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Does insect folivory vary with latitude among temperate deciduous forests?

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Abstract There is a widespread belief that warmer climate forests suffer more folivory, as a proportion of leaf area, than cooler climate forests. However, there is a need for closely standardized studies to test this assumption. In this study, we estimated total folivory as percentage area damaged in freshly fallen, undecayed autumn leaves from the forest floor during the lifetime of deciduous tree leaves, using scanner-linked software. Over a period of 2 years, 154 samples were taken at 96 forested localities in eastern North America, spanning 17° of latitude. In terms of percentage area damage per leaf, the results in both years sampled suggest that there is significantly more damage in warmer, lower latitude areas of eastern North America. The decreasing folivory rate is higher in northern than in southern regions. The observations of a latitudinal trend may suggest that ‘biotic’ interaction is indeed more important in warmer temperate climates compared to cool temperate climates.

Keywords Community · Folivory · Herbivore · Latitude · North America · Temperature

The first two authors have equal joint authorship and the order here is arbitrary.

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Introduction

It is widely believed that herbivore–plant interactions and plant defenses vary with latitude. Folivory is suggested as being more intense, and plant defenses better developed, at lower latitudes (Dobzhansky 1950; MacArthur 1969; Coley and Barone 1996; Pennings and Silliman 2005). However, direct evidence from field measurement is surprisingly scarce. Most studies on folivory do not focus on adult trees due to the difficulty of measuring folivory in the canopy. Hypotheses developed using tree seedlings or short statured plants on variation in folivory across climatic gradients (Janzen 1970; Connell 1971; Maron and Crone 2006) may not apply to adult forest trees. When compiled, such heterogeneous local studies do not clearly demonstrate any overall latitudinal/temperature gradient in the intensity and specificity of insect damage to forest tree seedlings. Studies on small spatial scales have shown that many factors can contribute to local gradients in folivory, e.g., successional stage and soil nutrient content (Crawley 1997; Fine et al. 2004; Forkner et al. 2004; Maron and Crone 2006), or distance from forest edges (Didham et al. 1996), but it is unclear whether such local gradients can scale up into latitudinal differences effectively. Such local studies have only limited usefulness in contributing to the broad picture, because individual studies tend to use quite different methods from one locality to another, greatly complicating comparison. In addition, each individual local study was carried out for local communities. When scaling up each individual study to a broad scale, the result will be biased by the scale-dependent issue of species distribution.

Findings as to how the folivory pattern changes with latitude/temperature vary among different studies. A literature review (Coley and Barone 1996) compiling the results of numerous local studies found evidence of higher folivory at low latitudes in tropical rainforest. But the study cautioned that the results are complicated by the different methodologies used. Some other studies

have used a standardized methodology to focus on a single species, or pairs of species, across a range of latitude/temperatures. In a standardized broad scale study, Andrew and Hughes (2005) found no evidence of a gradient in folivory along latitude in Australia. Also in eastern Australia, Sinclair and Hughes (2008) did not find any evidence of a change in the prevalence of leaf miner damage with latitude (or with rainfall) in 36 plant species. Lowman (1984) found that cooler climate forests had more folivory per unit area of leaf cover in eastern Australia. A trend of increasing foliar damage on *Betula pubescens* and *Betula pendula* along decreasing latitude was detected in Fennoscandinavea, while no geographical or climatic-related pattern in folivory was detected on *Betula pendula* in its more southerly natural range (e.g., Central Europe) (Kozlov 2008). A recent study of early summer leaves in four tree species, standardized for phenology, found that leaves from warmer low latitude locations in eastern North America actually suffer slightly (2–3%) less folivory than cooler high latitude locations (Adams and Zhang 2009). However, a latitudinal gradient of less folivory at higher latitudes in insect folivory was found in Norway maple (*Acer platanoides*) within its native range in Europe (Adams et al. 2009b).

Most studies that have assessed folivory have studied living leaves that were still attached to the tree and focused only on one or several species. Few studies have used fallen leaves to estimate folivory. Nor have results been taken at the community level rather than a selected subset of species (Adams et al. 2009b, c). While the approach using live leaves has advantages in terms of certainties about what exactly is being studied, it is relatively cumbersome to collect the leaves, which has limited the extent and replication of sampling. Furthermore, because leaf sampling tree by tree is inevitably patchy, it is difficult to know whether one is collecting a representative sample of leaves within the canopy. In addition, during the growing season, slight differences in leaf age can translate into large differences in amount of folivory (Coley and Barone 1996), making cross-comparison of sites difficult.

Using fallen leaf litter to address folivory would have several advantages over using live leaves attached to tree branches: (1) ease of collection, facilitating widespread sampling; (2) providing an integrated sample of leaves both through the depth of the canopy and across an area of forest; (3) providing a commonality in terms of what is being assessed, in the sense that it is total growing season folivory during the leaf's lifetime. Studies using fallen leaves have been used successfully to assess differences in folivory between native and invasive species, and between continents (Adams et al. 2009b, c).

The present study takes a complimentary approach to explore the community folivory pattern along latitude in North America. The study assessed folivory integrated across the whole growing season, and focused at a whole community level rather than particular tree species. To our knowledge, this is the first community-level

standardized study to compare different climate zones of the same biome. Our objective was to identify whether there exists a folivory trend at a community level in relation to latitude during the entire growing season.

Methods

Site selection

This study was based on sampling of autumn leaves under stands of wild trees at a range of different latitudes in eastern North America (Fig. 1) covering a wide latitudinal range in temperatures. Samples were chosen in large deciduous forested areas (>100 ha contiguous forest area) across a wide and broadly representative scatter of deciduous and mixed tree community types in the eastern United States and in eastern Canada. All stands sampled were greater than 50% estimated canopy coverage broadleaved deciduous species, rather than conifers or evergreen broadleaved species. Common trees throughout the latitudinal spread of sampling included *Acer rubrum*, *Fagus grandifolia* and *Quercus alba*. Also especially common in the north and the Mid-Atlantic States were such species as *Quercus rubrum* and *Quercus coccinea*, while species concentrated in the south included *Quercus falcata* and *Oxydendron* species. Only leaves from broadleaved deciduous species were sampled in this study. Most sampling sites were in state or national parks and forests, and some were on private

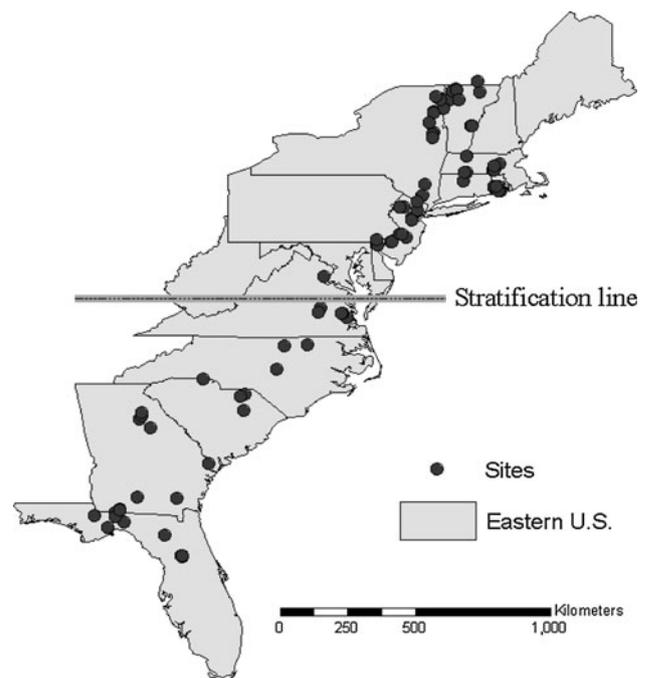


Fig. 1 Sampling sites from which leaves were collected in at least 1 year of this study. Some individual dots mark multiple sites located close together. Sites were located at least 5 km apart from one another. The stratification line divides the eastern North America into southern and northern clusters

land. Samples were taken mostly from areas below 330 m altitude, although in northern Vermont and New York State some higher altitude sites (up to 400 m) were sampled. A very wide range of landscapes and soil conditions were sampled within this scatter of sites (STATSGO 1994). Sites were located at least 5 km apart from one another, even when centered in a radius around a particular state park or geographical feature.

Leaf collection

Various caveats must be considered regarding the use of leaf litter: (1) physical degradation of leaf litter on the ground might give the false impression of herbivore damage. In this study, we were careful to use only fresh fallen leaves from the uppermost litter layer that were evidently undecayed and physically robust and unlikely to fall apart easily. In addition, we tried to avoid animal and hiker trails where dry leaves on the forest floor may be trampled. (2) For fallen dead leaves, it is impossible to check which herbivores are actually eating the leaves. However, vertebrate herbivore in the canopy of North America forests where most leaves are located is rare. The only mammalian herbivore that is known to climb to consume leaves is the porcupine (*Erethizon dorsatum*), but this mode of feeding is not common and porcupine biomass in forests is low. We can assume that the vast majority of folivore damage seen in the leaf litter layer comes from insect herbivores, given the small size of the damaged areas on most leaves, and the lack of any large populations of arboreal leaf-eating mammals at these sites (Adams and Zhang 2009).

Sample collection was timed depending on latitude in order to sample leaves within a week or two of them having fallen, to minimize accumulation of damage/decay after leaf fall. Different tree species to some extent tend to lose their leaves at different times (Borchert et al. 2005). Sampling in each region was timed according to observations, and conducted in the middle of the 'main' phase of leaf fall in that particular year. At each locality, a cluster of multiple samples, each > 5 km apart, were randomly assigned by the field worker putting a pencil onto a state road atlas map with the eyes closed. At each sample location arbitrarily chosen from the state map, the closest accessible area of forest at least 50 m from any roadside or clearing was selected. A hectare area was paced out and corner trees were marked with tape. Two collectors then walked diagonal tracks from one corner to the opposite corner. Each gathered a large handful of leaves from the uppermost fresh litter every 5 m and put the leaves into a bag. The two bags were then combined as the sample for that site. Bags of collected leaves were treated with care to avoid any crushing that might damage brittle leaves, and were stored dried in a cold room at 3°C until they could be sampled for herbivore damage.

Sampling from the bags was also carried out blindly to count 75 leaves. Folivory was identified as four types:

chewed-off, galls, skeletonized, and leaf mines (Labandeira et al. 2007). Folivory damage assessment took place using a scanner to scan in an image of each leaf, and Sigmascan (1995) software to calculate the area damaged. Sigmascan allows the user to draw a shape around the likely extent of the intact leaf, and then subtract areas identified as damage. As a result, a rigorous estimate of folivory loss can be achieved.

Data analysis

The annual total folivory (FOL, %) was plotted against latitude for the entire eastern north America. The statistical significance of the leaf folivory trend along latitude was tested at a 95% confidence level as a preliminary analysis. The leaf folivory percent value was arcsine-root transformed. The preliminary analysis indicated that there may be a linear relationship between total folivory and latitude (Lat), and different linear relationships may exist in the southern sites and northern sites. Furthermore, our sampling sites were less evenly spaced. Therefore, a second analysis (stratified regression model) was employed as the following for the total folivory:

$$y = (a_1 + b_1 \text{Lat})w + (a_2 + b_2 \text{Lat})(1 - w) \quad (1)$$

where y is arcsine-root transformed total folivory: $y = \arcsin(\sqrt{\text{FOL}/100})$; w is a dummy variable: $w = 1$ for the latitude of the folivory sampling site less than a specific latitude value (L_0), otherwise $w = 0$; a_1, b_1, a_2, b_2, L_0 are parameters to be estimated by minimizing the sum of squares of residuals (SSE).

The minimum SSE of Model (1) was also compared with the minimum SSE of a simple linear regression model $y = a + b\text{Lat}$ fitted for the whole data, in order to test the need to split the data and to perform this stratified regression. The significance and sign of b_1 and b_2 indicate the relationship between the folivory and latitude. Data analysis was conducted for total folivory sampled in winters of 2005–2006 and 2006–2007, respectively. The SAS procedure MODEL was used for all statistical analyses (SAS Institute 2008).

Results

Folivory loss comparison with latitude

Leaf folivory decreased significantly along rising latitude in the winter of 2005–2006 ($R^2 = 0.11$) and the winter of 2006–2007 ($R^2 = 0.09$) at a 95% confidence level for the entire eastern north American region (Fig. 2a).

Compared with the one linear regression fitted for the whole dataset without stratification, the stratified regression model (1) significantly reduced the minimum SSE (0.333 vs 0.252 and 0.064 vs 0.055 for data sampled in the winter of 2005–2006 and 2006–2007, respectively;

equivalent to 831.0 vs 632.4 and 122.2 vs 103.7 without taking arcsine-root transformation). This suggested that it is necessary to split the sampling sites along latitude, and that the stratified regression model is appropriate. The estimated value of L_0 from the fitted model was 37.3 and 37.4 for folivory data of winter of 2005–2006 and 2006–2007, respectively (Table 1). Our sampling

sites with latitude of less than 37.4° are from the southern states FL, GA, SC, NC and southern VA. The sampling sites with latitude of greater than 37.4° are from the northern area (Fig. 1).

For data sampled in the winter of 2005–2006, both the estimates of b_1 and b_2 were significant and negative ($P = 0.059$ and $P < 0.001$, respectively) (Table 1). This suggested that folivory decreased with the increase of latitude in both the southern and northern regions. The hypotheses of $b_1 = b_2$ was rejected ($P = 0.025$), which indicated the folivory decreasing rate was significantly different between these two regions (Fig. 2b). The decreasing rate in the northern region is greater than that in the southern region (Table 1).

For data sampled in the winter of 2006–2007, the estimates of b_1 and b_2 were significant and negative ($P = 0.012$ and $P < 0.046$, respectively) (Table 1). The same estimated value of b_1 and b_2 indicated the same folivory decreasing trend along rising latitude in both the southern and northern regions, but the a value is higher for the northern region than for the southern region.

While there was a decreasing trend of folivory along rising latitude in both years and in both regions, folivory variability between years was also obvious (Fig. 2b). In general, the folivory in the winter of 2005–2006 was significantly higher than in the winter of 2006–2007.

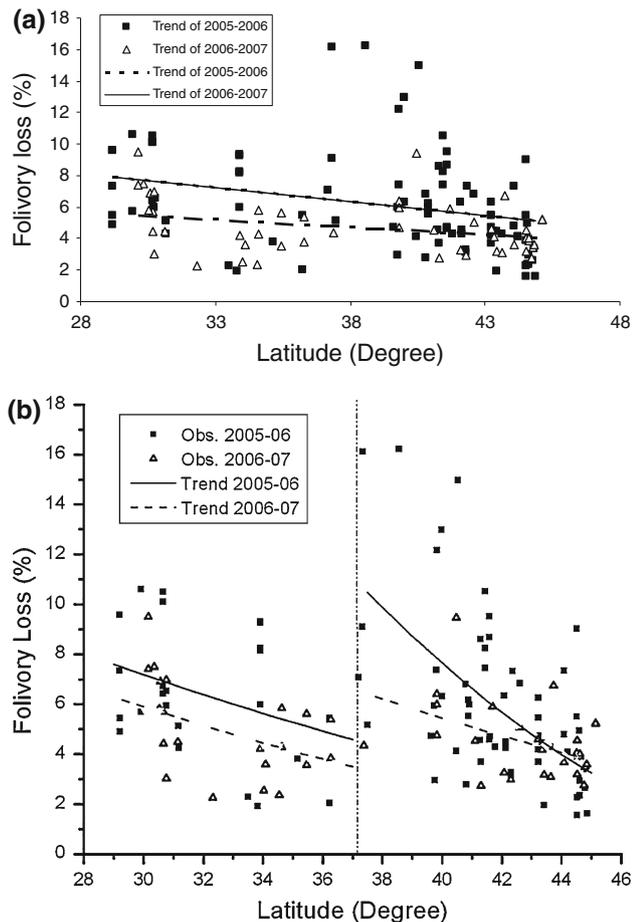


Fig. 2 a Observed folivory in winters of 2005–2006 and 2006–2007 and their corresponding predicted trends. The decreasing trends are both significant at 95% level. b Observed folivory in winters of 2005–2006 and 2006–2007 and their corresponding predicted trends from the stratified regression models. The decreasing trend is significant along rising latitude in the northern and southern regions and 2005–2006 and 2006–2007 periods at 90% confidence level

Relative frequency of types of leaf damage

Most folivory throughout the latitudinal gradient studied here was in form of the leaf material being chewed off (Fig. 3). Skeletonizing was the second most important form of folivory by leaf area. Folivory loss in the form of leaf galls and leaf miners accounted for a small proportion of the total folivory.

Discussion

The observation that there is more folivory on plants at lower latitudes (Coley and Barone 1996) has implications for many aspects of community and ecosystem theories (Adams et al. 2009a, c; Adams and Zhang 2009). At least at face value, the results presented here

Table 1 Parameter estimate, associated standard error and P value for stratified regression models fitted for folivory data sampled in winters of 2005–2006 and 2006–2007, respectively

Parameter	Folivory 2005–2006			Folivory 2006–2007		
	Estimate	Standard error	P value	Estimate	Standard error	P value
a_1	0.5086	0.1324	0.0002	0.4898	0.1055	< 0.0001
b_1	–0.0079	0.0041	0.0593	–0.0082	0.0032	0.0143
a_2	1.0726	0.1384	< 0.0001	0.5617	0.1713	0.0020
b_2	–0.0198	0.0033	< 0.001	–0.0082	0.0039	0.0463
R^2	0.3181			0.211		
L_0	37.3			37.4		

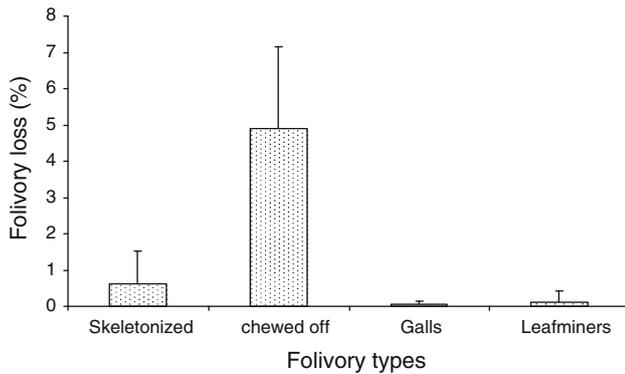


Fig. 3 Comparison of each category of folivory, by total leaf area lost, averaged for all sites. Bars 95% confidence interval

may tentatively be taken as supporting the hypothesis that there is more intense folivory in warm regions, for a greater proportion of leaf area is lost during the entire growing season.

There is some folivory variability from year to year. Folivory in 2005–2006 is significantly higher than that in 2006–2007 across the eastern US. Particular sequences of weather events or insect outbreaks could lead to this over broad areas (Turchin 1990). In our sampling years, especially high folivory was found at some mid-Atlantic sites. Especially in 2005–2006 in the latitudinal band between 40° and 43°N, several sites showed particularly high folivory (>9%). These sites may play an important role in raising the average folivory level in the north for 2005–2006, and in contributing to year-to-year variability within the whole combined sample of sites. None of the areas sampled were within 20 km of recorded gypsy moth (*Lymantria dispar*) outbreaks in that year based on individual state forest agency reports in the states sampled (e.g., <http://nj.gov/agriculture/divisions/pi/prog/gmhomeowners.html>). As gypsy moth is a non-native addition to the ecosystem, present from southern Virginia northwards, it is important to remove from the data any sites likely to have been in outbreak areas. It is likely that the high folivory (e.g., >8%) seen in several other sites was due to various native outbreaking herbivores such as tent caterpillar (*Malacosoma* spp.), although by autumn all diagnostic traces of any frass and ‘tents’ have disappeared. Subsequent work may examine the detailed possible causes of this year-to-year variation in terms of weather events in the years concerned.

One interesting finding in this study is the leaf folivory trend discontinuity around the latitude line of 37.4°, which might be caused by the following reasons. First, the leaf folivory spikes for the several sites around 38° are likely to lead to the statistical artifact of a steeper decreasing slope in the northern region than in the southern region. Second, the sampling sites are more clustered in the northern region than in the southern region, which can be seen as one limitation of this study. On average, there are 8.5 sampling points per latitudinal degree in the northern region and 3.9 sampling points

per latitudinal degree in the southern region in the winter of 2005–2006. In the winter of 2006–2007, there are 3.2 sampling points per latitudinal degree in the northern region and 3 sampling points per latitudinal degree in the southern region. The unevenly spaced sampling sites could result in the distinct decreasing rates between the two regions. Third, the steeper decreasing slope in the northern part might be related to its more dramatic climatic transition than in the southern region. Along the sampling site transect from north to south in the northern region, the temperature increased 1.02 and 1.3°C per latitudinal degree in 2005 and 2006, respectively, while the increasing rate was lowered to 0.71 and 0.69°C per latitudinal degree in the southern region in 2005 and 2006, respectively. The more dramatic climatic transition in the northern region would, accordingly, lead to more rapid biological responses as revealed in this study.

In a parallel study, Adams and Zhang (2009) took early summer leaves of four selected species along forest edges, and the leaf sampling was conducted at times computed to be at equivalent stages of the growing season. The present study is complimentary in focusing on the whole growing season, and working at a whole community level within the forest interior. It is interesting to note that the total growing season folivory in each year is slightly greater than the early summer folivory, as might be expected if leaf damage continues to accumulate at a low rate during the rest of the growing season.

An important question for the interpretation of these results is whether the proportion of leaves completely consumed—and thus not showing up in the litter layer—varies between different parts of the temperate zone. This is also a potential problem with studies of living leaves, where the ‘missing’ leaves are often not counted (Lowman 1984, 1985; Coley and Barone 1996). If many more leaves are completely consumed in warmer climates, this would tend to deflate the folivory estimates and would have caused us to underestimate tropical folivory. Lowman (1984, 1985), working on temperate and subtropical forests in Australia, suggested that many leaves that might have been thought to be senescing were actually being completely eaten, and that folivory in both temperate and subtropical systems was being greatly underestimated (by a factor between 1.8 and 3.5) if only ‘one time’ sampling of live leaf damage was being carried out instead of a cohort study on living leaves over time. Lowman’s work is often cited in reference to tropical forests as well (Coley and Barone 1996). However, Adams et al. (2009c) and Adams and Zhang (2009) have pointed out limitations of Lowman’s study that may greatly inflate the estimates of total leaf consumption. In any case, an important point is not to what extent consumption of whole leaves alters the overall estimation of folivory within each region, but whether it differs systematically between regions. If many more leaves were really being completely consumed in one climate zone than another, given that there is a lognormal curve in rank abundance of leaf damage

(Adams and Zhang 2009), we should also expect to see many more heavily damaged leaves as a proportion of the leaf litter showing up in the samples.

The concept that there is more folivory in the warm temperate zone seems intuitively reasonable to many ecologists, since there is only a mild winter to 'knock back' herbivorous insect populations (Dobzhansky 1950; MacArthur 1969; Pennings and Silliman 2005). Without density-independent population crashes, herbivores may then build up to levels at which density-dependent factors such as food limitation, disease and predation become important (Dobzhansky 1950). Though rarely mentioned explicitly in the literature, this viewpoint has permeated ecology. A shift in the relative importance of biotic and physical controls on populations is seen as a contrast between the tropics and temperate zone as a whole, and also within the temperate zone from grading warmer climates with mild winters to cooler climates with cold winters. Searching for a latitudinal difference in insect folivory becomes a means of testing one aspect of the important underlying hypothesis, i.e., that biotic interactions are more intense in warmer climates. It also becomes an indirect test of the mechanisms that are thought to follow on from more biotic interaction in warm climates (Janzen 1970; Connell 1971). Although 'outbreaks' of higher folivory, such as we may be seeing in some sites in the 40–43°N range, are generated partly through density-dependent processes (Turchin 1990), this may in part reflect the effects of release from herbivore pressure due to climate variability in areas with harder winters.

There is no clear evidence suggesting that a latitudinal folivory gradient that would otherwise be stronger is being suppressed by heavier investment in plant defenses towards lower latitudes (Adams et al. 2009a). Likewise, extensive analysis of samples of early summer leaves of *Acer rubrum* (from samples collected for a parallel study to this one) from a range of latitudes between Florida and the Canadian Border fails to show any latitudinal trend in leaf nitrogen content, another factor that might be expected to influence biotic interactions.

Another relevant observation is that, whichever way one chooses to interpret the results, the latitudinal trend in folivory in the transect we sampled down through eastern North America is in absolute terms fairly small, at around 2–3% of leaf area in the leaves found in the litter layer. Certainly it is considerably less than was proposed by Coley and Barone (1996) for temperate vs tropical ecosystems in their important review paper. It is a moot point whether such a small difference in folivory would be enough to significantly affect community functioning (Whittaker and Warrington 1985). It is lower than the order of 7–10% that has been found to relate to statistically significant differences in growth rate of the host plants (Bentley et al. 1980; Whittaker and Warrington 1985; Coley and Barone 1996). Across a longer north–south distance, it is possible that the latitudinal difference in absolute area lost from folivory would be greater, if equivalent deciduous broadleaved

forest types were to be compared. It would be interesting, for example, to extend the study up to the northern limit of temperate deciduous forest in eastern Canada, about 48°N.

Whichever the trend in folivory that one finds along a temperature/latitude gradient, it is not clear how ecologically important it would be in altering community composition and in affecting evolutionary processes. There is even an active debate in ecology about the significance of folivory in ecological processes on any scale, although in general studies do seem to support the view that it is important in most plant communities (Maron and Crone 2006). However, the findings in this study do emphasize the need for a reassessment of the widespread belief that herbivore pressure is necessarily much stronger in warmer low-latitude climates.

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