

Bottom-up manipulations alter the community structures of galling insects and gall morphs on *Neoboutonia macrocalyx* trees in a moist tropical rainforest

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- Abstract**
- 1 The effects of bottom-up forces on the community structure of tropical insect gallers and within species variation in gall morphotype assemblages are not well understood.
 - 2 We tested the roles of increased nutritional quality and density of host plants with respect to structuring the galling insect communities and gall morphotype assemblages on *Neoboutonia macrocalyx* trees in Uganda.
 - 3 Plant nutritional quality and resource concentration were manipulated with four levels of fertilization and the group size of trees, respectively. After applying these treatments in May 2011, gallers established naturally on experimental replicates. Five months later, we sampled gallers and recorded their numbers and the different morphotypes. We analyzed the effects of treatments on the structures of galler communities and gall morphotype assemblages.
 - 4 We recorded 5237 individuals, representing four galler species. One species, Cecidomyiid leaf galler, was represented by three morphologically distinct galls. Fertilization, host tree density and their interactions significantly changed the structures of galler species communities and gall morphotype assemblages.
 - 5 The results of the present study demonstrate the important role of bottom-up factors in structuring galler communities and the gall morphotype assemblages. These changes are likely caused by differential responses of different galler species and gall morphs to plant quality or quantity changes.

Keywords Adaptive radiation, barcoding, Cecidomyiid galler, Cecidomyiidae, community composition, galler guild, host specialization, plant vigor hypothesis, Psyllid galler, Psyllidae, resource concentration hypothesis, top-down forces.

Introduction

Understanding what factors regulate the community structure and phenotypic diversification of terrestrial phytophagous insects is important for ecosystem management. Some of the most potential factors that determine the community structure of herbivorous insects include soil nutrients, variation in host plant resource quality and quantity, variability in climate, mortality by natural enemies, competition for resources (Hunter & Price, 1992; Price *et al.*, 2011) and genetic differences among host plants (Wimp *et al.*, 2005; Crawford & Rudgers, 2013). For endophagous insect herbivores, such as galling and leaf mining insects, the two major factors considered to drive the patterns in

community structure are bottom-up forces from the host plant (host plant resource quality and quantity) and pressure from natural enemies (e.g. top-down effects) (Woodman & Price, 1992; Price, 2002; Araújo *et al.*, 2006; Cuevas-Reyes *et al.*, 2007; Price *et al.*, 2011). Resource availability (Hardy & Cook, 2010), sink strength (i.e. sites with strong sinks for nutrients) (Inbar *et al.*, 2004), natural enemies (Stone & Schönrogge, 2003; Inbar *et al.*, 2004) and intraspecific competition for galling or feeding sites (Inbar *et al.*, 2004) have also been suggested as potential drivers of phenotypic divergence in gall morphology.

In many studies, resource driven bottom-up effects feature as the over-riding force structuring communities of insect herbivores compared with top-down effects caused by natural enemies (Price, 2002; Cornelissen & Stiling, 2006). However, it is unclear which bottom-up factor, plant quality or quantity, is more important (Stiling & Moon, 2005), and two contrasting

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hypotheses have emerged. The plant vigour hypothesis (Price, 1991) argues that insect herbivores select and perform best on vigorously growing plants or plant modules. The resource concentration hypothesis (Root, 1973) argues that specialist herbivores are more likely to find suitable habitat, breed more successfully and increase in abundance where resources are concentrated. The relative importance of host plant quality or quantity for herbivorous insect abundance has been tested in many previous studies (Gonçalves-Alvim *et al.*, 1999; Nichols *et al.*, 1999; Stiling & Moon, 2005; Santos *et al.*, 2011; Tuller *et al.*, 2013; G. M. Malinga *et al.*, unpublished data) but less often at the community level (Wimp *et al.*, 2010). Enhanced plant nutritional quality can change the architectural complexity, as well as increase biomass and productivity of host plants (Gruner *et al.*, 2008; Chen *et al.*, 2010), and this in turn can influence the preference and performance of insect herbivores (Awmack & Leather, 2002; Sarfraz *et al.*, 2009; Chen *et al.*, 2010). Therefore, it is reasonable to expect changes in host plant nutritional quality and quantity to have extended effects on the community structures of insect herbivores.

Empirical tests investigating the importance of bottom-up versus top-down forces in structuring the communities of the poorly studied (mostly undescribed) tropical insect galls and associated gall morphotypes are lacking. In boreal and temperate systems, bottom-up effects could be more important for galls than top-down effects (Roininen *et al.*, 1996; Price & Hunter, 2005; Cornelissen & Stiling, 2006), although there is some indirect evidence that top-down effects could be important in tropical systems. For example, gall-forming Psyllids of the genus *Phytolyma* can prevent the growing of certain trees in nurseries and monoculture plantations (Nichols *et al.*, 1999; Bosu *et al.*, 2006). From a broader perspective, understanding the relative roles of bottom-up versus top-down effects is important for understanding how ecosystems function. For example, in modern manipulative environments, we should understand how nutrient cascades impact upon communities. Certain forest harvesting methods (e.g. clear-cutting and burning) can lead to nutrient cascades into the surrounding habitats (Giardina & Rhoades, 2001) and the intensive use of agrochemicals in the surrounding landscapes may cause nutrient leaching into natural systems.

In the present study, we investigated a guild of galling insects and their associated morphotypes living on *Neoboutonia macrocalyx* trees in Kibale National Park, Uganda. For clarity, we use the terms 'community' and 'assemblage' to describe galls and morphotypes, respectively (Magurran, 2004). The study aimed to examine how the variations in nutritional quality (plant vigour), host tree density (resource concentration), and their interactions influence the structure of galling insect communities and gall morphotype assemblages. Plant vigour was measured as the mean leaf size (Price, 1991; De Bruyn *et al.*, 2002; Santos *et al.*, 2011), whereas the total leaf area in each experimental unit represented the resource quantity (Low *et al.*, 2009). Specifically, we tested the predictions that increased fertilization and host tree density would lead to changes in the structure of galler communities (i.e. the relative proportions of galls) because different galler species may respond differently to quality changes as a result of their species-specific differences in life-history traits (e.g. growth and development time) and

colonization ability (Meyer & Root, 1996; Cornelissen & Stiling, 2006). Additionally, we tested whether variations in nutritional quality and host tree density or their interactions favour specific gall morphotypes (hereafter 'morphs') formed by Cecidomyiid leaf galls. We predicted that, if resource quality and quantity drives phenotypic diversification of galls, then the proportion of gall morphs should differ at different levels of fertilization and host density, respectively, because plant quality changes expand the species niche breadth (adaptive zones). Finally, we predicted that, if bottom-up effects are strong, then any possible change in the structures of galler communities and gall morph assemblages should correspond to the increasing gradients of leaf size (plant vigour) and total leaf area (resource concentration).

Materials and methods

Study area

Our experimental work was performed between May and November 2011 in a 1.30-ha former clear-cut of *Eucalyptus* plantation close to Makerere University Biological Field Station in Kibale National Park (0°13' to 0°41'N and 30°19' to 30°32'E), Uganda. Kibale (795 km²) represents a medium-altitude moist evergreen tropical forest. The mean daily minimum and maximum temperatures are 14.9 and 20.2 °C, respectively (Chapman *et al.*, 2005). The mean annual precipitation is 1696 mm (C. A. Chapman and L. J. Chapman, unpublished data, 1999–2011) with rainy seasons occurring from March to May and September to November (Struhsaker, 1997). The soils are classified as lixiv ferralsols (Majaliwa *et al.*, 2010), although there are local variations among sites. Valley bottoms are characterized by moderately deep, well drained and dark clay soils, with low pH and fertility; hillslopes have deep, red sandy loam, and hilltops have shallow, often rocky soils, or are covered in deep laterite (Lang-Brown & Harrop, 1962).

Study system

Neoboutonia macrocalyx (Euphorbiaceae) is a native deciduous pioneer tree species of medium-altitude tropical rainforests (Chapman *et al.*, 1999) growing up to 25 m in height (Lovett *et al.*, 2006) from 600 to 2500 m a. s. l. (Lovett, 1991; Fischer & Killmann, 2008). It grows in forest edges, regrowths, partially logged, primary and secondary forests (Kasenene & Roininen, 1999), as well as in light gaps of swamps and valley bottoms (Chapman *et al.*, 1999). The tree has a short trunk with an open crown and a canopy width of 7–12 m (Hamilton, 1991) and produces leaves continuously throughout the year (Kasenene & Roininen, 1999). According to G. M. Malinga *et al.* (unpublished data), *N. macrocalyx* trees are attacked by five galling species (four gall midges, Diptera, Cecidomyiidae; and one galling Psyllid, Homoptera). In the present study, we recorded four of those species, namely Cecidomyiid leaf galler, Cecidomyiid shoot galler, Cecidomyiid hairy stone galler and Psyllid leaf galler. Cecidomyiid leaf galler forms three distinctive gall morphs (namely; petiole gall, hard leaf gall and midrib gall). The species and gall morph status were confirmed by DNA Barcoding (G. M. Malinga *et al.*, unpublished data). The galls are multivoltine and gall formations are continuous throughout

the year, with peak abundance during the wet season, March to May and September to December (G.M. Malinga *et al.*, unpublished data).

Experimental design and sampling

We employed a 4 × 4 factorial manipulation with four levels of plant nutritional quality and group size of trees, respectively. Plant nutritional quality was manipulated by adding granulated nitrogen/phosphorus/potassium (NPK) (25 : 5 : 5) fertilizer to trenches dug at a radius of 15–20 cm and a depth of 5–10 cm around the tree base of 2-year-old *N. macrocalyx* trees, which ranged in height from 77.4 to 491.3 cm. P and N are the most limiting nutrients in tropical rainforests, and are the minerals most likely to regulate plant growth and determine soil fertility (Tanner *et al.*, 1998). In May 2011, we randomly assigned nine replicates of each combination of four levels of tree density (one, two, three and four trees per 1-m² plot) and four levels of fertilization (ambient level/control, 100, 200 and 400 g of NPK fertilizer added). This resulted in a total of 144 independent replicates for this experimental design. After applying treatments, we allowed gallers to establish on the experimental replicates naturally. In November 2011, 5 months after the treatments, we sampled gallers from all trees in each replicate. For each tree, we measured the number of different galler species per leaf, noting the gall morphs from which they came and the mid-rib length of all leaves. *Neoboutonia macrocalyx* leaf area (Y) is dependent on mid-rib length (x) and was estimated by the regression model, $Y = 5.03x + 0.83x^2$ (Savilakso *et al.*, 2009). In the laboratory, all galls were dissected under a stereomicroscope to justify the species morphological identification.

Statistical analysis

We tested for differences in the structures of galler communities or gall morph assemblages among levels of fertilization and host tree density, as well as their interactive effects, with permutational multivariate analysis of variance performed in PRIMER-E, version 6 (Clarke & Gorley, 2006), based on the Bray–Curtis similarity matrix computed from fourth-root transformed abundance data. Fourth-root transformation of data was used to reduce excessive contribution of the highly dominant species or gall morphs and to increase the contribution of rarer species or gall morphs in the multivariate analysis (Anderson *et al.*, 2008). P values were obtained with 999 permutations of residuals under a reduced model and type III sum of squares.

To illustrate differences and similarities in the structures of galler communities or gall morph assemblages among levels of fertilization, host tree density and their interactions, we used non-metric multidimensional scaling (NMDS; Clarke & Warwick, 2001). NMDS ordination was conducted using the Bray–Curtis similarity matrix computed from fourth-root transformed abundance data in PRIMER-E, version 6 (Clarke & Gorley, 2006). For clarity, the NMDS ordination graph generated using distances among centroids of each treatment combination is shown.

A similarity percentages routine (SIMPER, in PRIMER-E, version 6, Clarke & Warwick, 2001) was used to identify

which galler species or gall morphs primarily accounted for the observed differences in the structures of galler communities or gall morph assemblages between pairs of each treatment. SIMPER examines the percentage contribution that each species (or gall morph) makes to the mean Bray–Curtis dissimilarity between groups representing different combinations of treatments (Clarke, 1993).

Finally, a distance-based linear model (DisTLM, in PRIMER-E, version 6) was used to test whether the differences and similarities in the structures of galler communities or gall morph assemblages were explained by changes in the quality or quantity of host plants resulting from the experimental manipulations. To perform DisTLM, we modelled the Bray–Curtis similarity matrix (response variable) with the mean leaf size or total leaf area as the predictor variable.

Results

We recorded a total of 5237 individuals representing four species of gallers, namely cecidomyiid leaf galler (89.7% of individuals), cecidomyiid shoot galler (1.7%), cecidomyiid hairy stone galler (3.5%) and psyllid leaf galler (5.1%). Cecidomyiid leaf galler was represented by three morphologically distinct galls: a single-cavity hard leaf gall (85.4%), multiple-cavity petiole (13.6%) and midrib (0.96%) galls.

Impact of fertilization and host density on the structure of galler community

Both fertilization and tree density caused a significant effect on the community structure of gallers (Table 1). In addition, there was a significant fertilizer × tree density interaction effect on the community structure of gallers (Table 1), meaning that increasing fertilization caused different changes in the community structure of gallers at higher than at lower tree densities (Fig. 1). The largest source of variation in the community structure of gallers was explained by fertilization (21%), followed by the interaction between fertilization and tree density (17%), whereas tree density explained the least variation in the structure of galler communities (12%) (Table 1). Increasing fertilization rate enabled a more even proportional representation of galler species than at ambient nutrient level (Fig. 2A). A higher host density enabled an increased proportional representation of the rarer species in the community structure of gallers than at lowest tree density (Fig. 2B).

The mean leaf size and total leaf area significantly explained the variation in the community structure of gallers (DisTLM model; mean leaf area, $P = 0.003$, $R^2 = 0.06$; total leaf area, $P = 0.001$, $R^2 = 0.28$), which suggests that the change in structure of galler communities corresponds to a gradient of host plant quality and quantity.

SIMPER analysis indicated that three galler species (Cecidomyiid leaf galler, Cecidomyiid hairy stone galler and Psyllid leaf galler) made the strongest contributions to differences in galler community structure among levels of fertilization and host tree density. For both comparisons between control and highest level of fertilization, and the lowest and highest densities of host trees, Cecidomyiid leaf galler contributed > 70% to

Table 1 The differences in the community structures of gallers among levels of fertilization, host tree density and their interactions, analyzed by permutational multivariate analysis of variance based on the Bray–Curtis similarity from fourth-root transformed abundance data

Source of variation	d.f.	MS	Pseudo-F	P	U (perms)	Sq. var. (% of variation explained)
Host density	3	2060	3.0	0.009	999	6.2 (12%)
Fertilization	3	4827	7.0	0.001	999	10.7 (21%)
Host density × Fertilization	9	1345	2.0	0.021	999	8.5 (17%)
Residual	128	688	–	–	–	–
Total	143	–	–	–	–	–

MS, mean-squares; U (perms), unique permutations; Sq. var., square-root of the component of variation (percentage of the total variation explained in parentheses).

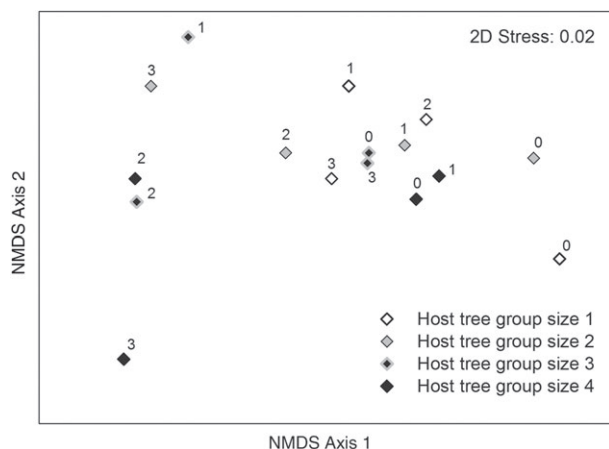


Figure 1 The ordination of non-metric multidimensional scaling (NMDS) on centroids of treatment combinations showing the separation in community structure of gallers among combinations of four levels of fertilization: 0, 1, 2 and 3, and four levels of host tree density: 1 (white), 2 (grey), 3 (grey with black dot) and 4 (black).

the dissimilarity, Cecidomyiid hairy stone galler contributed between 10% and 11% of the dissimilarity, and Psyllid leaf galler contributed 9% and 10% of the dissimilarity.

Impact of fertilization and host density on gall morph assemblages

Both fertilization and host tree density caused a significant effect on the structure of Cecidomyiid leaf gall morph assemblage (Table 2). Furthermore, there was a significant fertilizer × tree density interaction effect on the structure of gall morphs (Table 2), implying that increasing fertilization caused different changes in the structure of gall morphs at different levels of tree density (Fig. 3). Fertilization explained the largest source of variation in the structure of gall morphs (21%), followed by the interaction between fertilization and tree density (17%), whereas tree density explained the least variation in the structure of gall morphs (12%) (Table 2). The increasing fertilization rate enabled a more even proportional representation of the gall morphs than at ambient nutrient level (Fig. 4A), whereas a higher tree density caused an increase in the relative proportions of the rarer morphs rather than in lowest density of trees (Fig. 4B).

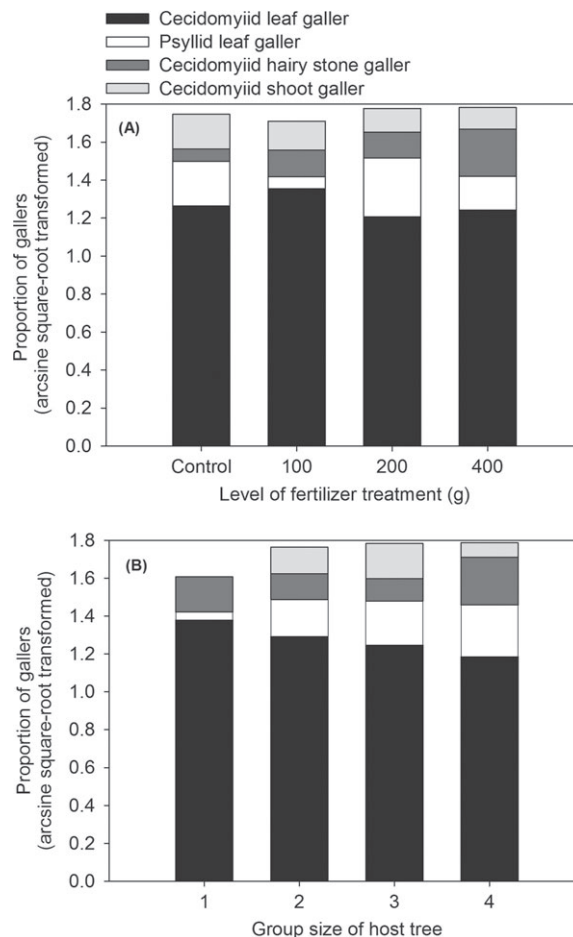


Figure 2 The proportion of each galler species (arcsine square root transformed) for each level of (A) fertilization and (B) host tree density.

Both mean leaf size and total leaf area significantly explained the variations in the structure of gall morph assemblages (Dis-TLM model; mean leaf area, $P = 0.001$, $R^2 = 0.08$; total leaf area, $P = 0.001$, $R^2 = 0.23$), suggesting that the change in structure of gall morph assemblages corresponds to a gradient of host plant quality or quantity.

According to SIMPER, two gall morphs (hard leaf gall, petiole gall) made the largest contributions to differences in gall morph assemblage structures among levels of fertilization and host tree

Table 2 The differences in the assemblage structures of Cecidomyiid leaf gall morphs among levels of fertilization, host tree density and their interactions, analyzed by permutational multivariate analysis of variance based on Bray–Curtis similarity from fourth-root transformed abundance data

Source of variation	d.f.	MS	Pseudo-F	P	U (perms)	Sq. var. (% of variation explained)
Host density	3	2257	2.9	0.021	999	6.4 (12%)
Fertilization	3	5387	6.9	0.001	999	11.3 (21%)
Host density × Fertilization	9	1561	2.0	0.022	997	9.3 (17%)
Residual	128	776	–	–	–	–
Total	143	–	–	–	–	–

MS, mean-squares; U (perms), unique permutations; Sq. var., square-root of the component of variation (percentage of the total variation explained in parentheses).

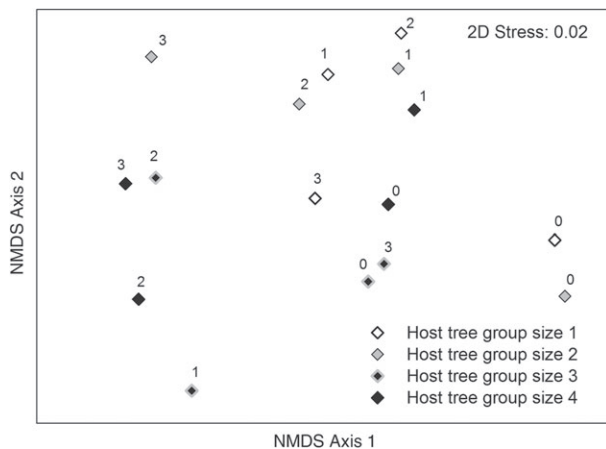


Figure 3 The ordination of non-metric multidimensional scaling (NMDS) on centroids of treatment combinations showing the separation in the structure of Cecidomyiid leaf gall morph assemblages among combinations of four levels of fertilization: 0, 1, 2 and 3, and four levels of host tree density: 1 (white), 2 (grey), 3 (grey with black dot) and 4 (black).

density. For both comparisons between control and highest level of fertilization and the lowest and highest tree density, hard leaf gall morph contributed > 60% to the dissimilarity, whereas petiole gall morph contributed between 26% and 29% to the dissimilarity.

Discussion

In the present study, we show that increasing levels of fertilization (plant nutritional quality) and host density (resource concentration) significantly changed the community structure of galls. The change in galler community structure was likely a response to the increased quality and quantity of host plants because measures of plant vigour (mean leaf size) and resource concentration (total leaf area) explained significant proportions of the variation in community structure of galls. Plant vigour is an important factor explaining the community structures of arthropods in other systems. For example, Wimp *et al.* (2010) demonstrated that increased primary production via nitrogen fertilization altered the composition of arthropod communities on *Spartina alterniflora* in salt marshes in New Jersey. The mechanisms by which these changes in community structure take place are unclear. One possible explanation could be that the different galler species differ in their resource ratio requirements and

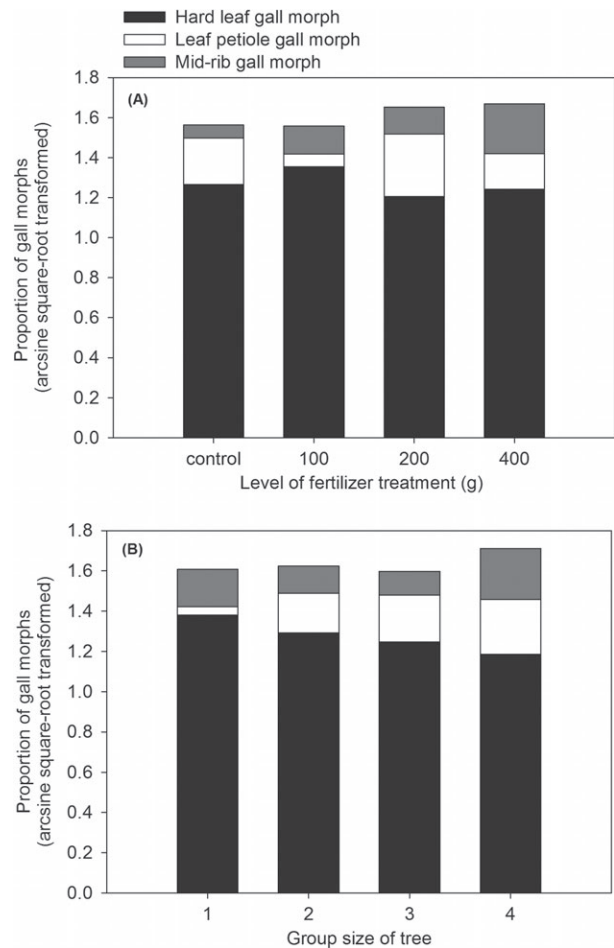


Figure 4 The proportion of each gall morph (arcsine square root transformed) for each level of (A) fertilization and (B) host tree density.

responses to plant quality changes. In our earlier work (G. M. Malinga *et al.*, unpublished data), we found that the density of one of the three species accounting for the differences in community structure of galls (Cecidomyiid leaf galler) was positively affected by increasing fertilization and host tree density. Whatever the mechanism, our results suggest that bottom-up pressure is fundamentally important in structuring communities of tropical galling insects, as indicated also in other previous studies (Araújo *et al.*, 2006).

The possible ecological forces driving divergence in gall morphology observed in the present study are uncertain. Morphological divergence in gall structures formed by one species within a host may be a response to enlarged surface area for feeding (Stone & Schönrogge, 2003) and intraspecific competition for gall sites (Inbar *et al.*, 2004). The key factors that facilitate gall morphological diversification are the availability of resources and adaptive zones (Price, 2005; Hardy & Cook, 2010). An increase in the levels of nutrient and host density could increase the number of vacant ecological niches for colonization and, hence, a higher rate of gall morphological diversification (McLeish *et al.*, 2007; Price *et al.*, 2011). Under an adaptive radiation model, the rate of diversification is governed by the amount of free space or ecological opportunities in an adaptive zone (Litosios *et al.*, 2012). Gall morphological diversification may comprise one possible mechanism for reducing gene flow, eventually leading to the emergence of reproductively isolated new races or species. For example, the gall inducing aphids (Hemiptera: Aphididae: Pemphiginae: Fordini) on the host plant *Pistacia* (Anacardiaceae) are considered to have radiated primarily by using different sites on the same host plant organ (Inbar *et al.*, 2004). Our results provide insight into the roles of bottom-up factors in driving adaptive radiations. Such within host diversification of gall morphs was also reported by Joy and Crespi (2007) on gall-inducing *Asphondylia* flies (Diptera: Cecidomyiidae) living on *Larrea tridentata* (creosote bush), as well as by Stireman *et al.* (2008) on *Asteromyia carbonifera* (Diptera: Cecidomyiidae) on the goldenrod *Solidago altissima* (Asteraceae).

In conclusion, in the present study, we have demonstrated the important role of bottom-up effects with respect to regulating the structures of galling insect communities and their associated gall morph assemblages. This knowledge might be useful when designing control strategies for galling insect pests (e.g. in nurseries and young plantations of tree species). Additionally, our results indicate the possible roles of plant nutritional quality and resource concentration in driving adaptive radiations in gall morphologies. Further studies are required to fully understand the mechanisms behind the observed effects of plant nutritional quality and resource concentration on the structure of galler communities and gall morph assemblages.

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