



The distribution of a host-specific canopy parasite is linked with local species diversity in a northern temperate forest

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CTFS; Forest dynamics plot; Galls; Hardwood forest; Herbivory; Plant–herbivore interactions; Richness; Spatial analysis; Stem density; Sugar maple

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Abstract

Question: Is the spatial distribution and density of the maple spindle gall mite *Vasates aceriscrumena* (MSGM) positively correlated with the distribution and density of its host? Is the distribution of MSGM influenced by non-host species and abiotic factors?

Location: Temperate mixed hardwood forest stand, Haliburton Forest and Wildlife Reserve, Ontario, Canada.

Methods: We used the mapped locations of host and non-host trees to investigate the cause of spatial variation in the density of MSGM within an 8.8-ha forest plot in central Ontario, Canada. Gall densities were determined from fallen leaves, collected at 20-m intervals. We used Mantel and partial Mantel tests to compute the correlation between gall density and several spatially variable biotic and abiotic factors: (1) host density and basal area, (2) density of non-host stems, (3) overall stem density, (4) stem species diversity and (5) topography.

Results: The density of leaf galls was weakly correlated with host density and basal area. Although the correlation with host density and basal area was statistically significant, leaf gall density was more strongly correlated with overall tree species richness and overall stem density. Gall densities were highest at the boundaries of neighbourhoods containing high and moderate sugar maple (*Acer saccharum*) densities. Partial Mantel tests indicated that the observed spatial correlations held when controlling for the potential influence of topography.

Conclusions: Based on the spatial relationships documented here, we speculate that the mechanism responsible for the correlation between the MSGM and non-host stems is parasite-induced host stress. Separate studies have established a strong negative impact of the MSGM parasite on sugar maple stem growth. We suggest that by weakening the competitive ability of its host, the parasite indirectly promotes local species diversity through competitive release. Given the high diversity and prevalence of leaf gall parasites in mixed hardwood stands, depression of host dominance by leaf parasites may represent an unexplored mechanism for the maintenance of species diversity in northern temperate forests.

Introduction

Forest trees worldwide host a variety of natural enemies, i.e. parasites, pathogens and herbivores. A large number of these are host-specific and are thought to be responsible, in part, for the maintenance of tree species richness in both tropical (Janzen 1970; Connell 1971; Wright 2002) and temperate (Packer & Clay 2000) forests through biotrophic density- and distance-dependent mechanisms (i.e. the

Janzen–Connell effect). While there is wide-ranging evidence for the role of density- and distance-related natural enemy impacts as mechanisms that maintain tree species richness (see Terborgh 2012 for a recent review), less is known about the various factors that influence abundances of (herbivorous) natural enemies in forests. Factors such as phylogenetic isolation of hosts (Yguel et al. 2011), host plant quality (Egan & Ott 2007), host genotypic variation (Tack et al. 2010), environmental conditions

(Cornelissen & Stiling 2006) and neighbourhood species richness (Jactel & Brockerhoff 2007) appear to be important in determining natural enemy establishment in forests. In temperate forests, familiar examples of host-specific natural enemies include fungal-like pathogens (Packer & Clay 2000), endophagous arthropods (leaf miners and gallers) and parasitic plants such as dwarf mistletoes (Hawksworth & Weins 1996).

Dispersal-limited canopy parasites such as dwarf mistletoes are known to have significant negative impacts on hosts, including reductions in growth (Filip et al. 1993) and physiological function (Meinzer et al. 2004). One important but overlooked guild of host-specific endophagous parasites in forest communities is the group of gall-inducing arthropods (insects and mites; hereafter GIA). Together with leaf miners, GIA comprise the most specialized group of phytophagous arthropods due to their extreme host specificity (Gaston et al. 1992; Gonçalves-Alvim & Fernandes 2001), but little is known about their spatial distribution and how this might influence local tree species richness in forest communities. Given their high host specificity, one might predict strong positive relationships between host and GIA densities (cf. the resource concentration hypothesis; Root 1973). Studies that have examined the association of individual species with their hosts, and with environmental correlates, provide some insight into the processes that govern GIA populations and communities. GIA species richness, for example, has been found to be positively correlated with sclerophyllous vegetation (Price et al. 1998), xeric habitats (Fernandes & Price 1988) and plant structural complexity (Cuevas-Reyes et al. 2004a), and negatively correlated with soil nutrient richness (Cuevas-Reyes et al. 2004b). In autecological studies on gall inducers, general patterns of GIA distributions remain unclear. For example, gall density may increase with host age in some species (Patanekar et al. 2011) and decrease in others (Fonseca et al. 2006; Ribeiro & Basset 2007). Other factors that influence the spatial distribution of GIA among individual hosts include the size (Thomas et al. 2010), light requirements (Basset 2001; Castellanos et al. 2006), canopy position (Kampichler & Teschner 2002; Thomas et al. 2010) and reproductive status (Ishihara et al. 2007) of the host, as well as its susceptibility and palatability (Egan & Ott 2007). GIA typically attack specific plant organs, e.g. leaves or stems, such that infestations are concentrated on certain parts of an individual plant. Prior studies have examined this within-plant spatial structure of GIA populations (Kampichler & Teschner 2002; Kuczynski & Skoracka 2005) with the aim of teasing out the microhabitat preferences of GIA and impacts on hosts. Only a few studies have examined GIA spatial distribution among the individuals of a host population (Biedermann 2007).

The GIA often show high fidelity to individual host plants, and such isolation may eventually lead to the formation of 'demes' or genetically distinct gall-inducer populations in some species (see Egan & Ott 2007). High host fidelity and isolation imply spatial structure (autocorrelation) in GIA distributions. However, prior studies have generally not accounted for the spatial processes that are characteristic of plant populations (see Dale 1999 for examples), and which give rise to spatial heterogeneity in host abundance and species association (Fuller & Enquist 2012). Most have essentially relied on simplistic linear models, while leaving out potentially important effects of spatial autocorrelation. Therefore, any positive or negative correlations identified with such models may suffer from a lack of independence from the underlying influence of spatial processes, such as dispersal (Legendre 1993). Moreover, these studies have generally sampled relatively few individual hosts; no large-scale GIA–host study accounting for spatial autocorrelation has yet been attempted.

Here, we use spatially explicit methods to examine associations between a GIA and the local forest community in a temperate mixed forest stand. The maple spindle gall mite (*Vasates aceriscrumena* Riley; hereafter MSGM) is a host-specific GIA common to the temperate mixed forests of northeastern North America. MSGM induces spindle or 'finger-shaped' galls exclusively (Jeppson et al. 1975) on the leaves of its host, sugar maple (*Acer saccharum* Marsh), a widely distributed and economically important broadleaf tree species. Emerged overwintering females induce galls on newly flushing leaves in the spring, and galls serve as habitat within which the mite's life cycle is carried out during the summer. Galls are abandoned (by a new generation of females) before leaf abscission in the autumn. At this point, mites are either transported passively by local wind events at the edge of the leaf surface or travel back along the leaf mid-vein and petiole in search of overwintering refugia (bud scales, bark crevices, etc.; for a detailed account of MSGM's life history see Patankar et al. 2012). Galling by this mite causes large declines in leaf-level gas exchange processes, and galling intensity is negatively correlated with radial increment growth of mature sugar maple trees (Patanekar et al. 2011). MSGM is found in conjunction with a congeneric gall inducer, *Vasates quadripedes* Shimer (the maple bladder gall mite) that induces bladder galls on both silver maple (*Acer saccharinum*) and red maple (*Acer rubrum* L.) (Jeppson et al. 1975; Keifer et al. 1982). Sugar maple is by far the most dominant tree species in the study area, with large stems (≥ 10 -cm diameter at breast height; DBH) alone comprising $\sim 41\%$ of the total basal area.

The aim of this paper is to estimate the influence of biotic and abiotic factors on the spatial distribution of MSGM, a host-specific natural enemy found in abundance on a

dominant tree species in a temperate forest plot. Specifically, we ask the following questions: (1) is MSGM gall density spatially clumped and, if so, at what scale; (2) is gall density correlated with underlying topographic features such as slope and aspect; (3) is gall density correlated with stem density and basal area of its host, sugar maple, and in particular with older maple trees; and (4) is gall density correlated to the abundance of other tree species, overall stem density or species richness in the study plot? Based upon prior observations of MSGM density patterns, we hypothesized that MSGM density would be most strongly related to host tree density (as proposed by the resource concentration hypothesis; Root 1973), and when examined across a range of host size classes, the oldest maples would carry the highest gall densities. We also predicted that areas with steeper slopes would be positively correlated with MSGM gall density, because these areas support shallow soils and rocky outcrops that represent poor habitat for the host, causing individual stems to be stressed and potentially more susceptible to infection by MSGM.

Methods

Study site description

The study was conducted within the forest mega-plot (13.5 ha) of Haliburton Forest and Wildlife Reserve, Ontario (45.2901° W, -78.6377° N), a recent addition to the system of long-term study plots established by the Center for Tropical Forest Science (CTFS). The site supports mixed hardwood forest, of the Great Lakes–St. Lawrence forest vegetation association. Tree species include sugar maple (*A. saccharum*), yellow birch (*Betula alleghaniensis* Britton), American beech (*Fagus grandifolia* Ehrh.), white ash (*Fraxinus americana* L.), red maple (*A. rubrum*), red oak (*Quercus rubra* L.), black cherry (*Prunus serotina* Ehrh.), eastern white pine (*Pinus strobus* L.) and eastern hemlock (*Tsuga canadensis* (L.) Carr.). The plot is situated near the west-central shoreline of a lake and is divided into 367 20 × 20 m grids with permanent grid-posts marking the northwest corner of each 20-m² quadrat. Prior to this study, all trees >10 cm DBH were identified, geo-referenced and assigned a permanent ID as part of the first census of the plot, completed in 2008. In total, there are 7211 stems ≥10 cm DBH in the entire plot. Sugar maple is the dominant species here, with 2545 stems comprising 35.3% of stems ≥10 cm DBH.

Data collection

We collected samples of dead (fallen) leaves, representing all tree species, from a subset of 231 grid posts, encompassing a rectangular area of 8.8 ha within the mega-plot. Leaf collection took place in early October 2008, immediately

after leaf fall. At each grid post of the subset, newly fallen leaves ($n \geq 50$) within a 1-m radius were collected from the forest floor and stored in paper bags. In addition to the samples collected at the grid posts, we collected leaves from an additional 20 'offset' points across the plot, located at 2, 5 or 10 m from the posts, in one of the four cardinal directions. The location (grid post ID), distance (2, 5 or 10 m) and direction (north, south, east, west) of these offset points were randomly generated with the purpose of gathering supplementary gall density data at known points to resolve spatial correlations at distances <20 m. Because the plot is bordered by lake margin on two sides, we restricted sampling to a minimum distance of 20 m from lake margins to minimize potential edge effects. Bagged leaves were transported to a laboratory, where they were dried. Sugar maple leaves were separated from each dried sample and individually scored for the number of galls. When possible, 50 sugar maple leaves were scored per bag, but for bags containing fewer than 50, all available sugar maple leaves were scored. Overall, a total of 12 342 sugar maple leaves were scored for MSGM galls. For each grid post, we calculated the mean MSGM gall density by dividing the total number of galls by the number of leaves counted. Slope and aspect were calculated from the mapped elevation of each grid post.

Spatial analyses

We quantified the relationship of MSGM gall densities with four biotic variables (overall stem density, species richness, sugar maple basal area and stem density) and two abiotic site features (slope and aspect). In addition to investigating associations with sugar maple, we examined the correlation between MSGM gall density and the stem density of seven other commonly occurring tree species within the plot. As the strength of relationships between MSGM gall density and the descriptors can vary with spatial scale (Greig-Smith 1952), we performed a scale analysis to determine the scale at which the correlation was strongest. Using the samples collected at the subset of grid posts, we computed separate Mantel test statistics (Fortin & Gurevitch 1993) for each of seven radii, ranging from 5 to 35 m from the centre of each post. We did not go beyond 35 m for any of our analyses, as the eastern and southern boundaries of the study plot were close to lake margins (<40 m), potentially leading to spurious correlation due to edge effects. The normalized Mantel statistic, r is calculated similar to Pearson's product-moment coefficient (by first normalizing each matrix), and depicts direction and the strength of linear association between distance (or similarity) matrices of any two given variables. Entries in a given matrix do not represent the original raw values but instead are based on a measure of distance (or similarity) between

individual 'points' of that particular variable (e.g. MSGM densities, maple densities, geographic distance etc.; Fortin & Gurevitch 1993).

Partial Mantel tests (Legendre & Fortin 1989) were used to examine the relationship between two variables while controlling for a third (e.g. the correlation between MSGM density and species richness controlled for overall stem density). The significance of the resulting Mantel statistic was assessed by comparing it with a reference distribution obtained by permuting the arrangement of the elements of any one of the distance matrices 999 times, each time recalculating the Mantel statistic (Fortin & Gurevitch 1993). Partial Mantel tests were then used, based on the appropriate scale, to examine MSGM gall density in relation to the above variables conditioned on space.

We constructed contour maps to visually detect areas with high gall densities within the sample plot. The contour maps were produced using bilinear interpolations (linear interpolations in two directions) of gall densities at individual posts. Additionally, we constructed contour maps of species richness, overall stem density and sugar maple density based upon 30-m circular sample plots, centred on the grid posts. All maps were created with the R software package (R Foundation for Statistical Computing, Vienna, AT); statistical analyses (Mantel and partial Mantel tests) were computed using the *vegan* package in R.

Results

The contour map centred on grid posts revealed that MSGM gall densities were highest in the southern end of the sample plot (Fig. 1a). Overall stem density (all species) and species richness (at 30-m radius) were similarly higher in these areas relative to the rest of the plot (Fig. 1b,c); sugar maple density (Fig. 1d) and basal area (not shown), however, did not correspond with high gall densities.

Scale analyses revealed that linear associations between MSGM gall density and (1) sugar maple density, (2) overall stem density and (3) tree species richness were strongest at 30 m (Fig. 2). At this scale, the Mantel tests revealed that species richness ($r = 0.3217$, $P = 0.001$) and overall stem density ($r = 0.3357$, $P = 0.001$) were most strongly positively correlated with MSGM gall density among the included descriptors (Table 1). Sugar maple basal area (across all tree sizes) did not correlate as strongly with gall density, although this relation was positive and significant ($r = 0.2232$, $P = 0.001$; Table 1). Sugar maple density (across all size classes) showed weaker significant positive correlations relative to basal area ($r = 0.1868$, $P = 0.001$; Table 1). When partitioned into DBH classes, the correlation between gall density and basal area was strongest at the smallest size class of 10–20 cm ($r = 0.2339$, $P = 0.001$; Fig. 3a). Gall density was not correlated with basal areas of

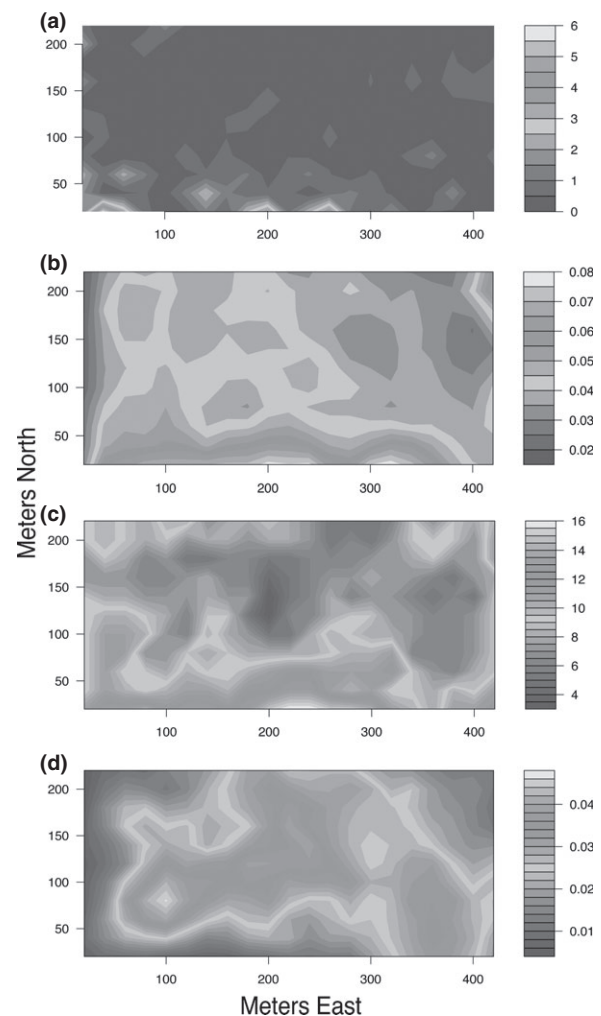


Fig. 1. Contour maps of (a) MSGM gall density (galls per leaf), (b) overall stem density (stems m^{-2}), (c) species diversity (number of species) and (d) sugar maple stem density (stems m^{-2}) from the 8.8-ha study area of the Haliburton forest mega-plot, Ontario. Sugar maple density, overall stem density and species diversity were calculated within a 30-m radius from 231 individual grid posts spaced 20 m apart. Gall densities were calculated at the grid posts.

the largest maple stems (50–80 cm; $r = -0.0622$, $P = 0.952$; Fig. 3a). The correlation between MSGM gall density and sugar maple density, when partitioned into DBH classes, was bimodal, with 10–20 and 30–40 cm DBH trees showing the strongest positive correlations amongst the size classes (r (10–20 cm) = 0.1965, $P = 0.001$; r (30–40 cm) = 0.1777, $P = 0.001$; Fig. 3b).

Mantel tests for the seven most common species (in addition to sugar maple) revealed that MSGM gall densities were positively and significantly correlated with only three additional species, of which red maple had the strongest association (Table 2a). The partial Mantel tests at 30 m conditioned on 'space' as the third factor produced slightly

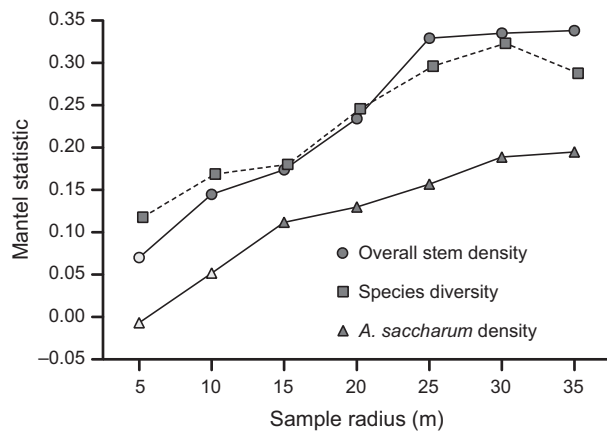


Fig. 2. Scale analysis of spatial correlation. Correlation coefficients between gall density and three descriptors: (1) species diversity, (2) overall stem density, (3) *A. saccharum* density from Mantel tests at six different scales (5–30 m) of analyses. Filled symbols represent values that are significant at $P = 0.05$.

lower correlation coefficients for the various descriptors, but the general pattern was the same as with the Mantel tests (Table 2a). Because tree species richness was strongly correlated with overall stem density, we repeated the partial Mantel test between MSGM gall density and species richness, this time accounting for the effect of overall stem density. The results revealed that the correlation of gall density on species richness was reduced when conditioned on overall stem density (Table 1). To test for the effect of richness on MSGM gall density, independent of species composition, we repeated the partial Mantels, this time controlling for the potential influence of red maple.

Species richness continued to show a strong positive correlation with MSGM gall density when we controlled for red maple density ($r = 0.3105$, $P = 0.001$; Table 1). We examined the relationship between MSGM gall density and two topographical variables at individual grid posts in the subset: (1) slope and (2) aspect. Aspect was not significantly correlated with corresponding gall density at posts ($r = -0.0574$, $P = 0.962$), however, slope was marginally positively correlated with MSGM density when accounting for spatial autocorrelation ($r = 0.1042$, $P = 0.05$; Table 2b).

Discussion

As expected, the distribution of galls in the plot followed an aggregated and non-random pattern within the study area, characterized by patches of high and low gall densities (Fig. 2a). The Mantel tests revealed that among the variables examined, species richness and overall stem density had the strongest positive associations with mite gall densities. This result persisted even when controlling for the influence of geographic distance (‘space’). It is well known that the species richness of a sample tends to increase asymptotically with sample size (Fisher et al. 1943); therefore, the positive influence of richness might simply reflect the species–density relationship. We found that the relationship between gall density and species richness was indeed reduced slightly when controlled for overall stem density; however, the positive association with richness remained highly significant. This association was stronger in magnitude to that between MSGM galls and the density of its host sugar maple, in analyses that

Table 1. Results (r and corresponding P in parenthesis) of Mantel (above the diagonal) and partial Mantel (below the diagonal) tests between gall density and four descriptor variables in the Haliburton Forest mega-plot. Partial Mantel statistics between gall density and space differed when conditioned on the remaining three descriptors. Hence, corresponding r - and P -values here are as follows (using superscripts): a = conditioned on stem density, b = species diversity, c = sugar maple density. Partial Mantel statistics between descriptors are conditioned on space.

| | Gall density | Stem density | Species diversity | Sugar maple density | Sugar maple basal area | Space |
|------------------------|--|-------------------|-------------------|---------------------|------------------------|-------------------|
| Gall density | – | 0.3357 (0.001) | 0.3217 (0.001) | 0.1868 (0.001) | 0.2231 (0.001) | 0.0944 (0.002) |
| Stem density | 0.3252 (0.001) | – | 0.4271 (0.001) | 0.2367 (0.001) | 0.3135 (0.001) | 0.1883 (0.001) |
| Species diversity | 0.3184, 0.3072*, 0.2094†, 0.3105#, 0.3157\$ | 0.4249 (0.001) | – | 0.1718 (0.001) | 0.3056 (0.001) | 0.0555 (0.006) |
| Sugar maple density | 0.1742 (0.001) | 0.2118 (0.001) | 0.1651 (0.001) | – | 0.7216 (0.001) | 0.1680 (0.001) |
| Sugar maple basal area | 0.2066 (0.001) | 0.2789 (0.001) | 0.302 (0.001) | 0.7121 (0.001) | – | 0.2599 (0.001) |
| Space | 0.0338 ^a , 0.065 ^b , 0.081 ^c (0.128, 0.012, 0.012) | n.a. | n.a. | n.a. | n.a. | – |

, †, #, \$ = Partial Mantel statistic between MSGM gall density and species diversity conditioned on slope, aspect\$, overall stem density† and *A. rubrum* density#. n.a., tests not applicable.

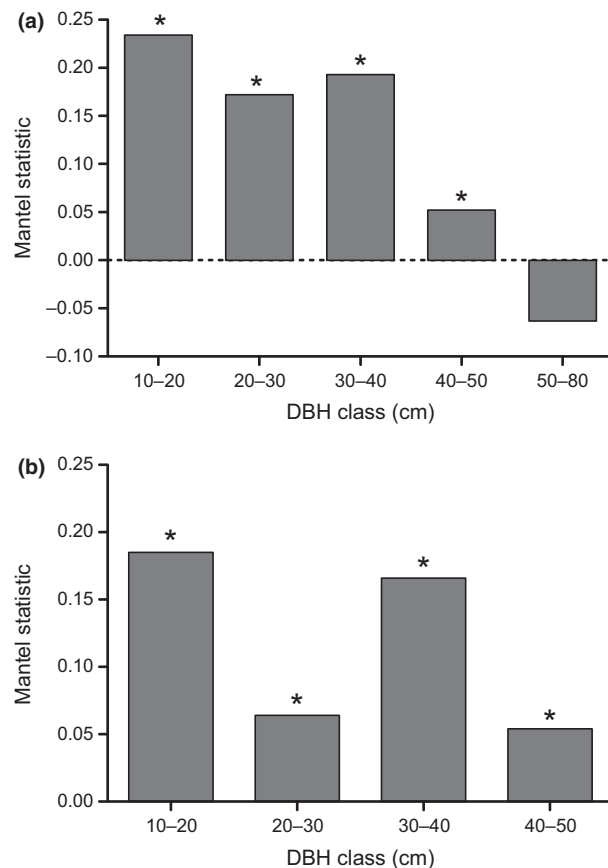


Fig. 3. Correlation coefficients of partial Mantel tests between MSGM gall density and (a) sugar maple basal areas (conditioned on space) partitioned into five size classes (10–20, 20–30, 30–40, 40–50, 50–80 cm DBH) and (b) sugar maple stem densities (conditioned on space) partitioned into four size classes (10–20, 20–30, 30–40, 40–50 cm DBH) from the Haliburton forest mega-plot. The y-axis represents the standardized partial Mantel statistic (Pearson's r). * = significant correlation with MSGM gall density at $P < 0.05$.

controlled for either total stem density or spatial effects as a third variable. Similarly, the association of MSGM gall density with richness remained strong when controlling for the potential influence of topographic slope or aspect. Because species composition may also have influenced the positive relationship of gall density and species richness, we performed an additional test, in which we controlled for the density of red maple, as this species had the strongest correlation (after sugar maple) with MSGM gall density among tree species in the plot. Again, the relationship between species richness and MSGM gall density remained strong when we controlled for red maple abundance.

The strong positive correlation of gall density with species richness was an unexpected result, contrary to our initial hypotheses. We had predicted that with increasing species richness in the plot, there would be fewer available sugar maple individuals for MSGM to colonize, potentially

Table 2. Mantel and partial Mantel statistics (r = Pearson correlation coefficient, P = significance value) between MSGM gall densities at grid posts and (a) seven tree species, and (b) two site features (slope and aspect) from the Haliburton Forest mega-plot. Tests between tree species and gall densities were based on individual tree densities calculated within a 30-m radius from grid posts. The partial Mantel test takes into account the effect of 'space' (geographic distance) when testing for associations between species densities/site features and gall mite densities.

| | Mantel statistic (r) | P -value | Partial mantel statistic (r) | P -value |
|------------------------------|--------------------------|------------|----------------------------------|------------|
| (a) Tree species | | | | |
| <i>Acer rubrum</i> | 0.1460 | 0.010 | 0.1470 | 0.015 |
| <i>Tsuga canadensis</i> | 0.1176 | 0.058 | 0.1178 | 0.045 |
| <i>Quercus rubra</i> | 0.1053 | 0.045 | 0.1077 | 0.047 |
| <i>Fagus grandifolia</i> | 0.0551 | 0.130 | 0.0498 | 0.163 |
| <i>Betula alleghaniensis</i> | -0.0285 | 0.682 | -0.0335 | 0.724 |
| <i>Fraxinus americana</i> | -0.0621 | 0.949 | -0.0593 | 0.934 |
| <i>Pinus strobus</i> | -0.0200 | 0.497 | -0.0171 | 0.448 |
| (b) Site features | | | | |
| Slope | 0.121 | 0.033 | 0.1042 | 0.053 |
| Aspect | -0.0574 | 0.962 | n.a. | n.a. |

n.a., tests not applied.

leading to reduced densities of MSGM galls on its host. Several possible alternative, but not mutually exclusive, explanations exist for the observed positive correlation between MSGM abundance and local tree species richness. First, isolation of susceptible sugar maples in species-rich areas could result in a build-up of gall densities on individual trees over time via local adaptation. Indeed, MSGM appears to display traits required for strong local adaptation of host-specific natural enemy populations to individuals within a host population. Sugar maple is a typically long-lived broadleaf species that can support several generations of MSGM populations (each lasting a year; Patankar et al. 2012) over time, thus plausibly allowing natural selection to occur (Edmunds & Alstad 1978). Further, endophagy, a trait common to all acarine gall inducers, appears likely to promote local adaptation due to continuous exposure of all life stages of the inducer to host plant tissues (Stiling & Rossi 1998). Indeed compelling examples of GIA local adaptation to individual hosts have been documented in recent literature (Egan & Ott 2007; Tack & Roslin 2010) pointing to the distinct possibility that, over time, GIA populations become locally adapted to individual hosts, leading to the formation of genetically distinct 'demes' (cf. Egan & Ott 2007). Isolated trees might also contribute to higher rates of GIA population establishment via escape from natural enemies; isolated trees might be harder to colonize at first, but it is possible that established populations of MSGM on isolated trees might in fact be released from selective pressures enforced by natural enemies that fail to migrate to and establish on such isolated trees. Faeth

& Simberloff (1981) observed that leaf miner survival in three species of oak (*Quercus* spp.) was significantly higher in isolated trees compared to non-isolated trees, possibly due to decreased parasitism rates on leaf miners. Similarly, Ozanne et al. (2000) observed that the composition of arthropods on isolated Scots pine (*Pinus sylvestris* L.) trees was significantly different from that in monospecific stands of this species, with certain herbivores attaining higher densities in isolated trees, also possibly due to lower impacts of predators (cf. Faeth & Simberloff 1981).

Along these lines, the primary natural enemy of MSGM appears to be the gall-invading tarsonemid mite *Tarsonemus acerbilis*. We found that >40% of MSGM galls (sampled across 2 yrs) contained this opportunistic gall invader, making it by far the most dominant arthropod species (after MSGM) found in MSGM galls (Patankar et al. 2012). The tarsonemid mite is more active than its prey, and is often seen roaming on the leaf phylloplane. It may therefore be vulnerable to other arthropod predators, such as phytoseiid mites and small insects, such as coccilids and thrips (for further examples see Lindquist 1986). An indirect 'release' from the gall invader by larger predatory arthropods might result in higher populations of MSGM in areas of high tree species richness. Alternatively, in patches comprised of sugar and red maple, gall invasion by *T. acerbilis* (a known facultative gall invader; Lindquist 1986) on *V. quadripedes* (a congeneric gall inducer found exclusively on red and silver maple) might in part contribute to release from MSGM gall invasion, leading to the observed results. Hence, future studies on variations in host plant quality and arthropod assemblages across a gradient of host densities might uncover strong local adaptation or multi-trophic mechanisms with respect to the observed increased densities of MSGM galls on isolated hosts in species-rich areas.

A second alternative explanation is that higher gall densities on maples could, in part, lead to greater tree species richness. This would be possible if galling resulted in reduced performance in individual trees, thereby reducing their competitive advantage over other species, leading to higher local species richness. Indeed, the influence of below-ground pathogens contributing to negative plant growth appears to support the notion that soil biota play an important role in weakening the competitive advantage of plant hosts (Klironomos 2002). We found that MSGM galling lead to significant declines in leaf gas exchange (>50% reduction in carbon dioxide uptake in infected leaves), and high levels of galling were also correlated with reduced radial incremental growth in MSGM-infected trees (Patankar et al. 2011). Hence it is plausible that isolation over time results in heavy gall loads (via local adaptation, described above), and heavily infected sugar maples might thus have reduced local competitive effects as a

consequence of impeded performance (through both above- and below-ground mechanisms), possibly encouraging the establishment of other species. If so, our results would support the growing evidence for the importance of natural enemy effects within temperate forests (Packer & Clay 2000; Hille Ris Lambers et al. 2002). Finally, high diversity patches could result in increased use of resources by competing tree species through niche complementarity, and this could result in higher stress on individuals, and therefore higher susceptibility to galling in sugar maple. Consistent with this explanation, increases in gall density in stressed vs. unstressed hosts have been observed in other systems (e.g. Fernandes & Price 1992; De Bruyn 1995; Price et al. 1998; Cuevas-Reyes et al. 2004b).

Increased densities of natural enemies in larger patches or higher densities of hosts would be expected from the standpoint of the resource concentration hypothesis (Root 1973). However, MSGM appears to show an alternative pattern, with a stronger association with high local species diversity. Although soil pathogens (Packer & Clay 2000) and mammalian herbivores (Myer & McCarthy 1989) have been shown to influence tree species density, studies that reveal density-dependent survival in temperate trees often fail to identify the specific cause of decreased survival (Hille Ris Lambers et al. 2002; Hyatt et al. 2003; Shibata et al. 2010). The results presented here and in Patankar et al. (2011) suggest that GIA may warrant inclusion in the list of organisms that potentially influence species diversity in forests where they are common. This observation is of particular interest given that MSGM is the single most common above-ground arthropod on sugar maple, itself the dominant tree species in the region (Thomas et al. 2010). What are the possible long-term implications of such a pattern on community dynamics? If patches of pure sugar maple show low galling impacts (densities), this may enhance the capacity of sugar maple to persist in these patches. Conversely, if patches with high species richness negatively impact sugar maple through increased galling, this should increase the capacity of high diversity patches to persist, by reducing the competitive effects of sugar maple on more light-demanding tree species. In a theoretical context, this dynamic could act to maintain diversity transiently, but is not dynamically stable (as it involves a positive feedback mechanism). Further long-term monitoring of infected and non-infected maples in patches and isolation might shed light on the responses of growth, reproductive success and local tree community dynamics to mite galling, and thus provide further insight on natural enemy-regulated processes that govern tree species diversity in temperate forests. In addition, experimental studies aimed at establishing the contribution of other variables, such as soil stability, tree mortality and turnover rates, and other natural enemies (both above- and below-ground)

may enable a more comprehensive understanding of the association between mite densities and forest stand characteristics.

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