

Insect–plant interactions in tropical dry deciduous forests: seasonality, chemical ecology, behavior, and climate-change challenges

Abstract

Tropical dry deciduous forests (TDFs) experience pronounced wet–dry cycles that change leaf availability, tissue age, plant traits, and insect activity. This seasonality provides a useful setting for examining when plants and insects interact, but direct mechanistic evidence is uneven across regions and taxa. This focused narrative review synthesizes field studies from southern India, Mexico, and Brazil alongside broader research on chemical ecology, climate effects, and dry-forest conservation. Field studies show that leaf flushing may precede the rains, herbivore activity can increase after rain onset, and evergreen trees may provide dry-season resources. Leaf age, phenology, physical defenses, and foliar phenolics are associated with herbivory, although effects vary among species and sites. One community-level study used plant–volatile associations and plant–herbivore records to develop an information-theory framework; it supports a testable explanation of chemical communication, not a universal arms-race rule. Mexican gall studies also associate gall presence with altered foliar phenolics and lower folivore damage on some hosts, without establishing causation. Warming, drought, altered rainfall timing, and fragmentation could shift plant resources and insect activity at different rates, but current evidence does not demonstrate a general climate-driven mismatch in TDFs. Because estimates of dry-forest extent depend on biome definitions, conservation figures are interpreted with their underlying assumptions. We conclude that repeated, place-based studies linking phenology, plant traits, insect behavior, and natural enemies are needed to identify vulnerable interactions and inform conservation.

Keywords: dry-season refugia, leaf cohorts, herbivore-induced plant volatiles, gall induction, trophic networks, plant–pollinator phenology, seasonal mismatch

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Introduction

Tropical dry deciduous forests (TDFs) experience a recurring dry season followed by rainfall that initiates leaf production and, in many locations, flowering and renewed insect activity. Water limitation and seasonal leaf loss restrict the timing and continuity of food and oviposition resources. The landscape is not uniformly leafless, however: evergreen and riparian plants can retain foliage and provide resources when deciduous hosts are unavailable. These contrasting phenologies create a temporal and spatial template for insect–plant encounters. Studies in southern India and Brazil show that leaf flushing and herbivore activity can be separated in time, while evergreen hosts can support insects during the dry season.^{1–3}

These interactions are mediated by more than timing. Insects may use plant odors, visual and structural cues, and contact chemicals when locating hosts; plants may reduce feeding through physical barriers, low nutritional quality, phenolics, other metabolites, or phenological escape. Volatile organic compounds (VOCs) can convey information about plant identity or herbivore attack, and herbivore-induced plant volatiles (HIPVs) can recruit predators and parasitoids. These mechanisms are well established in plant–insect research, but their effects cannot be assumed to be identical among TDF species or seasons. Direct evidence from TDFs includes field studies of leaf traits and herbivory and one community-level analysis of plant–VOC and plant–herbivore associations.^{4–6}

This review examines how seasonal resource pulses shape insect–plant encounters, how chemical and behavioral processes may mediate host use, and how climate change and habitat alteration could

affect those interactions. We prioritize peer-reviewed field studies conducted in tropical dry forests and use broader mechanistic and climate syntheses where local evidence is limited. We distinguish observed associations from causal mechanisms and from conservation outcomes that remain to be tested.

Review scope and evidence approach

We conducted a focused narrative search of published literature using PubMed/PMC, Crossref records, and scholarly search engines. Search terms were combined around “tropical dry forest” or “tropical deciduous forest” with “insect herbivory,” “insect seasonality,” “leaf phenology,” “plant volatile,” “gall induction,” “climate change,” and “conservation.” We prioritized peer-reviewed studies with identifiable publication records that directly examined plant–insect interactions in dry forests, including field studies from southern India, Mexico, and Brazil. Global assessments were included to provide conservation context. Broader reviews and mechanistic studies from other systems were used only to explain processes for which TDF-specific evidence was not available.

This is a narrative review, not a systematic review, bibliometric census, or meta-analysis. We did not apply a preregistered screening protocol or quantitative effect-size synthesis, so the selected studies should not be treated as an exhaustive inventory. In particular, the small number of regions represented here cannot establish the magnitude of global geographic or taxonomic research bias. Where mechanisms are supported mainly by crops, model plants, or non-dry forests, we identify them as plausible hypotheses rather than established TDF patterns.

Seasonality

Plant phenology and insect activity are seasonally linked, but the timing differs among forests and species. At two sites in Mudumalai, southern India, trees began flushing during the dry season and reached peak leaf production before the rains. Herbivorous insects emerged with the rains and reached peak biomass during wet months. Trees that flushed later experienced more insect damage than trees flushing early or near the community-wide peak, while species with waxy physical defenses suffered less damage.¹ These observations are consistent with temporal escape and physical defense, but they do not establish that either trait evolved in response to herbivory or that the same schedule applies across TDFs.

A Brazilian TDF study sampled 5,827 free-feeding canopy herbivores using 72 flight-interception traps. Herbivore diversity was greater in the dry season, with low overlap among seasons. During the dry season, evergreen trees supported greater herbivore richness and abundance than deciduous trees, and insects were more active at night; the diel difference was not observed in the rainy season.² This supports the hypothesis that evergreen hosts and nocturnal activity can buffer some insects from dry-season resource and microclimate constraints. Trap captures measure insect activity and occurrence, however, not feeding damage or population persistence by themselves.

In another Brazilian dry-forest study, researchers sampled 90 trees at the end of the dry season and 60 trees six days after the first rains.

Per-tree richness and abundance of herbivores were higher after the first rains.⁷ The rapid change is consistent with a seasonal pulse in leaf production and insect activity. Because rain onset also changes humidity and temperature, this short comparison cannot isolate which cue produced the response or demonstrate that leaf flushing alone caused it.

Leaf cohorts can differ in both traits and damage. In a two-year Brazilian study, leaves produced during the dry season by three stem-succulent deciduous species experienced less herbivore damage and had lower phenolic concentrations than rainy-season cohorts. The study also assessed 14 non-succulent deciduous species, and reported overall herbivory of 0.57–6.37%.⁸ The authors interpreted the low damage as evidence that escape through early leaf production may be a weak selective force in that community, where water-conservation strategies and other leaf traits also matter. The association between phenolics and damage does not, by itself, show that phenolics caused the seasonal damage pattern.

Together, these studies do not support a single-factor account of seasonal herbivory. Rainfall, leaf availability and age, host growth form, microclimate, and insect life history may act together. Abundance, richness, biomass, flight activity, and leaf damage are different response measures and should not be treated as interchangeable. Comparisons across sites therefore require repeated sampling before and after rain onset, across leaf cohorts and host phenological groups, and during both day and night (Table 1).

Table 1 Selected direct field evidence from tropical dry forests on seasonal insect–plant interactions

System/evidence	Reported result	What it supports	Interpretive limit
Mudumalai, southern India; 1988–1990	Trees flushed during the dry season and peaked before the rains; insect emergence and biomass peaked in wet months. Later-flushing trees had more damage; waxy-leaved species had less.	Temporal escape and physical defense are plausible explanations supported by local field associations.	Two sites; observational associations do not establish evolutionary cause or a universal schedule. (Murali & Sukumar, 1993)
Brazilian TDF; canopy sampling	5,827 herbivores were sampled in 72 traps. Diversity was greater in the dry season; evergreen trees supported greater dry-season richness and abundance; activity was more nocturnal in the dry season.	Evergreen hosts and activity-time shifts may help some insects persist through dry-season conditions.	One regional study; trap captures measure activity and occurrence, not feeding damage or persistence alone. (Silva et al., 2017)
Brazilian TDF; first-rain transition	Per-tree herbivore richness and abundance were higher six days after first rains than at the end of the dry season; 90 and 60 trees were sampled, respectively.	Rain onset is a rapid transition that merits high-frequency sampling.	Rainfall, humidity, temperature, and leaf flush covary; the short comparison cannot isolate a cause. (Novais et al., 2019)
Brazilian TDF; leaf-cohort comparisons	Dry-season cohorts of three stem-succulent species had lower damage and phenolics than rainy-season cohorts; reported overall herbivory was 0.57–6.37%.	Phenology–trait relationships are context dependent and may reflect water-conservation strategies as well as herbivory.	Study-specific species and site; trait associations do not prove that phenolics caused differences in damage. (Silva et al., 2020)
Chamela-Cuixmala, western Mexico; gall community	Gall-inducer richness was positively associated with plant richness; gall frequency and intensity were greater in deciduous than riparian habitat; host density was often a weaker predictor.	Host diversity, life form, plant age, and habitat conditions can shape gall communities.	Local community; most recorded galls were gall midges. (Cuevas-Reyes et al., 2004)
Chamela-Cuixmala, western Mexico; gall–folivore association	Four of five host species had higher phenolics in galled leaves, with lower folivore damage on galled leaves.	Gall induction may alter host traits and indirectly affect other herbivores.	Limited host set; association does not prove phenolic causation or universal protection. (Pascual-Alvarado et al., 2008)
Tropical dry forest; community chemical network	Field plant–VOC associations and plant–herbivore records supported an information-theory framework linking VOC redundancy and herbivore specialization.	Community-level chemical information is a useful, testable framework.	One community-level application; not a universal demonstration of an arms race or seasonal effect. (Zu et al., 2020)

Chemical ecology, host location, and plant defense

Plant VOCs are mixtures, not simple one-compound labels. Their composition can vary with plant species, developmental stage, tissue, herbivore damage, and environmental conditions. Insects detect and combine these cues, which may affect host recognition, attraction, or avoidance. HIPVs may also recruit predators and parasitoids, creating indirect plant defenses. These mechanisms are supported broadly in plant–insect research, but their direction and strength depend on the plant–insect–environment combination and should not be presumed for every TDF system.^{4,6}

Zu et al.⁵ provide a notable community-level application of chemical ecology in a tropical dry forest. They combined field records of plant–VOC associations with plant–herbivore interactions and used information theory to examine chemical information transfer across a community. Their analysis showed how VOC redundancy and herbivore specialization can arise within a conflicting information process. The contribution is to link chemical associations with community structure rather than studying a single plant–insect pair. It is a field-informed framework tested in one community; it does not establish that every TDF has the same information structure or show how seasonal drought changes VOC signals.

Nonvolatile traits also shape herbivory in TDFs. Leaf toughness, waxes, water content, nutritional quality, and phenolic chemistry can change as leaves expand and mature. The Mudumalai study associated waxy defenses with lower damage, while the Brazilian leaf-cohort study reported seasonal differences in phenolics and damage.^{1,8} These findings caution against using the concentration of one chemical class as a stand-alone measure of defense. A seasonal difference in phenolics may covary with leaf age, water status, insect abundance, or induced responses; controlled tests are needed to separate these explanations.

Future chemical-ecology studies should measure complete volatile blends alongside leaf age, water status, toughness, phenolics, and insect identity. Sampling should be repeated during the dry season, at first rains, and in the wet season. Field manipulations—such as adding or removing odors, paired-choice tests, and reciprocal presentations of leaf cohorts—can test whether a chemical cue changes host choice. Gas chromatography–mass spectrometry should be paired with direct behavioral observations and, where possible, insect performance and natural-enemy measures. A chemical profile alone is not evidence that an insect detects or responds to that profile (Figure 1).

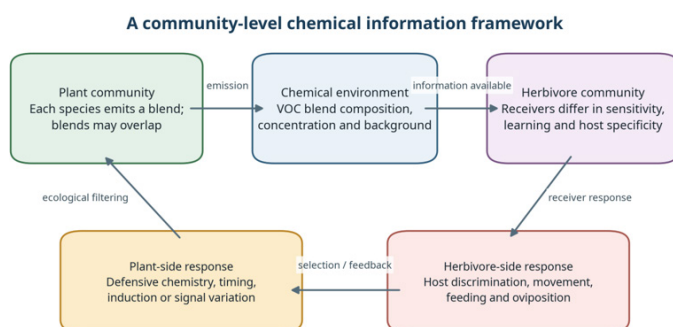


Figure 1 Community-level chemical-information framework.

Zu et al.⁵ tested an information-theory approach using plant–VOC and plant–herbivore records from one tropical dry-forest community. The framework is useful for generating hypotheses; its seasonal, taxonomic, and geographic generality remains untested.

Behavioral ecology, galling insects, and host use

Host use involves a sequence of encounters and choices. An insect may first encounter a plant, then assess it using odor, visual or structural cues, and contact chemicals. Female oviposition decisions may also depend on leaf age, plant water status, and the expected performance of offspring. In dry periods, some insects may shift among hosts, use evergreen plants, change activity times, or persist in inactive life stages. These are plausible strategies, but the TDF studies reviewed here more often measure seasonal occurrence or damage than directly test host choice. Preference tests should therefore be paired with larval survival, growth, or reproductive outcomes before preference is interpreted as fitness.

Gall-forming insects connect host selection with plant chemistry because the developing insect induces specialized tissue in its host. At Chamela-Cuixmala, western Mexico, a survey recorded 172 plant species, of which 39 hosted gall-inducing insects; 69.2% of identified gallers were gall midges. Gall-inducer richness was positively associated with plant-species richness in both deciduous and riparian habitats. Gall frequency and intensity were greater in deciduous habitat, and host-plant density was a weaker predictor for many gallers.⁹ The study indicates that host richness, plant form and age, and habitat conditions jointly help structure gall communities at this site.

In a related study of five host species in the same Mexican dry-forest system, galled leaves of four species had higher total phenolics and lower frequency and amount of folivore damage than ungalled leaves.¹⁰ This association is consistent with gall induction altering host traits in ways that may affect other herbivores. It does not show that gallers generally protect leaves or that phenolics caused the lower folivore damage. Gall position, leaf age, microhabitat, and insect behavior are alternative or contributing explanations. Matched manipulations across more host species and regions are needed to test how often this indirect effect occurs.

Ecological consequences and conservation context

Plant–insect interactions can be antagonistic, mutualistic, or context dependent. Herbivory transfers plant production to insects and can affect plant growth, reproduction, and recruitment; insect predators and parasitoids then connect herbivores to additional trophic levels. Pollination is a separate but complementary process that supports reproduction in many flowering plants. Herbivore-induced odors can also mediate indirect defenses by attracting natural enemies.^{4,11,12} The evidence reviewed here is strongest for herbivory. Pollination is noted as an important parallel interaction, but this article does not synthesize TDF pollination networks or quantify their responses.

The ecological consequences are not uniformly positive or negative. Defoliation can reduce plant growth and reproduction, while plant defenses and natural enemies can limit herbivore damage. Pollination outcomes depend on the identity and abundance of effective visitors, not simply on the presence of insects. Interaction networks can therefore influence regeneration and resource flow through several pathways, with effects that depend on species and environmental context. Conservation planning should retain diverse host plants, evergreen and riparian dry-season refuges, and habitat for natural enemies and pollinators. Such measures are plausible ways to maintain interaction opportunities, but their effectiveness should be evaluated rather than assumed.

TDF conservation estimates are sensitive to how the biome is defined. Miles et al.¹³ documented widespread conversion and long-

standing conservation concerns. A later comparison of four climatic definitions and two climate datasets found that only 40% of field plots fell within the World Wildlife Fund tropical and subtropical dry broadleaf forest ecoregions. The FAO definition paired with CHELSA climate data best matched the 540 field plots in that analysis. Under that definition, closed-canopy TDF with at least 40% forest cover was estimated at 4.93 million km² in 2000 and 4.37 million km² in 2020, a gross loss of about 562,000 km² (11.4%).¹⁴ A separate global assessment based on forest-height data found that less than one-third of the original tropical and subtropical dry broadleaf forest extent remained forested; more than 80% of remaining forest was exposed to edge effects, and 16% was in conservation or protection zones.¹⁵ These studies use different definitions and datasets, so their figures should not be combined as if they shared one baseline. For interaction research and conservation, the implication is to document local vegetation definitions and disturbance histories, and to sample edges, interiors, riparian strips, and evergreen patches separately.

Climate change, habitat alteration, and interaction mismatch

Climate change and land-use change could alter the timing and reliability of seasonal interactions. Rainfall onset, drought duration, and heat affect plant water balance and leaf production, while temperature and moisture also influence insect development and activity.¹⁶ If plants and insects respond at different rates, the period when suitable leaves, flowers, or host stages are available may shift. Fragmentation can further change edge microclimates and reduce the continuity of evergreen and riparian resources. These are credible pathways to altered encounter rates, but their strength will vary among sites and species.

Evidence supports concern, not a deterministic prediction for TDFs. A broad review and meta-analysis found that temperature, elevated carbon dioxide, drought, and nutrient conditions can affect herbivore consumption, plant damage, and development, with outcomes depending on plant life history and combinations of drivers. It also identified shifts in phenology and distribution as possible sources of mismatch and called for multifactorial experiments.¹⁷ This evidence is global rather than specific to TDF communities. The dry-forest field studies discussed above document seasonal coupling and local variation, but they do not show that climate change has already caused a general mismatch in TDFs.

Climate-sensitive changes in plant chemistry offer another possible pathway. Drought and heat can alter plant physiology and volatile emissions, which may affect how herbivores and natural enemies locate hosts; the outcome depends on the particular cue, receiver, and background odor.⁶ Climate can also affect flowering traits and pollinator traits, but a systematic global synthesis found diverse responses and noted that direct evidence for temporal plant–pollinator mismatches remains limited, especially in tropical and subtropical regions.¹⁸ Thus, it is premature to conclude that warming universally weakens plant defenses or reduces pollination in TDFs. The testable questions are whether climate shifts resource timing, changes chemical or floral cues, and alters the behavior or performance of the insects that receive those cues.

The country examples in this review are informative as local baselines, not as proof of climate impacts. In southern India, the Mudumalai study links leaf-flush timing and waxy traits with herbivore

damage. In Brazil, studies document dry-season host use, nocturnal activity, rapid changes after first rains, and differences between leaf cohorts. In western Mexico, gall diversity and folivore damage vary with host richness and habitat type. None of these studies attributes its observed pattern to a long-term climate trend. Their value is to identify which interactions should be monitored as heat, rainfall, and land cover change. Monitoring interaction timing alongside species presence may detect altered resource use before local extirpation is evident, while site-specific data are needed to identify which host plants and refuges warrant protection (Figure 2).

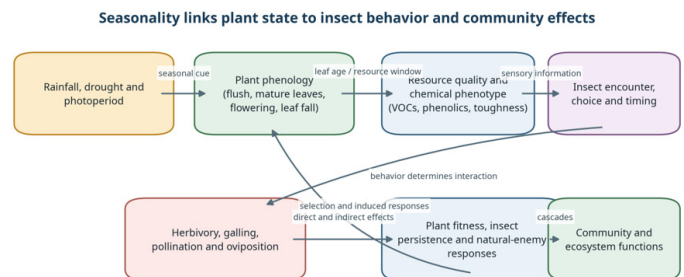


Figure 2 Proposed pathways linking seasonal forcing, plant phenology and traits, insect behavior, and community outcomes. The arrows synthesize mechanisms and hypotheses discussed in the review; they do not imply that every link has been demonstrated in every TDF. Land-use change and climate extremes may modify multiple links.

Priority research directions and methods

Future TDF studies should use seasonally repeated sampling rather than a single wet–dry comparison. Permanent plots can record rainfall, leaf flush, leaf age, flowering and fruiting, insect abundance, feeding guilds, and damage. Intensive surveys immediately before and after first rains are especially useful because one Brazilian study found differences in herbivore richness and abundance within six days.⁷ Sampling both day and night, and comparing evergreen with deciduous hosts and forest edges with interiors, can help separate phenology from microclimate effects.² Multi-year data are needed to distinguish climate trends from ordinary year-to-year variation.

Chemical studies should pair volatile blends and nonvolatile leaf traits with observed insect behavior. Replicated headspace collections should be linked to field choice assays, insect performance, and natural-enemy observations. Gall studies should compare galled and ungalled leaves matched by host species, leaf age, and position; exclusion, gall-induction, or phenolic-manipulation experiments can test whether chemical changes mediate folivore responses. Interaction networks should retain season and habitat as explicit dimensions rather than pooling them as background variation.

Climate-focused studies should measure naturally varying rainfall onset, temperature, drought, and land-use conditions, then use warming or rain-exclusion treatments where feasible to test causal pathways. Continuous monitoring and paired edge–interior sites can show whether plant phenology and insect activity shift synchronously. Low-cost cameras and community participation can extend observations where taxonomic expertise is limited, but voucher specimens and validated identifications remain important. Pollinator and natural-enemy sampling should be added where the study aims to test broader interaction networks, rather than inferred from herbivore data (Table 2).

Table 2 Priority questions, evidence designs, and the inference each design can support

Research question	Recommended evidence	Inference / conservation value
When do plants flush, and how closely does insect activity track first rains?	Multi-year phenology and insect sampling; intensive surveys before and after rain; record leaf cohort, guild, and weather.	Identify vulnerable interaction windows and distinguish repeatable patterns from year effects.
Which volatile and contact cues predict host choice in native dry-forest insects?	Seasonally repeated VOC sampling paired with field choice assays, leaf traits, and insect performance.	Separate odor association from behavioral function and test sensitivity to drought.
Do evergreen hosts buffer insects through the dry season?	Compare evergreen, deciduous, riparian, edge, and interior hosts across seasons and years; measure insect activity and feeding.	Identify resource refuges that may merit retention in restoration and conservation.
Do gall-induced chemical changes alter other folivores?	Match galled and ungalled leaves by host, age, and position; combine exclusion or induction with phenolic assays and folivore trials.	Test whether indirect effects extend beyond a small set of Mexican hosts and whether chemistry is causal.
Does climate change uncouple phenology and insect behavior?	Long-term rainfall and temperature monitoring, or factorial warming × drought experiments, with plant, insect, pollinator, and natural-enemy responses as relevant.	Distinguish climate effects from land use and annual variation; assess mismatch rather than assume it.
Which regions and insect guilds remain poorly sampled?	A reproducible bibliographic map plus standardized voucher collections and interaction datasets from underrepresented regions and guilds.	Quantify research gaps and improve geographic and taxonomic comparisons.

Conclusion

Tropical dry deciduous forests show that seasonality structures when plants and insects encounter one another and which tissues are available. Field studies from India and Brazil document different ways that insects persist through seasonal resource shortages: plants may flush before the rains, herbivore activity may rise after rain onset, evergreen hosts may support dry-season insects, and some activity may shift toward night. These patterns vary among communities and response measures, so no single seasonal strategy can be generalized to all TDFs. Chemical ecology provides tools for linking plant traits and volatile cues with host choice, while direct TDF evidence remains concentrated in a small number of systems. The information-theory framework and gall-associated changes in phenolics are useful hypotheses that require tests across additional taxa, regions, seasons, and years.

Climate change and fragmentation could alter seasonal resources and microclimates, but a climate-driven interaction mismatch has not been established as a general outcome in TDFs. Long-term, place-based monitoring should link plant phenology and chemistry with insect behavior, herbivory, pollination where relevant, and natural enemies. Such evidence can identify which species and seasonal refuges sustain interaction networks and support conservation decisions grounded in observed local responses.

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Conflicts of interest

The authors declare no conflict of interest.

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