



## Competition between managed honeybees and wild bumblebees depends on landscape context

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### Abstract

Honeybees might outcompete wild bees by depleting common resources, possibly more so in simplified landscapes where flower-rich habitats have been lost. We tested this by experimentally adding honeybee hives to nine sites while ensuring that ten additional sites were free from hives. The landscape surrounding each geographically separated site either held low (homogeneous landscape) or high (heterogeneous landscape) proportions of semi-natural grassland. Adding honeybees suppressed bumblebee densities in field borders and road verges in homogeneous landscapes whereas no such effect was detected in heterogeneous landscapes. The proportional abundance of bumblebee species with small foraging ranges was lower at honeybee sites than at control sites in heterogeneous landscapes, whereas bumblebee communities in homogeneous landscapes were dominated by a single species with long foraging range irrespective of if honeybees were added or not. We conclude that honeybees can impact bumblebee densities, but that landscape heterogeneity modified this effect.

### Zusammenfassung

Honigbienen können Wildbienen durch Konkurrenz verdrängen, indem sie häufige Ressourcen erschöpfen, was möglicherweise häufiger in einfach strukturierten Landschaften geschieht, in denen blütenreiche Habitate verloren gegangen sind. Wir testeten dies, indem wir experimentell Bienenstöcke an neun Standorten hinzufügten und in zehn weiteren sicherstellten, dass keine Bienenstöcke vorhanden waren. Die Landschaften, die die geographisch voneinander getrennten Standorte umgaben, enthielten entweder einen geringen (homogene Landschaft) oder einen hohen (heterogene Landschaft) Anteil von naturnahem Grasland. In homogenen Landschaften reduzierte die Hinzugabe von Honigbienen die Hummeldichten in Feldrainen und im Straßenbegleitgrün, während in heterogenen Landschaften kein derartiger Effekt beobachtet werden konnte. In heterogenen Landschaften war der proportionale Anteil von Hummelarten mit kleinem Sammelaktionsgebiet an Honigbienenstandorten geringer als an Kontrollstandorten. In homogenen Landschaften wurden die Hummelgemeinschaften dagegen von einer Art

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mit großem Sammelaktionsgebiet dominiert, unabhängig davon, ob Honigbienen hinzugefügt worden waren oder nicht. Wir schließen, dass Honigbienen Hummeldichten beeinflussen können, dass aber dieser Effekt durch die Heterogenität der Landschaft modifiziert wird.

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## Introduction

Declines in wild bee populations have been attributed to a combination of stressors including habitat loss and habitat degradation, parasites and pesticides (Goulson, Nicholls, Botías, & Rotheray, 2015). In addition, competition from managed honeybees has been suggested as aggravating the threats to wild bees by depleting common food resources (e.g. Goulson, 2003).

Many studies have attempted to assess impacts on wild bees of competition with honeybees, but observational studies can suffer from confounding factors and experimental studies are few and usually poorly replicated (Paini, 2004). Observed negative correlations between honeybee and wild bee densities might result from competition, but also from contrasting responses to human disturbance (Aizen & Feinsinger, 1994). Honeybees can displace foraging bumblebees (Walther-Hellwig et al., 2006) and negatively impact the reproduction of solitary bees (Hudewenz & Klein, 2015; Paini & Roberts, 2005) and bumblebees (Thomson, 2004). In addition, bumblebee workers are smaller when co-occurring with honeybees, probably due to lack of food during larval development (Goulson & Sparrow, 2009). Several studies have also failed to detect any impact (reviewed in Paini, 2004).

Competition between honeybees and bumblebees may be unlikely in Europe where both taxa are native (Paini, 2004), because coexistence of organisms initially sharing the same niche should result in niche differentiation (Lawlor & Smith, 1976). Multiple bee species may coexist because they vary in foraging-related attributes, resulting in differentiated flower choice (Ranta & Lundberg, 1980). However, food limitation can force competing bees to modify their foraging niche (Fontaine, Collin, & Dajoz, 2008). Thus, agricultural change, resulting in loss of semi-natural habitats and a consequential loss of flower resources, can have altered the conditions for coexistence of honeybees and bumblebees. This has to our knowledge not been examined.

Bumblebee species differ in foraging-related traits, which could affect how they respond to coexistence with honeybees (Walther-Hellwig et al., 2006). Bumblebees often prefer flowers with slightly shorter corolla tubes than their tongue-length (Brian, 1957), and interspecific tongue-length variation enables food niche separation (Ranta & Lundberg, 1980). Honeybees are short-tongued compared to bumblebees (Balfour, Garbuzov, & Ratnieks, 2013). Possibly for this reason, long-tongued bumblebee species respond to

competition from honeybees by shifting from open to deep flowers, whereas short-tongued species remain on open flowers but change to less profitable parts of the flower patch (Walther-Hellwig et al., 2006). Consequently, we expected the strongest competition between honeybees and short-tongued bumblebee species.

Furthermore, bumblebee species utilize forage resources at different spatial scales. Workers collect food and return to the central nest (Goulson, 2010), with foraging ranges being larger for species with larger body size and bigger colonies (Westphal, Steffan-Dewenter, & Tschamtkke, 2006). Short-distance foraging species depend on a continuous supply of flower resources near the nest, whereas long-distance foraging species can utilize distant patches (Walther-Hellwig & Frankl, 2000). Thus, we expected competition from honeybees to have a stronger negative impact on short-distance foragers.

We investigated effects of competition from managed honeybees on wild bumblebees by adding honeybee hives to field sites in two agricultural landscape contexts, defined by the proportion of agricultural land covered by grazed or mowed, permanent, semi-natural grasslands as either homogeneous (low proportion) or heterogeneous (high proportion) (Tschamtkke, Klein, Kruess, Steffan-Dewenter, & Thies, 2005). We compared bumblebee densities in road verges and field borders at sites to which honeybees had been experimentally added with densities at control sites that we ensured were free from hives. We hypothesized that honeybee supplementation reduces bumblebee density, particularly in homogeneous landscapes and for species with short tongues or small foraging ranges.

## Materials and methods

### Site selection

In 2012 we selected 19 geographically separated (>2.5 km) agricultural sites in southernmost Sweden (Fig. 1). Parts of the design were used earlier the same year to study rape-seed pollination (Lindström, Herbertsson, Rundlöf, Smith, & Bommarco, 2016). Therefore all sites were adjacent to an autumn sown withered rapeseed field.

We processed geographic land use information from the Integrated Administration and Control System, a yearly updated database on the use of agricultural land

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