Trends in
Plant Science

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Opinion

The evolution of plant cultivation by ants

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Outside humans, true agriculture was previously thought to be restricted to social insects farming fungus. However, obligate farming of plants by ants was recently discovered in Fiji, prompting a re-examination of plant cultivation by ants. Here, we generate a database of plant cultivation by ants, identify three main types, and show that these interactions evolved primarily for shelter rather than food. We find that plant cultivation evolved at least 65 times independently for crops (~200 plant species), and 15 times in farmer lineages (~37 ant taxa) in the Neotropics and Asia/Australasia. Because of their high evolutionary replication, and variation in partner dependence, these systems are powerful models to unveil the steps in the evolution and ecology of insect agriculture.

Highlights

True plant agriculture in non-human animals is exclusively known in the ant *Philidris nagasau*, which farms six species of *Squamellaria* in Fiji.

Plant cultivation by ants is widespread in the Neotropics and SE Asia/Australasia, with a minimum of 65 independent origins in plants, and 15 in ants, and involving nearly 200 plant species and ~37 ant species. It is apparently absent in Africa.

Plant-cultivating ants, even in obligate systems, overwhelmingly rely on their crops for structural support for nesting rather than food.

We provide a new evolutionary framework for agriculture to help to better reflect the diversity of farming mutualisms, evolutionary stages, and the divergent selective pressure shaping them.

Plant cultivation mutualisms are promising model systems to address many evolutionary and ecological questions in insect agriculture.

Insect agriculture: beyond fungiculture

Agriculture has been pivotal to the rise of a human-dominated world [1]. Outside of humans, 'farming-like' systems – in which organisms cultivate other species for food – have evolved across the tree of life [2–7]. However, true agriculture – which is defined by Mueller *et al*. as having four key characteristics: (i) habitual planting, (ii) cultivation, (iii) harvest, and (iv) obligate dependency on the crop for food – has only arisen in humans and three groups of social or subsocial insects, namely ants, termites, and beetles, all of which farm fungi [8].

Recently, an additional true, obligate agricultural system has been discovered in the Fiji Islands. The system is unique in that it is the only known example of insects farming plants. The Dolichoderine ant *Philidris nagasau* cultivates six species of the epiphytic plant genus *Squamellaria* [9]. This means that insect agriculture is not restricted to fungal crops as previously thought. Outside this obligate plant farming by ants, there is also the cultivation of epiphytic plants by ants. These so-called 'ant-gardens' were discovered over 100 years ago [10]. However, it is unclear how they fit within the framework of farming mutualisms, and whether they represent, or are ecologically close to, true agricultural systems.

In this opinion paper, we perform a systematic review of all forms of plant cultivation by ants and argue that (i) plant cultivation by ants involves a range of dependences, with partnerships ranging from loose facultative cultivation systems to tight obligate agricultures; (ii) several systems likely represent true agriculture systems, but quantifications are not possible yet as most of these symbioses are understudied; (iii) because plant cultivation partnerships range in their level of specialisation and dependence and involve many independent lineages of plants and ants, they are powerful model systems to study the ecological and evolutionary consequences of agriculture; (iv) a more inclusive ecoevolutionary framework focused on evolutionary stages is useful for understanding the evolution of farming behaviour across the tree of life.

Three types of plant cultivation by ants

Ants have coexisted with plants for at least 140 million years [11]. While they engage in a large diversity of mutualistic interactions with plants – including defence mutualisms based on **extrafloral nectaries** (**EFNs**) (see Glossary) or **domatia**, and seed dispersal mediated by **elaiosomes** [12–15] – actual plant cultivation only represents a small subset of these.

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We performed a systematic search and built a database of plants cultivated by ants and of plant-cultivating ants (see the supplemental information online) to ask the following questions. (i) How many types of plant cultivation mutualisms exist, and where are they located geographically? (ii) How taxonomically diverse are they? (iii) How do these plant cultivation systems compare in relation to taxonomic diversity, presence of domatia and food rewards, specificity and dependence? (iv) How do they compare to the conceptualisation of insect agriculture [8]?

We identified three types of plant cultivation mutualisms, which occur in three distinct geographical areas: (i) Neotropical ant-gardens, (ii) SE Asian and Australasian ant-gardens, and (iii) Fijian agriculture (Figures 1 and 2A–J). All three plant cultivation systems have the same core function: nutrient-stressed epiphytes receive nutritional resources in return for providing ants with nesting space; however, both nesting space and nutrients are provided in very different ways across the three types of cultivation mutualisms. Nutrients are provided to plants by being dispersed into a nutrient-rich **carton nest**, constructed by ant-garden ants (Neotropical and SE Asian ant-gardens) or by being actively fertilised with ant faeces (Fijian agriculture). The roots of planted epiphytes provide a scaffolding which increases the stabilisation of the carton nests – which allows for the construction of larger nests (Neotropical and SE Asian ant-gardens). In addition to the structural support from the roots, epiphytes also remove excess moisture via transpiration [16]. Additionally, nest space is provided with domatia (SE Asian ant-gardens and Fijian agriculture).

(i) Neotropical ant-gardens

Ant-gardens were first described in 1901 in Brazil by Ule who reported ants as being precise and active constructors of ant-gardens [10]. Ule posited that foundress queens first prepare their carton nests, and plant epiphyte seeds. However, this was challenged by Wheeler [17] and Weber [18] who both argued that young queens colonised the roots of already established epiphytes. Ule's hypothesis has subsequently been supported both by the presence of volatile compounds in ant-garden epiphyte seeds that exclusively attract ant-gardens ants in cafeteria experiments [19–22] and direct observations of ants collecting and planting seeds into their nests [21,23,24], fulfilling the first of the criteria for true agriculture set out by Mueller *et al.* [8], namely habitual planting of the crop.

The differential attractiveness of epiphyte seeds to ant-garden ants has been found to be directly correlated with the relative abundance of plants in ant-gardens [24]. Elaiosomes are almost always absent apart from five Neotropical plant species (<6% of Neotropical species) [25] and completely absent in other types of plant cultivation systems, strongly suggesting that ant-garden dispersal behaviour is not driven by food rewards. While some ant species do colonise established epiphytes [26] or abandoned ant-gardens [27,28], this behaviour is unusual and separate to the ontogeny of ant-gardens [23]. Additionally, many Neotropical ant-gardens contain an additional mutualism wherein two ant species co-occur in the same nest referred to as **parabiosis** [29]; whether it affects the farming mutualism is unknown (see Outstanding questions).

Neotropical ant-gardens also fulfil the second criterion – cultivation by providing a nutrient-rich environment in the form of a carton nest, which are made of organic debris (e.g., plant material, sand, soil, vertebrate faeces) cemented with ant secretions [30,31]. Such carton nests are rich in nitrogen, phosphorus, and potassium, thus providing a substrate that enhances plant growth. Not only do plants benefit from the nutrient-rich environment but, in at least some species, aggressive ant-garden ants also defend the plants against herbivory [30,32].

The third criterion – harvesting of the crop for food – is not ubiquitous (Figure 2C, Supplementary dataset 1 in the supplemental information online). However, it occurs in 41% of Neotropical ant-

Glossary

Ancestral state reconstruction (or estimation): a phylogenetic comparative method which infers back in time the evolution of a trait throughout a phylogenetic tree, based on the distribution of the trait in extant species.

By-product mutualism: a model of stable mutualism implying that the mutualistic service or reward is a by-product and hence cost-free. In theory, by-product mutualisms should be free of conflicts, but they can be the evolutionary starting point for more complex mutualisms with high costs and benefits.

Carton nests: nests actively built by the majority of arboreal ants. Carton nests are made of plant materials, other debris, and ant secretions.

Cheating: when an organism that is evolutionarily derived from a true mutualist obtains rewards from a partner without reciprocating in a way that increases their own fitness and decreases the inclusive fitness.

Domatia (singular domatium): evolutionary derived plant structures that are used by symbiotic ants for nesting. Domatia can be derived from a variety of modified plant structures including stems, leaves, rachis, thorns, root tubers, and hypocotyls.

Elaiosomes: nutrient-rich, fleshy structures attached to seeds. They are involved in seed dispersal mutualisms wherein ants are attracted by the food reward in return for dispersal.

Extrafloral nectaries (EFNs): plant structures that produce nectar outside of their flowers. Some plants produce EFNs as a nutrient reward to ants that defend them against herbivory.

Parabiosis: a symbiosis between two different ant species wherein two colonies nest together without showing any aggression to each other. Work in several systems shows that they are mutualistic, but very few have been studied.

Partner choice: a mutualism stabilisation mechanism wherein a mutualist partner exclusively rewards particular beneficial partner(s) and denies resources to others.

Partner fidelity feedback: a stabilisation mechanism wherein the fitness of mutualist partners is aligned, implying that 'cheating' a mutualist partner would harm their own fitness; therefore, there is no incentive to **cheat**.

Pearl bodies: small lustrous food rewards rich in lipids, protein, and carbohydrates. They are similar to EFNs;

some plants offer pearl bodies to elicit a defensive response from ants.

Phorophyte: a plant on which an epiphyte grows. It should be noted that epiphytes do not gain nutrients from their phorophytes, and instead just anchor themselves onto them, often to grow higher up in the forest canopy.

Polydomous: a nesting strategy in which an ant colony inhabits several spatially separated nests.

Post-anthetic nectar rewards: specialised food rewards of epiphytic Rubiaceae (Hydnophytinae), consisting of the large nectary discs, which become ant rewards once the corolla has fallen off. These nectaries maintain a high sucrose content by delaying fruit development. Symbiotic ants access these rewards by biting through the thick epidermis, which reduces attraction to opportunists.

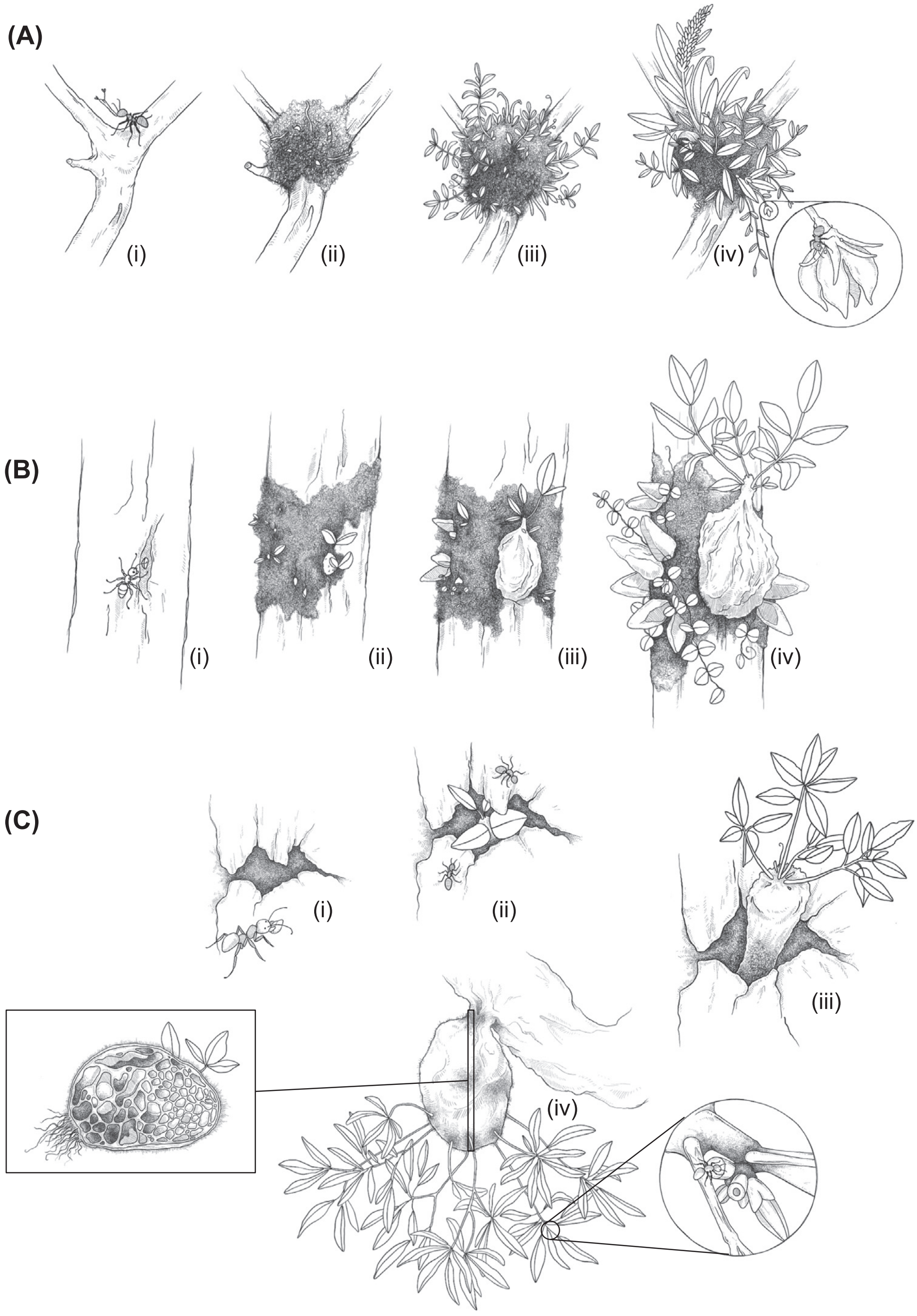

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Figure 1. Comparative development of the three main types of plant cultivation systems. (A) Neotropical ant-gardens. (i) Ant-garden ants build a carton nest, often aided by the **phorophyte** structure, such as here a branch fork, (ii) workers subsequently plant seeds inside the carton, (iii) the epiphyte roots stabilise the nest, and (iv) when epiphytes are mature, some provide rewards such as extrafloral nectar (inset). (B) SE Asian/Australasian ant-gardens. (i) Ant-garden ants build a carton nest, often directly on the bark, and (ii) plant seeds of ant-garden epiphytes, some with and others without domatia. The epiphytes grow and stabilise the nest, with some starting to develop domatia where part of the (**polydomous**) ant colony will

(Figure legend continued at the bottom of the next page.)

garden species, mostly through EFNs (Figure 2C). Finally, the fourth requirement – obligate dependence on the crop for food – does not occur. However, there is experimental evidence suggesting that ant-garden ants are obligately dependent on epiphytes to maintain their nest structure wherein ant-garden epiphytes were experimentally defoliated, which led the nests to deteriorate by losing 75% of the carton in a week, meaning that the ants could no longer nest and reproduce [16].

In terms of taxonomic diversity, we identified 75 records (including 69 identified at the species level) of ant-garden epiphytes from across 11 families (Araceae, Bromeliaceae, Cactaceae, Clusiaceae, Cyclanthaceae, Gesneriaceae, Moraceae, Orchidaceae, Piperaceae, Polypodiaceae, and Solanaceae), scattered across the plant tree of life (Figure 2B). The evidence for individual species to be true ant-garden epiphytes varies widely (Supplementary dataset 1 in the supplemental information online), mostly because of lack of data (see Outstanding questions). There are fewer ant species than plant species involved in these mutualisms: 17 records (15 reported at the species level) in four subfamilies Dolichoderinae, Formicinae, Myrmicinae, and Ponerinae (Supplementary dataset 2 in the supplemental information online).

(ii) SE Asian and Australasian Ant-gardens

While seed planting by ants was suspected in Central Java by Leeuwen in 1913 [33], it was previously believed that ant-gardens do not occur in SE Asia or Australasia – their presence was only confirmed more recently [34]. Similar to Neotropical ant-gardens, SE Asian and Australasian ant-gardens are founded by queens actively collecting and planting seeds into nutrient-rich carton nests [34], fulfilling the two first criteria for a true agriculture. Less than half of SE Asian and Australasian ant-garden epiphytes offer food rewards (Figure 2C, Supplementary dataset 1 in the supplemental information online), meaning that the third criterion – harvest of food rewards – is only sometimes met. The fourth criterion – obligate dependence – is also unclear; while SE Asian ant-garden ants have been described as obligate, there is inconsistency in how the term 'obligate' has been used, and further work should focus on better quantifying dependence in these systems (Box 1).

Given the longer history of research on Neotropical ant-gardens, it was surprising that our systematic review found more ant-garden species in SE Asia and Australasia – with 112 potential species from 12 plant families (Apocynaceae, Araceae, Araliaceae, Gesneriaceae, Melastomataceae, Moraceae, Orchidaceae, Piperaceae, Polypodiaceae, Rubiaceae, Urticaceae, and Zingiberaceae) (Supplementary dataset 1 in the supplemental information online). The taxonomic diversity of SE Asian ant-gardens differs drastically from their Neotropical counterparts, with only five out of 12 families in common (Araceae, Moreaceae, Orchidaceae, Piperaceae, and Polypodiaceae), but are similarly dispersed across the plant phylogeny (Figure 2B). Like Neotropical ant-gardens, there are far fewer ant species involved: four subfamilies and five genera Dolichoderinae, Formicinae, Myrmicinae, and Ponerinae with a total of 19 taxa, most of which are only described to the genus level (Supplementary dataset 2 in the supplemental information online). SE Asian ant-gardens also have the additional parabiotic mutualism. Interestingly, the same two genera (*Camponotus* and *Crematogaster*) that co-occur in the Neotropics also co-occur in SE Asia (E. Kaufmann, PhD

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live, expanding the nesting site area of the colony (iii). In the mature ant-garden, domatium-bearing epiphytes provide substantial nesting site area (iv), and a large part of the colony nest there, with the majority of epiphytic Rubiaceae providing food rewards too. (C) Fijian agriculture. (i) *Philidris nagasau* workers plant *Squamellaria* seeds directly in bark cracks, without a carton nest, and (ii) the seedlings emerge from the sunken cracks thanks to an adaptation of the hypocotyl ('hypocotyl foot'). Both seeds and seedlings are constantly monitored, and as soon as the domatium emerges, *P. nagasau* workers enter it to fertilise the plant by defaecation. As the *Squamellaria* plant grows (iii), it offers more nesting space to the colony, which typically consists of several dozen plants. Mature plants (iv) offer very large nesting sites in the domatia, which contain two types of wall: warty walls (in darker shade) where the ants defaecate, and smooth walls where the ants nest. They also offer post-anthetic nectar rewards, on which workers constantly feed. Drawings by Emma Hindhaugh.

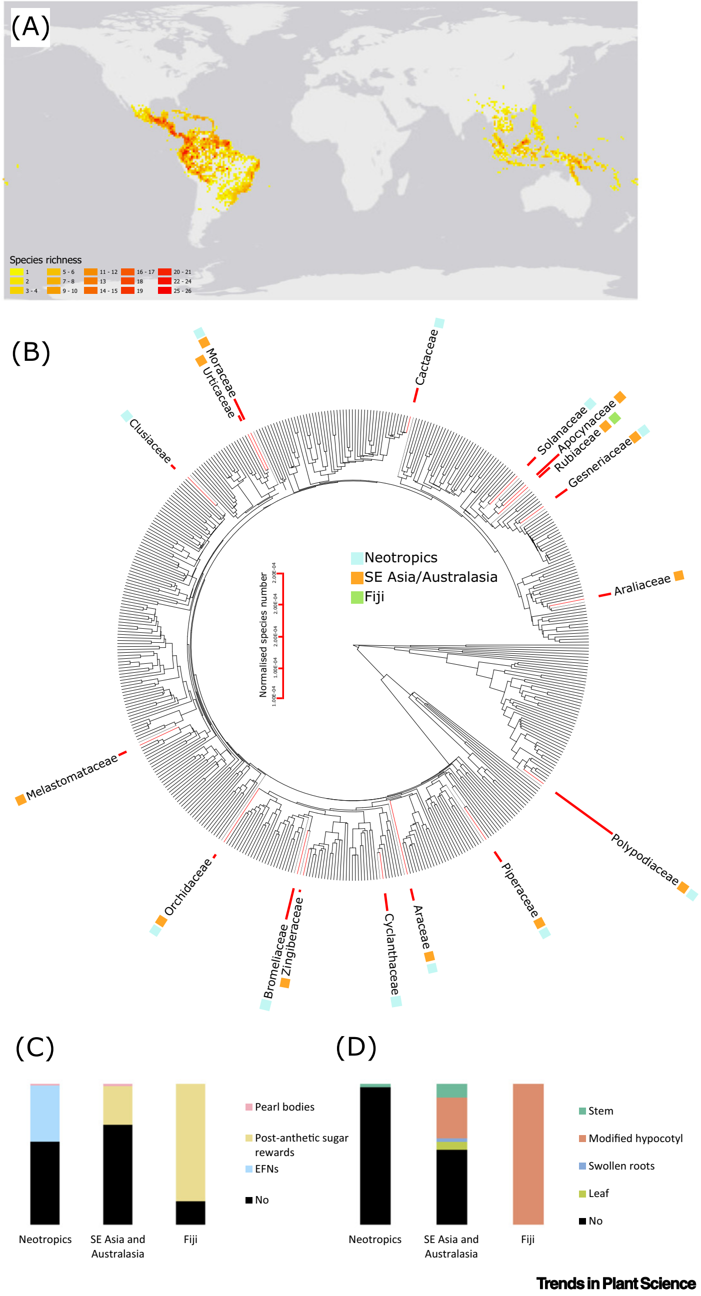
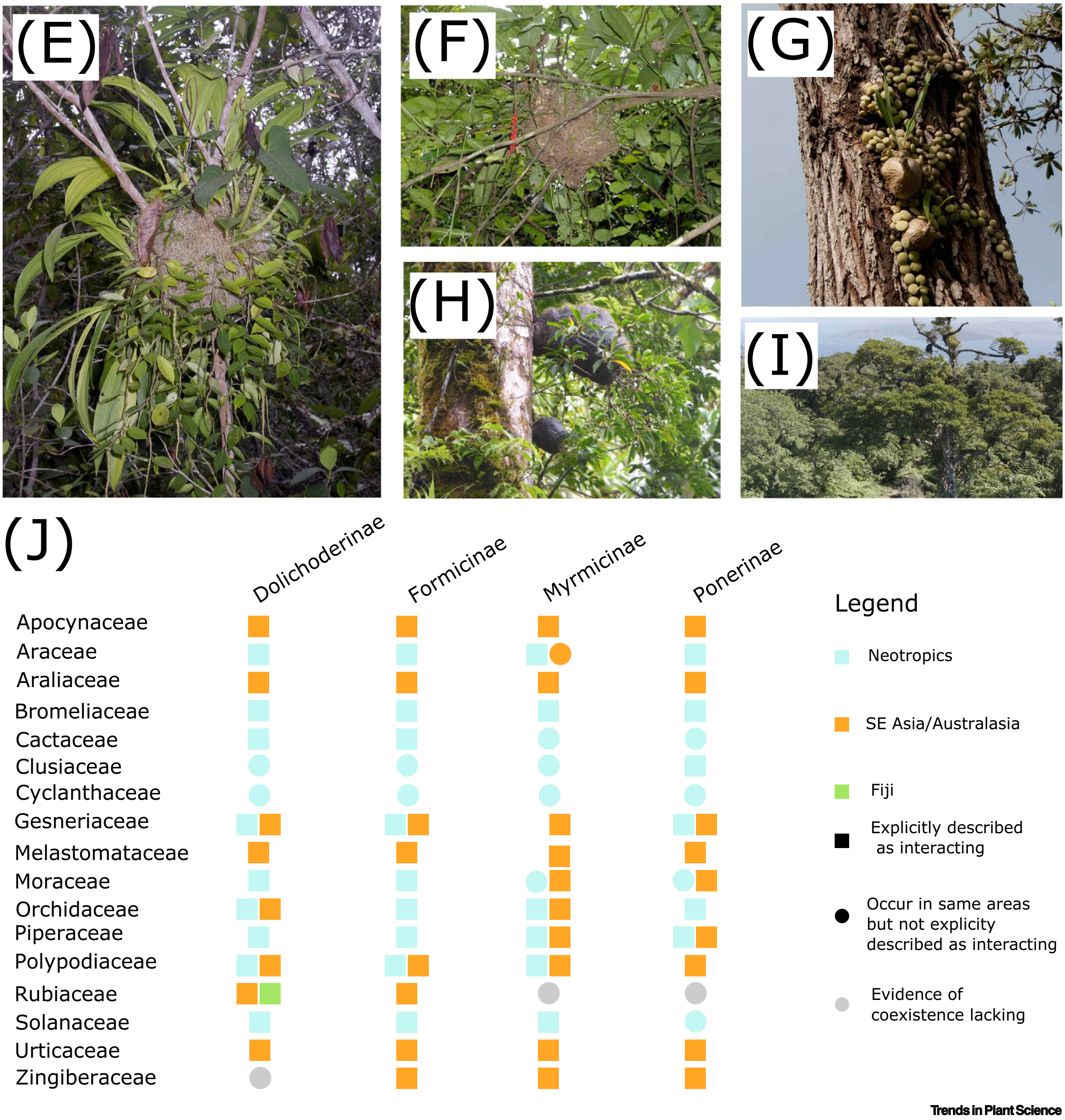


Figure 2. The diversity of plant cultivation mutualisms. (A) Species richness heatmap of ant-garden epiphytes based on Supplementary dataset 1 in the supplemental information online (see Table S3 in the supplemental information online for GBIF references). (B) Phylogeny of vascular plant families with families containing ant-garden plants coloured in red. Bars indicate the normalised number of ant-garden species in each family (see Methods in the supplemental information online for details of normalisation). (C) Percentages of ant-garden plants with food rewards and frequency of food reward type. (D) Percentages of ant-garden plants with domatia and frequency of domatia types. (E) Neotropical ant-garden with *Coryanthes leucocorys* in Peru. (F) Neotropical AG of parabiotic ants *Camponotus* and *Crematogaster*, (G) SE Asian ant-garden with *Myrmecodia tuberosa* and *Dischidia nummularia*, (H,I) *Squamellaria wilsonii* farmed by *Philidris nagasau*. (J) Interaction data of ant-garden ant subfamilies and ant-garden plant families. Squares indicate that there is strong evidence for these taxa interacting in ant-gardens, for example, explicit description of a plant family occurring in the ant-garden of an ant in a given subfamily. Circles indicate that these ants and plants may interact; for example, they are mentioned in the same ecological surveys. However, there is no explicit evidence of a given plant family occurring in the ant-gardens of a given ant subfamily. Grey circles indicate a lack of evidence of interaction, which, however, cannot be completely ruled out due to their co-occurrence in these geographic regions. Abbreviation: EFN, extrafloral nectary. Photographic credits: (E) Günter Gerlach; (F) Jerôme Orivel; (G) Milan Janda; (H) Guillaume Chomicki; (I) Benoît Chomicki.



	Dolichoderinae	Formicinae	Myrmicinae	Ponerinae
Apocynaceae	🟧	🟧	🟧	🟧
Araceae	🟦	🟦	🟦🟠	🟦
Araliaceae	🟧	🟧	🟧	🟧
Bromeliaceae	🟦	🟦	🟦	🟦
Cactaceae	🟦	🟦	🔵	🔵
Clusiaceae	🔵	🔵	🔵	🟦
Cyclanthaceae	🔵	🔵	🔵	🔵
Gesneriaceae	🟦🟧	🟦🟧	🟧	🟦🟧
Melastomataceae	🟧	🟧	🟧	🟧
Moraceae	🟦	🟦	🔵🟧	🔵🟧
Orchidaceae	🟦🟧	🟦	🟦🟧	🟦
Piperaceae	🟦	🟦	🟦🟧	🟦🟧
Polypodiaceae	🟦🟧	🟦🟧	🟦🟧	🟧
Rubiaceae	🟧🟩	🟧	⚪	⚪
Solanaceae	🟦	🟦	🟦	🔵
Urticaceae	🟧	🟧	🟧	🟧
Zingiberaceae	⚪	🟧	🟧	🟧

Legend

🟦 Neotropics

🟧 SE Asia/Australasia

🟩 Fiji

■ Explicitly described as interacting

● Occur in same areas but not explicity described as interacting

⚪ Evidence of coexistence lacking

Figure 2 (*continued*).

thesis, Goethe University Frankfurt, 2002; [35]). Ant-gardens solely occupied by *Crematogaster* seem to be much less successful than when occurring in parabiotic association with *Camponotus* (E. Kaufmann, PhD thesis, Goethe University Frankfurt, 2002; [20]), both in the Neotropics and SE Asia. *Camponotus* is larger and more aggressive than *Crematogaster*, but benefits from

Crematogaster's superior foraging abilities [29,36]; again, this has been noted in the Neotropics and SE Asia. Such differences in size and behaviour suggest that each species might play different roles in the ant-garden, for instance, in defence, seed planting, and cultivation. More work is needed to understand how parabiosis contributes to plant cultivation mutualisms (see Outstanding questions).

SE Asian ant-gardens differ from Neotropical ones in two key ways. First, SE Asian ant-gardens frequently involve stem or leaf domatia while these are absent in Neotropical ant-gardens, occurring in 46.7% of the SE Asian ant-garden plants, including four families and ten genera (Figure 2D). This correlates with the diversity of epiphytic ant-plants, which are concentrated in SE Asia and Australasia (E. Kaufmann, PhD thesis, Goethe University Frankfurt, 2002; [15]). Despite the high prevalence of domatia in SE Asian ant-gardens, queens are not usually found to nest in domatia and instead nest within the carton (E. Kaufmann, PhD thesis, Goethe University Frankfurt, 2002).

Second, SE Asian ant-garden epiphytes (E. Kaufmann, PhD thesis, Goethe University Frankfurt, 2002) contribute less to symbiotic ant nutrition than in Neotropical ant-gardens: only 29% of SE Asian ant-garden plant species have food rewards as compared to 41% in the Neotropics (Figure 2C, Supplementary dataset 1 in the supplemental information online). Perhaps more strikingly, EFNs are absent in SE Asian and Australasian ant-garden epiphytes (Figure 2C, Supplementary dataset 1 in the supplemental information online). Food reward in SE Asian and Australasia ant-gardens epiphytes is almost exclusively restricted to **post-anthetic nectar rewards**, found only in epiphytic Rubiaceae (34 species) [37], and **pearl bodies** occurring in two species [38].

Box 1. The challenge and opportunities of defining dependence in plant cultivation mutualisms

Comparing and quantifying levels of dependence of ant-garden species has proven difficult for two reasons.

First, specialisation (generalist vs. specialised) and dependence (facultative vs. obligate) are often conflated. This issue is not unique to the study of ant-gardens. A second problem is that there is little consistency about how authors have referred to systems as being 'obligate'. For example, Kaufmann (E. Kaufmann, PhD thesis, Goethe University Frankfurt, 2002) refers to ant species which plant epiphyte seeds as obligate mutualists, whereas Yu [16] refers to ant-garden ants as being obligate partners of epiphytes due to their nests falling apart following defoliation experiments. Youngsteadt regularly refers to ant-garden ants as obligate but does not define what it means to be obligate (E.K. Youngsteadt, PhD thesis, North Carolina State University, 2008). Determining whether a partnership is obligate typically requires experimentation. Experimental manipulations, such as the removal of epiphytes [16] or ants [39], permit us to ascertain the level of dependence of a plant cultivation mutualism. In SE Asia, some ant-garden ant species are observed to nest outside of ant-gardens (E. Kaufmann, PhD thesis, Goethe University Frankfurt, 2002; M. Janda pers. comm to G.C.) suggesting that there is a gradient of dependence amongst ant-garden ants.

Despite the difficulty in determining the level of dependence, plant cultivation mutualisms offer an unprecedented opportunity to probe how the level of dependence and specialisation affect farming mutualisms (Box 2).

Chomicki *et al.* [51] proposed a framework wherein dependence and specialisation are clearly differentiated, splitting mutualism into four categories with each of the four combinations of dependence and specialisation (facultative generalist, facultative specialist, obligate generalist, obligate specialist). Because both dependence and specialisation are frequently asymmetric, they have to be defined at the organism level rather than at the interaction level [51].

Specialisation is easier to assess, compared to dependence, as it concerns the number of mutualistic partners. Occurrence data can inform of the partner breadth of a species. However, this can vary locally and be unevenly distributed, implying that sampling at different locations could yield distinct partner species and species number. The evolutionary conceptualisation of specialisation [51] focuses on whether species associate with few specific (specialised) versus many unspecific partners (generalist). This places the emphasis on traits – which can in turn be traced along phylogenies – rather than on the absolute number of partners, which, in generalist interactions, can be a function of sampling effort. In SE Asian ant-gardens, the generalization of plant cultivation via the recruitment of (unrelated) new epiphyte species led to a specialisation of the mutualism in plant side, sometimes resulting in new traits [50]. Similar to attines which can differentiate between different fungal cultivars [52], it is clear that ant-garden ants can differentiate between seeds from ant-garden epiphytes and non-ant-garden epiphytes via chemical cues (E.K. Youngsteadt, PhD thesis, North Carolina State University, 2008), likely also mediating the level of specialisation of these mutualisms. Understanding how the level of specialisation affects the stability and efficiency of plant cultivation mutualisms is an open question, and this in turn has the potential to inform insect agriculture in general.

(iii) Fijian agriculture

The first known system that can be defined as true plant agriculture by a non-human animal was discovered in Fiji in 2016 [9]. In this system, *P. nagasau* (Dolichoderinae) obligately farms epiphytic *Squamellaria* plants (Rubiaceae). *P. nagasau* fulfils all four of the criteria for true agriculture. First, *P. nagasau* habitually collects and plants *Squamellaria* seeds under tree bark. Second, it actively fertilises *Squamellaria* plants throughout their entire lifetime [9,39] as well as protects them from herbivory and selects sites highly sun-exposed to optimise crop productivity [40]. Third, it harvests food rewards in the form of post-anthetic nectar rewards [37], but it does not obligately depend on crop-produced food, as workers can hunt insects when needed [9,37]. Fourth, the ant farmer, however, obligately depends on *Squamellaria* for nesting space due to an evolutionary loss of the ability to construct its own carton nests [39].

The Fijian farming system differs from both Neotropical and SE Asian/Australasian ant-gardens in being more specialised and reciprocally obligately dependent. *P. nagasau* cultivates six species of *Squamellaria*. Typically *Squamellaria* ‘farms’ are monocultures of a single species, and more rarely farmers can cultivate up to three closely related *Squamellaria* species [9,39], while in both Neotropical and SE Asian ant-gardens, these are typically diffuse assemblages spanning a large taxonomic breadth (Figure 2E–J, Supplementary dataset 1 in the supplemental information online). In addition to the taxonomic specialisation, farmed *Squamellaria* species show high levels of morphological specialisation, including differentiated areas within the domatia (smooth and highly absorptive areas, which defines different functions in the symbiosis: nesting and rearing brood for the former, and defaecating to fertilise the host in the latter [39]) as well the evolution of food rewards which can only be accessed by *P. nagasau* [37].

Fijian agriculture also differs in relation to dependence, both the ant *P. nagasau* and the *Squamellaria* plants are obligately dependent on the mutualism. The ant farmer dependence on the crop is mediated by the loss of carton nest building behaviour [9], while the dependence of the crop on the farmer is not fully clear, but ant-exclusion experiments suggest that it might be mediated by a role of the ant farmer in disease protection [39].

Agriculture beyond monoculture for food: a new evolutionary framework

Farming for shelter

A major finding from our database is that less than half of the epiphyte species cultivated by ants provide food rewards (Figure 2C, Supplementary dataset 1 in the supplemental information online), which strongly suggests that plant cultivation by ants is driven by an incentive for shelter rather than food. In contrast, structural support is ubiquitous. This is true across the gradient of specialisation and dependence of these partnerships. A key illustration of this occurs in one of the six obligately farmed Fijian *Squamellaria* species (*Squamellaria grayi*), which has secondarily lost food rewards, yet is still cultivated in the same way by *P. nagasau* farming ants [37].

The idea of obligate nutritional dependence [8] as one of the four steps of true agriculture put forward by Mueller *et al*. [8] stems from the fact that high-intensity agriculture for food generates food surpluses on which population size is dependent. In this regard, the fungiculture of attine ants and termites is remarkable, with attines having large colonies containing millions of workers and nests as large as 600 square metres [41]. This shows a striking convergence with human agriculture.

Our findings in plant cultivation mutualisms argue for the inclusion of services other than nutrition – such as shelter – in the definition of true agriculture by Mueller *et al.* [8]. The consequences for ants not having adequate access to nesting space are similar to not having adequate food: reduction in fitness/reproductive success. Not only are ants just as dependent on nesting space as they are on food, but nesting space is often the most limiting resource in tropical rainforest environments [42], largely because this is where ant abundance is maximal [43]. In rainforests, a large proportion of ants are cryptic herbivores, relying on the virtually unlimited plant carbon bank either directly by feeding on plant secretions such as extrafloral nectar or indirectly via cultivating honeydew-producing Hemipteran insects [43,44]. Given that food is not as limited, it makes sense to include farming for shelter within our understanding of agriculture. Besides the ecological relevance of farming for shelter, we humans also engage in agriculture for many non-nutritive purposes such as farming timber that is used for shelter, or for plants providing textiles such as cotton, or plants farmed for pleasure such as coffee, cannabis, or kava, or even ornament [45].

An evolutionary framework for agriculture

While what should or should not be considered 'true' agriculture may be considered semantics, we argue that including a broader diversity of farming mutualisms, including those that are not obligate, within the framework of agriculture is essential for three reasons. First, it offers evolutionary

Box 2. Plant cultivation mutualisms as model systems in insect agriculture

The study of insect fungiculture has provided many insights into mutualism, agriculture, and social evolution [53–57]. Here we argue that there are features of plant cultivation systems that have the potential to provide additional insights into insect agriculture for three main reasons.

First, it offers evolutionary replication to address various comparative questions on insect agriculture, such as the effect of agriculture on farmer demography (see Outstanding questions). Such level of replication is unique within farming systems: there are at least 65 independent origins in the plant lineages (31 in Neotropical ant-gardens, 33 in SE Asian ant-gardens, and one in Fijian agriculture), and minimally 15 origins in the ant lineages (ten in Neotropical ant-gardens and five in SE Asian ant-gardens) (Tables S1 and S2 in the supplemental information online). This compares to nine origins of fungiculture in insects (one in ants, one in termites, and seven in beetles) and six in fungal lineages (three farmed by ants, one farmed by termites, and two farmed by beetles [8]). Such evolutionary replication provides statistical support to ask a wide range of evolutionary and ecological questions on insect agriculture.

Second, it provides younger systems (and evolutionary replication) in which to dissect the early evolutionary stages of the evolution of agriculture. For example, which traits were preadaptations to agriculture, and which ones have evolved subsequently? What traits are prerequisite for agriculture to evolve? Phylogenetic comparative analyses can be used to compare agricultural systems with their close, nonagricultural relatives. Specifically, ancestral state reconstructions can be used to unveil the association and evolutionary directionality in the evolution of farming traits (e.g., [33,34]). For instance, seed and fruit traits have likely constrained the evolution of plant cultivation since there are maximum weight and minimal size that an ant can carry (and this varies across species as a function of traits such as body size). A tabulation of fruit types across plant-cultivated genera and their sister groups revealed that fleshy fruits are prevalent. Small dust-like seeds may not be suitable for ant dispersal (Table S4 in the supplemental information online). Food rewards, such as EFNs, do not appear to have facilitated the evolution of plant cultivation, consistent with the key role of nest support rather than food (Table S4 in the supplemental information online). The expression of plant compounds on seed cuticles that ants can identify, such as 6-MMS or oleic acid, might also play a role in the initial recruitment of epiphytes that become ant-cultivated.

Third, it provides farming systems with a wide range of dependence and specialisation (Box 1), which together with the evolutionary replication provides the opportunity to ask a number of evolutionary and ecological questions about how these two key variables shape insect agriculture. For example, how are farming mutualisms with different level of dependence stabilised? Recently, it has been shown that mutualisms with varying levels of dependence have been found to rely on different stabilising mechanisms, for example, mutualisms with low levels of dependence often rely on **byproduct mutualisms** whereas partner choice requires a closer association [51]. In the Fijian plant agriculture, two distinct mechanisms stabilise the partnership: (i) a crop-mediated mechanism involving the production of food rewards targeted to the farmer (partner choice) [37], and (ii) tight positive correlations between the ant colony size and the size of the domatium (**partner fidelity feedback) [**39]. How the more diffuse ant-gardens are stabilised is unclear.

Along these lines, one particularly interesting area would be to investigate how stabilising mechanisms relate to the diversity of the 'crops', especially since both fungus-farming insects and fungal crops appear to maintain high relatedness in fungiculture systems [56], whereas ant-cultivated plant monocultures are rare except in the Fijian system. *In vivo* experiments varying the number of epiphyte species in ant-gardens and probing the potential plant–plant conflict or cooperation could be used to address this question. Crop–crop negative interactions – wherein fungal crops are hostile to the presence of unrelated fungi – are an important component of higher attine–fungal farming [57], but whether it occurs at all in plant cultivation is unknown.

replication to address a number of comparative questions on insect agriculture. Second, it provides younger systems in which to dissect the early evolutionary stages of the evolution of agriculture. Third, it provides farming systems with a wide range of dependence and specialisation (Box 1), which allow us to ask how these two key variables shape the evolution of insect agriculture. We expand on the promise of plant cultivation mutualisms as models in insect agriculture (Box 2).

Rather than a focus on particular characteristics as the defining feature of true agriculture, we propose an ecoevolutionary framework for agriculture wherein we recognise stages in the evolution of agriculture. This approach allows us to encompass all types of farming mutualisms, including those considered to be 'farming-like' systems, while at the same time retain the distinctiveness of true agriculture that Mueller *et al*. [8] defined, and that we can further extend beyond other than food.

We recognise three stages in the evolution of agriculture, namely 'resource expansion', 'adaptive cultivation', and 'obligate agriculture'. The first stage – 'resource expansion' – involves one species expanding its resource (such as food), through the cultivation of another species. This farming behaviour results from preadaptation of the farmer and the crops, and does not involve any coevolutionary adaptation yet. This is seen in the damselfish farming mutualism, where the fish uses weeding to increase its algal crop resource [6], the cultivation of bacteria by social amoeba [3], or fungal farming in the marine snail [7]. This is also seen in three-toed sloths which engage in a three-partner mutualism involving moths and algae. Sloths descend from their trees once a week to defaecate, simultaneously delivering their mutualistic moths to their oviposition site. Adult moths actively seek out sloths, and their presence in sloth fur increases nutrient availability to algae via decomposition and mineralisation; this in turn increases the growth of nutritious algae which the sloths benefit from eating – thus sloth farm algae as a byproduct of this behaviour [5]. Another example involving ant/plant systems is the so-called 'devils gardens', which involve *Myrmelachista* ants generating single-species strands of their plant hosts by killing other plant species using an ant-made herbicide (formic acid), yet lacking any form of seed dispersal [46,47].

The second stage – 'adaptive cultivation' – involves systems which are often generalist or facultative and show some adaptations, yet lack reciprocal obligate dependence. Many Neotropical and SE Asian ant-gardens fit this category. Another example is the fungus *Morchella crassipes,* which farms the bacterium *Pseudomonas putida*. *P. putida* is dispersed throughout the *M. crassipes* fungal network; *M. crassipes* transfers carbon to *P. putida* which is then harvested and consumed [4]. Similarly, the polychaete worm *Platynereis dumerilii* attaches pieces of *Ulva* and *Cystoseria* algae to its own self-grown mucus tube which acts as a substrate for its algal crop [48,49].

Finally, we argue that obligate agriculture should involve the four farming steps that Mueller *et al*. [8] described, but with obligate dependency including services beyond nutrition, such as shelter – as discussed in the preceding text. This includes the classic fungus farming in attine ants, termites, and beetles, and the Fijian *Squamellaria* plant farming by *P. nagasau* ants.

We recognise that these stages may not always be clear-cut cases, nor stable states. However, we think that they are useful because they place the emphasis on processes in farming evolution. It is important to note that linear evolutionary transitions from resource expansion to adaptive cultivation to obligate agriculture may happen only rarely. Rather, most farming mutualisms may end in the first, or more rarely the second, category. Documenting transitions between these three stages may also prove difficult as transitional stages may be evolutionarily unstable. In the farming ant genus *Philidris*, a clear transition from adaptive cultivation to obligate agriculture occurred when ant-garden type ants from SE Asia colonised Fiji [50]. Here, adaptive cultivation

Outstanding questions

Are ant-gardens truly absent from Africa? Our systematic review suggests that ant-gardens are absent in Africa. Does this reflect a lack of research or a biological reality? While much fewer as compared to the Neotropics and SE Asia, there are still a wide range of ant–plant interactions in Africa, as well as a large number of vascular epiphytes. There are reports of arboreal ants nesting in the roots of epiphyte communities, which suggests that ant-gardens are biologically plausible in Africa, especially in the West African rainforests. Further ecological surveys are needed to test this.

What is the effect of agriculture on farmer demography? Demographic increase driven by the constant and large food production enabled by agriculture is often cited as the major reason for success of humans and leafcutter ants. Yet the extent to which agriculture truly contributes to demography has not been tested empirically. The evolutionary replication of plant cultivation mutualisms offers the opportunity to test this hypothesis. One approach would involve comparative phylogenetic analyses – comparisons of colony size of farming ants and their nonfarming closest relative. The ant genus *Philidris* would be a particularly useful as some species are facultative farmers, which would allow demographic comparisons at the population level. Experimental manipulations involving ant-garden epiphytes with and without food rewards could further dissect how shelter-only versus shelter plus food affects ant-farmer demography.

What drives the obligate dependence of plant on ants? While nutrient fertilization of *Squamellaria* by *P. nagasau* is highly efficient, nutrient starvation is unlikely the driver of obligate dependence on the farmers. Farmed *Squamellaria* species suffer more severe cases of disease than nonfarmed but ant-occupied generalist *Squamellaria* during ant exclusion experiments, suggesting that *P. nagasau* provides protection from disease. The mechanistic basis is entirely unknown. Could bacteria associated with ant farmers be driving this function, as in the attine ant fungiculture?

What cues drive epiphyte selection by ant-garden ants? An important study relied on a key preadaptation to farming (seed dispersal in carton nest) in SE Asian *Philidris*, but subsequent coevolution drove the origin of obligate agriculture in Fiji [9].

In light of our analysis, we propose defining agriculture as the full spectrum of behaviours through which a species (the farmer) cultivates another one (the crop) for a service, such as food, shelter, chemicals, ornament, pleasure. It applies to both humans and non-human farmers alike, and includes minimally two factors, namely, a form of cultivation, and a service harvested by the farmer. As explained in the preceding text, this allows us to encompass the whole ecoevolutionary process of agricultural evolution, rather than only the few highly specialised obligate coevolved systems. This includes the cultivation of nondomesticated species, and early stages where cultivation occurs because of ecological preadaptations rather than adaptation resulting from cultivation. Our framework retains the four steps, expanded to include functions other than nutrition, that Mueller *et al*. [8] envisioned for obligate agriculture. We argue that such a framework will help to shed light on the evolutionary processes and forces at play in agriculture. Because plant cultivation mutualisms show a range of stages, they provide important model systems to study the evolution of agriculture (Box 2).

Concluding remarks

Plant cultivation mutualisms include three main types: Neotropical and SE Asian ant-gardens, and Fijian obligate agriculture. In these systems, farming is for shelter, and is likely being driven by the limitation of nesting space in tropical forest canopies, rather than food. This forces us to reconsider our definition of agriculture to include the dependence on shelter rather than exclusively on food, and may in turn help us to decipher the evolutionary steps in the origin of agriculture. These farming systems have an unrivalled level of evolutionary replication, and they also vary greatly in the level of dependence and specialisation (Box 1) of both crop and farmers. This offers unique opportunities to study the ecology and evolution of agriculture, using a large cross-species comparative phylogenetic framework and field studies (Box 2). Despite the great promise of plant cultivation mutualisms as tools to study agriculture, many aspects of their biology remain unknown. We raise a few key outstanding issues, from fundamental research in the ecology and evolution of these interactions to the improvement of our own agriculture (see Outstanding questions).

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Declaration of interests

No interests are declared.

Supplemental information

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showed that seed odour consisting of five chemicals drives the seed-collecting behaviour in a Neotropical ant-garden. No such studies have been performed for SE Asian, Australasian, and Fijian systems. Are there convergent chemical signatures of seed odour across plant cultivation systems? Are all plant cultivation systems relying on odour or does morphology (e.g., seeds mimicking ant pupae) play a role? Do chemical cues drive the large epiphyte range of farmer specificity?

Ant-garden occupants or exploiters. Some common ant-garden occupants – such as some fern species (Supplementary dataset 1 in the supplemental information online) – have no evidence of being ant-dispersed. Are they still inadvertently ant-dispersed through spores sticking on the ant cuticle or are they wind-dispersed? Or could they represent a separate category: ant-garden occupants. Further work should confirm whether ant-garden occupants exist, specifically ferns. If they are not ant-dispersed, what is their ecological role: are they mutualists, commensal, or even parasites of ant-gardens?

Does parabiosis play a role in the ecology of ant-gardens? Parabiosis is a mutualism involving two ant species nesting together and sharing tasks. Some ant-gardens are cultivated by parabiotic ants (e.g., *Camponotus femoratus* and *Crematogaster* cf. *limata parabiotica*). Because, in a parabiosis, there is a dimorphism, with one of the ant species being larger-bodied than the other, does it play a role in ant-garden ecology?

Are there other obligate and specialised plant agricultural systems? Obligate *Squamellaria* plant farming by ants was discovered in Fiji in 2016. Yet, these plants belong to a clade where highly specialised interaction with the same ant subfamily evolved four times. The majority of these interactions occurs in remote areas of New Guinea and has not been studied. Moreover, our database revealed the existence of over 200 ant-garden plant species, some of which may form obligate relationships. More research is needed to study the level of dependence of these partnerships.

Could plant farming by ants inform human agriculture? The use of bacteria

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by fungus-farming ants to combat disease has inspired some crop breeding programs using root microbiomes. Understanding more about plant farming by ants could similarly inform human agriculture. For instance, the extreme efficiency of nitrogen uptake inside the domatium of ant-farmed *Squamellaria* could hold clues on increasing nitrogen-use efficiency on our crops. More research is needed to understand the genetic basis of nitrogen absorption in this system.