of annual plants. At later post-fire stages, however, as floral diversity decreases and woody vegetation recovers, bee diversity decreases (Petanidou & Ellis, 1996; Potts et al., 2003). Results from southern Switzerland (temperate forests dominated by *Castanea sativa*), showed that fire frequency had no effect on bee and wasp abundance but had a positive effect on their species richness, with repeatedly burnt sites showing the highest species richness (Moretti, Obrist, & Duelli, 2004). Grundel et al. (2010) also found a positive association between recent fire frequency and bee abundance across a habitat gradient (ranging from open grasslands to closed forests) in northwest Indiana, USA. However, there is a lack of studies on the effect of fire frequency on pollinator diversity and abundance in the Mediterranean or Mediterranean-type communities.

Recently, functional trait-based approaches have been used to unravel the responses of bees to disturbances and the underlying driving mechanisms (Moretti, De Bello, Roberts, & Potts, 2009; Williams, Crone, Minckley, Packer, & Potts, 2010). Trait-based approaches focus on the relationships between traits, environmental gradients, species interactions, and performance, to better understand community structure, effect of environmental change and the underlying biological processes (McGill, Enquist, Weiher, & Westoby, 2006). Such approaches quantify the distribution and abundances of species in a multidimensional functional space (Mouchet, Villeger, Mason, & Mouillot, 2010) through either functional diversity indices and their variation or methods evaluating trait responses to environmental variation such as the fourth-corner analysis (Legendre, Galzin, & Harmelin–Vivien, 1997; Dray & Legendre, 2008). Functional traits are defined as any trait affecting, directly or indirectly, individual performance and fitness of species (McGill et al., 2006; Violle et al., 2007). Generally, species are classified into functional groups according to their resource utilization and habitat requirements (Lavorel & Garnier, 2002; Papanikolaou et al., 2011). This functional classification can be informative about processes that determine patterns across different scales. Species traits reflect their behavior, physiology, and morphology, and thus formulate species responses to environmental change (McGill et al., 2006). So fire, a major ecological process, is expected to affect the trait