



## Research

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# Macroecological and macroevolutionary patterns of leaf herbivory across vascular plants

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The consumption of plants by animals underlies important evolutionary and ecological processes in nature. Arthropod herbivory evolved approximately 415 Ma and the ensuing coevolution between plants and herbivores is credited with generating much of the macroscopic diversity on the Earth. In contemporary ecosystems, herbivory provides the major conduit of energy from primary producers to consumers. Here, we show that when averaged across all major lineages of vascular plants, herbivores consume 5.3% of the leaf tissue produced annually by plants, whereas previous estimates are up to 3.8× higher. This result suggests that for many plant species, leaf herbivory may play a smaller role in energy and nutrient flow than currently thought. Comparative analyses of a diverse global sample of 1058 species across 2085 populations reveal that models of stabilizing selection best describe rates of leaf consumption, and that rates vary substantially within and among major plant lineages. A key determinant of this variation is plant growth form, where woody plant species experience 64% higher leaf herbivory than non-woody plants. Higher leaf herbivory in woody species supports a key prediction of the plant apparency theory. Our study provides insight into how a long history of coevolution has shaped the ecological and evolutionary relationships between plants and herbivores.

## 1. Introduction

Plant–herbivore interactions underlie some of the most important evolutionary and ecological processes in nature [1–3]. Arthropod herbivores have been consuming plants for over 415 Myr [4]. This long history of interaction, coupled with negative effects of herbivores on plant fitness [5], are credited with promoting the macroevolutionary diversification of defensive traits and elevating speciation rates in plants [3,6]. In turn, diversification of plant defences and species has promoted the diversification and specialization of herbivores [7,8]. Thus, plant–insect coevolution is thought to have given rise to much of the macroscopic diversity of life on the Earth [3,9,10]. Contemporary herbivore communities continue to have large ecological impacts on plant productivity, population dynamics, community composition, energy flow and nutrient cycling [2,11–15].

Despite the importance of plant–herbivore interactions for ecological and ecosystem processes, we lack robust estimates of rates of herbivory and how herbivory varies between major plant lineages, as well as among plants that differ in life-history traits. Previous estimates of the mean annual rate of leaf herbivory across plants range between 10 and 20% [1,13,16,17]. These estimates are limited by the number and taxonomic breadth of species examined. Here, we compile and compare variation in rates of leaf herbivory across a wide taxonomic breadth of vascular plant species. The mean per cent damage experienced across plant species provides important ecological insights into how much plant primary production is lost to higher macroscopic herbivores

or decomposed by detritivores in terrestrial ecosystems. Species-specific data can be used to analyse patterns of herbivory in a phylogenetic context and explore whether macroevolutionary history predicts contemporary patterns of herbivory. A better understanding of the importance of evolutionary history for rates of leaf herbivory can thus help to explain variation in nutrient and energy fluxes among ecosystems that differ in species composition [18], as well as the traits that might cause such variation.

Comparing rates of damage across species can help resolve one of the most important unanswered questions in the study of plant–herbivore interactions: why do species vary so dramatically in their susceptibility to herbivores [1,19–21]? With the realization that plant secondary metabolites play the dominant role in plant defence [22,23], it was initially believed that plants evolve to minimize damage and that variation among lineages was due to the presence of different secondary metabolites and insect counter-adaptations [9,24,25]. It was soon realized, however, that this view was too simplistic and did not account for the wide diversity of plant traits and life-history characteristics that also affect a plant's susceptibility and evolution of plant defences against herbivores. One of the first attempts to create a predictive framework that accounted for such complexity was the plant apparency theory (PAT) [26,27]. PAT predicts that woody species and other long-lived plants are more 'apparent' to herbivores and thus suffer more persistent attack than 'unapparent plants' [28], which subsequently causes selection for different types of defence [26]. Subsequent empirical research has not found strong support for the prediction that variation in apparency leads to the evolution of different types of defences [1,19]. However, tests of the prediction that apparent plants receive more damage than unapparent plants remain rare. The few studies that have tested this prediction failed to support the theory [28,29]. However, these studies focused mostly on a single growth form (i.e. woody long-lived plants) and large-scale tests of PAT across a wide phylogenetic breadth of vascular plants representing a diversity of growth forms are lacking.

Modern phylogenetic comparative analyses applied to contemporary rates of herbivory provide a powerful tool for evaluating alternative evolutionary hypotheses [3]. By comparing the fit of macroevolutionary models based on different mechanisms of evolution, we can elucidate the processes that probably drive variation in herbivory across plants. In the absence of strong selection by herbivores, rates of herbivory should evolve stochastically and thus covary with phylogenetic relationships among plant species. We can model such stochastic evolutionary dynamics using models of Brownian motion (BM). Alternatively, a combination of selection and drift could cause plants to evolve towards a single optimum that maximizes plant fitness. Another possibility is that species or entire lineages evolve towards different evolutionary optima. For example, species may adopt alternative defensive strategies, such as tolerance to damage, because they differ in growth form (e.g. trees or forbs). We can examine these selection-based hypotheses by fitting Ornstein–Uhlenbeck (OU) models that approximate stabilizing selection towards a single or multiple evolutionary optima [30].

We examined patterns of per cent leaf herbivory across 1058 vascular plant species that represent 455 Myr of evolutionary divergence using comparative phylogenetic

methods. Specifically, we asked: (i) What is the average amount of leaf herbivore damage received annually by vascular plants? (ii) What macroevolutionary processes best explain variation in leaf herbivory among plant lineages? (iii) How do plant life history and plant growth form influence natural rates of damage? The answers to these questions provide critical insights into the macroevolutionary processes that have shaped macroecological patterns of plant–herbivore interactions across vascular plants.

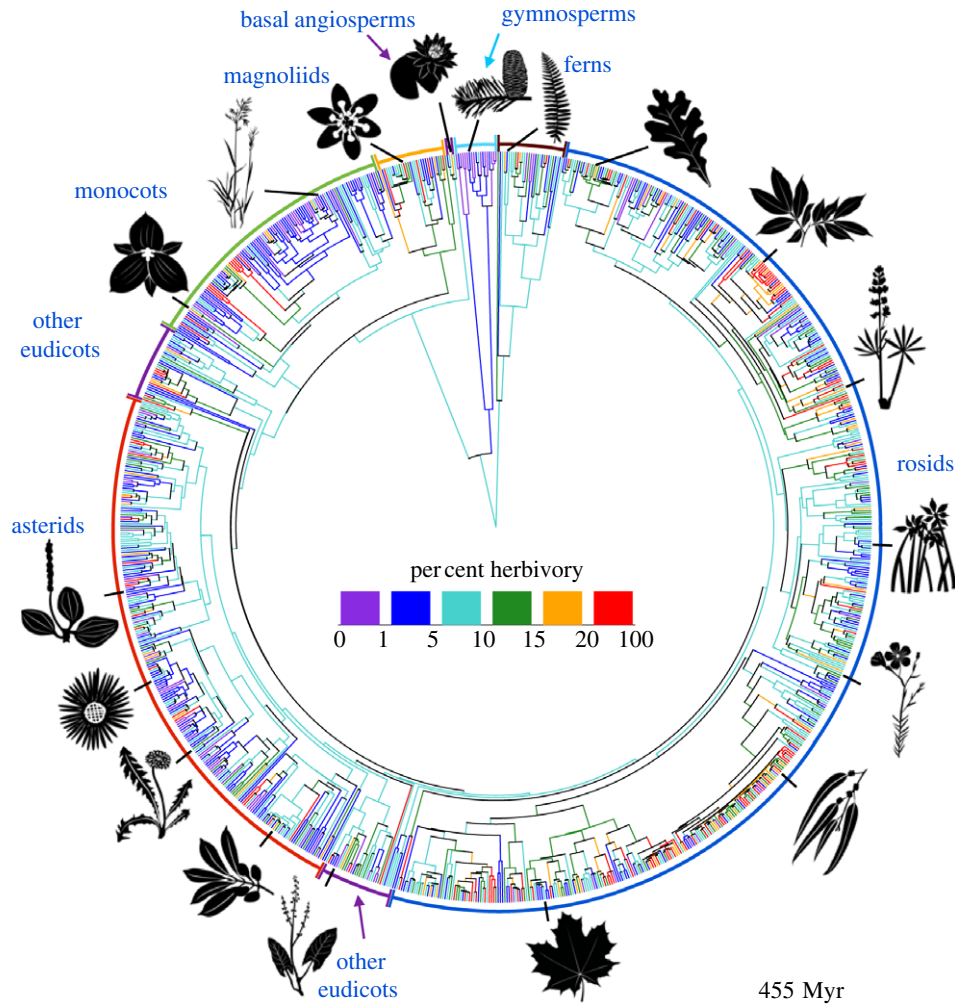
## 2. Material and methods

### (a) Leaf herbivory data acquisition

A major challenge in estimating rates of consumption is that herbivores attack every part of the plant, yet not all tissues are easily observed. For example, damage to leaves is relatively easy to quantify, while herbivory on flowers and fruits is complicated by their ephemeral production, and quantifying root herbivory on many species is virtually impossible [31–33]. Similarly, arthropods exhibit diverse feeding habits, from chewing entire tissues, to mining, to extracting out the contents of cells, phloem and xylem. Here, we focused on estimates of per cent leaf herbivory. This approach was based on three considerations: (i) leaf herbivory is important for fitness and ecosystem productivity [5,14,34,35]; (ii) it is a robust estimate of herbivory from a critically important feeding guild and (iii) it is the tissue from which herbivory is most commonly measured across species (see the electronic supplementary material).

On 28 October 2011, we searched titles, abstracts and keywords in the SciVerse Scopus database ([www.scopus.com](http://www.scopus.com)) for studies using a series of related combinations of terms for herbivory (see the electronic supplementary material for details). Of the 3371 studies identified, we focused on those from the 50 most frequent journals (electronic supplementary material, table S6), as well as studies that measured underrepresented lineages (e.g. gymnosperms). This narrowed the search to 1700 studies. We then determined whether these studies met our data selection criteria (electronic supplementary material). We also contacted a number of authors for species-level leaf herbivory rates that were not present in their manuscripts. Finally, we added unpublished measurements on 82 species from Trinidad and Eastern North America (electronic supplementary material, table S1). In all, we collated 2085 population-level estimates of per cent leaf herbivory caused by naturally colonizing herbivores on 1058 vascular plant species from 161 families, collected from 174 studies (electronic supplementary material, table S6), representing a combined dataset many times larger than previous compilations [1,13,16,17]. Turcotte *et al.* [36] recently published the population-level data for these 174 studies and an additional 15 studies.

To standardize data across all studies, we only included measurements that represent natural rates of annual leaf herbivory (see the electronic supplementary material for detailed descriptions and justifications). These values represented mean per cent damage from multiple replicate plants per species. When a study reported values for multiple populations or years for a given species, we recorded each estimate separately unless the authors provided an overall mean. From these data we calculated unweighted species mean annual leaf herbivory rates (see the electronic supplementary material, table S6 for mean values and sources of data). We also collected trait data from the source literature and online trait databases (e.g. <http://plants.usda.gov>). Life-history traits included: annual, intermediate or perennial reproduction. Plant growth form was classified as forb, shrub, tree, vine and graminoid, as well as whether the plant was woody or non-woody. Although monocots lack secondary growth that produces wood and bark, we classified monocots as



**Figure 1.** Annual rates of leaf herbivory mapped onto a phylogeny of 1058 species representing 455 Myr of vascular plant evolution using ancestral state reconstruction. Terminal branch lengths were extended by 10 Myr to aid visualization. The tree depicted is one of a posterior distribution of 1000 trees. Illustrated species include (starting from the ferns at the top and moving clockwise): *Polystichum acrostichoides*, *Quercus alba*, *Inga umbellifera*, *Lupinus argenteus*, *Rhizophora mangle*, *Linum lewisii*, *Eucalyptus globulus*, *Acer platanoides*, *Rumex acetosa*, *Pouteria cuspidate*, *Taraxacum officinale*, *Symphotrichum novae-angliae*, *Plantago major*, *Trillium grandiflorum*, *Bromus inermis*, *Persea americana*, *Nymphaea odorata* and *Abies grandis*. (Online version in colour.)

‘woody’ if they produced structures that provide similar functions to wood and bark (e.g. palms).

### (b) Phylogenetic inference and comparative analyses

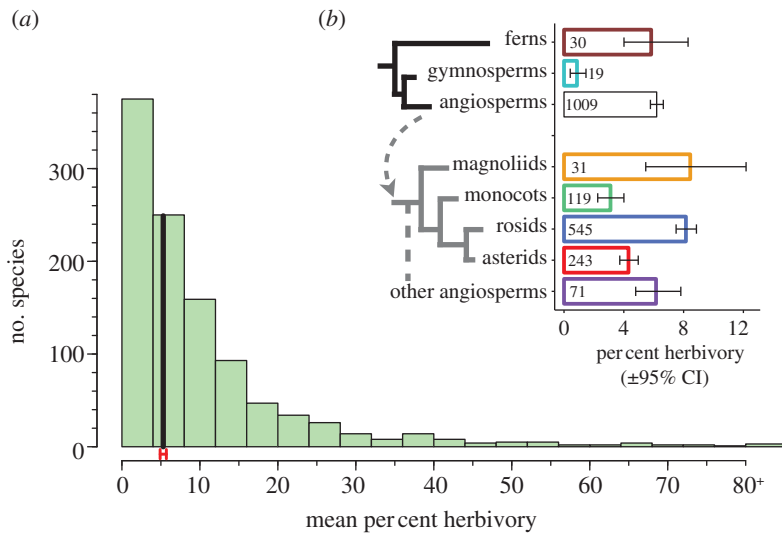
We first created a backbone family-level phylogeny using PHYLOMATIC [37]. We then resolved branches to the species level using maximum-likelihood (ML) methods [38] and *rbcL* sequence data obtained from Genbank. Species without sequence data were added to the tree as polytomies using accepted taxonomy [39]. Finally, we dated the tree and resolved polytomies using Bayesian methods to create a posterior distribution of 1000 fully resolved phylogenetic trees (e.g. figure 1; electronic supplementary material).

We compared the fit of alternative evolutionary models to observed patterns of leaf herbivory across species using AICc scores. We used several BM models to approximate stochastic evolution (i.e. genetic drift) and also OU models that approximate stabilizing selection with drift [30,40,41] (electronic supplementary material). We compared BM models with a single stochastic evolutionary rate (BM1) or with multiple rates (BMS) for plants that vary in life history and growth form. Similarly, we compared OU models with a single evolutionary optimum for the rate of herbivory (OU1) to models with multiple evolutionary optima (OUM). Each function was fitted separately for each major plant lineage so as to explore differences in the evolutionary model that best explains variation in herbivory across clades (electronic supplementary material).

Model fitting was conducted on each of the 1000 phylogenetic trees, thus taking into account uncertainty in phylogenetic inference and ancestral state reconstruction. We evaluated model fits by comparing median AICc values across all 1000 trees and alternatively, by comparing the frequency at which each model was favoured by AICc over the 1000 trees. We compared rates of leaf herbivory across major plant lineages using the estimated evolutionary optimal rate of herbivory ( $\theta$ ) according to the OU1 model [40] (electronic supplementary material). This value represents the phylogenetically corrected best estimate of mean herbivory for the clade [40]. For each lineage in each of the 1000 tree topologies, we extracted the optimum value estimate, and calculated 95% confidence intervals using the standard error of that optimum value. We then present median  $\theta$  values and median 95% confidence intervals across the 1000 tree topologies. In this way, we incorporate both phylogenetic uncertainty and uncertainty in the ML estimation. To compare rates of herbivory among plant species with different traits, we compared median and confidence intervals for optimal values ( $\theta$ ) from the OUM analyses, in which the evolutionary optima were allowed to vary with plant traits.

## 3. Results and discussion

We found that annual rates of leaf herbivory across vascular plants are substantially lower than previously estimated. Most



**Figure 2.** Annual rates of leaf herbivory across plant species and major lineages. (a) Histogram of annual rates of per cent leaf herbivory across 1058 species. The vertical black bar represents the geometric mean (5.3%) across all species and the whiskers below the x-axis (in red online) show the 95% confidence intervals (CI = 4.9–5.7%). (b) Comparison of evolutionary optimal rates of herbivory as estimated by stabilizing selection models (OU1) for each major plant lineage. Values are median estimates and median 95% CI over the distribution of 1000 phylogenetic trees. ‘Other angiosperms’ represent a paraphyletic group of species not contained within the other monophyletic angiosperm lineages. Numbers of species sampled are found within the bars. (Online version in colour.)

plant species receive little-to-no damage with 40% of species receiving less than 5% damage, and only a small number of species are heavily damaged (less than one-tenth of species receive more than 25% damage annually), suggesting that plant resistance to herbivores is generally high (figure 2a). The geometric mean rate of damage across vascular plants is 5.3% (95% confidence intervals (CI) = 4.9–5.7%, from 10 000 bootstrap iterations), whereas prior estimates that also averaged across ecosystems were 1.9–3.8× higher [1,13,16,17]. The discrepancy between our estimates and previous ones cannot be easily explained by differences in methodology. A secondary analysis using more stringent criteria for estimating annual rates of leaf herbivory (electronic supplementary material), assessed 958 of the initial 1058 species, and produced a nearly identical mean value of 5.2% (95% CI = 4.8–5.6%). We suggest that the difference between our estimate and previous measures likely reflects limited taxonomic or geographical sampling in earlier studies, some of which focused on taxa with high rates of leaf herbivory (e.g. *Eucalyptus* species or gap specialists species in the tropics). Because our study included substantially more data than previous efforts, we consider our estimates to be less biased by taxonomic sampling. In addition, few studies acknowledge the non-normal distribution of damage and instead present the arithmetic mean, which provides an upwardly biased estimate for right-skewed data.

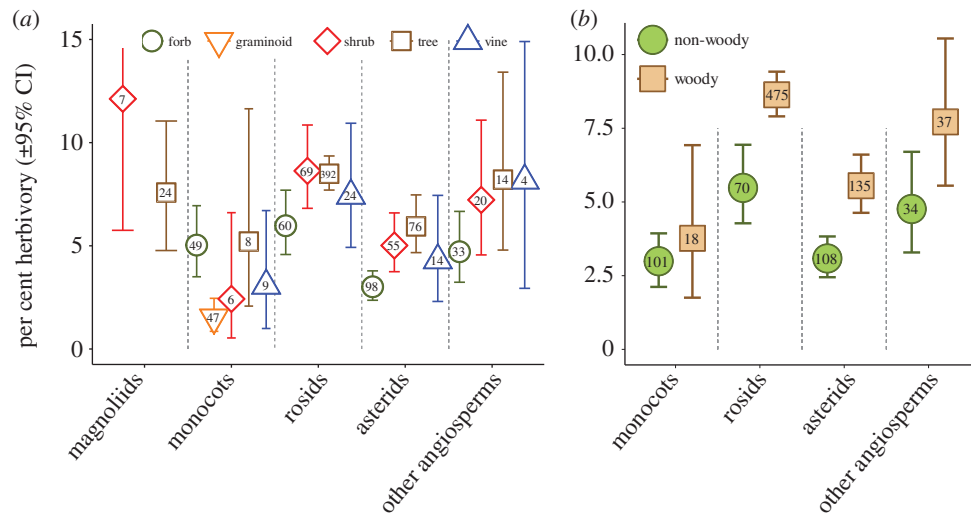
### (a) Macroevolutionary processes explaining patterns of leaf herbivory

OU models, which represent stabilizing selection plus drift, best described variation in rates of herbivory across the phylogeny in all analyses (electronic supplementary material, table S3), with the magnitude of annual rates significantly differing among plant lineages and among species (figures 1 and 2b). These results are consistent with the interpretation that stabilizing selection on resistance has caused plants to evolve towards one or more evolutionary optima, reflecting a trade-off between minimizing damage and investment in herbivore defences or investment in tolerance of damage.

This interpretation assumes that leaf damage indicates a plant’s investment in defences. This assumption is reasonable given that per cent tissue removed by herbivores is frequently used as a measure of a plant’s net level of resistance. The amount of herbivory is positively related to physiological and behavioural adaptations of herbivores that allow them to exploit plants and negatively related to a plant’s investment in direct (e.g. secondary metabolites) and indirect resistance traits (e.g. third trophic level) [1,24,35]. Although some specialist herbivores have overcome host defences [42,43], plants are thought to evolve defences in response to multiple herbivores and rates of damage should indicate investment in resistance [16]. While it is possible that alternative evolutionary processes could produce patterns that are consistent with the OU model, for example, fluctuating selection on investment in defence, it is not clear how such processes would result in the observed strong differences in herbivory rates among major plant lineages and on plants with different growth forms.

### (b) Leaf herbivory among major plant lineages

Our analyses reveal that major plant lineages significantly differed in annual rates of leaf herbivory (figure 2b; electronic supplementary material, table S4). The phylogenetic mean of herbivory for gymnosperms was only 0.9% (95% CI: 0.4–1.5%) leaf area damage annually, despite occasional pest outbreaks that cause large-scale defoliation [44]. Damage to gymnosperms is less than one-seventh that observed for angiosperms (6.2%; 95% CI: 5.8–6.6%). In contrast to long-held expectations [9,45], ferns experienced a statistically comparable rate of herbivory (5.8%; 95% CI: 4.0–8.3%) to angiosperms (figure 2b). Within angiosperms, lineages also differed significantly in rates of herbivory. Rosids and magnoliids were the most severely damaged clades, receiving 8.2% (95% CI: 7.5–8.9%) and 8.4% (95% CI: 5.5–12.2%) damage, respectively. Interestingly, the amount of damage on rosids and magnoliids approaches previous estimates of mean herbivory rates in the literature [1,13,16,17]. However, leaf herbivory in these clades is 2.7× higher than the rate of



**Figure 3.** Per cent leaf herbivory (a) across growth forms and (b) in woody and non-woody plant species in major plant lineages. Values were estimated as the evolutionary optima from multiple rate stabilizing selection models ('OUM Woodiness' and 'OUM Growth Form'; Appendix D: table D2). Values are median estimates and median 95% CI over the distribution of 1000 trees. Upper CI for magnoliids shrubs (23%) and other angiosperms vines (20%) extended beyond the limits of the figure. Number of species for each group is shown within each data point. (Online version in colour.)

damage on monocots (3.1%, 95% CI: 2.3–4.0%) and 1.9× higher than that on asterids (4.3%, 95% CI: 3.7–5.0%; figure 2b; electronic supplementary material, table S4). Our results suggest that selection is not simply driving all lineages to minimize rates of herbivory but instead supports lineage-specific optima (figure 2b). These differences in optimal rates could also reflect differences in the strengths of selection by the herbivore community, or differences in constraints such as the importance of genetic drift. We did find evidence for differences in the strength of selection and the rate of evolution among lineages (electronic supplementary material, figure S1). Notably, selection was significantly stronger and evolution was significantly faster in the more recently derived rosid and asterid clades than the older gymnosperm and basal angiosperm lineages. The strength of selection and rate of evolution were intermediate within ferns and monocots.

### (c) Plant traits and macroevolutionary patterns of leaf herbivory

Lineage-specific traits, including differences in secondary chemistry, leaf nutritional quality, morphology and phenology, likely explain the observed differences in herbivory among major lineages [46]. For example, lower leaf herbivory in monocots compared to dicots is attributed to greater leaf toughness, the presence of silica and growth features such as keeping young leaves rolled to reduce access by herbivores [29,47]. Low rates of leaf herbivory and weak selection on gymnosperms are likely due to tough needle tissue and the presence of terpenoid resins [48].

While mean leaf herbivory rates differed between major plant groups, we additionally found large variation in herbivory within these lineages, with species' mean leaf damage varying between 0 and 90% (figure 1). Models of stabilizing selection with multiple evolutionary optima (OUM) were often strongly favoured within most of the major plant lineages (electronic supplementary material, tables S3 and S4), supporting a link between plant traits and rates of herbivory. Among monocot species, forbs received 3.3× more damage than graminoids (figure 3a; electronic supplementary material, table S4). This

difference is probably explained by the presence of silica, which increases leaf toughness and decreases digestibility in graminoids [26]. Within asterids and rosids, forbs receive 45 and 30% less damage than shrubs and trees, respectively, and damage to vines was typically intermediate (figure 3a). In contrast to previous studies that used mostly woody species that differ in growth rate [28,29], our results are consistent with a key prediction of PAT [26,27]. We found that woody plants received on average 64% more leaf herbivory than non-woody plants in rosids, asterids and other angiosperms, and this effect was statistically significant in rosids and asterids (figure 3b; electronic supplementary material, table S4). This is result is surprising given that for mature woody plants, leaves represent a much smaller fraction of their biomass compared with herbaceous species, although this is not the case when comparing woody seedlings and saplings [49]. Perennial species also tended to have greater damage than species with annual and intermediate life-history strategies, but these effects were not statistically significant (electronic supplementary material, figure S2 and table S4). Our results suggest that different theories of plant defence might apply to different levels of comparison such as within plant growth forms (e.g. 'Resource Availability Hypothesis') [1,11,28] versus among plant growth forms (e.g. PAT).

## 4. Conclusion

Our study of over 1000 phylogenetically diverse vascular plant species shows that annual rates of leaf herbivory are on average substantially lower than previously estimated. These results suggest that herbivory might play a smaller role in the flux of energy through ecosystems than is often claimed [2,13,16], and this conclusion is consistent with the alternative view that most energy enters terrestrial ecosystems through the detrital pathway [12,17]. We acknowledge however, that this conclusion is limited to the average amount of herbivory per plant species and does not account for the relative abundance of each species in their ecosystems. Herbivory rates on more common species should have a greater impact on the rates of energy flux. A full understanding of the importance of

herbivory will also require similar extensive measurements of herbivory on other tissues [50].

Finally, our analyses suggest that the macroevolutionary processes driving rates of herbivory differ significantly within and among major plant lineages (figures 1 and 2*b*), and variation in damage may be partly explained by plant traits (figure 3). The distribution of damage among species is consistent with different selective regimes acting on plant lineages and leading to most species receiving very little damage (figure 2*a*). Even though leaf herbivory is low for most species, it can still have important impacts on plant fitness, performance and species composition [5,11,35], it can cause short-term evolutionary change [51–54], and influence

key elements of ecosystem function including nutrient cycling and primary production [2,12,13].

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**Data accessibility.** The phylogeny of the 1058 species before polytomies were resolved is to be found in the electronic supplementary material, as well as species mean leaf herbivory and sources of data.

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