Review of the Role of Bees as Ecosystem Engineers in Nature

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Abstract: Bees are a highly important group, providing a multitude of services to ecosystems, most notably through pollination. While much of the research on bees has traditionally focused on their role in pollinating a variety of wild and cultivated crops, this review paper expands the discourse by examining their functions as ecosystem engineers. Traditional definitions of ecosystem engineers exclude pollinators due to their non-physical modifications of habitats for other species. However, contemporary studies challenge this perspective, recognizing pollinators as integral ecosystem engineers who offer a range of direct and indirect ecological services. For instance, bees' pollination activities lead to the formation of dry fruits that subsequently serve as shelters for various organisms. In addition, ground-nesting bees modify soil composition through mechanisms such as aeration and bioturbation. This review aims to elucidate the transformative impact bees have as ecosystem engineers, thereby enhancing our understanding of their ecological importance.

Keywords: Ecosystem engineers, Ecosystem function, Habitat modification, Soil Bioturbation, Ground nesting soil

Introduction

Ecosystem engineers are organisms that modulate the availability of resources for other species, either directly or indirectly, by altering the physical state of biotic and abiotic materials within their ecosystem (Jones, Lawton, & Shachak, 1994). These engineers, through modifications of abiotic conditions, instigate changes in the biological responses of resident species, thereby influencing ecosystem functioning. Ecosystem functioning encompasses both physiochemical and biological processes within the ecosystem, which are closely associated to human well-being. This connection is evident in services such as carbon sequestration, productivity, and nutrient cycling (Byers, 2022).

Overview of Bees as Ecosystem Engineers

Mills, Soulé, and Doak (1993) identified five categories of keystone species, among which includes keystone habitat modifiers or ecosystem engineers (Lawton & Jones, 1995). These engineers are further classified as either autogenic or allogenic (Jones et al., 1994). Autogenic engineers modify environments with their physical structures, such as living or decaying tissues. Conversely, allogenic engineers transform environments by manipulating biotic or abiotic components through various activities (Jones et al., 1994; Jones, Lawton, & Shachak, 1997). However, the complexity inherent in species richness makes classifying certain organisms challenging. For instance, pollinators like bees were not traditionally considered ecosystem engineers by Jones et al. (1994) because they primarily modulate resources supply for seed and fruit consumers. Nonetheless, recent perspectives, such as those put forth by Wilby (2002), suggest expanding the term 'ecosystem engineering' to include organisms whose actions create or modify habitats, even if their influence does not align with traditional definitions of engineering (Casas-Crivillé & Valera, 2005). Under this broader definition, pollinators like bees can indeed be considered ecosystem engineers due to their direct and indirect impacts on ecosystems (Cardoso, Rezende, Caetano, & Oliveira, 2023; Casas-Crivillé & Valera, 2005).

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Bees form a monophyletic group of insects with over 20,000 described species across seven families, inhabiting a diverse array of latitudes and terrestrial ecosystems (Patel, Pauli, Biggs, Barbour, & Boruff, 2021). Globally, both wild bees and managed honeybees are economically significant as pollinators (Kremen & Chaplin-Kramer, 2007; Kremen, James, & Pitts-Singer, 2008). Their efficient pollen transport, reliance on floral resources, and social behaviors, from semi-social to eusocial classifications, enable them to be prolific pollinators for a wide spectrum of plant species (Klein, Boreux, Fornoff, Mupepele, & Pufal, 2018; Ollerton, 2017). Bees are responsible for pollinating more than 90% of the world's flowering crops (Klein et al., 2007). In addition to increasing crop yields (Aizen et al., 2019; Aizen & Harder, 2009), bees enhance the nutritional value and quality of fruits and vegetables (Ahmad et al., 2021; Khan et al., 2022; Klatt et al., 2014), indirectly mitigating food waste associated with aesthetic and quality imperfections (Gunders & Bloom, 2017). The crucial role of wild and managed bees in pollinating wild plants in forest ecosystems is also well-documented (Senapathi et al., 2015).

In this review, we aim to understand the role of bees as ecosystem engineers and explore their ecological functions across various ecosystems. While traditionally pollinators, specifically bees, were not acknowledged as ecosystem engineers due to their focus on resource provisioning (Jones et al., 1994), recent studies indicate that pollinator bees might fulfill the role of ecosystem engineers providing diverse environmental services. Bees also serve as bioindicators for contaminants resulting from increasing anthropogenic activities. The honeybee (Apis mellifera), in particular, is recognized as a valuable bioindicator due to its close association with the ecosystems it inhabits (Sadeghi, Mozafari, Bahmani, & Shokri, 2012). Bees encounter various contaminants during foraging, in flight, and through nectar and pollen consumption (Ruschioni et al., 2013). Analysis of the honeybees can reveal the presence of elements such as Cu, Cr, Zn, Mn, and Fe concentrations, which correlate with seasonal changes and agricultural practices (Skorbiłowicz, Skorbiłowicz, & Cieśluk, 2018).

Bees' Role in Pollination and Biodiversity

Pollination is important for the stability of natural ecosystems and the production of various vegetables and crops, forming a critical link between agriculture and the cycle of life. So the process of pollination significantly contributes to economic improvement (Gill et al., 2016; Hristov, Neov, Shumkova, & Palova, 2020). The term 'pollination' is the transfer of pollen from the male anthers to the female stigma, either within the same flower or between different flowers on same or on different plants.

Over 75% of food crops are partially or completely dependent on animal pollinators, with pollinating bees playing a crucial role in the production of fruits, vegetables, coffee, cocoa, and almonds (Klein et al., 2007). Pollinators such as bees are also key in supporting biodiversity, as evidenced by the positive correlation between plant and pollinator diversity (Ollerton, 2017). The abundance and species richness of pollinators in an area are considered as an indicator of the overall health of that ecosystem. Certain crops, including cherries, blueberries, and apples, solely rely on bee pollinators for up to 90 % of their yield, indicating the interdependence between bee pollinators and plant diversity (Biesmeijer et al., 2006).

Pollination as Ecosystem Engineering

For pollinators to function as ecosystem engineers, certain conditions must be met. Firstly, the plant species must require biotic factors for pollination. Secondly, the resultant fruits should be of a dry type that is not consumed by frugivores and predators, allowing them to remain in the environment for an extended period. Thirdly, post-seed dispersal, these fruits should create habitats for other organisms (Cardoso et al., 2023). In this scenario, a plant acts as an autogenic engineer, modifying the environment through its physical structures. Conversely, the pollinator serves as an allogenic engineer, effecting change through various activities (**Figure 1**) (Cardoso et al., 2023).

Habitat Construction and Maintenance

Bees from the Andrenidae, Fideliidae, Halicitidae, Melittidae, Oxaeidae, and Stenotritidae families build their nests underground across wide range of habitats. These habitats include weathered sandstone, prehistoric walls, dense clay, and sandy dunes of deserts and beaches (Custer, 1928; Roubik & Roubik, 1992; Stephen, 1965). Most species prefer soils that are well-drained, ranging from horizontal to vertical orientations for nesting (Linsley, 1958). However, species such as *Epicharis, Dasypoda*, and *Nomia*, are well-known for building nests in areas prone to submersion. In populated areas, solitary bees select nesting sites based on specific surface characteristics. For instance, *Nomia melanderi*, prefers soils with less than 8% clay content and minimal surface water seepage. This species digs deeper nests in hotter conditions to regulate temperature (Stephen, 1960). Similarly, species like *Colletes*, *Andrena*, and *halictine* bees often nest in soil with thinner organic layers compared to adjacent areas (Osgood Jr, 1972).

Nutrient Cycling and Soil Fertility

Bees contribute to nutrient cycling and soil fertility, in addition to their well-known role in pollinating diverse crops. In many terrestrial ecosystems, nitrogen is vital and often limiting factor for plant

growth and productivity. Research has shown that nitrogen supplementation can substantially increase both growth and productivity in plants (Vitousek & Howarth, 1991). Honeybees feces, rich in organic nitrogen, decomposes in the soil, releasing inorganic nitrogen that plants can readily assimilate (Mishra, Afik, Cabrera, Delaplane, & Mowrer, 2013). The wild bee, Osmia bicornis has been identified as a significant participant in the nutrient cycle. Biogeochemical niche analysis has underscored its role in this process. Pollen, the principal diet of bees, is a potent contributor to nutrient cycling due to its dense nutritional profile, which provides essential nutrients. The death of O. bicornis individuals also contributes to the flow of nutrients within ecosystems (Filipiak, 2023).



Figure 1: Schematic diagram of bees as ecosystem engineers.

Conservation Implications and Strategies

Bees, as important pollinators for both wild and cultivated crops, serve as ecosystem engineers in terrestrial environments (Klein et al., 2007). Despite their ecological significance, bees are declining, primarily due to anthropogenic activities (Biesmeijer et al., 2006; Fitzpatrick et al., 2007). Habitat loss emerges as the major factor in this decline, with habitat fragmentation exacerbating the situation by causing genetic isolation and inbreeding (Zayed, 2009). The potential decline of bee populations poses a substantial threat to ecosystem services, leading to concerns about disastrous impacts on the ecosystem functioning. This has prompted action from researchers, educators, and policymakers (Brown & Paxton, 2009; Dicks et al., 2013; Potts et al., 2016). Effective conservation strategies should prioritize mitigate habitat loss, promoting pollinator-friendly agricultural practices, and enhancing public awareness about the bees. The presence of natural patches of flowering plants can positively contribute to the species richness and abundance of bees by providing a continuous source of pollen, nectar, and shelter (Ruiz-Toledo, Vandame, Penilla-Navarro, Gómez, & Sánchez, 2020). A study conducted in Poland found that six ornamental flowering plants in the city of Lublin, each with different corolla lengths, attracted various species of pollinators (Jachuła, Denisow, & Strzałkowska-Abramek, 2019). Flowering plants in city gardens and parks act as a refuges for most pollinators, catering to their relatively small requirements such as habitat range, life cycle, and nesting behavior (Hall et al., 2017). Additional measures should focus on assessing the effects of invasive bee species on native bees and understanding the potential impacts of climatic changes on bee diversity and abundance. Conclusion

Bees are indispensable not only as pollinators of crops but also as ecosystem engineers, providing a range of multifaceted services. Beyond pollination, bees contribute to the ecosystem by creating habitats, such as hiding places for various organisms in abandoned fruits after seed dispersal. Additionally, they influence soil composition and aeration through their burrowing activities, which enhances plant root development. However, the full scope of bees' role as ecosystem engineers remains underexplored. This gap presents a critical area for future research to further elucidate their contributions to environmental processes and biodiversity.

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