



# Retention of green leaves not brown leaves increases spring cynipid diversity on large valley oaks

V. S. Pan<sup>1</sup> · A. Pepi<sup>1</sup> · J. Goidell<sup>1</sup> · R. Karban<sup>1</sup>

Received: 2 September 2020 / Accepted: 4 March 2021  
© The Author(s), under exclusive licence to Springer Nature B.V. 2021

## Abstract

Plants can retain either physiologically active green leaves or inactive brown leaves over winter. Research has suggested that leaf retention incurs a cost due to higher herbivore load in the following year; however, no distinction has, thus, far been made between retention of green and brown leaves. We surveyed the over-winter retention of physiologically active green and inactive brown leaves of valley oaks (*Quercus lobata*) and examined their relationship with the diversity and density of 15 gall-making cynipid wasp species. Cynipid diversity in the spring was 8.2-fold greater on larger trees with more green leaf retention. Brown leaf retention was not associated with spring cynipid diversity, but was related to a substantial 20-fold reduction in spring cynipid densities on large trees. Retention of either leaf type was generally a poor predictor of summer cynipid diversity and density. Overall, green leaf retention better explained cynipid diversity, but brown leaf retention better explained cynipid densities. These differing effects may be explained by the fact that green leaves provide a common cue used by herbivores to find a suitable host. Retained brown leaves, however, may be an ecological trap for over-winter gall wasps that normally drop to the ground.

**Keywords** Cynipidae · Deciduous · Evergreen · Leaf abscission · *Quercus*

## Introduction

As one of nature's more striking phenomena, winter-deciduous trees abscise leaves en masse every year, marking the end of a growing season. In more temperate climates, this leaf habit may have been an adaptation or pre-adaptation for trees to tolerate the cold and dry winter (Axelrod 1966) when opportunities for photosynthesis are limited anyway (Öquist and Huner 2003). In more Mediterranean climates, however, the adaptive value of winter-deciduousness seems less obvious. Trees in Mediterranean climate regions with wet and mild winters have faced less constraints due to temperature and water stress during winter (Mooney and Dunn 1970a). Therefore, plants in a Mediterranean climate often exhibit an evergreen leaf habit or leaf out soon after the start of the wet season in winter (Mooney and Dunn 1970b;

Di Castri et al. 1981; Shmida 1981). However, some dominant trees in Mediterranean habitats exhibit at least some degree of winter-deciduousness (Barbero et al. 1992; Blumler 2015; Escudero et al. 2017; Gil-Pelegrín et al. 2017), dropping most of their leaves in winter even while net positive photosynthesis would be possible (Mooney and Dunn 1970b). While the occurrence of the winter-deciduous trees in Mediterranean climates may have been a result of phylogenetic or physiological constraints and, therefore, non-adaptive (Eriksson et al. 1983; Ne'Eman 1993; Grove and Rackham 2003), some have noted their peculiar prevalence and hypothesized fitness benefits (Blumler 1991; Baldocchi et al. 2010; Escudero et al. 2017; Gil-Pelegrín et al. 2017).

One of the advantages proposed for winter-deciduousness in a Mediterranean climate posits that it defends plants against herbivores (Karbon 2007). By dropping leaves along with herbivores, plants can relocate, impose starvation, and promote predation and fungal infection risks for sessile folivores (Faeth et al. 1981a; Yamazaki and Sugiura 2008). Recolonizing herbivores that rely on retained leaves as an oviposition cue may also struggle to locate their hosts when leaves abscise (Moran and Whitham 1990; Karban 2007, 2008). Thus, deciduousness can reduce herbivory in

Handling Editor: Gimme Walter.

✉ V. S. Pan  
vsbpan@gmail.com

<sup>1</sup> Department of Entomology and Nematology, University of California- Davis, Davis, CA 95616, USA

the long term at the expense of some biomass loss in the short term by reducing herbivore densities. The first experimental evidence that leaf abscission during winter reduces herbivory in the following spring was reported in *Quercus lobata* and *Ceanothus velutinus*. Experimentally defoliated *C. velutinus* suffered lower chewing damage during the following spring (Karban 2008). Concordantly, two *Neuroterus* galling wasps and their galls occurred at lower densities on new leaves of *Q. lobata* that had been manually defoliated (Karban 2007). Moreover, a subsequent comparative study suggested that herbivory pressure from leaf miners may also have selected for the variation in leaf lifespan of the genus *Quercus* (Pearse and Karban 2013). Yet, despite these examples linking the deciduous habit with lower herbivory risks, the generality of this benefit and its precise mechanism remain not well understood.

The deciduous leaf habit consists of two co-occurring ecologically important phenomena: senescence and abscission. Senescence is when a leaf degrades its cellular structures and remobilizes its nutrients in a predictable and systemic fashion (Lim et al. 2007). Abscission is when a leaf detaches from the plant through biochemical and histological changes in the abscission zone of the petiole (Addicott and Lynch 1955). The two processes, although related, are nonetheless distinct, as senescence does not necessarily guarantee abscission. A petiole can abscise with only localized physiological changes in the abscission zone, in other words, prematurely abscise. Likewise, a leaf can senesce, but fail to detach from the plant, namely, marcescence (Table 1). We do not posit that leaf senescence and abscission are independent processes; indeed, in many systems, they necessarily co-occur. However, to conflate the ecological significance of deciduousness with abscission or senescence disregards the important distinction between these processes, and the many plant species cannot be categorized neatly as having a deciduous or evergreen leaf habit (Berkley 1931; Hoshaw and Guard 1949).

The distinction between senescence and abscission is important to consider when we examine the evolution and fitness trade-offs of various leaf habits in a Mediterranean climate, particularly since some herbivores and plants can remain active in the winter months (Kyparissis et al. 1997; Paine and Lieutier 2016). Whether a tree can benefit from reduced herbivory risks with leaf abscission may depend on the physiological activity of retained leaves. For instance,

the abscission of already senescent leaves may do little to impose starvation on developing herbivores, for it is senescence, not abscission, that limits leaf nutritional availability for herbivores. Insect herbivores often abandon deteriorating leaves when they sense a gradual decline in leaf quality, a phenomenon that has been well documented in studies on plant induction (Hoy et al. 1998; Karban 2011). Herbivores with limited mobility can accelerate development (Shafiei et al. 2001) or be selected to finish development before the predictable onset of senescence. In contrast, premature abscission of otherwise healthy leaves is more likely to induce herbivore starvation, especially for sessile insects. Herbivores have less time to react and fewer cues to anticipate leaf abscission. In the face of an unpredictable or damage-induced abscission schedule, the herbivores may more easily fall victim to abscising over-winter green leaves as they fail to optimize their phenology (Owen 1978; Faeth et al. 1981a; Williams and Whitham 1986; Zvereva and Kozlov 2014). Nevertheless, the loss of nutrients due to premature abscission of green leaves comes at a higher cost to the plant.

The cost of leaf retention also depends on whether the leaves are active green leaves or inactive brown leaves. While no clear demarcation exists in the spectrum of physiological activity that over-winter leaves exhibit, it is useful to consider the two extremes. For green leaves, the abundance of photosynthate and the supply of water and nitrogen-rich compounds that support photosynthate production (Weih 2009) means that the leaves may be at higher herbivory risk (Price 1991; Karban 2008). Conversely, for dead leaves, the general lack of nutritional value may limit herbivore performance (Kaiser et al. 2010; Body et al. 2013) and even deter herbivore feeding (Svendsen 2001; Mingo and Oesterheld 2009). Green leaves may also attract more herbivores than brown leaves. Whereas dead leaves remain relatively unchanged whether they are attached to the plant or relocated to a distance, green leaves rapidly senesce after abscission. As such, herbivores can use green leaves as a more reliable cue for host location. The higher concentration of volatile organic compounds emitted by younger and more photosynthetically active green leaves (Salomón et al. 2017; Portillo-Estrada et al. 2017) can further reveal the location of a host plant to its herbivores. Therefore, herbivores that rely on these cues may disproportionately aggregate on trees with higher green leaf retention. As herbivory can often lead to substantial reduction in fitness (Hawkes and Sullivan 2001; Agrawal et al. 2012), the strong selective pressure which herbivores impose could have facilitated the persistence of the winter-deciduous habit in Mediterranean climates.

Here, we examined whether leaf abscission can alleviate herbivory pressure for winter-deciduous trees in Mediterranean climates. We focused on the semi-deciduous *Q. lobata* system located in the central valley of California. *Q. lobata*

**Table 1** Four possible fates a leaf can have during winter and its associated leaf habit

	Leaf senescence (brown)	No leaf senescence (green)
Drop leaves	Deciduous leaf habit	Premature leaf abscission
Retain leaves	Marcescence	Evergreen leaf habit

exhibits considerable intraspecific variation in over-winter leaf density, degree of senescence, and load of galling wasps (Cynipidae: Cynipini). At high densities, galling herbivores have the potential to stunt oak growth (Russo 2006) and suppress acorn production (Crawley 1985). We tested the hypothesis that over-winter green, not brown leaf retention, drives the diversity and density patterns of herbivores in the following growing season.

## Materials and methods

### Study sites and natural history

The study was conducted at two sites in the Putah Creek Riparian Reserve at Davis, California, USA. With a Mediterranean climate, the sites are characterized by mild wet winters and hot dry summers. In early October, valley oaks at the study sites start dropping leaves at an increasing rate, eventually peaking in December (Karban 2007; Pearse and Karban 2013). Rain usually has arrived by October, so unlike other dry-deciduous trees in the region, drought avoidance does not clearly explain its deciduous habit. When new leaves begin to emerge in late March, less than 1% of leaves from the previous year are retained (Figure S1). Still, some leaves remain on the trees for several years, as evidenced by the presence of lichens on many dead leaves.

Depending on the species, adult cynipids usually emerge during spring or summer (Russo 2006). These wasps have overwintered in galls on the ground or still attached to the leaves or stems. Some, if not most, cynipids have two alternating spring and summer generations within a year (see discussion in Russo 2006). The spring generation makes up most of the herbivore community for *Q. lobata* at the study sites in the spring. Stem and bud galls can be seen to grow as early as a few weeks before budburst in late March, whereas leaf and flower galls rapidly develop as the leaves and flowers unfold in March and April. Male and female adults emerge from spring galls between late spring to late summer and produce a second asexual summer generation. Cynipid galls from the summer generation are much more conspicuous and numerous. While some aphids, leaf miners, leaf rollers, and free-living lepidopterans can be occasionally seen feeding on *Q. lobata* after late spring, the summer generations of cynipids occur at orders of magnitude higher densities than other herbivores.

### *Q. lobata* size, leaf phenologies, and cynipids surveys

We compared green and brown leaf retention using existing natural variation. We haphazardly selected 75 *Q. lobata* trees and characterized their size and level of green and brown

leaf retention from January 23 to 26. Tree size was estimated as diameter at breast height (DBH). To estimate a standardized measure of leaf retention across trees of different sizes, we haphazardly selected six branches on each *Q. lobata* and counted the presence/absence of green or brown leaves over the length of ten nodes. We then summed the number of nodes with leaves present for each tree before dividing by the total number of nodes surveyed to derive the proportion of leaf retention. To account for variation in budburst phenology, we surveyed bud development of *Q. lobata* biweekly from January 26 to April 22 and recorded when budburst occurred. We deemed budburst to occur when bud scales were open on more than one-third of the branches.

To characterize the variation in herbivore load on *Q. lobata* throughout the growing season, we surveyed the density and diversity of different spring and summer cynipid galls. During early May and August, we used a meter stick to run 8 transects on the lower branches. We pointed the meter stick from the branch tip towards the trunk for each tree to form a one meter transect. Every gall mass in the transects was counted and identified to morpho-species (Table S1). To ensure that our surveys accurately represented the density of active cynipids at a point in time, we excluded species that had already emerged and whose galls had senesced. Diversity was measured by the effective number of species. This index was calculated by raising Euler's number to the power of the Shannon's diversity index (Jost 2007).

### Data analysis

We analyzed the effect of green and brown leaf retention on gall density and diversity in the following year. Since spring and summer galls were analyzed individually, separate sets of models were fitted with either the proportion of green or brown leaf retention as the main effects. This was done because our measures of the proportions of green and brown leaf retention were not independent, and we wished to separately examine the effect of brown vs. green leaves.

We analyzed alpha diversity in the spring and summer using log-normal Bayesian generalized linear models with proportion leaf retention (either green or brown), DBH, date of budburst, and site as predictors (R package *brms*: Bürkner 2017, 2018). We included the interaction between DBH and proportion leaf retention to account for differences among large and small trees. We analyzed cynipid species densities using negative binomial Bayesian generalized linear multilevel models (R package *brms*: Bürkner 2017, 2018). We treated the densities during spring and summer as independent observations and analyzed them separately. Of the 15 species surveyed, only *Andricus quercuscalifornicus* and *Neuroterus saltatorius* occurred in both seasons; because galls that were seen in May had mostly senesced or abscised by August and

were therefore not counted, we felt confident that each measure represented a mutually exclusive subset. Rare species that appeared on less than 15 trees in one season were excluded, as insufficient data existed for meaningful analysis. For the analysis of spring and summer gall densities, we fitted gall density against proportion leaf retention, DBH, date of budburst, and site. Again, we included the interaction of DBH with proportion leaf retention. Species specific random intercepts and random slopes for each fixed effect were added to account for the differences among cynipid species. Tree individuals were also included as a random effect to account for spatial non-independence.

Using a leave-one-out cross-validation-derived information criterion (*LOOIC*), we were able to compare models with either green or brown leaf retention and determine which type of leaf retention better predicted gall density and diversity (Vehtari et al. 2017). In order to estimate the *LOOIC* for which there were  $n$  observations with Pareto  $k > 0.7$ , we refitted the model  $n$  times, each time leaving out one of the problematic observations (R package *loo*: Vehtari et al. 2019).

In analyses with leaf retention as the predictor, we transformed the proportion of green and brown leaf retention by  $\ln(x + 0.01)$  to reduce heteroscedasticity. We also removed insignificant interactions and refitted the models when necessary (Table S2). All Bayesian models were performed with 3 chains each with 3000 iterations. We set a weakly normalizing normal prior distribution (centered at zero with a standard deviation of 100) for all intercepts and parameters.

Model assumptions were checked using trace plots, autocorrelation plots, and residual plots. All analyses were executed in R version 3.6.0 (R Core Team 2019).

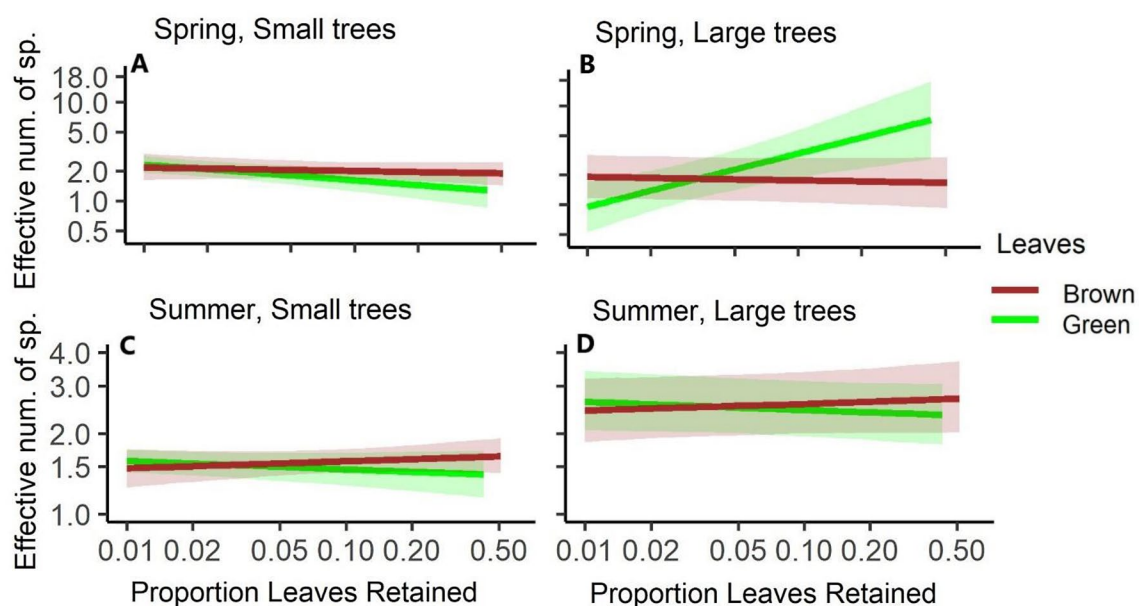
## Results

### *Q. lobata* traits

Trees of a variety of sizes were surveyed; DBH averaged  $22 \pm 18$  (*SD*) cm and ranged from 3 to 99 cm. The levels of leaf retention were generally low at  $13 \pm 11\%$ , with brown leaves being the majority of the leaves retained (*green*:  $3.1 \pm 7.4\%$ ; *brown*:  $9.4 \pm 9.1\%$ ).

### Cynipid diversities

We found seven species of cynipids in the spring (Table S1). Higher green leaf retention was associated with higher diversity of cynipids on large trees, and lower diversity on smaller trees ( $\beta_{\text{Retention} \times \text{DBH}} = 0.0072$ , 95% Credible Interval (CI) = [0.0032, 0.011]; Fig. 1a, b). The magnitude of the positive effect of green leaf retention on diversity on larger trees was much greater than the negative effect on diversity on smaller trees. Our model estimates that retaining 50% green leaves compared to retaining only 1% green leaves was associated with a large 8.2-fold increase in cynipid diversity at the largest tree, but a smaller 1.9-fold decrease at the smallest tree. On the other hand, brown leaf retention did not appear to explain variation in spring



**Fig. 1** Spring and summer cynipid diversity on *Q. lobata* ( $n=75$ ) in relation to the proportion of leaves retained (green or brown) in January. The ribbons indicate the 95% credible intervals



cynipid diversity well ( $\beta_{Retention} = -0.035$ , 95% CI =  $[-0.15, 0.078]$ ) even after removing an insignificant interaction between retention and DBH ( $\beta_{Retention \times DBH} = -0.0044$ , 95% CI =  $[-0.0096, 0.0006]$ ). Hence, green leaf retention better explained cynipid diversity in the spring (Table 2), although much variation remained unaccounted for ( $R^2 = 0.26$ ;  $\Delta R^2_{Retention} = 0.15$ ).

We found 10 species of cynipids in the summer (Table S1). In the summer, green ( $\beta_{Retention} = -0.030$ ,

95% CI =  $[-0.080, 0.022]$ ) and brown leaf retention ( $\beta_{Retention} = 0.027$ , 95% CI =  $[-0.034, 0.090]$ ) were both poor predictors of cynipid diversity and neither the effect of green ( $\beta_{Retention \times DBH} = 0.00062$ , 95% CI =  $[-0.0017, 0.0029]$ ) nor brown leaf retention ( $\beta_{Retention \times DBH} = 0.00025$ , 95% CI =  $[-0.0025, 0.0030]$ ) depended on tree size (Fig. 1c, d). Rather, the diversity of cynipids appeared to vary primarily by tree size alone ( $\beta_{DBH} = 0.0037$ , 95% CI =  $[0.00038, 0.0063]$ ), with approximately a 0.37% increase in the species diversity for each centimeter increase in DBH.

**Table 2** Comparison of the best green and brown leaf models' fit using LOOIC

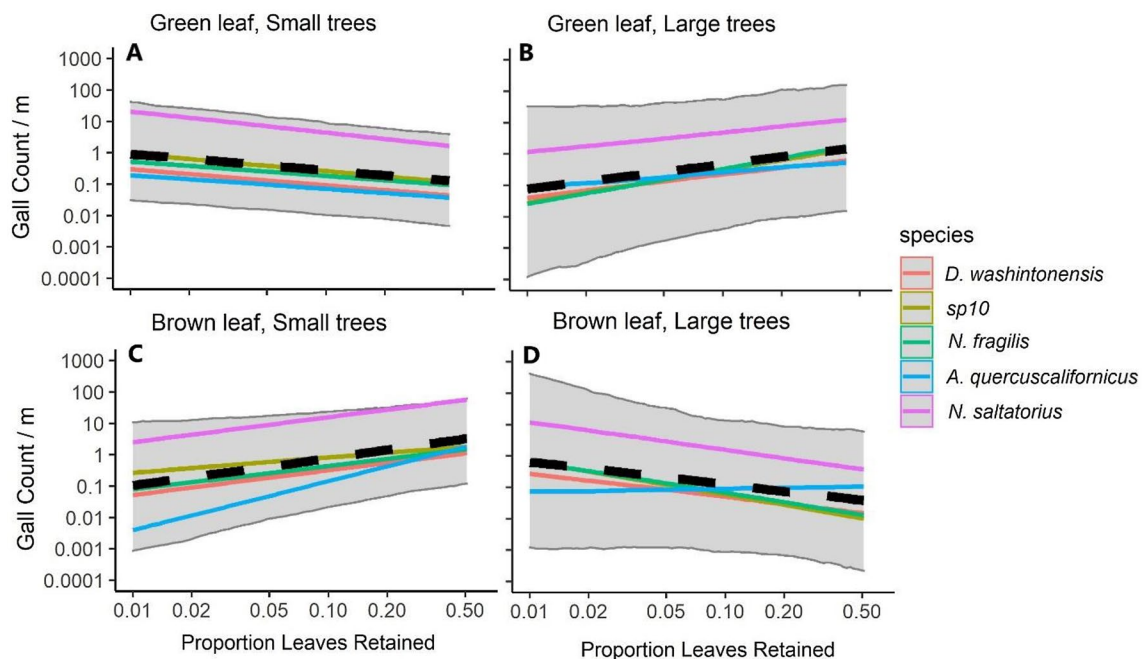
	Green leaf model ( $LOOIC \pm SE$ )	Brown leaf model ( $LOOIC \pm SE$ )	Comparison ( $\Delta LOOIC \pm SE$ )
Spring diversity	<b>168.96 <math>\pm</math> 16.21*</b>	182.34 $\pm$ 16.76	-13.38 $\pm$ 11.25
Summer diversity	80.13 $\pm$ 11.76	81.68 $\pm$ 11.46	-1.55 $\pm$ 2.87
Spring density	1683.89 $\pm$ 79.73	<b>1669.95 <math>\pm</math> 80.13*</b>	13.93 $\pm$ 11.23
Summer density	3105.38 $\pm$ 133.71	3096.96 $\pm$ 133.27	8.42 $\pm$ 9.96

$\Delta LOOIC$  is the LOOIC of the green leaf model minus the brown leaf model. For comparisons in which  $|\Delta LOOIC| > 1 SE$ , the best model is bolded

An asterisk indicates an inclusion of DBH  $\times$  retention interaction term in the model, otherwise the interaction is removed due to non-significance

## Cynipid densities

Unlike cynipid diversity, brown rather than green leaf retention better explained cynipid densities (Table 2). In the spring, higher brown leaf retention was associated with a substantial reduction in cynipid densities for large trees, but the relationship was reversed for small trees ( $\beta_{Retention} = 0.19$ , 95% CI =  $[0.32, 1.6]$ ,  $\beta_{Retention \times DBH} = -0.017$ , 95% CI =  $[-0.034, -0.00014]$ ; Fig. 2a–d). Our model estimates that retaining 50% brown leaves compared to retaining only 1% of brown leaves was associated with 20-fold lower cynipid densities for the largest trees and 30-fold higher cynipid densities for the smallest trees. Green leaf retention had no detectable relationship with spring cynipid densities ( $\beta_{Retention} = -0.25$ , 95% CI =  $[-0.68, 0.24]$ ) and its effect was not dependent on DBH ( $\beta_{Retention \times DBH} = 0.014$ , 95% CI =  $[-0.0013, 0.029]$ ). Our best model explained 28% of



**Fig. 2** Average spring gall densities on large and small trees with more green or brown leaves. The black dashed lines indicate the average response for all species. The gray ribbons represent the 95% credible intervals. Only species that occurred on more than 15 trees are shown

the variation, while leaf retention alone explained 8.8% of the variation in spring densities. In the summer, both green and brown leaf retention were again poor predictors of cynipid densities (*green*:  $\beta_{\text{Retention}} = 0.077$ , 95% CI = [−0.18, 0.34]; *brown*:  $\beta_{\text{Retention}} = 0.21$ , 95% CI = [−0.20, 0.61]; Fig. 3a–d) after an unsupported interaction with DBH was removed (*green*:  $\beta_{\text{Retention} \times \text{DBH}} = 0.0011$ , 95% CI = [−0.010, 0.012]; *brown*:  $\beta_{\text{Retention} \times \text{DBH}} = -0.0018$ , 95% CI = [−0.013, 0.0097]).

## Discussion

In this study, we showed that leaf abscission may alleviate herbivory pressure for large evergreen and small deciduous valley oaks, but for others, leaf abscission may instead incur a cost of higher herbivory risk. This difference appears to depend on tree size and the degree of leaf senescence. Indeed, contrary to our expectation, the retention of green leaves was not solely responsible for driving the patterns in cynipid diversity and density, but only cynipid diversity. Cynipid densities were instead driven by the retention of brown leaves. Thus, our results highlight the importance of recognizing the physiological differences between overwinter leaves when the costs and benefits of leaf retention or abscission are evaluated. Prior studies examining only leaf permanence may have overlooked important differences between individuals and led to misleading conclusions.

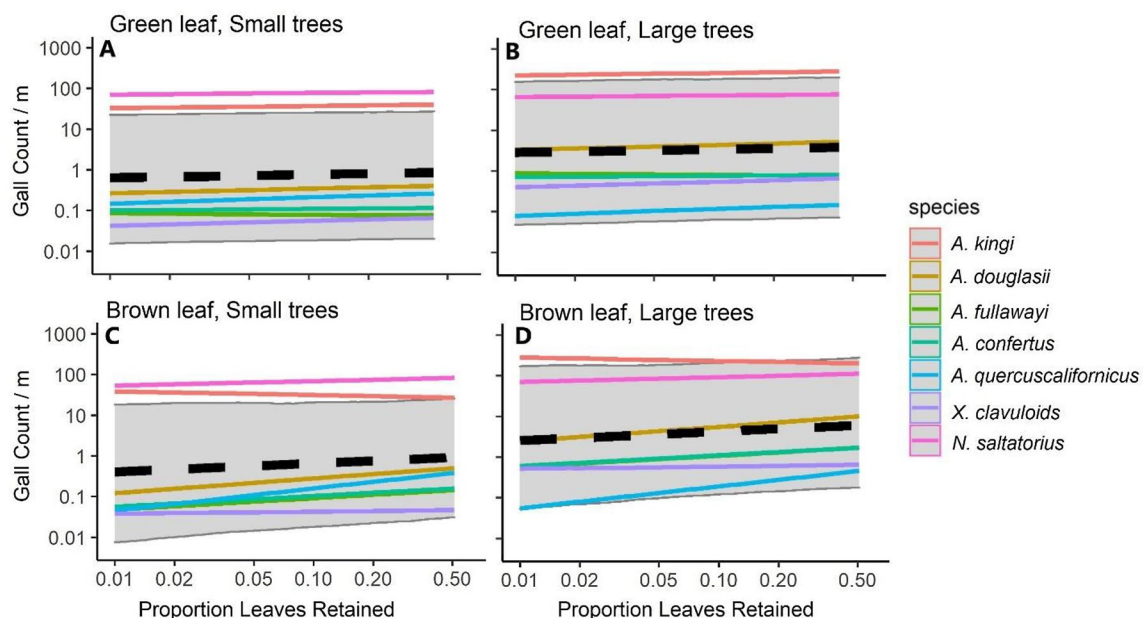
We are certainly not the first to bring this physiological distinction into consideration. Many earlier workers have

already extensively discussed the leaf lifespan in the context of different leaf traits including retention (Opler 1978; Faeth et al. 1981b; Pearse and Karban 2013). However, less attention has been placed on the relationship between herbivory risk and leaves of different physiological activity levels. By considering both senescence and abscission, we may begin to understand the adaptive value of winter leaf habits, such as marcescence and premature leaf abscission, both of which have largely been left out of previous discussions.

## Herbivory cost of green leaf retention

It may seem counter-intuitive for trees to abscise whole green leaves since herbivores cannot normally eat more tissue than the plant is shedding. There are several possible explanations. First, holding green leaves may attract and maintain herbivores that will consume considerable plant tissue in the following season (see below). Second, maintaining leaves is metabolically costly and may make the tree more susceptible to damage by wind and ice. Third, retaining damaged leaves may make the tree more vulnerable to infection by pathogens and increases water loss (Zvereva and Kozlov 2014).

In our system, many gall makers emerge during late winter at a time when few green leaves are present (Russo 2006). Accordingly, the few green leaves that are present pose an extraordinary liability to the trees that retain them. Not only do the green leaves lend refuge to resident herbivores, but they also provide recruitment cues to colonizing herbivores from afar (Moran and Whitham 1990; Karban 2007, 2008).



**Fig. 3** Average summer gall densities on large and small trees with more green or brown leaves. The black dashed lines indicate the average response for all species. The gray ribbons represent the standard error interval. Only species that occurred on more than 15 trees are shown

This liability may explain why larger *Q. lobata* in the spring saw a large increase in cynipid diversity when the level of green leaf retention was high (Fig. 1b). Perhaps guided by the sight or scent of green leaves, female cynipids, including non-leaf galls (Figure S2; Table S1), located their host and deposited the eggs for the spring generation. Subsequently, with the resources provided by the new leaf flush, ovipositing females from the spring generation placed eggs of the summer generation independently of winter leaf retention, since these leaves were gone by this time. For smaller trees, however, the retention of green leaves was associated with a lower increase, if not a slight decline in cynipid diversity (Fig. 1a). This difference may be because herbivore recruitment to green leaves only occurs on a large scale. Small trees, even with complete green leaf retention, still retain only a trivial number of leaves to attract colonizing herbivores from afar, so the effect may be masked by other factors.

We do not believe that green leaf abscission reduced cynipid diversity through starvation or relocation as have been observed in many studies on sessile folivores (Faeth et al. 1981a; Williams and Whitham 1986; Pearse and Karban 2013). Observations made in early January 2020 found that retained green leaves generally lacked galls or any sign of scars from leaf galls. On the other hand, brown leaves carried leaf galls similar to the densities seen in the summer. Ovipositing cynipids were unlikely to systematically avoid the green leaves. Therefore, the lack of galls on green leaves suggests that these leaves were probably produced later in the growing season after peak cynipid oviposition in the summer. Leaves that flushed in early spring were probably dropped or senesced by the start of winter. This is consistent with the leaf phenology noted for other woody plants in similar Mediterranean environments (Kyparissis et al. 1997). These plants put out a spring leaf flush followed by an autumn flush, coinciding with the two most productive periods of the year.

### Herbivory cost of brown leaf retention

Our result suggests that brown leaves better predicted cynipid densities (Table 2; Table S3), but this pattern was driven by very strong effects on a few herbivore species (Figure S2). This may be why brown leaf retention explained cynipid diversity poorly (Table 2). For large oaks, higher brown leaf retention was associated with substantially lower spring cynipid densities (Fig. 2d). This result contrasts with earlier reports and discussions of the anti-herbivore function of leaf abscission which are based upon the notion that being dropped to the ground incurs a fitness cost to the herbivore (Faeth et al. 1981a; Williams and Whitham 1986; Pearse and Karban 2013). In the *Q. lobata* galler community, many cynipid species drop to the ground months ahead of peak

leaf fall and over-winter on the ground naturally. Therefore, assuming a fitness cost to the herbivore of being dropped seems inappropriate.

Indeed, some authors have challenged this assumption about abscission and herbivore performance and reported very little abscission induced mortality (Pritchard and James 1984). Others have even found that leaf abscission reduced herbivore mortality by moving the endophagous herbivores to a parasitoid-free space (Kahn and Cornell 1989). More recently, some have speculated that increased plant structural complexity may provide a habitat for predators (Wetzel et al. 2016; Pearse et al. 2020). Retained brown leaves may serve as a reservoir for the natural enemies of galls while providing no nutritional value to herbivores. Thus, abscission of these leaf reservoirs may be a mechanism that alleviates top-down pressures on the cynipids, particularly considering that parasitoids often kill the vast majority of the galls (Joseph et al. 2011; Prior and Hellmann 2013). Leaf abscission may also promote cynipid survival by relocating the sessile pupa to a more suitable overwintering site. Underneath layers of leaves, the pupa may be protected from cold winter air, solar radiation, dry wind, predators, and high daily temperature fluctuations. For example, working with *Q. lobata*, Herrmann et al. (2012) found that leaf litter correlated with cynipid richness and suggested leaving litter intact over winter as a conservation method. Further, there is some evidence to suggest that *N. saltatorius* actively seeks shelter on the ground to avoid heat and desiccation (Duncan 1997; Manier and Deamer 2014). This behavior is consistent with the negative correlation between leaf retention and *N. saltatorius* densities we saw on large trees. During the winter, we saw a considerable number of galls remain attached to the marcescent leaves. Collection of these galls in December 2018 revealed that some were still viable, although most failed to emerge (pers. obs.). Still, by retaining brown leaves on their branches, large valley oaks can sequester leaf galling cynipids in a more vulnerable location, thereby suppressing local densities.

Juvenile oaks, on the other hand, are capable of holding fewer leaves and a lower density of galls. Retaining brown leaves as a way of sequestering galls may therefore not be as important, because the numbers of cynipids that exist locally are probably determined predominantly by neighboring large *Q. lobata*. Why then, might marcescence be especially bad for smaller valley oaks? We are unsure. By fall, most cynipids have already finished development, so starvation is unlikely to explain the difference. Neither does physical relocation, as that would only contribute minor effects to local densities. One explanation may be that marcescence does not pose a direct cost per se, but is a consequence of water stress, which is related to a higher plant quality preferred by the galls. During the dry summer in Mediterranean climates, maintaining leaf activity without an adequate

supply of water runs the risk of drought stress, especially for small trees without deep roots. Juvenile trees with highly active leaves during this unfavorable time may succumb to water stress and fail to properly develop the abscission layer (Berkley 1931; Dunberg 1982; Abadia et al. 1996).

Patterns in winter leaf retention did not predict summer cynipid densities. A lack of relationship is expected because leaves that dropped by budburst (Figure S1) cannot directly interact with the temporally segregated spring and summer generations of cynipids of the same year. Indirect interactions mediated by the host plant may also have attenuated by summer. Accordingly, the herbivory consequences of over-winter leaf retention may be limited to the spring (Figure S2), although enough damage may have already been done during spring to reduce plant performance, especially in the early season when leaves are particularly valuable and support the development of acorns on the same branch.

## Conclusion

Herbivory pressure that shapes leaf habits may be inconsistent across years, individuals, and ecoregions (Leckey et al. 2014). As we have shown with our system, the herbivory associated with different leaf habits depends on the tree ontogeny, season, the local herbivore community, and possibly individual location. Understanding the true herbivory cost of different leaf habits may require extensive sampling across multiple dimensions and/or manipulative experiments. Thus, proponents of a general cost–benefit model for leaf habits that account for herbivory may be disappointed to find the task prohibitively challenging and uninformative (Chabot and Hicks 1982; Karban 2007, 2008). When selective regimes are variable, even large fitness effects may fail to provide patterns that are clear (Cvijović et al. 2015; Graves and Weinreich 2017). Thus, herbivory is unlikely to be a sufficient selective force to drive the persistence or transition to certain leaf habits, especially since abiotic forces are known to exert a strong influence on leaf habits (Axelrod 1966; Wright et al. 2004). However, even if the risk of herbivory cannot predict different leaf habits and easily explain the prevalence of winter-deciduous trees in Mediterranean environments, our study shows that winter leaf habits may explain large differences in herbivory load among individual trees. However, it is possible that differences in physiology, chemistry, or other unmeasured traits between trees that differed in leaf retention were the true cause of difference in gall communities.

Finally, our study emphasizes the unique ecological role that green and brown leaves each play at determining herbivore density and diversity. Thus, the herbivore load associated with winter-leaf abscission cannot be understood without consideration of leaf physiological activity. Further

explorations of physiological activity and other mechanisms may prove invaluable to insect ecologists attempting to explain insect herbivore distributions.

**Supplementary Information** The online version contains supplementary material available at <https://doi.org/10.1007/s11829-021-09815-7>.

**Acknowledgements** We thank the Putah Creek Reserve staff Andrew Fulks and Jean-Philippe Marie for helping us work at our field sites, Louie Yang, Neil Willits, and Emilio Laca for providing statistical advice, Steve Heydon for helping identify cynipids, Naomi Murray and Danielle Rutkowski for helping improve the manuscript, and the two anonymous reviewers for their invaluable comments.

**Author contributions** VSP and RK conceived and designed the experiments. VSP and JG performed the fieldwork. VSP and AP analyzed the data. VSP wrote the manuscript. AP and RK provided editorial advice.

**Funding** This work was funded by NSF LTREB (Grant No. 1456225) and USDA Regional projects (Grant No. NC-7 and NE-1501).

**Data availability** Data file is available online as a supplementary material.

**Code availability** R code used to analyze data may be provided upon request.

## Declarations

**Conflict of interest** We declare no conflict of interest.

**Consent for publication** All authors approve the publication of this manuscript.

## References

- Abadia A, Gil E, Morales F, Montanes L, Montserrat G, Abadia J (1996) Marcescence and senescence in a submediterranean oak (*Quercus subpyrenaica* E.H. del Villar): photosynthetic characteristics and nutrient composition. *Plant Cell Environ* 19:685–694
- Addicott FT, Lynch RS (1955) Physiology of abscission. *Ann Rev Plant Physiol* 6:211–238
- Agrawal AA, Hastings AP, Johnson MTJ, Maron JL, Salminen J-P (2012) Insect herbivores drive real-time ecological and evolutionary change in plant populations. *Science* 338:113–116
- Axelrod DI (1966) Origin of deciduous and evergreen habits in temperate forests. *Evolution* 20:1–15
- Baldocchi DD, Ma S, Rambal S, Misson L, Ourcival J-M, Limousin J-M, Pereira J, Papale D (2010) On the differential advantages of evergreenness and deciduousness in mediterranean oak woodlands: a flux perspective. *Ecol Appl* 20:1583–1597
- Barbero M, Loisel R, Quézel P (1992) Biogeography, ecology and history of mediterranean *Quercus ilex* ecosystems. *Vegetatio* 99:19–34
- Berkley EE (1931) Marcescent leaves of certain species of *Quercus*. *Bot Gaz* 92:85–93
- Blumler MA (1991) Winter-deciduous versus evergreen habit in mediterranean regions: a model. In: Standiford RB, Technical Coordinator (eds) Proceedings of the symposium on oak woodlands and hardwood rangeland management; October 31–November 2,



- 1990; Davis, California Gen Tech Rep PSW-GTR-126. Pacific Southwest Research Station, Forest Service, US Department of Agriculture, Berkeley, CA, pp 194–197
- Blumler MA (2015) Deciduous woodlands in Mediterranean California. In: Box EO, Fujiwara K (eds) Warm-temperate deciduous forests around the Northern Hemisphere. Springer, Cham, pp 257–266
- Body M, Kaiser W, Dubreuil G, Casas J, Giron D (2013) Leaf-miners co-opt microorganisms to enhance their nutritional environment. *J Chem Ecol* 39:969–977
- Boege K, Barton K, Dirzo R (2011) Influence of tree ontogeny on plant-herbivore interactions. In: Meinzer FC, Lachenbruch B, Dawson TE (eds) Size- and age-related changes in tree structure and function. Springer, Dordrecht, pp 193–214
- Bürkner P-C (2017) brms: an r package for Bayesian multilevel models using Stan. *J Stat Softw* 80:1–28
- Bürkner P-C (2018) Advanced Bayesian multilevel modeling with the R package brms. *R J* 10:395–411
- Chabot BF, Hicks DJ (1982) The ecology of leaf life spans. *Annu Rev Ecol Syst* 13:229–259
- Crawley MJ (1985) Reduction of oak fecundity by low-density herbivore populations. *Nature* 314:163–164
- Cvijović I, Good BH, Jerison ER, Desai MM (2015) Fate of a mutation in a fluctuating environment. *PNAS* 112:E5021–E5028
- Di Castri F, Goodall DW, Specht RL (1981) Mediterranean-type shrublands. Elsevier, New York
- Dunberg A (1982) Why beech and oak trees retain leaves until spring: a comment on the contribution by Otto and Nilsson. *Oikos* 39:275–277
- Duncan RW (1997) Jumping gall wasp. Natural Resources Canada, Canadian Forest Service, Pacific Forestry Centre, Victoria, BC
- Eriksson O, Inghe O, Jerling L, Tapper P-G, Telenius A, Torstensson P (1983) A note on non-adaptation hypotheses in plant ecology. *Oikos* 41:155–156
- Escudero A, Mediavilla S, Olmo M, Villar R, Merino J (2017) Coexistence of deciduous and evergreen oak species in mediterranean environments: costs associated with the leaf and root traits of both habits. In: Gil-Pelegrín E, Peguero-Pina JJ, Sancho-Knapik D (eds) Oaks physiological ecology. Exploring the functional diversity of genus *Quercus* L. Springer, Cham, pp 195–237
- Faeth SH, Connor EF, Simberloff D (1981a) Early leaf abscission: a neglected source of mortality for folivores. *Am Nat* 117:409–415
- Faeth SH, Mopper S, Simberloff D (1981b) Abundances and diversity of leaf-mining insects on three oak host species: effects of host-plant phenology and nitrogen content of leaves. *Oikos* 37:238
- Feeny P (1970) Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. *Ecology* 51:565–581. <https://doi.org/10.2307/1934037>
- Gil-Pelegrín E, Saz MÁ, Cuadrat JM, Peguero-Pina JJ, Sancho-Knapik D (2017) Oaks under mediterranean-type climates: functional response to summer aridity. In: Gil-Pelegrín E, Peguero-Pina JJ, Sancho-Knapik D (eds) Oaks physiological ecology. Exploring the functional diversity of genus *Quercus* L. Springer, Cham, pp 137–193
- Graves CJ, Weinreich DM (2017) Variability in fitness effects can preclude selection of the fittest. *Annu Rev Ecol Evol Syst* 48:399–417
- Grove AT, Rackham O (2003) The nature of Mediterranean Europe: an ecological history. Yale University Press, London
- Hawkes CV, Sullivan JJ (2001) The impact of herbivory on plants in different resource conditions: a meta-analysis. *Ecology* 82:2045–2058
- Herrmann DL, Pearse IS, Baty JH (2012) Drivers of specialist herbivore diversity across 10 cities. *Landsc Urban Plann* 108:123–130
- Hoy CW, Head GP, Hall FR (1998) Spatial heterogeneity and insect adaptation to toxins. *Annu Rev Entomol* 43:571–594. <https://doi.org/10.1146/annurev.ento.43.1.571>
- Hoshaw RW, Guard AT (1949) Abscission of marcescent leaves of *Quercus palustris* and *Q. coccinea*. *Bot Gaz* 110:587–593
- Joseph MB, Gentles M, Pearse IS (2011) The parasitoid community of *Andricus quercuscalifornicus* and its association with gall size, phenology, and location. *Biodivers Conserv* 20:203–216
- Jost L (2007) Partitioning diversity into independent alpha and beta components. *Ecology* 88:2427–2439
- Kaiser W, Hugué E, Casas J, Commin C, Giron D (2010) Plant green-island phenotype induced by leaf-miners is mediated by bacterial symbionts. *Proc R Soc B: Biol Sci* 277:2311–2319
- Karban R (2007) Deciduous leaf drop reduces insect herbivory. *Oecologia* 153:81–88
- Karban R (2008) Leaf drop in evergreen *ceanothus velutinus* as a means of reducing herbivory. *Ecology* 89:2446–2452
- Karban R (2011) The ecology and evolution of induced resistance against herbivores. *Funct Ecol* 25:339–347
- Kahn DM, Cornell HV (1989) Leafminers, early leaf abscission, and parasitoids: a tritrophic interaction. *Ecology* 70:1219–1226
- Kyparissis A, Grammatikopoulos G, Manetas Y (1997) Leaf demography and photosynthesis as affected by the environment in the drought semi-deciduous Mediterranean shrub *Phlomis fruticosa* L. *Acta Oecol* 18:543–555
- Leckey EH, Smith DM, Nufio CR, Fornash KF (2014) Oak-insect herbivore interactions along a temperature and precipitation gradient. *Acta Oecol* 61:1–8
- Lim PO, Kim HJ, Gil Nam H (2007) Leaf senescence. *Annu Rev Plant Biol* 58:115–136
- Manier S, Deamer D (2014) Jumping galls: a novel mechanism for motility. *J Insect Behav* 27:716–721
- Mingo A, Oosterheld M (2009) Retention of dead leaves by grasses as a defense against herbivores. A test on the palatable grass *Paspalum dilatatum*. *Oikos* 118:753–757
- Mooney HA, Dunn EL (1970a) Photosynthetic systems of Mediterranean-climate shrubs and trees of California and Chile. *Am Nat* 104:447–453
- Mooney HA, Dunn EL (1970b) Convergent evolution of Mediterranean-climate evergreen Sclerophyll Shrubs. *Evolution* 24:292–303
- Moran NA, Whitham TG (1990) Differential colonization of resistant and susceptible host plants: pempfigus and populus. *Ecology* 71:1059–1067
- Ne'Eman G (1993) Variation in leaf phenology and habit in *Quercus Ithaburensis*, a Mediterranean deciduous tree. *J Ecol* 81:627–634
- Opler PA (1978) Interaction of plant life history components as related to arboreal herbivory. In: Montgomery GG (ed) The Ecology of arboreal folivores: a symposium held at the Conservation and Research Center, National Zoological Park, Smithsonian Institution, May 29–31, 1975. Smithsonian Institution Press, Washington, pp 23–31
- Öquist G, Huner NPA (2003) Photosynthesis of overwintering evergreen plants. *Annu Rev Plant Biol* 54:329–355
- Owen DF (1978) The effect of a consumer, *Phytomyza ilicis*, on seasonal leaf-fall in the Holly, *Ilex*. *Aquifol Oikos* 31:268
- Paine TD, Lieutier F (2016I) Insects and diseases of mediterranean forest systems: introduction. Springer, New York
- Pearse IS, Karban R (2013) Leaf drop affects herbivory in oaks. *Oecologia* 173:925–932
- Pearse IS, LoPresti E, Schaeffer RN, Wetzel WC, Mooney KA, Ali JG, Ode PI, Eubanks MD, Bronstein JL, Weber MG (2020) Generalising indirect defence and resistance of plants. *Ecol Lett* 23:1137–1152

- Portillo-Estrada M, Kazantsev T, Niinemets Ü (2017) Fading of wound-induced volatile release during *Populus tremula* leaf expansion. *J Plant Res* 130:157–165
- Price PW (1991) The plant vigor hypothesis and herbivore attack. *Oikos* 62:244
- Prior KM, Hellmann JJ (2013) Does enemy loss cause release? A biogeographical comparison of parasitoid effects on an introduced insect. *Ecology* 94:1015–1024
- Pritchard IM, James R (1984) Leaf fall as a source of leaf miner mortality. *Oecologia* 64:140–141
- R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Russo R (2006) Field guide to plant galls of California and Other Western States, 1st edn. University of California Press, Oakland
- Salomón RL, Rodríguez-Valcárcel J, Staudt M (2017) Carbon losses from respiration and emission of volatile organic compounds—the overlooked side of tree carbon budgets. In: Gil-Pelegrín E, Peguero-Pina JJ, Sancho-Knapik D (eds) Oaks physiological ecology. Exploring the functional diversity of Genus *Quercus* L. Springer, Cham, pp 327–359
- Shafiei M, Moczek AP, Nijhout HF (2001) Food availability controls the onset of metamorphosis in the dung beetle *Onthophagus taurus* (Coleoptera: Scarabaeidae). *Physiol Entomol* 26:173–180
- Shmida A (1981) Mediterranean vegetation in California and Israel: similarities and differences. *Isr J Bot* 30:105–123
- Svendsen CR (2001) Effects of marcescent leaves on winter browsing by large herbivores in northern temperate deciduous forests. *Alces* 37:475–482
- Vehtari A, Gelman A, Gabry J (2017) Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. *Stat Comput* 27:1413–1432
- Vehtari A, Gabry J, Magnusson M, Yao Y, Gelman A (2019) Efficient LOO-CV and WAIC for Bayesian models—loo-package. <http://mc-stan.org/loo/reference/loo-package.html>. Accessed 28 Jan 2021
- Weih M (2009) Genetic and environmental variation in spring and autumn phenology of biomass willows (*Salix* spp.): effects on shoot growth and nitrogen economy. *Tree Physiol* 29:1479–1490
- Wetzel WC, Screen RM, Li I, McKenzie J, Phillips KA, Cruz M, Zhang W, Greene A, Lee E, Singh N, Tran C, Yang LH (2016) Ecosystem engineering by a gall-forming wasp indirectly suppresses diversity and density of herbivores on oak trees. *Ecology* 97:427–438
- Williams AG, Whitham TG (1986) Premature leaf abscission: an induced plant defense against gall aphids. *Ecology* 67:1619–1627
- Wright IJ, Reich PB, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, Flexas J, Garnier E, Groom PK, Gulias J, Hikosaka K, Lamont BB, Lee T, Lee W, Lusk C, Midgley JJ, Navas M-L, Niinemets Ü, Oleksyn J, Osada N, Poorter H, Poot P, Prior L, Pyankov VI, Roumet C, Thomas SC, Tjoelker MG, Veneklaas EJ, Villar R (2004) The worldwide leaf economics spectrum. *Nature* 428:821
- Yamazaki K, Sugiura S (2008) Deer predation on leaf miners via leaf abscission. *Naturwissenschaften* 95:263–268
- Zvereva EL, Kozlov MV (2014) Effects of herbivory on leaf life span in woody plants: a meta-analysis. *J Ecol* 102:873–881

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.