Chapter 5
Multitrophic and Indirect Interactions in the *Baccharis dracunculifolia* System

Milton Barbosa, Graziella França Monteiro, and G. Wilson Fernandes

Abstract The *Baccharis dracunculifolia* (Asteraceae) system is a reasonably self-contained community including the host plant and its rich fauna of arthropods. Over the last three decades, ecological researchers in Brazil have intensively used the system as a study model. Several interactions, across multiple trophic levels, among the plant species *B. dracunculifolia* and associated arthropods, have been empirically demonstrated. Half of these interactions are indirect and include effects propagated via changes in density, trait, habitat or interaction strength. Here we describe the components of this system and summarize their interactions in a network. We hope that this work will spark new ideas for experimental tests of ecological hypotheses on the role of indirect interactions at the level of the whole community in the field.

Keywords Experimental ecology · Insect herbivory · Interaction modification · Network · Non-trophic inter0actions

1 Multitrophic and Indirect Interactions

Species affect each other in countless ways. The most evident and easily visible influences are the direct trophic interactions, those involving feeding relationships between two species. On the other hand, indirect trophic interactions require the presence of a third species as an intermediary (Wootton 1994) and are propagated through feeding relationships. In a trophic cascade, a predator affects the density and/or behaviour of a prey and, therefore, indirectly affects the rate of consumption of a species in the next lower trophic level (Estes and Palmisano 1974). These interaction chains or indirect effects mediated by density (e.g. trophic cascades, keystone species, apparent competition) have been broadly demonstrated (e.g. Wootton 1994, 2002; Morris et al. 2004; van Veen et al. 2006). Indirect trophic interactions

---

M. Barbosa (✉) · G. F. Monteiro · G. W. Fernandes
Ecologia Evolutiva & Biodiversidade/DGEE, Universidade Federal de Minas Gerais,
Belo Horizonte, Minas Gerais, Brazil

G. W. Fernandes et al. (eds.), *Baccharis*,
https://doi.org/10.1007/978-3-030-83511-8_5

play an important role in structuring communities and have generally not been taken into account in traditional studies (Bukovinszky et al. 2008).

Indirect interactions between species can also happen in non-trophic ways (e.g. via habitat, trait or behaviour modification: Wootton 1994). However, these interactions remain largely ignored (Ogushi 2008). Indirect effects can cause changes in species density (e.g., interference competition, facilitation: Prugh and Brashares 2012; Wetzel et al. 2016) or changes in species interactions (interaction modification: Wootton 1994, 2002; Prasad and Snyder 2010; Pagès et al. 2012; Hammill et al. 2015). Species can modify interactions by modifying a trait of one of the interacting species (e.g. fear effects associated with predator presence; plant-mediated interactions: Prasad and Snyder 2010; Hammill et al. 2015) or by changing the biotic or abiotic physical environment where the interaction takes place (Pagès et al. 2012; Barbosa et al. 2019).

Indirect effects have received increasing attention in ecological research, and their role in structuring ecological communities has been demonstrated experimentally (Tompkins et al. 2000; Morris et al. 2004; Sanders et al. 2015; Barbosa et al. 2019). For example, the positive indirect effects that consumer species have on each other, reducing competition among their respective resource species, can help maintain the diversity of consumer species (Sanders et al. 2015). In addition, indirect interactions can be the cause of unexpected results often found in experimental manipulations of direct interactions (Doak et al. 2008). Barbosa et al. (2017), for instance, found that the experimental reduction in abundance of a species affects other unrelated species in a food web. In addition, many of the effects that have been interpreted in the past as the result of competition can be caused by other indirect interactions (Holt 1977). For example, in the so-called apparent competition (Holt 1977; Morris et al. 2004), the negative effect of one herbivore on another, mediated by a common predator, may produce a result that resembles competition. Thus, it has become clear that the structure and dynamics of ecological communities cannot be fully understood without taking indirect interactions into account.

2 The *Baccharis dracunculifolia* System

The *Baccharis dracunculifolia* D.C. (Asteraceae) system is a self-contained assemblage of arthropods living on this host shrub species (Figs. 5.1 and 5.2). The plant species is a perennial, evergreen, dioecious shrub, 2–3 m high, widely distributed in the south-central portion of South America (Espírito-Santo et al. 2003). In some parts of Brazil, *B. dracunculifolia* produces flowers twice a year from March to June and from November to December (Collevatti and Sperber 1997). *B. dracunculifolia* frequently forms distinct patches that vary from 18 to 12,000 m^2 in area (Collevatti and Sperber 1997). This plant is fundamental to natural succession and regeneration (Fernandes et al. 2016) playing an important role in promoting biodiversity and ecosystem functioning (Perea et al. 2019).

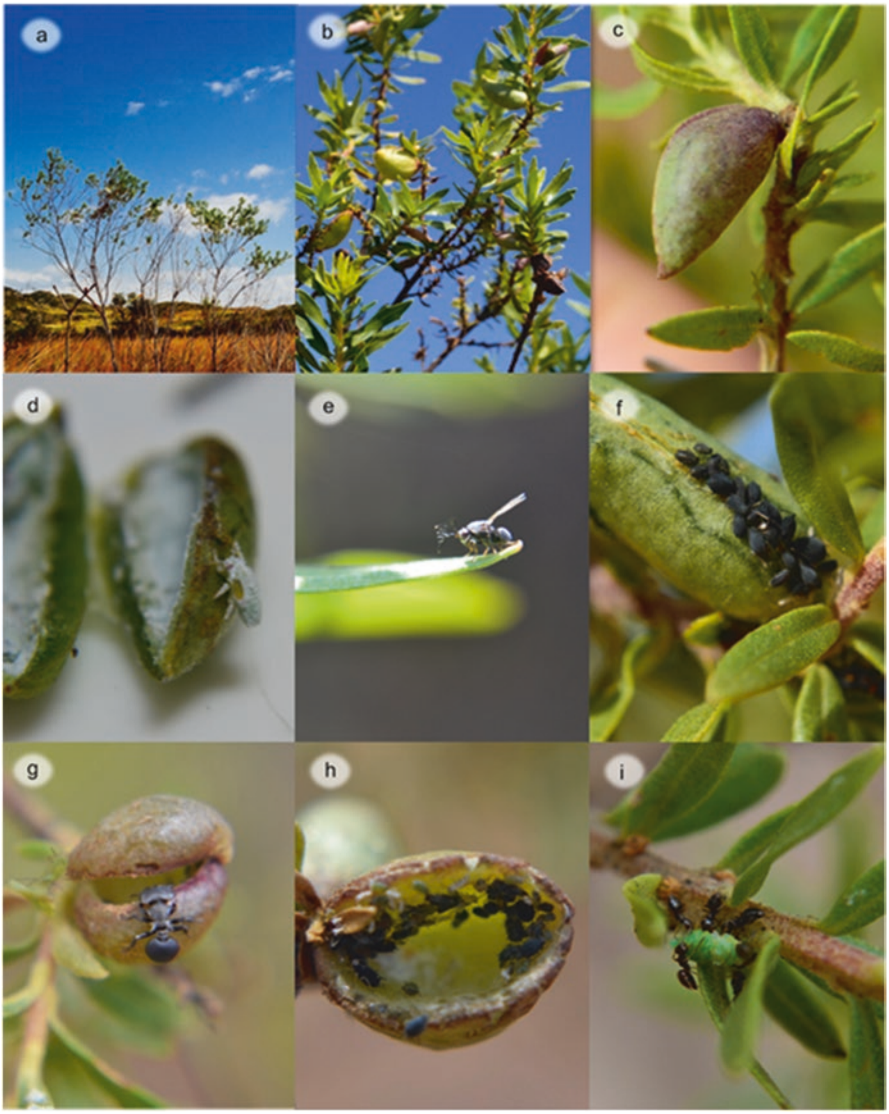

Fig. 5.1 Species engaged in multitrophic and indirect interactions in the *Baccharis dracunculifolia* system: (**a**) *B. dracunculifolia*; (**b**) and (**c**) galls induced by *Baccharopelma dracunculifoliae*; (**d**) nymph of the galler *B. dracunculifoliae*; (**e**) parasitoid wasp; (**f**) aphids *Uroleucon tucumani* invading a gall; (**g**) ant tending aphids inside a post-emergence gall; (**h**) aphids inside a post-emergence gall; (**i**) ants removing a free-feeding herbivore. Photos by Milton Barbosa

The species *B. dracunculifolia* hosts many species of free-feeding herbivores, 17 gall-inducing species and also many species of predators, including the orders Araneae, Coleoptera, Mantodea and Hymenoptera (Fagundes et al. 2005; Fagundes and Fernandes 2011; Barbosa et al. 2017, 2019; Monteiro et al. 2020a). In Brazil,

Fig. 5.2 Species engaged in multitrophic and indirect interactions in the *Baccharis dracunculifolia* system: (**a**) spider using a post-emergence gall as shelter; (**b**) ladybird; (**c**) weevil; (**d**–**f**) mistletoe *Struthanthus flexicaulis* and its germinating seeds. (Photos a–c by Milton Barbosa and d-f by António Cruz)

over the past three decades *B. dracunculifolia* has been extensively used in community ecology research. The diverse associated fauna, and the wide distribution, usually at high frequency and through gradients (elevational, higrothermal, and habitat disturbance), make the species an attractive study model (e.g. Fernandes and Price 1988; Ribeiro-Mendes et al. 2002; Fagundes et al. 2005; Julião et al. 2005; Barbosa et al. 2017, 2019; Monteiro et al. 2020a, b). As a result, several multitrophic and indirect interactions have been revealed in the system, involving *B. dracunculifolia*, its associated arthropods and a mistletoe species (Collevatti and Sperber 1997; Fernandes et al. 1999; Espírito-Santo and Fernandes 2002; Fagundes et al. 2005; Neves et al. 2011; Bahia et al. 2015; Monteiro et al. 2020b). Below, we describe the *B. dracunculifolia* system and its interactions, summarizing them in an interaction network (Table 5.1, Fig. 5.3).

Table 5.1 Empirically demonstrated interactions involving arthropods and plants in the *Baccharis dracunculifolia* system, in Brazil. Interaction codes correspond to the links in the interaction network (Fig. 5.3)

Interaction code	Affecting	Affected	Interaction type	Outcome	Effect
1	Free-feeding herbivores	Host plant	Direct trophic	Negative	Herbivory (Neves et al. 2011)
2	Galler	Host plant	Direct trophic	Negative	Nutrient sinking (Espirito Santo and Fernandes 2002)
3	Host plant	Galler	Direct non-trophic	Negative	Plant resistance; gall dropping (Espirito-Santo and Fernandes 2002)
4	Parasitoid	Galler	Direct trophic	Negative	Parasitism (Tavares and Perioto 1993)
5	Parasitoid	Galler	Direct trophic	Positive	Unparasitized nymphs sharing a gall with parasitized nymphs are larger (Espírito-Santo et al. 2004)
6	Parasitoid	Host plant	Indirect trophic	Positive	Parasitism controls gall population (Espírito-Santo et al. 2004)
7	Parasitoid	Host plant	Indirect non-trophic	Negative	Increase gall size and nutrient sinking (Espírito-Santo et al. 2004)
8	Galler	Aphid	Indirect non-trophic	Positive	Gall provides shelter (Collevatti and Sperber 1997)
9	Aphid/ galler	Galler/aphid	Indirect non-trophic	Negative	Competition for plant photoassimilates (Fagundes et al. 2005)
10	Aphid	Galler	Direct non-trophic	Negative	Inquilines kill galler nymphs (Espirito Santo and Fernandes 2002)
11	Aphid	Interaction 4	Interaction modification	Negative	Inquiline aphids preferably kill parasitized galling larvae (Barbosa et al. 2019)
12	Post-emergence gall	Interaction 8	Interaction modification	Positive/ Negative	Providing extra habitat for aphids (Barbosa et al. 2019)

(continued)

Table 5.1 (continued)

Interaction code	Affecting	Affected	Interaction type	Outcome	Effect
13	Post-emergence gall	Interaction 11	Modification of an interaction modification	Positive/ Negative	Interference with the negative effect of aphids on parasitism (Barbosa et al. 2019)
14	Ants/ Aphids	Aphids/Ants	Direct non-trophic	Positive	Trophobiosis (Fagundes et al. 2005; Neves et al. 2011)
15	Ants	Galler	Direct non-trophic	Negative	Fewer nymphs per gall due to interference with oviposition (Neves et al. 2011)
16	Ants	Free-feeding herbivores	Direct trophic; Direct non-trophic	Negative	Predation or interference (Neves et al. 2011)
17	Aphid	Free-feeding herbivores	Indirect non-trophic	Negative	Ants attracted reduce number of herbivores (Neves et al. 2011)
18	Aphid	Host plant	Direct trophic	Negative	Sap sucking; nutrient sinking affects shoot growth (Neves et al. 2011)
19	Mistletoe	Host plant	Direct trophic	Negative	Parasitism; increased plant mortality (Bahia et al. 2015; Monteiro et al. 2020a, b)
20	Mistletoe	Interaction 2	Interaction modification	Positive	Increase abundance of galls of *B. dracunculifoliae* (Bahia et al. 2015)

Plant–Free-Feeding Herbivore Interaction

The most frequent orders of free-feeding herbivores found on *B. dracunculifolia* are Hemiptera, Coleoptera and Orthoptera (Interaction 1; see Table 5.1 and Figs. 5.1, 5.2 and 5.3, as for all interactions described hereafter). Among the chewing insects, the most common families are Chrysomelidae and Curculionidae. Chrysomelidae is one of the most numerous herbivorous insect families and has the greatest ecological and economic importance (e.g. monoculture pests: Riley et al. 2002, Chaboo 2007). The sucking insects most commonly found on *B. dracunculifolia* are from the families Cicadellidae, Membracidae and Psyllidae. These sucking insects often have a trophobiontic relationship with ants, which chase away other free-feeding herbivores. Ant effects depend on the context, the environment and the species of ants involved and influence the presence of other insects (Fagundes et al. 2005; Neves et al. 2011).

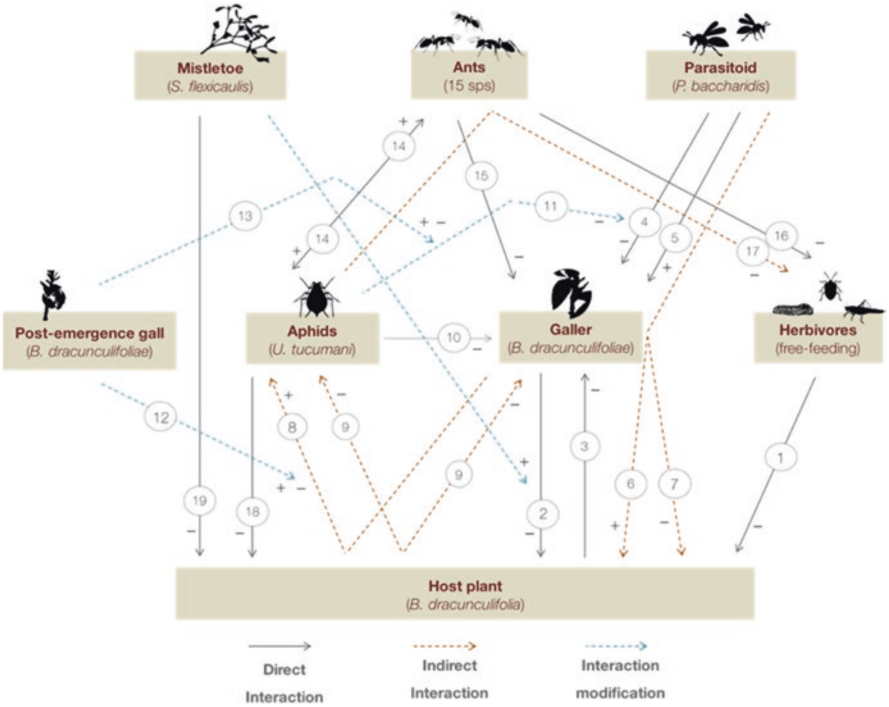

Fig. 5.3 Interaction network of arthropods and plants in the *Baccharis dracunculifolia* system, in Brazil. Links are categorized into direct interactions (solid arrows), indirect interactions (dashed orange arrows) and interaction modifications (dashed blue arrows). The link numbers refer to the interaction descriptions in Table 5.1

Interactions between herbivorous insects and their host plants can be affected by characteristics of the host plants or by changes in environmental conditions (Novotny et al. 2003; Fernandes 2016; Nunes et al. 2016a, b; Peters et al. 2016; Longino and Branstetter 2018). Monteiro et al. (2020a) investigated how the interaction between insect herbivores and *B. dracunculifolia* changed along an elevational gradient in the *campo rupestre* (rupestrian grassland) in Serra do Cipó, Brazil. In this study, the composition, diversity of interactions and specialization of insect herbivores changed with altitude. The richness and abundance of chewing insects increased with elevation, while the richness and abundance of sucking insects were higher at intermediate elevations. The change in diversity of insects associated with *B. dracunculifolia* along the elevation was due to abiotic and biotic factors. Abiotic factors such as increased wind speed and solar radiation and decreased temperature at higher elevations functioned as an environmental filter for many species. On the other hand, biotic factors such as the relationship between the richness of trophobiont ants and herbivores associated with *B. dracunculifolia* influenced the distribution of insect herbivore species.

Plant–Galler Interactions

The genus *Baccharis* supports the richest galling insect fauna recorded so far in the Neotropics, with 121 galling insect species found on 40 host species (Fernandes et al. 1996, 2014; Carneiro et al. 2009a, b). Among the several host species, *B. dracunculifolia* has the largest fauna of galling insects, with a total of 17 species recorded considering various locations (Fernandes et al. 1996, 2014; Barbosa et al. 2017). Galling insects represent appropriate model systems as they are usually straightforward to identify and count, which makes their populations easy to manipulate and monitor in the field (Barbosa et al. 2017, 2019). Galling insects also present very high specialization to their host plants and very persistent morphology, and, therefore, taxonomic identification can be indirectly made through the gall's external morphology and through the identity of their host (Rohfritsch and Shorthouse 1982; Carneiro et al. 2009b). In addition, the fact that parasitoids do not cause immediate damage to the galler allows the quantification of interaction frequency (van Veen et al. 2006).

Baccharopelma dracunculifoliae (Sternorrhyncha: Psyllidae) is by far the most common galling insect, inducing up to 83% of galls on *B. dracunculifolia* (Araújo et al. 1995; Barbosa et al. 2017) (Interaction 2). This psyllid induces a gall on the central rib of the leaf, which folds over itself until the borders are joined, forming an elliptical, green, glabrous, unicameral gall, which usually houses up to 4 nymphs, although up to 21 have already been recorded (Lara and Fernandes 1994; Arduin et al. 2005). The gall is not completely sealed because the edges of the leaves are joined but not fused. The galls of *B. dracunculifoliae* are colonized by several inquiline arthropods (species that occupy a living space produced by another species – e.g., a gall), such as Diptera, Hemiptera (Aphididae), Neuroptera (Chrysopidae), Thysanoptera and Acarina immature (Collevatti and Sperber 1997; Espírito Santo and Fernandes 2002; Barbosa et al. 2019). The post-emergence galls can persist on the plant and dry out but are still occupied by inquilines (Espírito-Santo and Fernandes 1998; Barbosa et al. 2019). These post-emergence galls can trigger indirect effects that feedback to the galler modifying its interactions with other species (discussed below in Sect. 2.4; Barbosa et al. 2019).

According to Espírito-Santo and Fernandes (2002), the host plant *B. dracunculifolia* has strong bottom-up control over the galling population. Plant-mediated mortality in the galling insect *B. dracunculifoliae*, due to gall drop and plant resistance, represented 40.7% of the initial cohort studied (Interaction 3).

Galler–Parasitoid Interaction

The performance of the galling psyllid *B. dracunculifoliae* is strongly controlled by top-down effects. Espírito-Santo et al. (2004) found that parasitoid attack was the main cause (45.2%) of mortality of the galls of *B. dracunculifoliae* that survived plant defences. At least ten wasp species have been known to parasitize galls of *B. dracunculifoliae* (Barbosa et al. 2017), the main ones are *Lyrcus* sp. (Hymenoptera: Pteromalidae), *Brasema* sp. (Hymenoptera: Eupelmidae), Platygastridae sp. (Hymenoptera: Platygastridae) and *Psyllaephagus baccharidis* (Hymenoptera: Encyrtidae) (Tavares and Perioto 1993; Sperber and Collevatti 1996; Barbosa et al. 2017).

Psyllaephagus baccharidis is the most common parasitoid of the galling psyllid. In the survey carried out by Espírito-Santo et al. (2004), this parasitoid was responsible for 93% of the parasitism recorded in galls of *B. dracunculifoliae* (Interaction 4). *P. baccharidis* is a solitary koinobiont endoparasitoid that consumes the nymph and pupates inside the host's cuticle, causing a so-called 'nymph mummification' (Espírito-Santo et al. 2004). The parasitoid attacks galls in the early stages of development, making them increase in size. Mortality by parasitism is clearly recognizable as parasitized nymphs have a distinct colour and shape (Espírito-Santo et al. 2004).

Apparently, the parasitoid *P. baccharidis* stimulates the nymphs to feed, increasing their size and also the size of the gall induced by *B. dracunculifoliae* (Espírito-Santo et al. 2004). This can decrease the performance of the plant, since larger galls represent larger nutrient sinks. In addition, unparasitized nymphs of *B. dracunculifoliae* sharing a gall with parasitized nymphs were larger than the ones found in unparasitized galls. This can result in adults of the gall inducer with greater survival and reproductive success (Espírito-Santo et al. 2004) (Interaction 5). Thus, the parasitoid *P. baccharidis* can have a positive indirect effect on the host plant, controlling the population of the gall inducer *B. dracunculifoliae* (Interaction 6), and a negative indirect effect, increasing the sinking of nutrients by the gall and the fitness of the galler (Espírito-Santo et al. 2004) (Interaction 7).

Barbosa et al. (2017) investigated the role of direct and indirect interactions in the structure and robustness (tolerance to species loss) of galler-parasitoid food webs on *B. dracunculifolia*. Theoretical models from previous works suggest that the loss or reduction in abundance of individual species can lead to secondary and cascading extinctions (Saavedra et al. 2008; Staniczenko et al. 2010). The authors experimentally manipulated quantitative host-parasitoid food webs to reduce the abundance of the main galler, *B. dracunculifoliae*. The perturbation resonated throughout the food web, affecting the food web structure and robustness (tolerance to species loss). Since there was no possibility for these effects to be propagated directly or indirectly via the documented trophic interactions, the effects must have spread non-trophically and/or through trophic links not included in the webs. The results emphasize that, even for a relatively simple ecological community, indirect interactions (trophic and non-trophic) are fundamental to their structure and dynamics (Fontaine et al. 2011; Kéfi et al. 2012).

Galler–Aphid Interaction

In addition to parasitoids, galls of *B. dracunculifoliae* can be occupied by many inquiline arthropods (Collevatti and Sperber 1997; Espírito-Santo and Fernandes 2002; Barbosa et al. 2019). These inquilines use the gall as shelter and sometimes as a food source, consuming silk made by the galler or other plant products. Some inquilines can enter the pre-emergence galls through the longitudinal opening, while others enter the gall through the characteristic exit hole left in the gall wall when parasitoids emerge (Espírito-Santo et al. 2004). Thus, the colonization of parasitized galls by inquilines can be facilitated by parasitoids (MB *unpublished data*). Post-emergence galls remain attached to the plant, sometimes for a few generations, and gradually become dry and woody (Lara and Fernandes 1994; Espírito-Santo and Fernandes 1998) and are still colonized by many species.

The aphid *Uroleucon tucumani* (Sternorrhyncha: Aphididae) is the main inquiline species found in galls of *B. dracunculifoliae* (Collevatti and Sperber 1997; Fagundes et al. 2005) (Interaction 8). This aphid species also feeds and reproduces on the apical meristems of the host plant, forming dense colonies that produce honeydew (sugary secretions). Fagundes et al. (2005) showed that aphids can have a negative indirect effect on gall development: in their absence, galls were heavier. Gall size may be related to the performance of the galling insect (Weis 1988). Therefore, this suggests exploitation competition between the galler *B. dracunculifoliae* and the aphid *U. tucumani* for sap assimilates and young leaves from terminal buds (Fagundes et al. 2005) (Interaction 9). Inquilinism by the aphid *U. tucumani* is also common and can be indirectly responsible for the death of the nymphs of the galler *B. dracunculifoliae* (Espírito-Santo and Fernandes 2002) (Interaction 10).

Theory suggests that indirect effects may be an important mechanism for community stability and persistence, but empirical data are scarce (Strauss 1991; Kéfi et al. 2012). Barbosa et al. (2019) examined the propagation of indirect effects in the *B. dracunculifolia* system. The authors investigated whether the indirect effects initiated by ecosystem engineering – physical changes in the biotic or abiotic environment caused by a species – can feedback to the engineer, changing the magnitude and direction of its interactions with other species. Gallers can be seen as ecosystem engineers since galls serve as habitat for other species, particularly aphids, which occupy hatches and unhatched galls of the most common galler on B. *dracunculifolia.* Barbosa et al. (2017) raised the hypothesis that the hatched galls could generate feedbacks on the galler – e.g. increasing the availability of shelter for aphids and, therefore, positively affecting the galler by decreasing the occupation of live galls by aphids. In a field experiment, they generated treatments with reduced or elevated ecosystem engineering, removing or adding hatched galls. Inquilism by aphids negatively affected parasitism rates (interaction modification) likely by killing parasitized galling larvae (Interaction 11) since they preferentially colonize parasitized galls (MB *unpublished data*). Post-emergence galls changed the interaction between aphid inquilines and the galler (positively or negatively, depending on gall density), probably by providing extra shelter for aphids

(Interaction 12) and also altered (positively or negatively, depending on gall density) the negative effect that aphids had on parasitism (modification of an interaction modification) (Interaction 13). The results show that hatched galls of the dominant galler can trigger indirect interactions that feedback to the galler, modifying its interactions with parasitoids and inquiline aphids. In addition, the results suggest that these interaction modifications are dependent on the context, which changes with species densities.

Ant–Aphid Interaction

At least 15 species of ants have been recorded foraging on *B. dracunculifolia*, many of them tend and protect the aphid *U. tucumani* in a trophobiotic relationship (Fagundes et al. 2005; Neves et al. 2011; MB *unpublished data*) (Interaction 14). Fagundes et al. (2005) experimentally excluded ants, aphids or both from shoots of *B. dracunculifolia*. Ants had a direct negative effect on the performance of *B. dracunculifoliae*. When ants were present, a smaller number of nymphs were found in each gall of *B. dracunculifoliae*, most likely because ants interfered with the female galler during oviposition (Fagundes et al. 2005) (Interaction 15). Neves et al. (2011) observed that the presence of ants and *U. tucumani* aphids on *B. dracunculifolia* also decreased the abundance of other free-feeding herbivores and that the presence of aphids decreased the growth of plant shoots (Interactions 16, 17, and 18).

Monteiro et al. (2020a) studying the community of insect herbivores associated with *B. dracunculifolia* also found that ant abundance was positively related to the abundance of trophobionts and negatively associated with the richness of chewing herbivores. Ants protecting aphids can directly affect herbivores negatively, preying or interfering with them (Abe 1988; Fernandes et al. 1999). However, aphids on their own can reduce the abundance of fluid-sucking and chewing insects due to exploitation competition or by altering the nutritional quality of the host plant (Fay et al. 1996; Larson and Whitham 1997). Thus, aphids can potentially reduce herbivory and indirectly benefit the host plant. Also, as chewing insects can attack the gall and kill the galling nymph, aphids can also positively affect the galling species *B. dracunculifolia* (Espírito-Santo and Fernandes 2002).

Mistletoe–Plant Interaction

The hemiparasitic *Struthanthus flexicaulis* frequently colonizes *B. dracunculifolia* (Monteiro et al. 2020b; Fig. 5.2). *S. flexicaulis* represents an important stress factor for the host plant. Over time *S. flexicaulis* can cause significant reduction in growth and fitness or irreversible and sublethal damage to the host plants, increasing mortality (Press and Phoenix 2005; Cameron et al. 2008; Bahia et al. 2015; Mourão et al. 2016; Monteiro et al. 2020b) (Interaction 19).

Bahia et al. (2015) showed that *S. flexicaulis* can reduce the number of leaves of *B. dracunculifolia* and cause the death of occupied branches or even of the entire plant. The water imbalance caused by this hemiparasite may be a factor responsible for affecting growth and increased mortality of parasitized host plants (Bahia et al. 2015; Mourão et al. 2016; Monteiro et al. 2020b). In addition, when the plant faces water restriction, there is a tendency to decrease leaf size to prevent water loss through transpiration (Lincoln and Zeiger 2013). The effect of lower water availability on the vegetative development of host plants can also decrease the specific leaf area (SLA) of the host or even lead to increased senescence of the leaves (e.g. Figueirôa et al. 2004; Lincoln and Zeiger 2013). This water imbalance can affect the plant's ability to store water in the leaves and can also compromise leaf succulence (Cruz et al. 2018) due to the lower water supply for the hydration of the leaves (e.g. Scatena and Scremin-Dias 2003, Cruz et al. 2018).

A study by Monteiro et al. (*unpublished*) found that the rate of fluorescence in *B. dracunculifolia* is affected by the presence of *S. flexicaulis*. The photosynthetic rate of *B. dracunculifolia* was reduced in the most critical period of the day (12:00 noon to 3:00 pm); however, the host plant was unable to recover itself in the early evening. The percentage of chlorophyll was not affected by the presence of the hemiparasite on individuals of the host *B. dracunculifolia*. The percentage of nitrogen balance (NBI) was higher in non-parasitized individuals than in parasitized individuals. The percentage of flavonoids was higher in parasitized individuals than in non-parasitized individuals. Thus, parasitism affected the N/flavonoid balance of the host plant, representing a source of damage. The *S. flexicaulis* mistletoe has a much higher rate of transpiration than the host *B. dracunculifolia*. In addition, the mistletoes have the homeostatic control of their hosts and intensify the withdrawal of water throughout the day (Glatzel and Geils 2009). Plants parasitized by the mistletoe have a higher water potential than non-parasitized plants as a way to guarantee their hydration, since the mistletoe removes a large volume of water at noon.

The effects of parasitism on physiology also affect the architecture of the host *B. dracunculifolia*. Monteiro et al. (2020b) showed that individuals parasitized by the hemiparasite presented lower crown growth and height. These effects on the host are related to the fact that the hemiparasite obtains water and nutrients directly from the xylem, reducing the resources available for the host's own metabolism (Press and Phoenix 2005; Westwood et al. 2010; Guerra and Pizo 2014), which can affect their fitness and even lead to their death (Mallams and Mathiasen 2010; Mourão et al. 2016; Monteiro et al. 2020b). In fact, Monteiro et al. (2020b) found a high mortality of parasitized *B. dracunculifolia* individuals, 61%, after 2 years. The high mortality of abundant species such as the host *B. dracunculifolia* can lead to a restructuring of the community of woody plants in the environment in which they occur in high frequency, increasing plant diversity.

In addition, the presence of the hemiparasite *S. flexicaulis* can affect the host in indirect ways. The presence of the parasitic plant alters the interactions of *B. dracunculifolia* with its associated insect community. Bahia et al. (2015) found that branches occupied by mistletoe showed a greater abundance of galls induced by *B. dracunculifoliae* (Interaction 20). Although parasitic plants are known to cause deleterious effects on plant communities, a broader view of these relationship reveals several positive direct and indirect effects on the community (e.g. Watson 2009; Watson et al. 2011; Mellado et al. 2016; Ndagurwa et al. 2016; Mellado and Zamora 2017; Hódar et al. 2018). Mistletoes can be an important source of nectar and fleshy fruits, arthropods, nesting sites and perches for birds (Guerra and Pizo 2014; Watson et al. 2011). The abundance of ants and trophobionts can be increased since insects can benefit from the large flow of water and nutrients that come from parasites and, therefore, become more abundant (Guerra et al. 2011; Freitas and Rossi 2015). Mistletoes can also have positive impacts on soil microbial communities, increasing the diversity, quality and quantity of organic matter that enters the soil next to the host (Mellado et al. 2016). This mechanism also promotes an increase in diversity and in leaf cover of herbaceous vegetation next to the host tree (Watson 2009; Ndagurwa et al. 2016), which can lead to the presence of vertebrates in the area (Hódar et al. 2018).

3 Concluding Remarks

The *B. dracunculifolia* system is well studied and comprehended, as described here. The focal community represents a very appropriate model system for the study of indirect interactions under natural field conditions. The aggregated distribution of the host plant combined with a diverse and fairly specialized fauna of arthropods creates a discrete and highly self-contained multi-trophic community. These characteristics not only facilitate the manipulation and monitoring of species densities but also increase the chances of observing their effects, since they are more likely to be a result of local ecological processes, rather than being entangled with external processes (e.g. compensatory migration). In addition, contrary to experimental manipulations in laboratory conditions, where sets of interacting species are studied in isolation, in this system the propagation of systemic indirect effects is possible. We hope that this work inspires and facilitates the design of further empirical investigations on the role of indirect interactions in community structure and dynamics.

Acknowledgements M.B. and G.F.M. were supported by Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES), and G.W.F. by CNPq and Fapemig. We also thank Reserva Vellozia and Planta Ltda.

References

Abe Y (1988) Trophobiosis between the gall wasp, *Andricus symbioticus*, and the gall-attending ant, *Lasius niger*. Appl Entomol Zool 23:41–44

Araújo AM, Fernandes GW, Bedê LC (1995) Influência do sexo e fenologia de *Baccharis dracuncufolia* D. C. (Asteraceae) sobre insetos herbívoros. Rev Bras Entomol 39:347–353

Arduin M, Fernandes GW, Kraus JE (2005) Morphogenesis of galls induced by *Baccharopelma dracunculifoliae* (Hemiptera: Psyllidae) on *Baccharis dracunculifolia* (Asteraceae) leaves. Braz J Biol 65:559–571. https://doi.org//S1519-69842005000400002

Bahia T d O, Zúñiga IG, Souza ML et al (2015) Hemiparasitism effect on *Baccharis dracunculifolia* DC. and consequences to its major galling herbivore. Acta Bot Bras 29:339–345. https://doi.org/10.1590/0102-33062014abb0008

Barbosa M, Fernandes GW, Lewis OT, Morris RJ (2017) Experimentally reducing species abundance indirectly affects food web structure and robustness. J Anim Ecol 86:327–336. https://doi.org/10.1111/1365-2656.12626

Barbosa M, Fernandes GW, Morris RJ (2019) Interaction engineering: non-trophic effects modify interactions in an insect galler community. J Anim Ecol 88:1168–1177. https://doi.org/10.1111/1365-2656.13025

Bukovinszky T, Van Veen FJF, Jongema Y, Dicke M (2008) Direct and indirect effects of resource quality on food web structure. Science 319:804–807. https://doi.org/10.1126/science.1148310

Cameron DD, Geniez JM, Seel WE et al (2008) Suppression of host photosynthesis by the parasitic plant *Rhinanthus minor*. Ann Bot 101:573–578. https://doi.org/10.1093/aob/mcm324

Carneiro MAA, Borges RAX, Araújo APA, Fernandes GW (2009a) Insetos indutores de galhas da porção sul da Cadeia do Espinhaço, Minas Gerais, Brasil. Rev Bras Entomol 53:570–592. https://doi.org/10.1590/s0085-56262009000400007

Carneiro MAA, Branco CSA, Braga CED et al (2009b) Are gall midge species (Diptera, Cecidomyiidae) host-plant specialists? Rev Bras Entomol 53:365–378. https://doi.org/10.1590/S0085-56262009000300010

Chaboo CS (2007) Biology and phylogeny of the Cassidinae Gyllenhal sensu lato (tortoise and leaf-mining beetles) (Coleoptera: Chrysomelidae). Bull Am Mus Nat Hist 350:189–233

Collevatti RG, Sperber CF (1997) The gall maker *Neopelma baccharidis* Burck. (Homoptera:Psyllidae) on *Baccharis dracunculifolia* DC. (Asteraceae): individual, local, and regional patterns. An Soc Entomol Bras 26:45–53. https://doi.org/10.1590/S0301-80591997000100006

Cruz AF, da Silva G, Silva EFF et al (2018) Stress index, water potentials and leaf succulence in cauliflower cultivated hydroponically with brackish water. Rev Bras Eng Agríc Ambient 22:622–627. https://doi.org/10.1590/1807-1929/agriambi.v22n9p622-627

Doak DF, Estes JA, Halpern BS et al (2008) Understanding and predicting ecological dynamics: are major surprises inevitable. Ecology 89:952–961. https://doi.org/10.1890/07-0965.1

Espirito-Santo MM, Fernandes GW (1998) Abundance of *Neopelma baccharidis* (Homoptera: Psyllidae) Galls on the Dioecious Shrub *Baccharis dracunculifolia* (Asteraceae). Environ Entomol 27:870–876

Espírito-Santo MM, Fernandes GW (2002) Host plant effects on the development and survivorship of the galling insect *Neopelma baccharidis* (Homoptera: Psyllidae). Austral Ecol 27:249–257. https://doi.org/10.1046/j.1442-9993.2002.01185.x

Espírito-Santo MM, Faria ML, Fernandes GW (2004) Parasitoid attack and its consequences to the development of the galling psyllid *Baccharopelma dracunculifoliae*. Basic Appl Ecol 5:475–484. https://doi.org/10.1016/j.baae.2004.04.010

Espírito-Santo MM, Madeira BG, Neves FS et al (2003) Sexual differences in reproductive phenology and their consequences for the demography of *Baccharis dracunculifolia* (Asteraceae), a dioecious tropical shrub. Ann Bot 91:13–19. https://doi.org/10.1093/aob/mcg001

Estes JA, Palmisano JF (1974) Sea otters: their role in structuring nearshore communities. Science 185:1058–1060. https://doi.org/10.1126/science.185.4156.1058

Fagundes M, Fernandes GW (2011) Insect herbivores associated with *Baccharis dracunculifolia* (Asteraceae): responses of gall-forming and free-feeding insects to latitudinal variation. Rev Biol Trop 59:1419–1432

Fagundes M, Neves FS, Fernandes GW (2005) Direct and indirect interactions involving ants, insect herbivores, parasitoids, and the host plant *Baccharis dracunculifolia* (Asteraceae). Ecol Entomol 30:28–35. https://doi.org/10.1111/j.0307-6946.2005.00668.x

Fay PA, Hartnett DC, Knapp AK (1996) Plant tolerance of gall-insect attack and gall-insect performance. Ecology 77:521–534. https://doi.org/10.2307/2265627

Fernandes GW (2016) Ecology and conservation of mountaintop grasslands in Brazil. Springer, Switzerland

Fernandes GW, Price PW (1988) Biogeographical gradients in galling species richness – tests of hypotheses. Oecologia 76:161–167. https://doi.org/10.1007/BF00379948

Fernandes GW, Carneiro MAA, Lara ACF et al (1996) Galling insects on neotropical species of *Baccharis* (Asteraceae). Trop Zool 9:315–332. https://doi.org/10.1080/03946975.1996.10539315

Fernandes GW, Fagundes M, Woodman RL, Price PW (1999) Ant effects on three-trophic level interactions: plant, galls, and parasitoids. Ecol Entomol 24:411–415. https://doi.org/10.1046/j.1365-2311.1999.00218.x

Fernandes GW, Silva JO, Espírito-Santo MM et al (2014) *Baccharis*: a Neotropical model system to study insect plant interactions. In: Fernandes WG, Santos CJ (eds) Neotropical insect galls. Springer Netherlands, Dordrecht, pp 193–219

Fernandes GW, Toma TSP, Angrisano P, Overbeck G (2016) Challenges in therestoration of quartzitic and ironstone rupestrian grasslands. In: Fernandes GW (Ed.) Ecology and conservation of mountaintop grasslands in Brazil. Springer, Switzerland, pp. 449–477

Figueirôa JM, Barbosa DCA, Simabukuro EA (2004) Crescimento de plantas jovens de (*Myracrodurum urundeuva* Allemão) Anacardiaceae sob diferentes regimes hídricos. Acta Bot Bras 18:573–580. https://doi.org/10.1590/S0102-33062004000300015

Fontaine C, Guimarães PR, Kéfi S et al (2011) The ecological and evolutionary implications of merging different types of networks. Ecol Lett 14:1170–1181. https://doi.org/10.1111/j.1461-0248.2011.01688.x

Freitas JD, Rossi MN (2015) Interaction between trophobiont insects and ants: the effect of mutualism on the associated arthropod community. J Insect Conserv 19:627–638. https://doi.org/10.1007/s10841-015-9785-2

Glatzel G, Geils BW (2009) Mistletoe ecophysiology: host-parasite interactions. Botany 87:10–15. https://doi.org/10.1139/B08-096

Guerra TJ, Pizo MA (2014) Asymmetrical dependence between a Neotropical mistletoe and its avian seed disperser. Biotropica 46:285–293. https://doi.org/10.1111/btp.12112

Guerra TJ, Camarota F, Castro FS et al (2011) Trophobiosis between ants and *Eurystethus microlobatus* Ruckes 1966 (Hemiptera: Heteroptera: Pentatomidae) a cryptic, gregarious and subsocial stinkbug. J Nat Hist 45:1101–1117. https://doi.org/10.1080/00222933.2011.552800

Hammill E, Kratina P, Vos M et al (2015) Food web persistence is enhanced by non-trophic interactions. Oecologia 178:549–556. https://doi.org/10.1007/s00442-015-3244-3

Hódar JA, Lázaro-González A, Zamora R (2018) Beneath the mistletoe: parasitized trees host a more diverse herbaceous vegetation and are more visited by rabbits. Ann For Sci 75:77. https://doi.org/10.1007/s13595-018-0761-3

Holt RD (1977) Predation, apparent competition, and the structure of prey communities. Theor Popul Biol 12:197–229. https://doi.org/10.1016/0040-5809(77)90042-9

Julião GR, Fernandes GW, Negreiros D et al (2005) Insetos galhadores associados a duas espécies de plantas invasoras de áreas urbanas e peri-urbanas. Rev Bras Entomol 49:97–106. https://doi.org/10.1590/S0085-56262005000100010

Kéfi S, Berlow EL, Wieters EA et al (2012) More than a meal… integrating non-feeding interactions into food webs. Ecol Lett 15:291–300. https://doi.org/10.1111/j.1461-0248.2011.01732.x

Lara CF, Fernandes GW (1994) Distribuição de galhas de *Neopelma baccharidis* (Homoptera: Psyllidae) em *Baccharis dracunculifolia* (Asteraceae). Rev Bras Biol 54:661–668

Larson KC, Whitham TG (1997) Competition between gall aphids and natural plant sinks: plant architecture affects resistance to galling. Oecologia 109:575–582. https://doi.org/10.1007/s004420050119

Lincoln T, Zeiger E (2013) Fisiologia Vegetal, 5th edn. Artmed, Porto Alegre

Longino JT, Branstetter MG (2018) The truncated bell: an enigmatic but pervasive elevational diversity pattern in Middle American ants. Ecography 41:1–12. https://doi.org/10.1111/ecog.03871

Mallams KM, Mathiasen RL (2010) Mistletoes on hardwoods in the United States. Forest Insect & Disease Leaflet, Portland, pp 1–12

Mellado A, Zamora R (2017) Parasites structuring ecological communities: the mistletoe footprint in Mediterranean pine forests. Funct Ecol 31:2167–2176. https://doi.org/10.1111/1365-2435.12907

Mellado A, Morillas L, Gallardo A et al (2016) Temporal dynamic of parasite-mediated linkages between the forest canopy and soil processes and the microbial community. New Phytol 211:1382–1392. https://doi.org/10.1111/nph.13984

Monteiro GF, Macedo-Reis LE, Dáttilo W et al (2020a) Ecological interactions among insect herbivores, ants and the host plant *Baccharis dracunculifolia* in a Brazilian mountain ecosystem. Austral Ecol 45:158–167. https://doi.org/10.1111/aec.12839

Monteiro GF, Novais S, Barbosa M, et al (2020b) The mistletoe Struthanthus flexicaulis reduces dominance and increases diversity of plants in campo rupestre. Flora 271:151690. https://doi.org/10.1016/j.flora.2020.151690

Morris RJ, Lewis OT, Godfray HCJ (2004) Experimental evidence for apparent competition in a tropical forest food web. Nature 428:310–313. https://doi.org/10.1038/nature02394

Mourão FA, Pinheiro RBP, Jacobi CM et al (2016) Host preference of the hemiparasite *Struthanthus flexicaulis* (Loranthaceae) in ironstone outcrop plant communities Southeast Brazil. Acta Bot Bras 30:41–46. https://doi.org/10.1590/0102-33062015abb0177

Ndagurwa HG, Ndarevani P, Muvengwi J et al (2016) Mistletoes via input of nutrient-rich litter increases nutrient supply and enhance plant species composition and growth in a semi-arid savanna, Southwest Zimbabwe. Plant Ecol 217:1095–1104. https://doi.org/10.1007/s11258-016-0635-4

Neves FS, Fagundes M, Sperber CF, Fernandes GW (2011) Tri-trophic level interactions affect host plant development and abundance of insect herbivores. Arthropod Plant Interact 5:351–357. https://doi.org/10.1007/s11829-011-9139-2

Novotny V, Basset Y, Kitching R (2003) Herbivore assemblage and their food resources. In: Basset Y, Novotny V, Miller S, Kitching R (eds) Arthropods of tropical forests: Spatio-temporal dynamics and resource use in the canopy. Cambridge University Press, Cambridge

Nunes CA, Quintino AV, Constantino R et al (2016a) Patterns of taxonomic and functional diversity of termites along a tropical elevational gradiente. Biotropica 49:186–194. https://doi.org/10.1111/btp.12365

Nunes CA, Braga RF, Figueira JEC et al (2016b) Dung beetles along a tropical altitudinal gradient: environmental filtering on taxonomic and functional diversity. PLoS One 11:e0157442

Ohgushi T (2008) Herbivore-induced indirect interaction webs on terrestrial plants: the importance of non-trophic, indirect, and facilitative interactions. Entomol Exp Appl 128:217–229. https://doi.org/10.1111/j.1570-7458.2008.00705.x

Pagès JF, Farina S, Gera A et al (2012) Indirect interactions in seagrasses: fish herbivores increase predation risk to sea urchins by modifying plant traits. Funct Ecol 26:1015–1023. https://doi.org/10.1111/j.1365-2435.2012.02038.x

Perea R, Cunha JS, Spadeto C et al (2019) Nurse shrubs to mitigate plant invasion along roads of montane Neotropics. Ecol Eng 136:193–196. https://doi.org/10.1016/j.ecoleng.2019.06.024

Peters MK, Hemp A, Appelhans T et al (2016) Predictors of elevational biodiversity gradients change from single taxa to the multi-taxa community level. Nat Commun 7:13736. https://doi.org/10.1038/ncomms13736

Prasad RP, Snyder WE (2010) A non-trophic interaction chain links predators in different spatial niches. Oecologia 162:747–753. https://doi.org/10.1007/s00442-009-1486-7

Press MC, Phoenix GK (2005) Impacts of parasitic plants on natural communities. New Phytol 166:737–751. https://doi.org/10.1111/j.1469-8137.2005.01358.x

Prugh LR, Brashares JS (2012) Partitioning the effects of an ecosystem engineer: kangaroo rats control community structure via multiple pathways. J Anim Ecol 81:667–678. https://doi.org/10.1111/j.1365-2656.2011.01930.x

Ribeiro-Mendes HN, Marques ESA, Silva IM, Fernandes GW (2002) Influence of host-plant sex and habitat on survivorship of insect galls within the geographical range of the host-plant. Trop Zool 15:5–15. https://doi.org/10.1080/03946975.2002.10531163

Riley EG, Clark SM, Flowers RW et al (2002) Family 124. Chrysomelidae Latreille 180. In: Arnett RH Jr, Thomas MC, Skelley PE et al (eds) American beetles: Polyphaga: Scarabaeoidea through Curculionoidea. CRC Press, Boca Raton

Rohfritsch O, Shorthouse JD (1982) Molecular biology of plant tumors. New York : Academic Press

Saavedra S, Reed-Tsochas F, Uzzi B (2008) Asymmetric disassembly and robustness in declining networks. Proc Natl Acad Sci U S A 105:16466–16471. https://doi.org/10.1073/pnas.0804740105

Sanders D, Kehoe R, van Veen FJF (2015) Experimental evidence for the population-dynamic mechanisms underlying extinction cascades of carnivores. Curr Biol 25:3106–3109. https://doi.org/10.1016/j.cub.2015.10.017

Scatena VL, Scremin-Dias E (2003) Parênquima, Colênquima e Esclerênquima. In: Appezzato-da-Glória B, Carmello-Guerreiro SM (eds) Anatomia Vegetal. UFV, Viçosa, pp 109–127

Sperber CF, Collevatti RG (1996) The gall maker *Neopelma baccharidis* (Homoptera) on *Baccharis dracunculifolia* (Asteraceae): success and parasitoidism density dependence. An Soc Entomol Bras 25:59–63

Staniczenko PPA, Lewis OT, Jones NS, Reed-Tsochas F (2010) Structural dynamics and robustness of food webs. Ecol Lett 13:891–899. https://doi.org/10.1111/j.1461-0248.2010.01485.x

Strauss SY (1991) Indirect effects in community ecology: their definition, study and importance. Trends Ecol Evol 6:206–210. https://doi.org/10.1016/0169-5347(91)90023-Q

Tavares MT, Perioto NW (1993) *Psyllaephagus baccharidis* n. sp. (Hymenoptera, Encyrtidae), a nymphal parasitoid of *Neopelma baccharidis* Burckhardt (Homoptera, Psyllidae). Rev Bras Entomol 37:317–320

Tompkins DM, Draycott RAH, Hudson PJ (2000) Field evidence for apparent competition mediated via the shared parasites of two gamebird species. Ecol Lett 3:10–14. https://doi.org/10.1046/j.1461-0248.2000.00117.x

Van Veen FJF, Morris RJ, Godfray HCJ (2006) Apparent competition, quantitative food webs, and the structure of phytophagous insect communities. Annu Rev Entomol 51:187–208

Watson DM (2009) Parasitic plants as facilitators: more dryad than Dracula? J Ecol 97:1151–1159. https://doi.org/10.1111/j.1365-2745.2009.01576.x

Watson DM, McGregor HW, Spooner PG (2011) Hemiparasitic shrubs increase resource availability and multi-trophic diversity of eucalypt forest birds. Funct Ecol 150:889–899

Weis A (1988) Reactive plant tissue sites and the population biology of gall makers. Annu Rev Entomol 33:467–486. https://doi.org/10.1146/annurev.ento.33.1.467

Westwood JH, Yoder JI, de Pamplhilis CD (2010) The evolution of parasitism in plants. Trends Plant Sci 15:227–235. https://doi.org/10.1016/j.tplants.2010.01.004

Wetzel WC et al (2016) Ecosystem engineering by a gall-forming wasp indirectly suppresses diversity and density of herbivores on oak trees. Ecology 97:1–5. https://doi.org/10.1007/s13398-014-0173-7.2

Wootton JT (1994) The nature and consequences of indirect effects in ecological communities. Annu Rev Ecol Syst 25:443–466. https://doi.org/10.1146/annurev.es.25.110194.002303

Wootton JT (2002) Indirect effects in complex ecosystems: recent progress and future challenges. J Sea Res 48:157–172. https://doi.org/10.1016/S1385-1101(02)00149-1