Honeybees collect pollen from the buzz-pollinated invasive *Solanum elaeagnifolium* in Northern Greece

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Abstract

Around 6% of flowering plants, including most solanaceous species, have flowers specialized for buzz-pollination (sonication). The poricidal anthers of these flowers release pollen in response to frequency-specific vibrations that buzz-pollinating bees, including bumble bees and many solitary bees, generate via rapid oscillation of flight muscles. Honeybees are incapable of sonication and typically avoid buzz-pollinated plants in natural settings. Here, we report a novel interaction in which honeybees consistently visit and extract pollen from flowers of *Solanum elaeagnifolium* (silverleaf nightshade) within a large invasive plant population in Northern Greece. We postulate that honeybee foraging effort on *S. elaeagnifolium* reflects a shortage of alternative floral resources at the peak of the Mediterranean summer, consistent with observations for pollen-starved bees in captivity. This recent behavioral shift may have important implications for plant invasions, particularly under climate change, and suggests a need for further investigation to elucidate its ecological and evolutionary driver

Text

1. Honeybees cannot buzz-pollinate

"…the polylectic honeybee does not seem able to learn the process."

Linsley (1978)

Buzz-pollinated flowers occur in around 20,000 species across various angiosperm clades (~6% of species), including key crops such as tomato, eggplant, blueberry, cranberry, and kiwi (Buchmann 1983; Cooley and Vallejo-Marín 2021; De Luca and Vallejo-Marín 2013; Pritchard and Vallejo-Marín 2020). Owing to their unique floral morphology, the poricidal anthers of these flowers require vibration at specific frequencies (sonication) to release pollen. Buzz pollination is hypothesized to serve as an adaptation for preventing pollen access by relatively inefficient, non-specialist pollinators (Pritchard and Vallejo-Marín 2020), although the morphology of buzz-pollinated flowers may also deter herbivory by making pollen less accessible (Hargreaves et al. 2009). A capacity for sonication via rapid oscillation of the thoracic indirect flight muscles has evolved independently ca. 45 times within bees (Cardinal et al. 2018), enabling approximately 58% of bee species (at least 74 genera) to efficiently extract pollen from buzz-pollinated flowers (Buchmann 1983; De Luca and Vallejo-Marín 2013; Jankauski et al. 2022; Pritchard and Vallejo-Marín 2020). However, honeybees, the most frequent floral visitors in both natural and agricultural systems worldwide (Hung et al. 2018), are incapable of sonication, and their limited interaction with buzz-pollinated plant species

has been widely discussed by pollination biologists (Buchmann 1983; De Luca and Vallejo-Marín 2013; Linsley 1978).

The proximate mechanisms preventing honeybees from effectively collecting pollen from buzz-pollinated flowers appear to be based in physiological constraints—specifically relating to the maximum sustained frequency of thoracic vibrations (King and Buchmann 2003)—rather than a lack of behavioral flexibility or learning capacity, as had previously been suggested (Linsley 1978). In any case, honeybees typically avoid buzz-pollinated flowers in natural settings, and particularly those of species that do not offer nectar, as in the genus *Solanum* (Buchmann 1983; Buchmann and Cane 1989; Linsley 1978; Michener 1962; Petanidou et al. 2018; Tayal and Kariyat 2021; Tscheulin and Petanidou 2013; Tscheulin et al. 2009). On rare occasions in which honeybees have been observed to visit buzz-pollinated flowers in the wild, they have primarily been reported to glean leftover pollen from petals following visits by buzz-pollinators (Buchmann 1983; Buchmann and Cane 1989; Gross and Mackay 1998; Mesquita-Neto et al. 2018; Petanidou et al. 2018; Rocha et al. 2023; Solís-Montero et al. 2015; Wille 1963), and sometimes to steal already deposited pollen from the stigma, presumably reducing plant fitness (e.g., Gross and Mackay 1998).

Despite their limited ability to utilize buzz-pollinated flowers, honeybees can be induced to visit such flowers under conditions of pollen deprivation and are sometimes utilized for pollination of buzz-pollinated agricultural crops. In the case of buzz-pollinated flowers that do not offer nectar (e.g., tomato, eggplant, potato, tamarillo),

managed honeybees will visit only when confined into greenhouses or flight cages with no access to other pollen sources (Cane et al. 1993; Cane and Schiffhauer 2003; Miyamoto et al. 2006; Neiswander 1956). However, honeybees will spontaneously visit only the nectar-offering buzz-pollinated crops (e.g., blueberry, cranberry), in which case they can be used in open environments (Cane et al. 1993; Dogterom and Winston 1999). The reported pollinating efficiency of honeybees on buzz-pollinated crops ranges from zero (avoided the flowers, although pollen-deprived; e.g, Amala and Shivalingaswamy 2017; Banda and Paxton 1990; Rijo et al. 2022; Sanford and Hanneman 1981; Zhang et al. 2020), to inconsistent (Cooley and Vallejo-Marín 2021; Courcelles et al. 2013; Dos Santos et al. 2009; Higo et al. 2004), or sometimes satisfactory provided that hives are used in high densities and honeybee workers do not steal nectar (Cane and Schiffhauer 2003; Cooley and Vallejo-Marín 2021; Courcelles et al. 2013; Cribb et al. 1993; Delaplane and Mayer 2000; MacKenzie 1994; Miyamoto et al. 2006; Neiswander 1956; Sabara and Winston 2003).

The observation that managed honeybees will visit and attempt to collect pollen from buzz-pollinated flowers under pollen deprivation, raises the possibility that similar behaviors may occur in nature, particularly in environments where honeybees have limited access to other pollen sources or, conversely, where other potential pollinators are absent or rare. Both conditions might arise in the context of plant invasion (Albrecht et al. 2016; Davis et al. 2018). Yet, as noted above, reports of honeybee visitation of buzz-pollinated flowers in nature are rare and generally limited to observations of bees collecting residual pollen from petals, following visitation by other, buzz-pollinating

species. In the current study, we report the large-scale extraction and utilization by honeybees of pollen from a buzz-pollinated plant (*Solanum elaeagnifolium*), which forms large monocultures in its invaded (Mediterranean) range and produces flowers in a seasonal period when other flowers are scarce. We also provide evidence that this honeybee behavior has become widespread within the last decade and discuss potential ecological and evolutionary implications within the context of plant invasion.

2. Honeybees consistently visit the buzz-pollinated flowers of an invasive plant population

Solanum elaeagnifolium (silverleaf nightshade) is currently among the top-noxious invasive plants worldwide (Roberts and Florentine 2022; Uludag et al. 2016). A perennial herbaceous species originating in N Mexico and SW USA, *S. elaeagnifolium* has been rapidly expanding to almost all continents over the past century, posing serious threats to native biodiversity and causing significant losses in agricultural and livestock production in many countries (Roberts and Florentine 2022; Uludag et al. 2016). Its uncontrollable expansion has severely affected the Mediterranean Basin, making it one of the most impacted regions (Krigas et al. 2021; Uludag et al. 2016). In croplands and urban areas of N Greece, this species forms numerous extensive monospecific stands (of >10,000 individuals) (Petanidou et al. 2018) (Figure 1).

Since 2015, we have observed honeybees to frequently visit *S. elaeagnifolium* flowers across the entire metropolitan area of the city of Thessaloniki (N Greece) and to actively extract pollen from the poricidal anthers in three ways: (a) shaking/drumming

the anthers using their forelegs; (b) biting off pieces of anthers with their mandibles; (c) holding the anthers with their forelegs and inserting their proboscis through the pores of the anthers (Videos S1-S3). As a result, pollen of silverleaf nightshade adheres on the bodies of honeybees and is used to fill up the corbiculae (Videos S1-S3) (Figure 2c-d). These modes of behavior have previously been reported for honeybees trying to exploit buzz-pollinated flowers in cultivation, and Cane et al. (1993) hypothesized that the foreleg drumming behavior is a permutation of pollen-grooming movements that bees perform to transfer pollen grains from their upper body parts to the corbiculae.

As documented in agricultural settings, honeybees spend more time on visitation of buzz-pollinated flowers than they usually do on other types of flowers, presumably due to the low efficiency of pollen extraction (Kendall et al. 2022). However, honeybee interactions with *S. elaeagnifolium* entail a high level of settings, physical effort and an exceptionally long-duration of floral visits. Indeed, in Thessaloniki, we recorded visits on single flowers lasting as long as 224 s (Video S1), whereas known maximum visitation times of honeybees on buzz-pollinated species are 100 s, observed on blueberry flowers (Kendall et al. 2022). Instead, for non-buzz-pollinated species, handling times are considerably shorter, typically ranging from 2.6 s per flower (oregano) and 4 s (lavender) (Hennessy et al. 2021) to 40 s (melon) (Ribeiro et al. 2017).

Furthermore, especially during the latter part of the flowering season (August), honeybees in Thessaloniki regularly visited *S. elaeagnifolium* flowers that were in poor condition, (e.g., heavily damaged by florivores, wilting, or deformed), which otherwise is

known to reduce attractiveness to pollinators (e.g., Sõber et al. 2010; Vega-Polanco et al. 2020). Finally, it should be noted that honeybees are now by far the most frequent visitors of these flowers, outnumbering buzz-pollinating bees in the area (i.e., *Bombus, Pseudapis, Xylocopa,* and *Amegilla*) (RRK and GN personal observations). To our knowledge, this is the first report of honeybees consistently extracting pollen from a buzz-pollinated plant in a natural community.

3. An extraordinary consequence of plant invasion?

The striking similarity of the behavior reported here with that previously reported for pollen-starved honeybees in confined agricultural settings (see above), suggests that it might be linked to severe limitation of other pollen sources. This is highly plausible given the magnitude of the invasion of silverleaf nightshade in the study area (Petanidou et al. 2018). It has been estimated that *S. elaeagnifolium* reached current population sizes in and around Thessaloniki city within 50 years after its first unintentional introduction (most probably from Texas) in the 1930s, forming one of the most heavily invaded areas in Europe (Krigas and Kokkini 2004; Roberts and Florentine 2022; Uludag et al. 2016). While we cannot be certain about when the widespread utilization of *S. elaeagnifolium* flowers by honeybees in Thessaloniki began, we can be confident that it started later than 2007, based on previous extensive surveys of pollinator activity in this area (Petanidou et al. 2012; Petanidou et al. 2018). While these surveys reported that other wild bees were scarce (Petanidou et al. 2018), honeybee interactions with *S. elaeagnifolium* were also rare, and restricted to gleaning leftover pollen from petals, presumably following visits

162 by other pollinators (Petanidou et al. 2012; Petanidou et al. 2018). Similar behavior has
163 been repeatedly reported for silverleaf nightshade both in Greece (Tscheulin and
164 Petanidou 2013; Tscheulin et al. 2009) and in its native range, i.e., Texas and Arizona
165 (Buchmann and Cane 1989; Tayal and Kariyat 2021). Besides, this fits the typical
166 interaction of honeybees with *Solanum*-type flowers in the wild, where they have been
167 reported to either avoid (*S. wedlandii*) (Michener 1962), or glean pollen leftovers (*S.*
168 *rostratum*) (Solís-Montero et al. 2015) from flowers of *Solanum* species.

169 Since the successful establishment of silverleaf nightshade in Thessaloniki, local
170 honeybee populations have presumably been exposed to a novel "operative environment"
171 (Agosta and Klemens 2008; Spomer 1973), including a super-abundant pollen source,
172 which, despite being challenging to exploit, is available during the most adverse time of
173 year. Given the relative scarcity of other insect-pollinated species in flower in the
174 lowlands of the Mediterranean at the peak of the dry summer (Kantsa et al. 2023b),
175 silverleaf nightshade is by far the dominant pollen source in the invaded habitats.
176 Therefore, we assume that the observed utilization of *S. elaeagnifolium* is a consequence
177 of plant invasion in an area with limited alternative pollen sources, although it remains
178 unclear why the behavior appears to have become widespread only in recent years.

179 The well-known aversion of honeybees towards buzz-pollinated flowers suggests
180 that the utilization of nectarless, buzz-pollinated flowers is not adaptive in typical
181 environments, likely because the ratio of pollen rewards obtained to effort expended is
182 unattractive, relative to that provided by other flower types (Buchmann and Cane 1989).

If utilization of *S. elaeagnifolium* flowers has been adaptive under the novel conditions in Thessaloniki, a question is whether this arises due to pre-existing behavioral flexibility or entails genetic adaptation. The apparently similar exploitation of buzz-pollinated flowers by pollen-starved honeybees in agricultural settings suggests that the former is plausible; the employment of different techniques by the honeybees (viz., drumming, "milking", or biting; Videos S1-S3) is consistent with ecological fitting (Agosta and Klemens 2008; Janzen 1985), suggesting that the eventual mode of action depends on individual decision-making ability, agility, or both. These behaviors may thus represent a notable example of behavioral plasticity of the honeybees, facilitating exploration of novel areas of fitness space created by the massive invasive populations of *S. elaeagnifolium* in Northern Greece.

Regarding why the reported behavior was not observed prior to 2015, it may be useful to explore the potential preference of relevant colony-level heritable traits (e.g., pollen hoarding) in the local beekeeping market. For instance, Cane and Schiffhauer (2001; 2003) suggested that when honeybee queens are genetically predisposed for pollen hoarding (Rueppell 2014) pollen-foraging trips on buzz-pollinating flowers are significantly more frequent. Furthermore, the previously mentioned hypothesis by Cane et al. (1993) that the movement of foreleg drumming in honeybees is a permutation of pollen-grooming movements that bees perform to transfer pollen grains from their upper body parts to the corbiculae, suggests the possibility of an existing pre-adaptation. This could indicate a case of exaptation, where a trait originally evolved for one function (pollen grooming) has been co-opted for another (buzz-pollination). A similar example is

the woodpecker finches (*Camarhynchus pallidus*, Thraupidae) at the Galápagos Islands, in which beak morphology originally suited for cracking seeds or eating insects has been co-opted for tool utilization, a behavior which varies according to habitat type (i.e., operative environment), is not acquired with social learning (but possibly with trial-and-error learning at a young age), and is believed to be based on genetic predisposition (Tebbich et al. 2001). In any case, whether honeybees have established a novel interaction circumventing adaptive processes (through phenotypic plasticity), or we are witnessing the real-time establishment of an exapted behavior, possibly conveying a more subtle and complex genetic background (e.g., pleiotropic traits), this phenomenon requires in-depth investigation.

Honeybees are globally abundant, frequently utilized in agriculture, and highly competitive with wild bees, often with adverse effects on native bee faunae (Goulson 2003; Lázaro et al. 2021). Given that they are generally among the first pollinators to interact with newly introduced plants in natural communities (Kantsa et al. 2023a), these behavioral shifts can be directly linked with invasion status and dynamics, with *S. elaeagnifolium* providing a characteristic example. In general, the rapid geographical expansion of this species is thought to be promoted largely by its ability to propagate vegetatively with root fragments (Roberts and Florentine 2022). The invasive populations of silverleaf nightshade are known to be self-incompatible, and (at least until 2007) pollen-limited (Petanidou et al. 2012; Petanidou et al. 2018). Based on these observations, it had been suggested that sexual reproduction was less important for the expansion of this plant in the invaded area. Yet, if this condition is overturned, and

227 honeybee visitation can now convey the advantages of outcrossing, the genetic
228 robustness of this vast invasive population is expected to be even further enhanced, with
229 potentially even more disastrous effects on the native wildlife and landscape. For
230 example, in the genus *Solanum,* outcrossing maintains high chemodiversity of volatile
231 emissions, and it relates to better performance in chemically repelling herbivores and in
232 recruiting predators (Kariyat et al. 2012a; Kariyat et al. 2013; Kariyat et al. 2012b).

233 **4. Outlook**

234 Here we report a new foraging behavior in honeybees, which has emerged during
235 the past decade, probably owing to the substantial expansion of *S. elaeagnifolium*,
236 resulting in an overabundance of pollen during the most adverse period of the year in the
237 Mediterranean in terms of floral resources. We have argued that our observation, likely
238 involving a complex interplay of honeybee biology and floral ecology, has important
239 implications both for the invasion status of silverleaf nightshade and for honeybee
240 biology.

241 The enormous invasive populations of silverleaf nightshade in Northern Greece
242 (and probably elsewhere) in fact represent large-scale natural experiments, which can
243 reveal fascinating aspects of the evolution of plant–pollinator interactions. For instance,
244 we know that buzz-pollination is not a dead-end, and novel floral forms (that do not even
245 require bees) can evolve from bee-buzz-pollinated flowers (Dellinger et al. 2019). In the
246 system examined here, we see the archetypical buzz-pollinated flower form (the
247 *Solanum*-type) potentially experiencing a pollinator shift with apparently no phenotypic

transition. Further investigation is needed to determine if this indeed represents a functional transition, the extent floral phenotype has been modified, and the drivers (e.g., floral abundance, abiotic conditions, honeybee plasticity, etc.) of these transitions.

Beyond basic research questions, it should also be kept in mind that silverleaf nightshade is a top-noxious weed that is adversely affecting natural, agricultural-, and urban ecosystems across the world. Moreover, its invasive potential remains high, especially in the context of global change: spatial models simulating climatic suitability for this plant indicate numerous currently invadable regions in all continents, with poleward expansions predicted in a warmer atmosphere (Kriticos et al. 2010). Given that honeybees occur with generally high population densities in almost all continents, their impact on the realized fitness of invasive populations of *S. elaeagnifolium*, and the broader implications for natural communities should be explored.

Conflict of interest statement

The Authors declare no conflict of interest.

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Figure captions

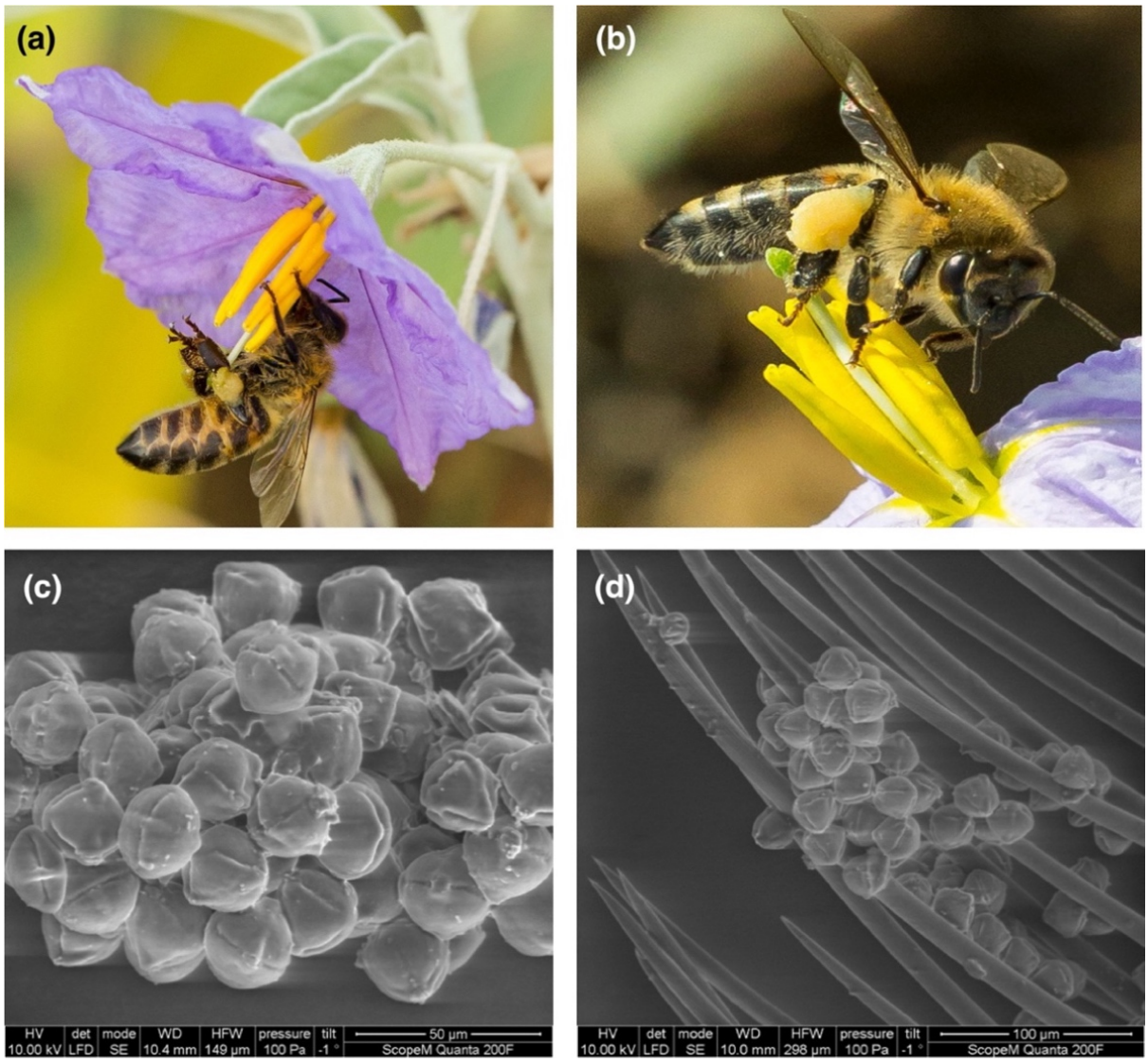
Figure 1. Invasive population stands in an agricultural (up) and an urban residential area (down) in the Metropolitan area of Thessaloniki, N Greece (photos: photos: R.R. Kariyat, G. Nakas).

Figure 2. (a-b) Honeybees foraging for pollen on *Solanum elaeagnifolium*; their corbiculae (pollen baskets) are replete with the pollen of the plant (photos: R.R. Kariyat). (c-d) SEM images showing the pollen grains, and how these accumulate among the bristles on the body of the bee (imaging was performed at the Scientific Center for Optical and Electron Microscopy of ETH Zurich).

447 Figures

448 Figure 1

Figure 2


(a)
(b)
(c)
HV 10.00 kV
det LFD
mode SE
WD 10.4 mm
HFW 149 µm
pressure 100 Pa
tilt -1 °
50 µm
ScopeM Quanta 200F
(d)
HV 10.00 kV
det LFD
mode SE
WD 10.0 mm
HFW 298 µm
pressure 100 Pa
tilt -1 °
100 µm
ScopeM Quanta 200F

Electronic Supplementary Material

Video S1. A honeybee worker attempting to extract pollen from the flowers of silverleaf nightshade by biting the anthers. Videographer: G. Nakas. (https://polybox.ethz.ch/index.php/s/YHb7WMsZNAoJCwY)

Video S2. A honeybee worker attempting to extract pollen from the flowers of silverleaf nightshade by holding the anthers with their forelegs and inserting their proboscis through the pores of the anthers ("milking" behavior). Videographer: G. Nakas. (https://polybox.ethz.ch/index.php/s/YHb7WMsZNAoJCwY)

Video S3. A honeybee worker attempting to extract pollen from the flowers of silverleaf nightshade by shaking the anthers. Videographer: G. Nakas. (https://polybox.ethz.ch/index.php/s/YHb7WMsZNAoJCwY)