Beyond Bees: A Critical Narrative Review of Ant-Mediated Pollination in Indian Flora

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Abstract

Ants are ubiquitous floral visitors, yet their contribution to pollination has historically been regarded as exceptional because worker ants are flightless, often forage over short distances, may groom pollen from their bodies, and can carry antimicrobial secretions that impair pollen function. Indian evidence complicates this conventional view. This critical narrative review evaluates when ants act as pollinators, when they merely visit flowers, and when they disrupt established pollination mutualisms in Indian flora. Literature was selected through transparent searches of multidisciplinary, biological and agricultural scholarly sources, complemented by citation searching, with emphasis on Indian field studies and global mechanistic evidence from 1974 to 27 June 2026. The strongest Indian demonstrations occur in the Western Ghats rainforest tree *Syzygium occidentale* and the ant-adapted herb *Euphorbia hirta*, where exclusion or access experiments link ant visitation to reproductive output. Earlier work on *Euphorbia heterophylla* reported substantial ant visitation and preserved pollen viability but provides a less complete causal chain. By contrast, observations in monsoon cucurbits are hypothesis-generating rather than definitive, while studies of pumpkin and cashew show that ants can deter legitimate pollinators, prey on bees, damage reproductive structures or exploit nectar. Re-examination of evidence from *Salacia gambleana* and *Salacia oblonga* also illustrates why ant abundance at flowers should not be equated with pollination. Across systems, outcome depends on ant identity, floral architecture, pollen tolerance, reward placement, mating system, weather, phenology and the competing pollinator assemblage. The Indian literature is therefore better interpreted as a context-dependent continuum from mutualism to antagonism than as evidence for a uniform ant-pollination syndrome. Future progress requires species-level ant identification, manipulative exclusions, direct measurement of pollen deposition, pollen viability, seed quality and genetic mating outcomes across replicated habitats and seasons. Ants deserve greater attention in Indian pollination ecology, but functional claims should be made only when visitation is connected experimentally to plant reproduction.

Keywords: Ant pollination; Formicidae; Indian flora; myrmecophily; pollinator effectiveness; pollen viability; pollinator interference; Western Ghats

1. Introduction

Pollination biology is often narrated around bees, but flowers are embedded in much broader interaction networks. Ants are especially conspicuous members of those networks: they are abundant, taxonomically diverse, behaviourally dominant at many food resources and frequent visitors to nectar-bearing structures. In India, a national checklist documented 828 valid ant species and subspecies in 100 genera, while also emphasising uneven geographic sampling and unresolved distributional records (Bharti *et al*., 2016). That diversity creates substantial opportunity for ants to encounter reproductive structures across forests, grasslands, disturbed habitats and agroecosystems. Floral visitation, however, is not synonymous with pollination. A visitor becomes a pollinator only when it transfers viable conspecific pollen to receptive stigmas in a manner that contributes to reproduction, and its ecological importance depends on the quantity and quality of that contribution relative to alternatives.

The traditional expectation that ants should be poor pollinators has several biological foundations. Workers lack wings and often move over shorter distances than volant insects, which can increase within-plant pollen transfer and reduce gene flow. Their small, relatively smooth bodies may carry little pollen, and grooming can further reduce loads. Most influentially, experiments demonstrated that brief contact with ants can reduce pollen viability, germination, pollen-tube growth and subsequent seed set, giving rise to the antibiotic hypothesis for the rarity of ant pollination (Beattie *et al*., 1984). Later comparative tests found strong pollen-germination reductions after contact with multiple ant species and showed that the effect was not reproduced by bees, while also suggesting geographic variation in its severity (Dutton & Frederickson, 2012). These mechanisms made ant pollination appear not simply uncommon but biologically constrained.

Field evidence nevertheless shows that the constraint is conditional rather than absolute. The classic demonstration in *Polygonum cascadense* linked a low-growing plant in a dry environment with ant-mediated pollen transfer and helped define an early ant-pollination syndrome (Hickman, 1974). Subsequent studies documented effective ant pollination in unrelated taxa and habitats, including the granite-outcrop endemic *Diamorpha smallii* (Wyatt, 1981), the orchid *Microtis parviflora* (Peakall & Beattie, 1989),

the dioecious geophyte *Borderea pyrenaica* (García *et al*., 1995), Mediterranean herbs under contrasting mountain and arid conditions (Gómez *et al*., 1996), and the alpine orchid *Chamorchis alpina* (Schiestl & Glaser, 2012). These cases show that ant pollination can emerge through different combinations of floral accessibility, ant abundance, chemical attraction, pollen protection and ecological circumstances rather than through one invariant syndrome. Recent studies outside India continue to broaden the ecological settings in which ants are considered potential or functional pollen vectors, including additional tree and non-photosynthetic plant systems (Pereyra *et al*., 2024; Suetsugu & Hashiwaki, 2025).

India is particularly informative because its direct evidence includes both a humid rainforest tree and small herbs, while crop studies reveal strong antagonistic effects. In the Western Ghats, *Technomyrmex albipes* was shown experimentally to be an important pollinator of *Syzygium occidentale*, an endemic rainforest tree, despite the presence of bees and birds (Kuriakose *et al*., 2018). In northern India, *Euphorbia hirta* exhibits several traits conventionally associated with ant pollination, and field exclusions linked ant access to higher fruit production (Samuel & Rastogi, 2022). An earlier Himalayan study of a plant reported as *Euphorbia geniculata* likewise associated seed production with abundant *Camponotus compressus* visitation and found no significant reduction in pollen viability after ant contact (Araf *et al*., 2010). Current taxonomic resources treat *Euphorbia geniculata* Ortega as a synonym of the accepted name *Euphorbia heterophylla* L. (Royal Botanic Gardens, Kew, n.d.), illustrating the need for nomenclatural as well as ecological verification in synthesis.

The same Indian literature also cautions against a celebratory reinterpretation of ants as overlooked substitutes for bees. Mixed outcomes within a single plant species have also been demonstrated elsewhere; in gynodioecious wild strawberry, ant visitation was associated with both positive and negative components of seed production depending on floral sex and context (Ashman & King, 2005). Yellow crazy ants, *Anoplolepis gracilipes*, sharply reduced honey-bee activity on pumpkin flowers in southern India and were associated with failure of colonised pistillate flowers to develop fruit; predation on lingering bees provided an additional mechanism of interference (Sinu *et al*., 2017). A broader comparison of native and invasive ants in pumpkin found that both groups reduced honey-bee visitation rate and visit duration, with stronger effects from invasive species (Unni *et al*., 2021). In cashew, *Crematogaster subnuda* has been observed damaging reproductive parts and taking floral nectar without evidence that such activity compensates through pollination (Vanitha *et al*., 2024). Globally, experimental and meta-analytic work similarly shows that ants can deter pollinators directly or through scent cues and that the net effect of protective ants on pollination varies with floral visitors and the placement of extrafloral nectaries (Cembrowski *et al*., 2014; Vieira da Silva *et al*., 2025; Villamil *et al*., 2018, 2019).

A central problem is therefore evidentiary. Some reviews have assembled long lists of ant-visited or allegedly ant-pollinated plants, but the underlying studies differ markedly in design. A flower census establishes visitation; pollen on an ant establishes vector plausibility; pollen on a stigma after a controlled visit establishes delivery; reproductive output under ant-only access demonstrates functional contribution; and progeny performance or genetic paternity can reveal whether that contribution extends beyond immediate fruit or seed set. These are not interchangeable endpoints. The distinction matters acutely in India, where the small number of direct experiments is surrounded by observations that are ecologically suggestive but causally incomplete. Recent global reviews have renewed attention to ants as pollinators (Das & Das, 2023; Torezan-Silingardi & Del-Claro, 2025), but a focused critical appraisal of the Indian evidence, including negative interactions and the strength of inference behind individual claims, remains needed. Recent experimental and applied work further supports a context-dependent interpretation by showing that the consequences of ant presence can depend on ant identity and by examining the potential contribution of ants to crop pollination (Calixto *et al*., 2024; Díaz *et al*., 2025).

1.1 Scope, Research Gap and Objectives

This review focuses on ant-mediated pollen transfer in flowering plants occurring in India, including native flora, weeds and cultivated plants where Indian field evidence informs the interaction. It distinguishes experimentally supported pollination from floral visitation, pollen carriage, nectar exploitation and ant-mediated interference with other pollinators. Global studies are used selectively to evaluate mechanisms, evolutionary interpretation and methodological standards that help explain Indian cases. The review does not attempt an exhaustive account of ant seed dispersal, plant defence by ants, domatia-based mutualisms or general myrmecophily except where these processes alter floral access and pollination. The principal gap addressed is the mismatch between frequent ant–flower observations and the small number of Indian studies that establish a causal pathway from ant visitation to successful reproduction. The objectives are to appraise the strength of the Indian evidence, identify the traits and ecological conditions under which ants are likely to function as pollinators or antagonists, clarify methodological requirements for future claims, and develop research priorities suited to India's taxonomic and ecological diversity.

2. Methods for Literature Selection

This review used a critical narrative design because the central question is not a single intervention-effect comparison amenable to pooled estimation. Indian evidence spans descriptive natural history, visitor censuses, exclusion experiments, pollen-viability tests, reproductive-biology studies and crop interaction experiments, while the mechanistic literature includes behavioural, chemical, genetic and meta-analytic approaches. A narrative framework permits these heterogeneous evidence types to be integrated without pretending that they estimate a common effect. Transparency, explicit selection logic and appraisal remain essential to narrative synthesis; the procedure was therefore informed by recommendations for evidence-oriented narrative reviewing and by the SANRA quality domains concerning search description, referencing, scientific reasoning and presentation of relevant evidence (Baethge *et al*., 2019; Green *et al*., 2006).

Literature discovery used Google Scholar, Semantic Scholar, OpenAlex, the Directory of Open Access Journals, CORE, PubMed and AGRIS. India-centred discovery was supplemented with searches of Indian agricultural and institutional scholarly repositories, including ICAR e-publication resources and KrishiKosh, when they were relevant to crop or regional evidence. Backward citation searching of key Indian articles and recent ant-pollination reviews, forward searching of influential primary studies, related-article searching and targeted searches for corrected taxonomic names were also undertaken. Bibliographic identity and DOI information were checked against article records, DOI landing pages, PubMed or other authoritative scholarly metadata where available. The search sources were used for discovery and verification rather than treated as evidence in themselves.

The principal search period was 1974 to 27 June 2026. The starting year corresponds to Hickman's modern experimental formulation of ant pollination as a low-energy system and provides a coherent historical point from which the contemporary mechanistic literature developed. Representative combinations included ("ant pollinat*" OR "ant-mediated pollinat*" OR "Formicidae pollinat*") AND (India OR Indian OR "Western Ghats" OR Himalaya* OR Bengal OR Kerala); (ant* AND (flower* OR anthesis OR stigma OR pollen) AND (pollinat* OR "fruit set" OR "seed set")) AND (India OR Indian); (ant* AND (exclusion OR "single visit" OR pollen OR stigma OR "fruit set" OR "seed set")) AND pollinat*; and ant* AND flower* AND ("extrafloral nectar*" OR "nectar thie*" OR deterr* OR interfer* OR antimicrobial OR "pollen germination"). Crop-specific combinations added cucurbit, pumpkin, cashew and agroecosystem terms. Searches were iteratively refined around plant and ant names identified in relevant records.

Eligible sources were peer-reviewed primary studies and high-quality reviews directly relevant to ant visitation, pollen transport, pollen viability, stigmatic deposition, reproductive output, pollinator interference or the evolution and ecology of ant pollination. Indian studies received priority for the empirical synthesis; international studies were included when they supplied mechanistic tests, methodological benchmarks or comparators not available from India. Foundational studies before or near the start of the main period were retained when essential to the history of the field. Sources were excluded when bibliographic identity could not be verified, when an ant was mentioned without information relevant to floral function, when an account merely repeated a secondary claim without traceable primary evidence, or when the publication quality was insufficient for a substantive inference. A small number of locally published Indian studies without DOIs were retained only when the article itself and stable scholarly source could be verified and the evidence was uniquely relevant; their methodological limitations were weighted accordingly.

Titles and abstracts were first assessed for relevance, followed by examination of available full text or sufficiently detailed scholarly records for studies likely to influence the synthesis. Duplicate records were reconciled using DOI, exact title, author order, year and journal metadata. Where the same study appeared in several repositories, the primary article or authoritative record was used. No screening counts are reported because the selection process was designed for critical narrative synthesis rather than a prospectively registered systematic review with a fixed deduplicated record set. English-language literature predominated; a non-English review was used only where its bibliographic identity and relevant concepts could be confirmed. Inaccessible or bibliographically uncertain items were not used to support substantive claims.

Evidence appraisal centred on the inferential chain from visitation to plant fitness. Studies were judged qualitatively by whether they identified ants to an informative taxonomic level; quantified ant visitation relative to other visitors; documented contact with anthers and stigmas; measured pollen load, viability or stigmatic deposition; used selective exclusion, ant-only or single-visit treatments; measured fruit set, seed set, germination or recruitment; considered mating system and autonomous selfing; replicated across plants, sites, seasons or weather conditions; and separated direct ant pollination from indirect effects on other pollinators. Genetic evidence on outcrossing was treated as especially informative for consequences of short-range ant movement. No formal risk-of-bias score was assigned because designs and outcomes were too heterogeneous for a single validated instrument. Themes were developed by comparing causal strength, mechanisms and ecological context, with contradictory findings treated as evidence of conditionality rather than averaged into a false consensus.

3. From Floral Visitation to Effective Pollination: Concepts and Evidentiary Thresholds

The most important conceptual distinction in this literature is between being on a flower and functioning as a pollinator. Ants may visit flowers to drink nectar, collect secretions, hunt other arthropods or patrol plant surfaces. Such behaviour can bring the body into contact with reproductive structures, but it may also bypass anthers and stigmas entirely. A census therefore establishes an interaction but not its reproductive sign. This distinction is particularly important for ants because they can impose simultaneous positive and negative effects: an ant may carry pollen yet deter a bee; it may promote self-pollination while reducing outcrossing; or it may protect a plant from herbivores while damaging floral tissues. The correct unit of inference is consequently not 'ant present' but the net pathway linking a particular ant species, a particular floral phenotype and a defined reproductive outcome.

Table 1. Operational criteria for interpreting ant–flower interactions

Evidence category	Minimum observation	What it can support	Principal limitation	Supporting references
Floral visitation	Ants occur on flowers or floral rewards	Presence of an ant–flower interaction and candidate taxa for further study	Does not establish contact with reproductive organs, pollen transfer or reproductive benefit	Das & Das, 2023; Torezan-Silingardi & Del-Claro, 2025
Vector plausibility	Ant contacts anthers/stigmas or	Mechanistic possibility of pollen transport	Carried pollen may not reach a receptive	Beattie *et al.*, 1984; Delnevo *et*

	carries conspecific pollen; pollen viability may be measured		stigma; viable pollen does not prove deposition	*al*., 2020; Luo *et al*., 2012
Pollen delivery	Conspecific pollen is deposited on a receptive stigma after a controlled ant visit	Direct pollen-transfer function	Does not by itself establish fruit, seed or offspring quality	Luo *et al*., 2012; Sugiura *et al*., 2006
Reproductive contribution	Ant-only or selective-access treatment increases fruit/seed production above complete exclusion or autonomous baseline	Functional pollination contribution	May largely reflect selfing, geitonogamy or low-quality seed	Gómez, 2000; Kuriakose *et al*., 2018; Samuel & Rastogi, 2022
Effective mutualism	Reproductive contribution is accompanied by viable progeny, recruitment or appropriate genetic outcrossing relative to alternatives	Contribution to sequential plant fitness	Requires longer, more demanding experiments and may still be context-dependent	Gómez, 2000; Peakall & Beattie, 1991; Rostás *et al*., 2018
Antagonism/interference	Ant presence reduces legitimate pollinator activity, damages flowers or lowers reproductive output	Negative or conflicting effect on pollination	Net effect still requires simultaneous measurement of any ant-delivered pollen	Cembrowski *et al*., 2014; Sinu *et al*., 2017; Unni *et al*., 2021

Note. Categories are interpretive thresholds for this review, not a formal risk-of-bias scale.

Pollen carriage represents the next level of evidence, but even this remains incomplete. The amount of pollen on an ant varies with body size, pilosity, grooming, floral architecture and where the ant contacts the flower. Luo *et al*. (2012) showed in *Jatropha curcas* that ant species differed in pollen loads and that larger ants carried more pollen, while ants also deposited pollen on stigmas and made a measurable contribution to fruit set. In common buckwheat, *Fagopyrum esculentum*, exclusion of ants reduced seed set and pollen of both floral morphs was found on the two common ant visitors, giving concordant behavioural and reproductive evidence (Natsume *et al*., 2022). These studies demonstrate why pollen load is strongest when paired with a manipulation that estimates the contribution of ants to plant reproduction.

Pollen quality is equally important. The antibiotic hypothesis predicts that antimicrobial compounds associated with ants can impair pollen after contact, and early controlled work supported effects on several functional stages (Beattie *et al*., 1984). Dutton and Frederickson (2012) extended the argument across multiple plant and ant species. Yet ant contact is not universally destructive. In the Western Australian proteaceous plant *Conospermum undulatum*, pollen remained highly germinable after contact with ant bodies and ant visitors carried substantial numbers of grains suitable for pollination, consistent with adaptation of pollen to an ant vector (Delnevo *et al*., 2020). In the orchid *Leporella fimbriata*, plant traits associated with pollinium attachment and stigmatic secretions allowed normal pollen function even though ant contact under artificial conditions could be disruptive (Peakall *et al*., 1990). The relevant question in an Indian system is therefore empirical: what happens to that plant's pollen after contact with that ant under natural floral conditions?

Reproductive endpoints provide stronger evidence but also require interpretation. Ant-only access that produces more fruit or seed than complete exclusion demonstrates that ants can contribute to reproduction, but the benefit may be predominantly selfing. In *Blandfordia grandiflora*, ants increased seed set above autonomous self-pollination yet did not effectively cross-pollinate emasculated flowers, indicating mainly self-pollination (Ramsey, 1995). In *Microtis parviflora*, worker-ant pollination produced high seed set, but genetic analysis revealed strong selfing, short pollen-flow distances and highly inbred population structure in the clonal study system (Peakall & Beattie, 1989, 1991). Thus, fruit or seed number is not necessarily equivalent to genetic-quality benefit.

The highest-confidence evaluation follows sequential fitness components beyond initial reproduction. Gómez (2000) assessed ant effects in *Lobularia maritima* from visitation through seed production, germination, seedling performance and recruitment, showing that ant-pollinated offspring performed comparably to those from other pollination treatments. By contrast, in *Euphorbia seguieriana*, ants contributed to pollen transfer and fruit formation but seeds produced after ant-only visitation showed extremely poor germination compared with winged-insect pollination (Rostás *et al*., 2018). The contrast is decisive: an ant can satisfy a narrow definition of pollination while failing to deliver equivalent reproductive value. Indian studies rarely extend that far, which limits claims about long-term fitness, gene flow and population persistence.

For this review, evidence is therefore interpreted as a hierarchy of causal sufficiency rather than a binary label. Table 1 summarises the operational thresholds used. The categories are not formal risk-of-bias scores; they are a guide to what a given observation can legitimately establish. Their main implication is that 'ant pollination' should be reserved for studies that connect ant access or controlled visitation to pollen delivery or reproductive output, while visitor records should remain explicitly provisional.

4. Evidence for Ant-Mediated Pollination in Indian Flora

The direct Indian evidence is small enough to examine closely, and its narrowness is itself an important finding. Three wild or naturalised plant systems provide the clearest positive evidence, but they differ markedly in ecological setting and inferential strength. *Syzygium occidentale* offers a strong field demonstration in a tropical rainforest tree; *Euphorbia hirta* provides a modern study of an ant-adapted herb with exclusion experiments and morphological evidence for pollen carriage; and *Euphorbia heterophylla*, studied under the name *Euphorbia geniculata*, provides an earlier Himalayan case in which ant abundance and pollen viability were examined but the causal chain is less complete. A later report from deltaic Bengal expands the list of ant-visited cucurbits but remains observational. Together these studies support ant-mediated pollination as a real component of Indian flora while also showing why the national evidence base cannot yet support broad prevalence estimates.

The Western Ghats study of *Syzygium occidentale* is the strongest challenge to the classical image of ant pollination as confined to short herbs in hot, dry sites. The plant is an endemic tree of tropical rainforest, and its flowers were visited by several potential pollinators, including bees and birds. Among these visitors, *Technomyrmex albipes* was dominant. Crucially, Kuriakose *et al*. (2018) did not stop at frequency: flowers exposed exclusively to this ant achieved higher fruit set than flowers assigned to other visitor-specific treatments, and experiments that allowed ant access during day or night supported a role across the diel cycle. The ant was also reported as the only active nocturnal floral visitor. These results connect abundance, exclusive access and fruiting response in a way that meets a high evidentiary threshold for functional pollination.

The importance of the *Syzygium* case lies as much in mechanism as in novelty. A tree canopy does not fit the early low-growing 'ant-pollination syndrome', and the humid Western Ghats do not fit the dry or alpine settings in which ant activity has often been viewed as a reliable substitute for flying insects. The result therefore favours an ecological rather than purely syndromic interpretation. Where a common arboreal or trunk-foraging ant encounters accessible flowers repeatedly, its local abundance and persistent activity can outweigh assumptions based on body plan. The plant's partial self-compatibility and capacity for autonomous reproduction complicate the fitness interpretation, because fruit set does not by itself reveal the proportion of cross-pollination. Even so, the visitor-specific experimental comparison establishes that ants were not merely incidental occupants of the flowers (Kuriakose *et al*., 2018).

Euphorbia hirta represents a different route to the same functional outcome. Samuel and Rastogi (2022) described an annual herb with inconspicuous cyathia arranged in compact globose cymes, tiny inflorescence-associated nectaries and a short, semi-erect growth form, traits that make floral resources physically accessible to ground-foraging ants. Seven ant species from five genera and three subfamilies visited the plants. Field manipulations showed higher fruit production when ants were included than in treatments allowing only winged insects or relying on self-pollination, while scanning electron microscopy demonstrated pollen grains attached to bristles and grooves around ant mouthparts. Observations of ants visiting multiple plants within a foraging bout also provided behavioural plausibility for cross-pollen movement rather than strictly within-plant transfer.
This evidence is strong because independent components converge: floral architecture predicts access, ant foraging connects plants, pollen is physically carried, and exclusion treatments link ant presence to fruit production. Nonetheless, key uncertainties remain. Fruit set cannot quantify realised outcrossing, and ant species may differ substantially in effectiveness. Pooling 'ants' can conceal whether one species provides most service while others are neutral or antagonistic. The study also concerns a ruderal herb in a human-modified setting, so its ecological dynamics cannot be assumed to represent forest herbs or endemic plants. Even within *Euphorbia*, the balance among autogamy, geitonogamy and cross-pollination can differ among species and populations. These limitations do not negate the result; they define the next questions needed to move from functional pollination to evolutionary significance.

The north-west Himalayan study by Araf *et al*. (2010) is historically important but methodologically more modest. The plant was published as *Euphorbia geniculata* Ortega, a name now treated as a synonym of *Euphorbia heterophylla* L. (Royal Botanic Gardens, Kew, n.d.). *Camponotus compressus* comprised just over half of recorded hymenopteran visitors and was the exclusive visitor at two sites. Pollen exposed to ants did not show a significant reduction in viability, directly addressing a major proposed constraint on ant pollination. The authors also described seed set as pollen-limited and interpreted ants as the principal source of pollen delivery (Araf *et al*., 2010). These observations are consistent with ant-mediated pollination and, importantly, show that the antibiotic constraint need not operate strongly in every Indian *Euphorbia* system.

Table 2. Indian evidence supporting or suggesting ant-mediated pollination

Plant and setting	Principal ants reported	Study design / evidence	Interpretive strength	Key limitation	Supporting references
Syzygium occidentale; tropical rainforest tree, Western Ghats	*Technomyrmex albipes*	Visitor comparisons; visitor-specific access; day/night ant access; fruit set	Strong experimental support for functional ant pollination	Genetic outcrossing and longer-term progeny quality not measured	Kuriakose *et al*., 2018
Euphorbia hirta; ruderal annual herb, northern India	Seven species across five genera; species-level visitors reported in study	Exclusion/access treatments; multi-plant foraging; scanning electron microscopy of pollen on mouthparts; fruit production	Strong support for ants as pollination vectors	Relative effectiveness among ant species and realised outcrossing	Samuel & Rastogi, 2022

				remain unresolved	
Euphorbia heterophylla (published as *E. geniculata*); north-west Himalaya	*Camponotus compressus*	Visitor abundance; exclusive visitation at two sites; ant-exposed pollen viability; seed limitation interpreted in relation to ants	Moderate supportive evidence	Lacks the same degree of selective ant-only reproductive isolation as later studies	Araf *et al*., 2010; Royal Botanic Gardens, Kew, n.d.
Eight cucurbit species; deltaic Bengal during monsoon	Multiple genera including *Camponotus*, *Diacamma*, *Monomorium*, *Odontomachus* and *Trichomyrmex*	Repeated field observations across years and diel periods	Hypothesis-generating only	No ant-exclusion/single-visit test linking ants uniquely to stigma pollen or reproductive output	Saradar *et al*., 2024

Note. "Strong" and "moderate" are qualitative summaries of causal evidence, not formal quality scores

Yet the evidence should not be inflated. A high proportion of visits and preserved pollen viability establish opportunity and mechanistic compatibility, but they do not isolate the reproductive contribution of ants as cleanly as selective exclusion or single-visit treatments. If ant dominance covaries with site, weather or scarcity of winged insects, ant visitation can correlate with seed production without being the sole cause. The study's value is therefore best classified as moderate supportive evidence rather than equivalent to the experimental strength of the *S. occidentale* and *E. hirta* studies. This distinction is useful because it prevents the historical literature from being either dismissed for lacking contemporary design or over-read as proof beyond what was measured.
A more recent short communication from deltaic Bengal described ants visiting eight cucurbit species during monsoon conditions and suggested that extrafloral nectar and seasonal weather could favour ant involvement in pollination (Saradar *et al*., 2024). The observations are ecologically interesting because rain, high humidity and low-light periods may reduce activity of some flying pollinators while ants remain available, a phenomenon analogous to the supplementary role documented for *Camponotus japonicus* in the orchid *Epipactis thunbergii* during cool or cloudy conditions in Japan (Sugiura *et al*., 2006). The Bengal study also broadens attention beyond a single crop and encourages observation across day and night.

It does not, however, establish ant-mediated pollination for those cucurbits. Cucurbits frequently have specialised floral sex roles and rely on effective movement of relatively large pollen loads between staminate and pistillate flowers. Without ant exclusion, ant-only access, measured stigmatic deposition or reproductive comparison, ant presence near extrafloral or floral rewards can as readily indicate defence, nectar use or interference. That caution is reinforced by pumpkin studies from southern India in which abundant ants reduced rather than enhanced honey-bee pollination (Sinu *et al*., 2017; Unni *et al*., 2021). The proper conclusion is that monsoon cucurbits are promising experimental systems, not that ant pollination has already been demonstrated across the crop group.

Table 2 places the Indian positive and putative cases on the same evidentiary scale. The contrast is informative: only a few studies link ant access directly to reproductive output, whereas several plausible interactions remain at the levels of visitation, pollen compatibility or ecological circumstance. This pattern argues for expanding field experimentation rather than expanding lists of 'ant-pollinated' Indian species from observational records.

5. Ants as Pollination Antagonists and Ambiguous Floral Associates in India

The Indian evidence is not a one-directional story of overlooked mutualism. Some of the most rigorous field experiments show ants disrupting pollination. In southern Indian pumpkin, *Cucurbita maxima*, the invasive yellow crazy ant *Anoplolepis gracilipes* occupied flowers for nectar and strongly altered interactions with honey bees. Bee visitation frequency and time spent in ant-colonised flowers were reduced, none of the ant-colonised flowers in the reported comparison developed fruit, and ants preyed on a fraction of bees that remained in occupied flowers (Sinu *et al*., 2017). Because pumpkin depends on movement between separate staminate and pistillate flowers, deterring or killing legitimate pollinators can have immediate reproductive consequences even if ants themselves occasionally contact pollen.

The later comparison by Unni *et al*. (2021) strengthens the conclusion by showing that interference is not unique to a single invasive species. Nine ant species were recorded in pumpkin flowers, and both native and invasive ants negatively influenced honey-bee visitation rate and visit duration, with invasive ants producing the stronger effect. *Apis cerana* represented the large majority of observed bee visits, with *Apis dorsata* a smaller component. The mechanism is therefore best understood as context-dependent competition at a limiting floral resource: nectar draws ants into flowers, while bee pollinators respond to ant presence as a risk or obstruction. In such a system, an ant's presence at floral reproductive structures cannot be scored as a positive pollination event without quantifying its net effect on bee-mediated pollen transfer.

Cashew provides a second antagonistic example. Vanitha *et al*. (2024) documented *Crematogaster subnuda* on cashew flowers and reported nectar thieving together with damage to reproductive structures. The study was a research note and did not estimate whole-tree pollination loss or compare ant exclusion with open pollination, so the magnitude of crop-level impact remains uncertain. Its importance lies in mechanism: floral occupancy by ants can create direct costs even before interactions with bees are considered.

Damage to stamens or pistils and removal of nectar without effective pollen transfer both weaken the assumption that high visitation should be interpreted as a pollination service.

Table 3. Indian evidence for antagonistic or ambiguous ant–flower interactions

Plant/system	Ant association	Observed effect	Interpretation	Main uncertainty	Supporting references
Pumpkin, *Cucurbita maxima*; southern India	Invasive *Anoplolepis gracilipes* in flowers	Reduced honey-bee visitation and foraging time; predation on lingering bees; ant-colonised flowers failed to fruit in reported comparison	Strong interference with bee-mediated pollination	Direct ant pollen deposition was not the focus, so net ant-only pollination was not quantified	Sinu *et al*., 2017
Pumpkin, *Cucurbita maxima*	Nine native and invasive ant species	Both native and invasive ants reduced honey-bee visitation rate and duration; invasive effects stronger	General ant–bee interference with species-dependent intensity	Reproductive consequences require integration with ant-only pollen transfer	Unni *et al*., 2021
Cashew, *Anacardium occidentale*	*Crematogaster subnuda*	Nectar thieving and damage to reproductive parts	Antagonistic floral use rather than demonstrated pollination service	Research note did not quantify field-scale yield loss or exclusion effect	Vanitha *et al*., 2024
Salacia gambleana and *Salacia oblonga*; Western Ghats	*Oecophylla smaragdina*, *Tetraponera* sp., *Anoplolepis gracilipes*	Abundant ant foraging coincided with absence/scarcity of other visitors and low fruiting; weaver ants proposed as a possible deterrent	Ambiguous to potentially antagonistic; not experimental evidence of ant pollination	No demonstration that ants deposited pollen or improved fruit/seed set	Krishnasree *et al*., 2022

Note. Ambiguous cases are retained because they illustrate the risk of equating ant abundance with pollination

A more subtle interpretive problem arises in two threatened medicinal climbers of the Western Ghats, *Salacia gambleana* and *Salacia oblonga*. Their reproductive-biology study recorded foraging by *Tetraponera* sp., *Oecophylla smaragdina* and *Anoplolepis gracilipes*, with weaver ants especially abundant during flowering. At the same time, the study described obligatory entomophily, low fruiting and an insufficiency of pollinators, and explicitly considered abundant weaver ants as a possible reason other floral visitors were absent (Krishnasree *et al*., 2022). That combination does not demonstrate ant pollination. It is equally, and perhaps more, compatible with ant presence suppressing access by effective pollinators. Secondary compilations that classify such a system as ant-pollinated risk converting co-occurrence into function.

These Indian examples mirror broader experimental evidence. Bumblebees transferred less pollen analogue to and from artificial flowers containing ants, and even residual ant scent reduced pollen removal, showing that interference can occur without direct attack (Cembrowski *et al*., 2014). In *Turnera velutina*, field manipulation of extrafloral nectaries supported the 'distraction' hypothesis: preventing extrafloral nectar secretion increased ant occupancy of flowers and raised fruit abortion, consistent with a plant benefit from keeping defensive ants away from reproductive structures (Villamil *et al*., 2019). A 2025 meta-analysis across 27 studies found a generally negative effect of protective ants on floral visitation, particularly for bees, but no uniform reduction in reproductive performance; the size and direction of costs were moderated by extrafloral nectary location and visitor type (Vieira da Silva *et al*., 2025). Thus, pollinator deterrence is real, but its translation to plant fitness is variable.

The practical implication is that Indian ant–flower associations should be assessed as interaction networks, not pairwise anecdotes. A species can defend foliage, exploit floral nectar, kill pollinators and transport some pollen within the same flowering episode. The net outcome depends on relative effect sizes and plant mating requirements. Table 3 therefore classifies the best Indian evidence for antagonism or ambiguity according to mechanism and causal strength. It also highlights a recurrent asymmetry: negative effects on bee behaviour are often measured more directly than positive ant-mediated pollen deposition, making net reproductive comparisons an urgent priority.

6. Mechanistic Filters Governing When Ant Pollination Works

Ant pollination is best understood as the outcome of a series of filters rather than the possession of a single floral syndrome. An ant must first reach the flower, then contact reproductive structures, retain viable pollen, move to a receptive stigma, and do so at a spatial and temporal scale compatible with the plant's mating system. At the same time, its presence must not impose larger costs through tissue damage, reward theft or deterrence of more effective pollinators. Failure at any stage can convert a potential mutualist into a neutral visitor or antagonist. The Indian cases are particularly useful because they occupy different positions along this sequence.

Floral architecture and reward accessibility form the first filter. Small, open or compact flowers close to foraging surfaces are readily entered by workers, which helps explain classic associations with low herbs and dense inflorescences (Hickman, 1974). *Euphorbia hirta* conforms well to this expectation: its cyathia, clustered inflorescences, small nectaries and low stature place rewards directly within the working range of terrestrial ants (Samuel & Rastogi, 2022). Yet *Syzygium occidentale* demonstrates that architecture operates relative to ant foraging ecology. A rainforest tree can be highly accessible to arboreal ants even though it violates the low-growth-form heuristic (Kuriakose *et al*., 2018). 'Low to the ground' should therefore be replaced by the more general concept of low access cost from the ants' normal foraging substrate.

The second filter is morphological fit and pollen retention. Ant bodies are not uniformly poor pollen carriers. Size, pilosity, cuticular sculpturing and mouthpart structures influence how much pollen is acquired and where it is retained. In *Jatropha curcas*, pollen loads differed among ant species and increased with body length, while ant-only access still produced substantial fruit set even though winged visitors were more effective (Luo *et al*., 2012). Samuel and Rastogi (2022) visualised pollen lodged in bristles and grooves around ant mouthparts in *E. hirta*, providing a direct morphological pathway from feeding to transport. Conversely, species that groom intensively or contact nectar without brushing anthers and stigmas may be frequent visitors with little vector value. Species-level behavioural observation is therefore more informative than treating Formicidae as a homogeneous pollinator guild.

Pollen physiology forms the third and historically most influential filter. Ants maintain microbial hygiene through antimicrobial compounds, and contact with their bodies can reduce pollen germination and pollen-tube performance (Beattie *et al*., 1984; Dutton & Frederickson, 2012). This mechanism explains why ant abundance alone has not led to widespread ant pollination. Yet several routes can bypass it. Plant pollen may be tolerant to ant-associated compounds, as in *Conospermum undulatum* (Delnevo *et al*., 2020). Pollen packages or floral secretions can limit harmful contact, as suggested by the *Leporella fimbriata* system (Peakall *et al*., 1990). The Indian *E. heterophylla* study found no significant reduction in pollen viability after ant exposure (Araf *et al*., 2010), indicating that tolerance or weak toxicity is plausible in at least one local system. The crucial methodological point is that pollen viability should be measured after contact with the actual ant species and under realistic exposure, not inferred from the antibiotic hypothesis.

Chemical signalling adds a fourth filter. Floral volatiles often help plants repel ants from reproductive tissues while retaining ants elsewhere for defence. Willmer *et al*. (2009) showed that pollen- and flower-derived volatiles can alter ant behaviour and reviewed multiple strategies by which plants spatially control ants. Yet chemical signals can also evolve towards attraction when ants are reliable pollen vectors. In *Chamorchis alpina*, floral scent helped explain specific attraction of pollinating ants (Schiestl & Glaser, 2012), and in *Cytinus hypocistis* electrophysiological and field assays showed that floral volatile blends attracted effective ant pollinators (de Vega *et al*., 2014). Indian studies have rarely tested floral chemistry in ant-pollinated plants. This is a major gap because the same chemical channel can mediate either exclusion or recruitment depending on ecological function.

Reward placement is closely related but deserves separate treatment because extrafloral nectar can either recruit ants near flowers or distract them away from reproductive tissues. Ant-guarded plants face a conflict: the same workers that reduce herbivory may threaten pollinators. Field experiments in *Turnera velutina* showed that functioning extrafloral nectaries can reduce ant occupancy of flowers and associated fruit abortion (Villamil *et al*., 2019). Meta-analysis indicates that negative effects on floral visitors become stronger when extrafloral nectaries are closer to inflorescences, although effects on plant reproductive performance are not uniformly negative (Vieira da Silva *et al*., 2025). For Indian flora, especially plants with ant defence and extrafloral nectaries, the relevant mapping is therefore three-dimensional: where rewards are located, when they secrete and which ant species they recruit.

Mating system and movement distance form a fifth filter that determines the genetic quality of service. Flightless workers often move among neighbouring flowers and plants, which can be adequate for self-compatible or densely distributed species but problematic for obligate outcrossers, self-incompatible plants or sparse populations. Genetic work in *Microtis parviflora* documented a high proportion of self-pollen transfers, short mean movement distances and low realised outcrossing in clonal patches (Peakall & Beattie, 1991). Ramsey (1995) similarly showed ant-mediated seed set in *Blandfordia grandiflora* without meaningful cross-pollination. In contrast, dioecious *Borderea pyrenaica* demonstrates that ants can also transfer pollen effectively between male and female plants when spatial arrangement and foraging behaviour permit it (García *et al*., 1995). For Indian endemic plants, counting fruit without measuring outcrossing could therefore overestimate conservation value.

Table 4. Mechanistic filters and testable predictions for ant-mediated pollination in Indian flora

Mechanistic filter	Prediction favouring pollination	Prediction favouring neutrality/antagonism	Priority Indian measurement	Supporting references
Floral access and architecture	Flowers are readily reached from normal ant foraging substrates and force contact with anthers/stigmas	Rewards can be taken without reproductive contact or flowers are inaccessible to workers	Map ant routes and quantify anther/stigma contact by visitor species	Hickman, 1974; Kuriakose *et al*., 2018; Samuel & Rastogi, 2022
Ant morphology and behaviour	Pilosity, body size or mouthpart structures retain pollen; low grooming; movement among plants	Low pollen retention, intensive grooming or repeated within-flower feeding	Species-resolved pollen loads, grooming rate and movement trajectories	Luo *et al*., 2012; Samuel & Rastogi, 2022
Pollen tolerance	Pollen germination remains high after	Ant-associated secretions reduce germination or	Paired control-versus-ant-contact viability and	Beattie *et al*., 1984; Delnevo *et*

	realistic ant contact or pollen is physically protected	pollen-tube growth	germination assays	*al*., 2020; Dutton & Frederickson, 2012
Chemical signalling	Floral volatiles selectively attract effective ant vectors	Floral scent repels ants or ant odour deters other pollinators	Floral volatile profiles plus field/olfactometer behavioural tests	de Vega *et al*., 2014; Schiestl & Glaser, 2012; Willmer *et al*., 2009
Reward placement	Rewards promote visits that cross reproductive structures, or extrafloral rewards keep defensive ants away from flowers	Rewards concentrate aggressive ants inside flowers and interfere with bees	Manipulate floral/extrafloral nectar access and record net reproduction	Vieira da Silva *et al*., 2025; Villamil *et al*., 2019
Mating system and spatial structure	Short-range movements still connect compatible genotypes or sexes	Geitonogamy and selfing dominate, reducing genetic pollen flow	Paternity/outcrossing estimates linked to ant movement distance	García *et al*., 1995; Peakall & Beattie, 1991; Ramsey, 1995
Weather and diel niche	Ants remain active when flying pollinators are limited or flowers are receptive at night	Ants overlap with and deter superior pollinators during peak anthesis	Repeated day/night and weather-stratified exclusion experiments	Kuriakose *et al*., 2018; Sugiura *et al*., 2006
Pollinator-community context	Ant activity adds service where alternative visitors are scarce	Ants reduce visitation or performance of more effective pollinators	Simultaneous ant-only, winged-only and open-pollination comparisons	Gómez *et al*., 1996; Sinu *et al*., 2017; Unni *et al*., 2021

Note. Predictions are intended for empirical testing and should not be inferred from floral appearance alone

Temporal and weather conditions form a sixth filter. Ants may provide redundancy when flying insects are suppressed by cool, cloudy or wet weather, or when flowers remain receptive outside peak bee activity. *Camponotus japonicus* contributed supplementary pollination to *Epipactis thunbergii* under conditions in which hover-fly activity varied, illustrating how an ant can be a secondary rather than primary pollinator (Sugiura *et al*., 2006). The diel activity of *T. albipes* in *S. occidentale* is similarly important because it extends pollen transfer into the night (Kuriakose *et al*., 2018). Monsoon observations in Bengal may reflect the same ecological opportunity, but controlled comparisons across rain, humidity, temperature and light are needed before weather-dependent pollination can be claimed (Saradar *et al*., 2024).

Finally, the competing visitor assemblage determines whether ant activity adds to or subtracts from total pollination. In Mediterranean communities, Gómez *et al*. (1996) found ant pollination in five of seven plant species and argued that ant effectiveness was strongly related to their abundance relative to other visitors. In *Lobularia maritima*, ants became especially important in summer and produced offspring with performance comparable to that from other pollination routes (Gómez, 2000). Conversely, pumpkin in India shows the opposite outcome: when specialised bee service is available, ant occupation can reduce legitimate visitation and fruiting (Sinu *et al*., 2017; Unni *et al*., 2021). The same ant trait, persistence at a nectar source, can therefore be beneficial in one network and costly in another.

Table 4 integrates these filters as testable predictions for Indian flora. Its main value is prospective: it converts general explanations into measurements that can be taken in the field. A convincing study should not attempt to prove a syndrome from floral appearance; it should identify where in the causal sequence ant identity, plant phenotype and environment permit or block effective pollen transfer.

7. Evolutionary and Biogeographical Interpretation

The idea of an 'ant-pollination syndrome' remains useful as a hypothesis generator but weak as a diagnostic rule. Hickman's (1974) low-energy model emphasised small stature, overlapping inflorescences and habitats in which abundant ants could move efficiently among flowers. Many later cases fit parts of that pattern, particularly dryland or alpine herbs. Yet the global literature now includes orchids, geophytes, shrubs, parasitic plants, trees and crops, and experimental work shows that ant pollination may arise through ecological opportunity rather than a single convergent phenotype (Gómez *et al*., 1996; Torezan-Silingardi & Del-Claro, 2025). Indian evidence reinforces this pluralism because *E. hirta* resembles the classic syndrome whereas *S. occidentale* does not.

This diversity suggests at least three evolutionary routes. First, specialised ant pollination can evolve when floral traits actively recruit a reliable ant vector and protect pollen from ant-associated costs. Chemical attraction in *Cytinus hypocistis* and *Chamorchis alpina* illustrates this route (de Vega *et al*., 2014; Schiestl & Glaser, 2012). Second, pre-existing plant and ant traits can be co-opted: in *Leporella fimbriata*, pollen packaging and stigmatic secretions enable successful interaction even though the traits need not have originated specifically for ant pollination (Peakall *et al*., 1990). Third, facultative or opportunistic ant pollination can emerge where ant abundance and environmental conditions make ants quantitatively important without strong reciprocal specialisation, as in Mediterranean assemblages (Gómez *et al*., 1996). The Indian *S. occidentale* case appears closer to this ecological-opportunity end of the spectrum than to a highly specialised syndrome, although comparative phylogenetic evidence is lacking.

The distinction between ecological service and evolutionary adaptation is critical. A plant can benefit from ants in the present without having evolved 'for' ants. Likewise, a floral trait that correlates with ant visitation may have evolved under selection from other agents. Compact flowers, accessible nectar and extended anthesis can serve multiple functions. Demonstrating adaptation would require comparative evidence that trait states are associated with ant dependence across lineages, experimental evidence of fitness consequences, or historical evidence of correlated evolution. No Indian study currently provides such a comparative evolutionary test. Claims that Indian plants possess an ant-pollination syndrome should therefore be framed as functional resemblance rather than proof of evolutionary causation.

Biogeography also requires caution. The antibiotic hypothesis led to expectations that ant pollination might be less likely in warm, pathogen-rich environments if tropical ants evolve stronger antimicrobial defences (Dutton & Frederickson, 2012). Yet ant pollination occurs in tropical systems, including the Western Ghats rainforest. That exception does not falsify the hypothesis; it shows that pollen tolerance, floral architecture, ant species identity and local abundance can override a general constraint. The relevant biogeographic prediction is not a simple tropical-versus-temperate contrast but a distribution of compatible ant–pollen combinations. India, spanning tropical rainforest, monsoon dry forest, savanna, alpine environments and agroecosystems, offers an unusually powerful natural laboratory for testing that prediction.

Genetic consequences further complicate evolutionary interpretation. Short-range worker movement can increase geitonogamy, defined as pollen transfer among flowers of the same genetic individual, and can limit between-genotype pollen flow. In a clonal orchid, this behaviour contributed to high selfing and low outcrossing (Peakall & Beattie, 1991). Yet ants can also pollinate dioecious plants and produce cross-pollen movement when male and female individuals are interspersed (García *et al*., 1995). The evolutionary outcome therefore depends on plant spatial structure, self-compatibility and the fitness cost of selfing. For rare Indian endemics, especially fragmented populations, ant-mediated fruit set should not automatically be equated with maintenance of genetic diversity.

The most defensible synthesis is consequently pluralistic. Ant pollination is neither an evolutionary anomaly explained by one exception nor a hidden universal service overlooked because of bee-centric research. It is a conditional interaction that repeatedly emerges when multiple filters align. The value of Indian evidence lies precisely in showing both ends of that continuum: effective pollination by a common ant in a rainforest tree and marked pollinator disruption by invasive ants in a crop. An evolutionary framework that cannot accommodate both outcomes is too simple for the evidence.

8. Methodological Weaknesses and Minimum Standards for Demonstrating Ant Pollination

The principal methodological weakness in the Indian literature is not lack of interesting natural history but insufficient progression from observation to causal demonstration. Flower-visiting ants are easy to record, especially on accessible inflorescences and nectar-rich crops. What is harder, and far more informative, is to show that those ants deposit viable conspecific pollen on receptive stigmas and increase reproduction under conditions that exclude other explanations. A national research programme should therefore prioritise inferential depth over species-list expansion.

Visitor censuses remain necessary because pollinator importance contains both quantity and quality components. They should record ant identity, abundance, visit duration, contact with anthers and stigmas, movement among flowers and plants, time of day and weather, while simultaneously sampling other visitor groups. Ant identification should reach species where feasible, with voucher specimens or verifiable images, because congeners can differ in body size, aggression, grooming, nesting habitat and chemical secretions. The contrast among *Technomyrmex albipes*, *Camponotus compressus*, *Anoplolepis gracilipes* and *Crematogaster subnuda* in Indian studies illustrates why 'ant' is not a sufficient functional identity (Araf *et al*., 2010; Kuriakose *et al*., 2018; Sinu *et al*., 2017; Vanitha *et al*., 2024).

A second minimum standard is direct vector evidence. Pollen loads should be quantified on ant body regions likely to contact stigmas, and pollen should be identified as conspecific where mixed flowering communities make contamination plausible. Pollen viability or germination after realistic ant contact should be measured rather than assumed. The antibiotic hypothesis is important precisely because a large pollen load can be functionally worthless if most grains are damaged (Beattie *et al*., 1984; Dutton & Frederickson, 2012). Conversely, preserved viability should not be presented as proof of pollination without evidence of deposition. The strongest design pairs body-load analysis with stigmatic pollen counts after controlled visits, as demonstrated in studies such as *Jatropha curcas* (Luo *et al*., 2012).

Third, selective access experiments must isolate ant contribution. Complete bagging estimates autonomous reproduction; ant-only or size-selective access estimates the result when flying visitors are excluded; winged-insect access provides a comparator; open flowers estimate the natural combined outcome; and, where feasible, single-visit experiments estimate per-visit effectiveness. Treatments need to avoid artefacts such as changing microclimate, damaging flowers or altering scent. The best Indian evidence already moves in this direction: *S. occidentale* used visitor-specific and diel access treatments, while *E. hirta* compared ant-included, winged-insect and self-pollination conditions (Kuriakose *et al*., 2018; Samuel & Rastogi, 2022). Future studies should replicate such designs across populations and years rather than relying on one flowering season.

Fourth, outcomes should extend beyond fruit presence. Fruit set can reflect selfing, resource reallocation or selective abortion, and seed count can obscure viability. At minimum, studies should measure seeds per fruit, filled or viable seed, germination and early seedling performance. Where conservation or mating-system questions are central, genetic markers should estimate paternity or multilocus outcrossing. Global work shows why this matters: ant-only visitation can yield fruit with poor germination in *Euphorbia seguieriana* (Rostás *et al*., 2018), whereas ant-pollinated offspring of *Lobularia maritima* performed comparably through

recruitment (Gómez, 2000). Peakall and Beattie (1991) further demonstrated that high pollination success can coexist with restricted pollen flow and strong inbreeding. Indian studies have not yet routinely followed this full fitness sequence.

Fifth, net interaction effects must be measured when other pollinators are present. Ants can both move pollen and deter bees. A design that quantifies only ant-carried pollen will miss that trade-off, while a design that records only bee avoidance may miss compensatory ant pollination. Pumpkin research provides a model for measuring interference through visitation and fruiting responses, but a complete network experiment would add ant-only reproductive treatments and pollen deposition (Sinu *et al*., 2017; Unni *et al*., 2021). The 2025 meta-analysis showing strong negative effects on visitation but variable reproductive consequences underscores the need to measure both behavioural and plant-fitness endpoints (Vieira da Silva *et al*., 2025).

Sixth, temporal replication should be treated as biologically necessary rather than optional. Ant importance can shift with rainfall, cloud, temperature, season and the abundance of competing pollinators. *Epipactis thunbergii* illustrates supplementary pollination under weather conditions unfavourable to hover flies (Sugiura *et al*., 2006), and *S. occidentale* shows the value of nocturnal observations (Kuriakose *et al*., 2018). Indian monsoon systems in particular require sampling before, during and after rainfall and across multiple years if claims are made about weather-mediated reliability. A few hours of daytime observation can systematically underestimate both nocturnal service and weather-dependent substitution.

Finally, reporting standards should separate observations from conclusions. If ants are the most abundant visitors, the manuscript should say so. If they carry pollen, that should be reported separately. If their exclusion reduces seed set, the causal inference can then be stated. Each step should include uncertainty and alternative explanations. This discipline would prevent ambiguous cases such as *Salacia* from being transformed by secondary citation into definitive ant-pollination records. It would also make Indian data more comparable internationally and allow future quantitative synthesis when enough replicated studies accumulate.

9. Ecological, Conservation and Agricultural Significance

Recognising ants as potential pollinators changes the ecological questions asked about Indian plant reproduction, but it should not lead to indiscriminate promotion of ants. In natural systems, the immediate significance is functional redundancy. Persistent ants may provide pollen transfer when bees, flies or birds are scarce, inactive at night or suppressed by adverse weather. The *S. occidentale* study demonstrates that such redundancy can occur in a rainforest tree, and *E. hirta* shows that a ruderal herb can receive a substantial contribution from ants (Kuriakose *et al*., 2018; Samuel & Rastogi, 2022). These cases argue for including ants in pollinator censuses rather than excluding them analytically as non-pollinating visitors by default.

For conservation, however, the quality of pollen movement is as important as its quantity. A rare plant can set fruit through ant-mediated selfing yet still suffer loss of heterozygosity or inbreeding depression. This concern is especially relevant to fragmented Western Ghats populations and threatened taxa. The reproductive constraints reported for *Salacia gambleana* and *S. oblonga* show how easy it is to misread ant abundance as rescue when the plants remain pollinator-limited (Krishnasree *et al*., 2022). Conservation assessments should therefore combine visitor identity with stigma loads, seed viability and, where feasible, genetic estimates of outcrossing. Ants may be part of a plant's reproductive solution, part of its limitation, or both under different conditions.
Agricultural implications are similarly conditional. International studies show genuine crop contributions: ants can add substantially to fruit set in *Jatropha curcas*, common buckwheat and protected raspberry, although open pollination or winged visitors may still provide greater overall service (Luo *et al*., 2012; Malm *et al*., 2026; Natsume *et al*., 2022). These findings justify testing ants as components of crop pollinator communities. They do not justify deliberate ant augmentation without species-specific evidence. Indian pumpkin shows that invasive and even native ants can suppress honey-bee visitation, while cashew observations demonstrate damage and nectar theft (Sinu *et al*., 2017; Unni *et al*., 2021; Vanitha *et al*., 2024). Management that increases an aggressive ant could therefore reduce rather than stabilise yield.

The most useful agricultural approach is habitat- and species-specific monitoring. Flower-visiting ants should be identified, their effect on legitimate pollinators quantified, and net fruit or seed outcomes measured before they are classified as beneficial or harmful. In protected cultivation, where ant densities can become high and pollinator communities simplified, this is especially important. Malm *et al*. (2026) found that ants contributed to raspberry pollination in commercial protected systems but did not outperform open pollination, illustrating a possible supplementary role. Comparable replicated studies in Indian protected horticulture could reveal where ants provide insurance and where they create conflict.

There is also an invasive-species dimension. Aggressive invasive ants can dominate nectar resources, displace native ants and interfere with pollinators. The *A. gracilipes* pumpkin result shows that pollination should be included among ecosystem functions considered in invasive-ant management (Sinu *et al*., 2017). Because India's ant fauna is diverse but incompletely sampled at fine scales (Bharti *et al*., 2016), conservation and agricultural monitoring should distinguish native functional diversity from invasive dominance. Pollination research can thereby contribute not only to plant reproductive ecology but also to early detection of interaction-network disruption.

A cautious expansion of the pollinator concept is therefore warranted. Bees remain central to many crop and wild-plant systems, but the 'beyond bees' perspective is valuable when it increases functional resolution rather than replacing one taxonomic bias with another. Ants should be counted when they transfer pollen, discounted when they merely forage, and treated as costs when they damage flowers or deter more effective pollinators. The ecological significance of ants lies in this conditionality.

10. Future Directions

The first priority is a geographically replicated inventory of candidate systems built around functional evidence rather than visitor lists. India's climatic range makes it possible to test whether ant contribution increases under dry heat, monsoon rain, cool high-elevation conditions, nocturnal flowering or simplified agricultural communities. Candidate plants should be selected from contrasting growth forms and mating systems, and each study should couple standardised visitor censuses with manipulative access treatments. Replication across at least two flowering seasons and multiple populations would distinguish a stable pollination relationship from a transient response to local scarcity of bees or flies. The immediate outcome should be a map of where ants contribute measurably to seed production, not a catalogue of where ants have been seen on flowers.

A second priority is species-resolved functional ecology of the ants themselves. Current Indian work often identifies dominant species but rarely compares their pollination efficiency within the same plant. Experiments should measure body size, pilosity, grooming rate, floral handling, pollen load by body region, movement distance and aggression towards other visitors. Pollen viability should be tested after contact with each common ant species because antimicrobial effects vary and cannot safely be generalised from the family level (Beattie *et al*., 1984; Dutton & Frederickson, 2012; Delnevo *et al*., 2020). This work would identify which ant traits predict beneficial pollen transfer and which predict antagonism, allowing functional classification to replace taxonomic assumption.

A third priority is direct measurement of pollen delivery. Stigmas collected after single controlled ant visits can be analysed for conspecific pollen quantity and germination, while fluorescent dye or labelled pollen can quantify transfer distances. These measurements should be paired with ant-only, winged-insect-only and open treatments. Studies such as *Jatropha curcas* and common buckwheat show the value of combining pollen load with reproductive response (Luo *et al*., 2012; Natsume *et al*., 2022). Applied to Indian *Euphorbia*, *Syzygium* and cucurbit systems, this design would resolve whether high ant visitation reflects effective deposition, redundant selfing or incidental carriage.

A fourth priority is to extend reproductive endpoints to seed quality and mating outcomes. The difference between pollination and useful reproduction is clear from global studies in which ant-mediated fruits yielded either comparable recruitment or poor germination (Gómez, 2000; Rostás *et al*., 2018). Indian research should routinely measure filled seed, germination and early survival. For self-compatible, clonal, rare or fragmented plants, microsatellite, single-nucleotide polymorphism or other appropriate marker systems should estimate outcrossing and pollen-dispersal distance. The objective is not molecular sophistication for its own sake; it is to determine whether ants maintain gene flow or mainly convert available ovules into selfed seeds.

A fifth priority is chemical ecology. Indian ant-pollinated plants have not been tested systematically for floral volatiles that attract or repel ants, despite strong evidence that scent can regulate ant access to flowers (de Vega *et al*., 2014; Schiestl & Glaser, 2012; Willmer *et al*., 2009). Coupled gas chromatography, electrophysiology and behavioural assays could identify compounds that recruit effective ants or exclude antagonists. Equivalent experiments should test whether pollen or stigmatic secretions buffer ant-associated antimicrobials. Such work would move the field from descriptive syndrome matching to mechanisms of compatibility.

A sixth priority is explicit study of mutualism conflict in plants with extrafloral nectaries. India contains many ant-associated tropical plants, yet the spatial relationship among extrafloral rewards, ant patrol routes and flowers has rarely been integrated with pollinator behaviour. Experiments that temporarily block extrafloral nectaries, alter reward access or exclude particular ants can test whether plants use nectar to divert workers away from flowers, as demonstrated in *Turnera velutina* (Villamil *et al*., 2019). The 2025 meta-analysis predicts stronger floral-visitation costs when extrafloral nectaries are close to inflorescences (Vieira da Silva *et al*., 2025). Testing that prediction across Indian lineages would link plant defence and pollination ecology in a common conceptual framework.

A seventh priority is climate and weather sensitivity. Monsoon systems provide a natural experiment because rainfall and humidity can rapidly alter the activity of winged pollinators while ground- or canopy-foraging ants may respond differently. Continuous or repeated observations should relate pollinator composition and pollen deposition to rainfall, temperature, humidity and light, including nocturnal sampling. The supplementary role of ants in *Epipactis thunbergii* under poor flying-insect conditions and the day-night contribution of *T. albipes* to *S. occidentale* provide testable precedents (Kuriakose *et al*., 2018; Sugiura *et al*., 2006). The deltaic Bengal cucurbit observations can become a rigorous climate-context study if followed by exclusion experiments and reproductive endpoints (Saradar *et al*., 2024).

Table 5. Prioritised research agenda for ant-mediated pollination in India

Priority problem	Recommended design	Core outcomes	Contexts needing replication	Decision value	Supporting references
Unknown geographic and taxonomic prevalence	Replicated visitor censuses plus selective ant access/exclusion across candidate species	Visitation, stigma pollen, fruit and seed set	Western Ghats, Himalaya, central Indian drylands, north-east India, monsoon coasts	Separates true pollination from frequent visitation and identifies robust candidate systems	Kuriakose *et al*., 2018; Samuel & Rastogi, 2022

Ant species differ in pollen compatibility and handling	Within-plant comparisons among common ant species with pollen viability and behavioural assays	Body pollen load, germination, grooming, plant-to-plant movement	Natural and agricultural systems with multiple ant species	Identifies functional traits and prevents family-level generalisation	Beattie *et al*., 1984; Delnevo *et al*., 2020; Dutton & Frederickson, 2012
Fruit set may overstate reproductive value	Sequential fitness studies and genetic mating analysis	Filled seed, germination, recruitment, outcrossing and pollen-flow distance	Rare, clonal, self-compatible and fragmented plants	Determines conservation value rather than immediate pollination alone	Gómez, 2000; Peakall & Beattie, 1991; Rostás *et al*., 2018
Chemical basis of attraction/repellence is unknown	Floral volatile chemistry, electrophysiology and field behavioural manipulation	Ant attraction, specificity, pollinator avoidance, pollen protection	Confirmed Indian ant-pollinated plants and close relatives	Tests mechanisms of specialisation and compatibility	de Vega *et al*., 2014; Schiestl & Glaser, 2012; Willmer *et al*., 2009
Defensive ants may conflict with pollination	Manipulate extrafloral rewards and ant access while monitoring pollinators and reproduction	Flower occupancy, bee visitation, herbivory, fruit/seed set	Indian EFN-bearing trees, shrubs and crops	Quantifies trade-offs between defence and reproduction	Vieira da Silva *et al*., 2025; Villamil *et al*., 2019
Climate and weather dependence is poorly known	Multi-season day/night observation and exclusion stratified by rainfall, humidity and temperature	Visitor turnover, stigma pollen, fruit/seed set	Monsoon crops, alpine systems, nocturnally active flowers	Tests whether ants provide temporal insurance under climate variability	Kuriakose *et al*., 2018; Saradar *et al*., 2024; Sugiura *et al*., 2006
Invasive ants may alter crop pollination networks	Density manipulation or natural-gradient studies measuring direct and indirect effects	Ant pollen transfer, bee behaviour, fruit set, yield and quality	Pumpkin and other nectar-rich crops; protected cultivation	Supports evidence-based invasive-ant and crop-pollinator management	Malm *et al*., 2026; Sinu *et al*., 2017; Unni *et al*., 2021

Note. Priorities are ordered conceptually rather than by a numerical rank because urgency depends on ecosystem and management context

An eighth priority is to integrate ant pollination with invasive-species management and crop protection. For invasive ants such as *A. gracilipes*, field experiments should quantify both direct ant pollen transfer and indirect loss of bee service, then model the net yield consequence under different ant densities. Similar designs should evaluate native aggressive ants so that management does not assume nativity equals neutrality. In protected crops, where both ant and managed-pollinator densities can be manipulated, factorial experiments could test when ants add insurance and when they undermine primary pollination. Such evidence is required before any recommendation to conserve, suppress or augment particular ants in crop fields.

A final priority is data standardisation. Indian studies should report observation effort, plant and ant voucher information, treatment sample sizes, weather, floral sex or morph, pollinator access dimensions, pollen-load methods and all reproductive outcomes in comparable units. Raw or supplementary data should distinguish visits from unique visitors and individual flowers from plant-level replication. This would reduce pseudoreplication and enable future meta-analysis. It would also make negative results publishable and useful, countering the likely bias towards striking examples of ant pollination. Table 5 summarises these priorities and links each to the design most likely to close the present evidentiary gap.

11. Conclusions

Ant-mediated pollination is a genuine but highly conditional component of Indian floral ecology. The strongest evidence comes from *Syzygium occidentale* in the Western Ghats and *Euphorbia hirta* in northern India, where experimental access or exclusion treatments connect ant visitation to reproductive output and are supported by behavioural or pollen-transport observations. Evidence from *Euphorbia heterophylla* is supportive but less complete, while monsoon cucurbit observations remain hypotheses requiring manipulative confirmation. These cases are sufficient to reject the assumption that ants in Indian flowers are invariably irrelevant to pollination, but they are insufficient to infer that ant pollination is widespread.

The same literature demonstrates why the ecological sign of ant visitation cannot be predicted from abundance alone. Pumpkin studies show strong interference with honey-bee visitation, an invasive ant can impose predation risk on pollinators, and cashew observations document nectar theft and floral damage. Ant-rich flowers of threatened *Salacia* species illustrate a further danger: abundant foraging may coexist with pollinator limitation and should not be reclassified as pollination without direct evidence. Indian ant–flower interactions therefore form a continuum from mutualism through redundancy and neutrality to antagonism.

A mechanistic synthesis explains that continuum. Effective ant pollination requires alignment among floral access, ant morphology and behaviour, pollen tolerance, chemical signalling, reward placement, plant mating system, weather and the surrounding pollinator assemblage. No single 'ant-pollination syndrome' captures all successful cases, and the rainforest-tree evidence is particularly important in breaking the historical association with low herbs in dry habitats. Future progress depends on moving beyond visitation towards single-visit pollen deposition, selective access experiments, viable seed production, progeny performance and genetic mating outcomes. The most productive 'beyond bees' perspective is therefore not to replace bees with ants in pollinator narratives, but to measure ants by the same functional standard applied to any pollinator: demonstrable, context-specific contribution to pollen transfer and plant reproduction.

12. Limitations

As a critical narrative review, this synthesis is intrinsically vulnerable to selection and interpretive bias despite a transparent search strategy, explicit evidentiary thresholds and repeated bibliographic verification. It does not provide a formally exhaustive, prospectively registered systematic search or quantitative meta-analysis. The Indian primary evidence is sparse, methodologically heterogeneous and concentrated in a small number of plant taxa, regions and crop systems, which limits national generalisability. Several locally relevant studies use observational designs or older methods, and not all report comparable outcomes such as pollen deposition, seed quality or genetic outcrossing. The literature is also likely affected by publication bias because unusual positive cases of ant pollination may be more publishable than neutral interactions. Rapid changes in taxonomy and incomplete fine-scale knowledge of Indian ant distributions add further uncertainty. Consequently, absence of documented ant pollination in a region or lineage should not be interpreted as evidence of absence, and apparent positive cases based only on visitation should remain provisional until experimentally confirmed.

Declaration of AI Use

This manuscript was prepared through the intellectual contributions of the author(s) to the study design, data analysis, interpretation of results, and scholarly content. Grammarly and ChatGPT were used solely to assist with grammatical refinement and reference formatting during manuscript revision. The author(s) accept full responsibility for the accuracy, integrity, and final content of the manuscript.

Competing Interests

Authors have declared that no competing interests exist.

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