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The role of soils on pollination and seed dispersal

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Ongoing environmental changes are affecting physical, chemical and biological soil components. Evidence of impacts of soil changes on pollinators' and seed dispersers' behaviour, fitness and density is scarce, but growing. Here, we reviewed information on such impacts and on a number of mechanisms that may explain its propagation, taking into account the full range of resources required by the large and diverse number of species of these two important functional groups. We show that while there is substantial evidence on the effects of soil nitrogen enrichment and changes in soil water content on the quality and quantity of floral and fruit resources, little is known on the effects of changes of other soil properties (e.g. soil pH, soil structure, other nutrients). Also, the few studies showing correlations between soil changes and pollinator and seed disperser foraging behaviour or fitness do not clearly identify the mechanisms that explain such correlation. Finally, most studies (including those with nitrogen and water) are local and limited to a small number of species, and it remains unclear how variable such effects are across time and geographical regions, and the strength of interactive effects between soil properties. Increasing research on this topic, taking into consideration how impacts propagate through species interaction networks, will provide essential information to predict impacts of ongoing environmental changes and help guide conservation plans that aim to minimize impacts on ecosystem functioning.

This article is part of the theme issue 'The role of soils in delivering Nature's Contributions to People'.

1. Introduction

Pollination and seed dispersal are essential ecosystem functions upon which the reproduction of most plants depends [1,2] both being performed by a vast group of animals including a diverse set of invertebrates and vertebrates (figure 1). These functions make an important contribution to humankind, increasing production and quality of the vast majority of crops [3,4] and maintaining the populations of many plants [2] essential for several ecosystem services. Human activities have changed immensely chemical [5,6], physical [7,8] and biological [9] properties of the soil affecting plants at the species [10,11] and community level [12]. Yet, compared to other global changes (e.g. biological invasions, pollution, climate and land use changes [13,14]), little is known about how impacts of such changes in soil properties propagate through trophic levels and even less about the direct impacts on pollinators and seed dispersers [15,16]. In addition, the scarce existing information shows that impacts of soil changes vary in strength and direction depending on the species of the consumer evaluated. For example, some flower visitor species increase their visitation rates with nitrogen enrichment, while other species have their visitation rates maintained

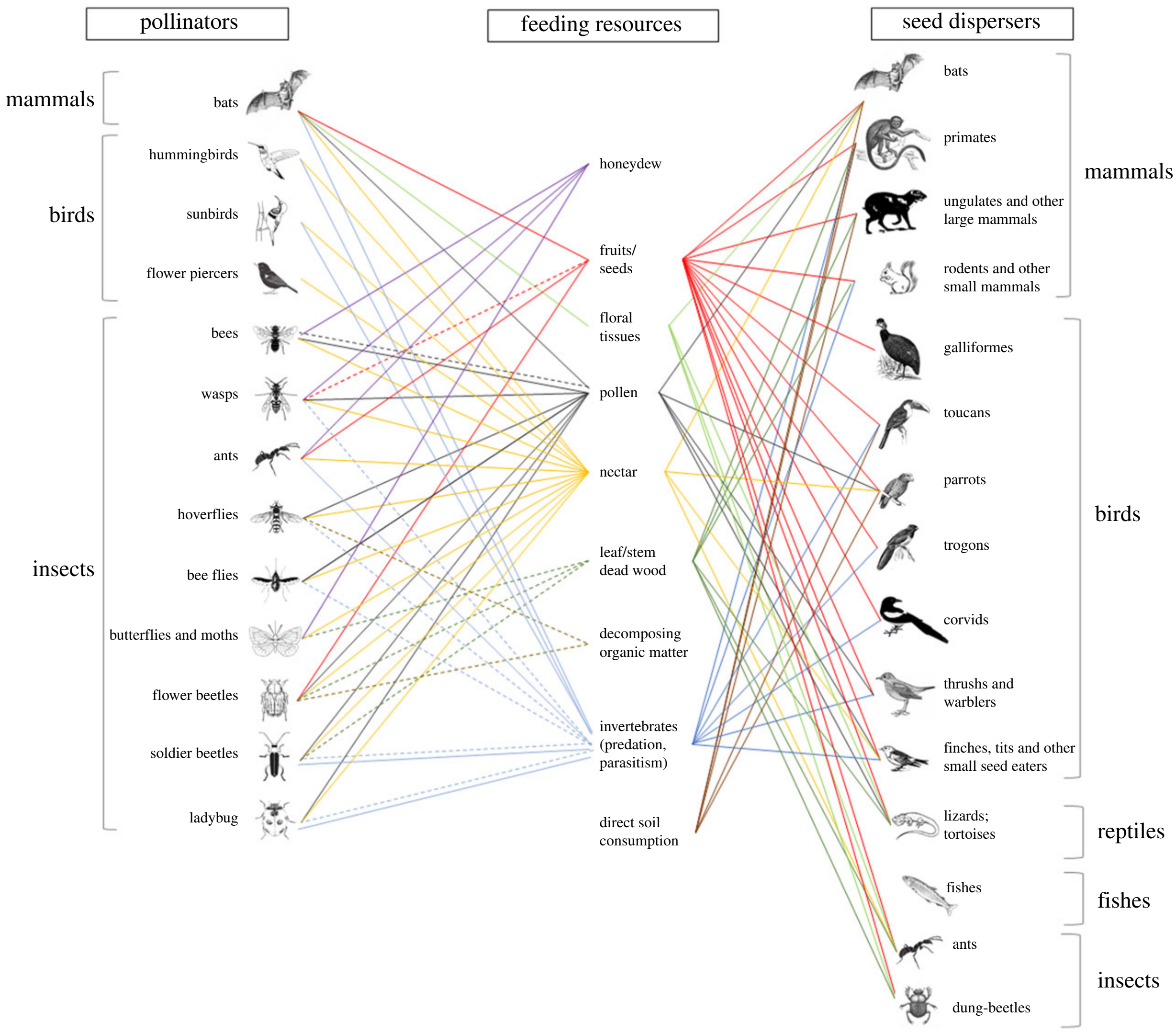

Figure 1. Diversity of feeding resources used by pollinators, during larval or adult stages, that can be affected by soil properties. Dashed lines represent resources used during larval stages. References used for the construction of this figure are listed in the electronic supplementary material.

or even reduced [17,18]. Similarly, some vertebrate dispersers benefit from soil nutrient enrichment, while ant dispersers seem more frequent on infertile soils [16,19]. Diet preferences may partly explain such variability in species responses [20,21], which effects scale up to shape communities (e.g. increased dominance [18], reduced density and richness [21–23] and changes in overall interaction network patterns [24]). Understanding the mechanisms that mediate the propagation of soil changes to pollinators and seed dispersers is essential to improve our ability to predict impacts of ongoing environmental changes and define adequate conservation plans. Here, we explore potential mechanisms mediating impacts on pollinators and seed dispersers by summarizing the existing information on the impacts of changes of several soil properties on the great diversity of dietary (figure 1) and nesting resources of these important functional groups and how such changes can explain the reported effects on them (figure 2).

2. Effects mediated by changes on abundance and diversity of floral and fruit resources

Soil abiotic and biotic characteristics are important regulators of plant physiology and affect the spatial abundance and diversity of flowers and fruits [25–28]. While the effects of increasing water availability on flower and fruit production tend to be generally positive, most plant species are better adapted to soils with low levels of nutrients, with nitrogen enrichment leading to local losses of plant diversity and promoting the expansion of invasive plants [25,26]. Similarly, soil phosphorous enrichment, which facilitates nitrogen uptake by plants [6], can lead to losses of plant richness [29]. Even in regions where plant richness is recovering (e.g. northwest Europe), increases of species are dominated by nitrophilous plants, benefitting only those pollinators that are able to make use of such species [21]. Other important macronutrients (phosphorus, potassium, calcium) may also affect flower availability, but are still poorly studied. On the other hand, whereas fertile soils have a higher percentage of fleshy-fruit species, infertile soils are more likely to have a community of plants that develop elaiosomes and arils (important rewards for many dispersers, including ants, birds and mammals [16,30,31]). Indeed, soils rich in potassium, calcium and phosphorus, are associated with vertebrate-attracting fleshy fruits, while in the nutrient-poor soil, seed dispersal communities may have a greater proportion of ants [19].

Effects of changes in soil microbiota on individual flower production can also vary among species. A reduction in the activity of soil microbiota may hence induce accentuated changes in plant community composition [32], the flower

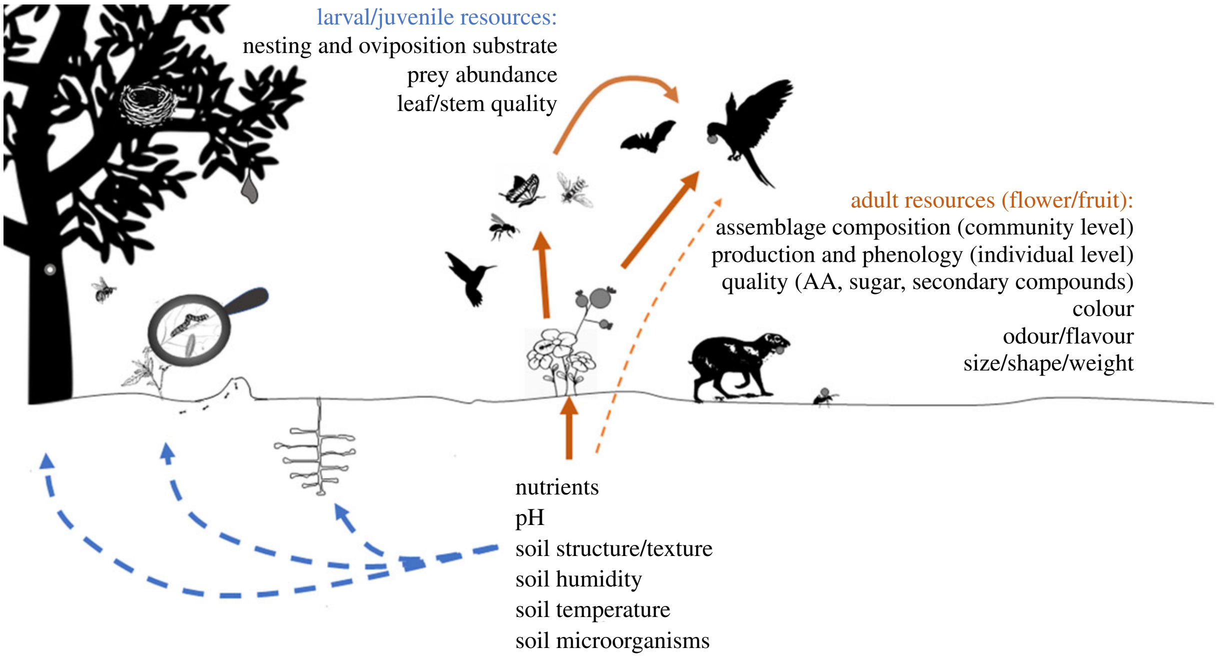

Figure 2. Pathways through which changes in soil properties (chemical, physical and biotic) may affect pollinators and seed dispersers. Blue dashed arrows represent effects on nesting and dietary resources used mostly by immature stages, orange solid arrows represent effects on dietary resources collected by adult individuals and orange thin dashed line represents direct consumption of soil by adults.

abundance of some species being positively affected by mycorrhizal fungi colonization ([33,34]), while others exhibit a negative or null response [33].

Phenology can also be affected by soil changes (e.g. nutrients [35], soil microclimate [36–38]), affecting the abundance of flowers and fruits through time, potentially creating temporal mismatches between plants and their pollinators and seed dispersers [39,40]. Some species have their flowering periods anticipated by increased nitrogen availability [41,42], while in others, flowering may be delayed or shortened [43,44]. Drought may delay the flowering period of certain plant species (e.g. [36–38]).

The changes in plant distribution, flower production and phenology described above may affect the availability of dietary resources with adequate nutritional content for pollinators and seed dispersers. Moreover, even when flower resource availability and assemblage composition are not affected, soil-driven changes in plant morphology, physiology and chemistry can have strong impacts on their consumers [45]. Below we describe in more detail effects of soil changes on such properties.

3. Effects mediated by changes on fruit and flower morphology

Alteration of soil nutrient levels [15,46], pH [47] and humidity [36,48] may change flower and fruit morphology. For example, under water restriction, certain plant species produce smaller flowers [36,48], while under lower soil pH, some species produce smaller inflorescences [47]. Nutrient increases have been related both to increases [46,49] and decreases [50] in fruit and flower size (e.g. corolla length, petal width), and soil changes may also affect flower and fruit colour [51,52]. Such changes can affect attractiveness to pollinators [53,54] and seed dispersers [16], or access of pollinators to floral resources [36,48]. Other morphological changes caused by soil changes (e.g. nutrient level, mycorrhizal fungi) may involve pollen sculpture [55] and size [33,56], which can affect pollen adherence to pollinator body and their performance as pollinators [57,58].

4. Effects mediated by changes on nutritional value of resources

Similar to other guilds of primary consumers, to satiate the dietary needs of pollinators and dispersers, the nutritional composition of plant resources consumed must match, at least partially, the requirements of those animals, which can greatly vary across species [21,59–62]. Nutrient enrichment may affect nectar [49,63,64] and pollen [56] production per flower, negative effects on nectar volume being more likely when nitrogen input is high [49,50]. Nectar and pollen quality [65–67] (i.e. amino acid (AA) content, sugar or secondary compounds levels) may also be affected by nutrient enrichment. For example, increasing nitrogen availability can increase nectar AAs and sugar content, some AAs being more affected than others [42,64,68–71], with climate mediating the strength of such effects [42]. Indeed, Gardener & Gillman [68] showed that glutamine and proline, key AAs in pollinator nectar selection, exhibit a large and significant increase under fertilizer treatment. Soil fertility (especially nitrogen and phosphorus) and irrigation may also affect the production of essential oils consumed by multiple flower visitor species [72–74]. For example, soil phosphorous increased the yield of essential oil in *Achillea millefolium* L. [75]. Yet, it is unclear if similar effects can be detected in non-volatile (fatty) floral oils, and if such effects depend on soil nutrients and water levels. Changes on mycorrhizal fungi root colonization can also affect the quality of nectar, affecting sugar content [33,34,76], flavonoids and other secondary compounds (e.g. [77–80]) found in floral resources.

Fruit quality may also be affected by soil nutrient enrichment [30,31]. An increase in potassium level may lead to more nutritious fruits [46], rich in sugars and AAs [30,81], and overall benefits for fleshy-fruited plants [19,82]. Increases in secondary compounds caused by nitrogen enrichment can be toxic when ingested [83,84], which many dispersers can counter by ingesting clay [83]. Soil ingestion may also help to compensate for fruit deficits in nitrogen and calcium [85,86]. In addition, soils with low nutrient levels tend to have plants with drier and harder fruits [30,31] and elaiosomes and arils are more common [19]. The production of edible fruits can also be limited by soil water stress, reducing fruit fleshiness and energetic content available to animals [87,88].

While many species of these two groups of animals have a generalized diet, resource quality changes mentioned above can have a strong influence on the foraging behaviour and fitness of pollinators [89,90] and seed dispersers [19,68,90–92], and potentially lead to local losses of diversity [93]. However, these effects may greatly vary among species. Low levels of nitrogen enrichment may be beneficial to some pollinator species (e.g. by reducing parasite loads [94,95]), but repel pollinators and negatively affect their physiology at high concentrations [96]. Finally, plants growing in heavy-metal-rich soils can accumulate metals into their nectar, shortening foraging time of pollinators and nectar robbers, leading to an overall positive effect on fitness of some plant species (e.g. [97]), possibly owing to increased cross-pollination.

5. Effects mediated by changes on floral and fruit scent

While vastly understudied, there is evidence that soil property changes can affect secondary compounds related to floral volatile compounds. Nitrogen enrichment can increase a phenylpropanoid floral volatile (eugenol) that attracts pollinators [17], while the number of floral volatiles and total fragrance emission can decrease with mycorrhizal fungi colonization rate [76]. Earthworm-mediated changes in soil properties can also affect the production of defence-related phytohormone jasmonic acid and of phenolic compounds [98]. Reduced soil humidity is also thought to limit the emission of olfactory cues used by dispersers to find seeds [59]. Given the importance of floral and fruit scent for detecting the presence of resources [60–62,84], any change in chemical composition of olfactory cues can affect pollinator and seed disperser foraging activity. Indeed, previous studies have suggested nitrogen-induced changes in floral volatiles increase pollinator visitation rates [17] and overall plant–pollinator communication [99].

6. Effects mediated by changes on dietary non-floral and non-fruit resources

Recognizing the diversity of resources used by consumers is essential to understand the mechanisms by which soil changes can affect them. While tight coevolutionary processes have resulted in highly specialized relationships between animals and plants [100], many pollinators feed on multiple species across multiple families [101,102], some including a variety of non-floral resources, especially during immature life stages (figure 1). Among seed dispersers, there is also variation in specialization levels, some being almost exclusive frugivorous species [1], while others include multiple alternative resources (figure 1). For pollinators that feed on leaves, decaying material, soil fungi and plant roots during immature stages (e.g. Lepidoptera and Syrphidae [103–107]), changes in leaf biomass, nutritious content and chemical clues caused by increased nutrient level or other soil changes affect the behaviour (e.g. oviposition, consumption patterns) and physiology of those insects [107–110]. Some species of pollinators also act as predators during larval stages, hence, depending on the populations of their prey. Such prey are frequently herbivores (e.g. aphids [110]) and, consequently are highly susceptible to plant chemical properties which are affected by soil properties [111]. Moreover, for pollinators highly specialized in their oviposition locations (e.g. on nitrophobous plant species [21,112]), any change in plant community composition will change oviposition opportunities. However, little is known on how changes in soil chemical and physical conditions affect larval stages of pollinators and seed dispersers and their role in ecosystem functioning.

7. Effects mediated by changes on nesting resources

Several pollinators and seed dispersers have a central place foraging pattern around a nesting location (e.g. bees, ants and vertebrates). For species constructing nests aboveground, nesting requirements are related to habitat structural complexity [28,113], which can be affected by soil properties (e.g. [114,115]). For those directly using soil as nesting substrate (e.g. the vast majority of non-parasitic bees [116,117] and several ant species) and for those that use soil to construct their cells above ground (e.g. Megachillidae [118]), the impacts of altered soil properties can be profound [119].

Although ground-nesting species can adapt to distinct soil types [120–122], some studies suggest soil texture is important. For example, many bee species tend to prefer sandy soils [122,123], deserts and dunes hosting a large diversity of bees, while clay or silt soils are less favourable. Slope [124] and soil compaction [125] also influence choice of nesting sites. While some bee communities prefer flat areas with little compaction [126], others require steep and sloping ground [127], or compacted soil in irregular surfaces [123,125]. Soil temperature and humidity can affect oviposition and the availability of nesting area for pollinators and seed dispersers (e.g. [128–131]). Central place foragers tend to minimize the difference between nest microclimate and optimal environmental foraging conditions [132], and exposed bare ground [126,127], litter cover [133], or direct sunlight and warmth [125] are documented to be preferred by some species.

Anthropogenic activities (e.g. agriculture, pasture or mining) can constrain nest availability [130,134] owing to intense soil disturbance and changes in the physical characteristics of soils and habitat structure [134]. Agricultural soils are known nesting sites of pollinators (wild bees) and seed dispersers (ants, birds) and, despite the limited knowledge, agricultural practices such as tillage or pesticide use may directly harm nest sites. Anecdotal evidence suggests that tillage can directly impact bee survival and delay emergence time [125,135]. For example, for squash bees, *Peponapis pruinose*, it has been reported that tilling can halve offspring survival owing to direct destruction of nests which, if males and females are at different depths, may also affect sex ratios [136]. However, tillage may also have positive effects on soil properties for ground-nesting by creating open bare ground, loosening compacted soils or changing the predator community [137]. In addition, in agricultural land, ground-nesting pollinators and seed dispersers can also be exposed to pesticides that accumulate in the soil (e.g. [138]). Substantial knowledge gaps remain around the toxicity and effects of neonicotinoids to arthropods, including ground-nesting bees. Further research on pollinator and seed disperser soil preferences is needed, and citizen science approaches integrating large-scale nesting occurrences documented by volunteers [139] with soil texture maps is a promising avenue to advance in this regard.

8. Effects of pollinators and seed dispersers on soil properties

Pollinators and seed dispersers are important in soil formation and maintenance. Soil nesting species impact soil characteristics owing to their excavation activities promoting vertical and horizontal mobilization of soil [116,140,141]. For example, a single bee species (*Nomia meander*) can move around 95 t yr^{-1} in the Touchet Valley of southeastern Washington [142]. Such activity may affect soil physical, chemical and hydrological profiles [141], as demonstrated in soils surrounding ants' nests [143]. This can be particularly relevant in arid and semi-arid ecosystems, where soil changes promoted by ants can generate islands of fertility [144]. Moreover, the ramified nests of communal nesters (i.e. bees nesting in aggregations) create an extensive network of tunnels that contribute to soil aeration. In addition, bees are known to bring in external soil into nests to complement its construction, contributing to soil mixing [121]. Overall, like earthworms, bees and ants contribute largely to soil aeration and rejuvenation.

9. Pathways for future research

Ongoing environmental changes are affecting soil in all its components. Evidence of impacts of soil changes on pollinators' and seed dispersers' behaviour, fitness and density is growing. While we have reviewed a number of mechanisms that may explain how such impacts propagate to these important groups of ecosystem service providers, most studies focus only on a subset of the pathways (e.g. effect of soil changes on resources, effects of resource changes on consumers). More experimental studies testing the full chain of effects from soil changes to both resources and consumers are needed. Moreover, it is likely that there is plenty of geographical variation in such impacts. Indeed, Zhong *et al.* [145] found differences in effects of nitrogen enrichment on soil respiration across biomes, with stronger negative effects in forests than in deserts. Global studies comparing strength and type of effects across climates and biomes are essential to better understand temporal and spatial variations of such effects. Moreover, much of the evidence on potential mechanisms presented here comes from a limited number of studies, and substantial knowledge gaps exist on the effects of most soil characteristics. Also, most studies focus on changes in nitrogen and water content, with more limited evidence on the effects of soil structure, pH, biota and other soil nutrients and pollutants. Experimental manipulation of other soil variables would help to disentangle interactive effects between multiple soil characteristics. Finally, multidisciplinary studies involving different guilds would help understand the indirect impacts of soil changes on pollinators and seed dispersers. For example, as pollinators have a strong influence on fruit abundance and quality, it is likely that any impact of soil changes on pollinators propagate to frugivores, affecting seed dispersal.

Data accessibility. This article has no additional data.

Authors' contributions. L.G.C. and I.B. conceived the initial structure of the manuscript. All authors contributed to the literature review and manuscript writing. L.G.C. coordinated and integrated all contributions.

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