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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 $3.8 \times$ 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

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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 counteradaptations [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) 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 populationlevel 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, Symphyotrichum 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 (θ) 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 θ 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 (θ_i) 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% Cl 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 10000 bootstrap iterations), whereas prior estimates that also averaged across ecosystems were $1.9-3.8 \times$ 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 longheld 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 $2.7 \times$ 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% Cl over the distribution of 1000 trees. Upper Cl 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 lineagespecific 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 $3.3 \times$ more damage than graminoids (figure 3*a*; 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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1	Electronic Supplementary Material
2	
3	Details of methodology and analyses
4	(a) Literature search
5	We searched for relevant data on SciVerse Scopus database using the following series of
6	related combinations of terms for herbivory:
7	TITLE-ABS-KEY("rate* of grazing" OR "grazing rate" OR "amount of grazing" OR "level*
8	of grazing" OR "grazing level*" OR "rate* of herbivor*" OR "herbivor* rate" OR "amount of
9	herbivor*" OR "herbivory level*" OR "level* of herbivory" OR "degree of herbivor*" OR
10	"rate* of defoliat*" OR "defoliat* rate" OR "amount of defoliat*" OR "defoliation level*" OR
11	"level* of defoliation" OR "foli* damage*" OR "foli* level*" OR "level* of foli*" OR "leaf
12	min* damag*" OR "leaf area remov*" OR "leaf damage" OR "damage to lea*" OR "percent
13	leaf area" OR "leaf area damage" OR "removal of leaf" OR "leaf consumption" OR
14	"consumption of leaves" OR "leaf herbivor*" OR "canopy consumption" OR "consumption of
15	canopy" OR "canopy damag*" OR "canopy defoliation" OR "foliage damag*" OR "foliage
16	consum*" OR "consumption of foliage" AND NOT *plankton* AND NOT alga*) AND
17	DOCTYPE(ar OR ip OR cp OR le OR no OR sh)
18	* Truncated words with all possible ending will be identified
19	
20	(b) Data selection criteria
21	In collecting data our aim was to obtain measurements of leaf herbivory that were comparable

22 across all plant species and ecosystems. We therefore only retained data that was likely to

represent the amount of natural herbivory that a typical leaf from a given species would experience

24 in a single year. We excluded studies or treatments within studies that added herbivores to plants. In order to conduct a phylogenetically explicit analysis we focused on species-level estimates. 25 Finally, we excluded studies that only reported leaf herbivory during an outbreak year without 26 baseline data because these extreme events do not represent natural herbivory rates unless 27 corrected for frequency of occurrence. One caveat to our method is that our estimates of herbivory 28 might be lower than historical averages if taxa that acted as major herbivores in the past recently 29 went extinct. This might be especially true for some large grassland herbivores (e.g., Bison) and 30 other megafauna (e.g., Moa, Woolly Mammoth and Giant Sloth), which were hunted to extinction 31 32 or functionally removed from their native ecosystems. Even so, our estimates should accurately reflect modern rates of herbivory and the loss of these herbivores should not affect our ability to 33 make inferences about evolutionary differences in herbivory and defence among plant lineages. 34 35 We focused on damage to leaf tissue for multiple reasons. First, leaf herbivory has strong 36 impacts on individual plants and communities [1-3]. Studies show that even small amounts of leaf 37 herbivory can reduce plant fitness [4, 5]. Although herbivory can cause variable impacts on plant 38 growth, recent meta-analyses of experimental studies find that aboveground leaf herbivory 39 frequently causes reduced plant growth, photosynthesis, and fitness compared to protected plants with effects as large as competition between plants [6, 7]. Leaf herbivory has also been shown to 40 41 influence the evolution of defensive traits [8-10], plant population dynamics [3], species distributions and community composition [3, 11], and ecosystem productivity [12-14]. Second, 42 quantifying leaf damage is easier and thus much more common than quantifying damage on roots, 43 reproductive tissues, or damage caused by piercing herbivores [15, 16]. For example, damage 44 caused by phloem feeders might only be apparent if one quantifies the loss of growth potential 45 compared to undamaged plants. Third, leaf damage is easier to standardize across species since 46 leaves are almost always present in the growing season, unlike some other tissues [e.g., flowers 47

and fruits; 17]. It is difficult to say whether damage to leaves is representative of other tissues 48 because few studies have compared damage rates directly [18]. The few studies that have made 49 such comparisons suggest that leaf herbivory is usually higher than root herbivory and similar to 50 or lower than damage to flowers and fruits [17, 19]. Fourth, we focused on percent leaf area lost 51 caused by chewing, grazing, leaf mining, and scraping but excluded damage due to galling, 52 phloem and xylem feeding because quantifying tissue loss due to these processes is difficult to do 53 across many species [15, 16, 20]. The study of herbivory at the scale we present here, both in 54 phylogenetic breadth and number of species, is currently only possible using percent leaf area 55 56 damage.

To effectively compare rates of leaf herbivory across species we collected estimates of 57 annual percent damage. In deciduous species, the limited growing season limits leaf life-span to a 58 59 single year and measures collected towards the end of the growing season accurately reflect annual rates of damage [20]. In evergreen species, leaves can survive for multiple years, which could 60 61 cause an overestimation of annual damage. This is probably a minor effect because most damage 62 to leaves occurs within their first year [21]. A more complex issue occurs in species that continually produce new leaves because annual rates of herbivory will depend on the rate of leaf 63 production. This issue has motivated researchers to present herbivory as a daily rate of damage 64 65 usually measured over several months with regular sampling [22, 23]. These values are not easily converted into annual leaf herbivory because rates of damage change with leaf age and season. 66 One cannot simply sum daily rates of damage over a year, which can reach over 100% [22], 67 without correcting for leaf production and [the number of leaf flushes; 24]. Given these 68 limitations, our approach for this type of data was to estimate total herbivory received by a leaf 69 during its lifetime, most of which occurs within its first year of growth as an estimate of the 70 proportion of annual primary production consumed (see below). 71

72 The various methodologies used to measure percent leaf herbivory have received much attention [20-22, 25]. The two most common sampling approaches are: i) single measures of 73 herbivory on standing leaves, and ii) the quantification of herbivory on marked leaves over an 74 extended period of time. Both methods have potential shortcomings. Standing measures of 75 herbivory can underestimate annual herbivory when completely consumed leaves are not 76 measured [20, 22, 25-27]. The marking approach can overestimate damage when missing leaves 77 are assumed to have been completely consumed when in fact some leaves might have been 78 dropped by the plant after a smaller amount of damage [20, 28]. In addition, marking leaves can 79 80 alter rates of herbivory because repeated human visitation can increase rates of herbivory for some species [29, 30]. 81

We included data collected using both the standing and marked methods. This was justified 82 83 because standing measures of leaf herbivory are the most commonly reported and often the only available data for most species. Furthermore, some authors do account for completely consumed 84 leaves by looking for evidence of chewing damage on petioles [31-33]. Most studies however, do 85 86 not explicitly state how they deal with missing leaves and others reveal that it was impossible to 87 determine the cause of damage even with careful observation [20]. However, when both types of data were available, we used that from marked leaves, assuming the total damage received at the 88 end of the sampling period as a measure of annual herbivory. Details of the studies included in the 89 database, including habitat, location, climate, and sampling methodology, can be found in Turcotte 90 et al. [34]. 91

To account for potential methodological biases, we created two datasets of different stringency. In temperate systems, studies that reported herbivory at the end of the summer or fall were included in the stringent dataset whereas a less-stringent dataset also included measurements made in mid-summer (7 studies, data on 22 species). In tropical systems we excluded studies that

96	measured herbivory only during the first month of growth of new leaves. We did so because for
97	most species this period represents an underestimate of annual herbivory; Coley and Barone [21]
98	report that 68%, 47%, and 29% of damage occurs during leaf expansion of species found in
99	tropical wet forests (shade-tolerant species), tropical wet forests (gap specialists), and tropical dry
100	forests, respectively. For tropical systems, we only included data on mature leaves (standing or
101	marked measures) in the stringent dataset. In the less stringent dataset we also included studies of
102	young and old leaves, or of an unknown mixture of leaves (13 studies, 104 species), plus studies
103	measuring herbivory on leaves that were two months old (2 studies, 22 species).
104	Leaf herbivory values were often extracted directly from figures using Web Plot Digitizer
105	(http://arohatgi.info/WebPlotDigitizer/). We also took note when studies mentioned the main
106	herbivores but few studies explicitly quantified herbivore visitation rates especially on different
107	plant species. Of the studies that noted the type of damage, 45% report that insects are the main
108	herbivores (32% Lepidoptera, 20% Coleoptera, and 6% Orthoptera), while 5% identify
109	crustaceans, and 4% report vertebrates as the principal consumer. We acknowledge that our
110	selection criteria might exclude the impact of certain herbivores, such as grassland grazers for
111	which herbivory is not commonly studied by measuring percent leaf area damaged.

112

113 (c) Phylogenetic inference

We first created a backbone family-level phylogeny for the 161 families in the database using the Phylomatic v.3 online tool based on the APG megatree [http://phylodiversity.net/phylomatic; 35]. Species were then added to the tree as polytomies using currently accepted taxonomy [e.g., 36]. We resolved this tree to the species level based on published plastid *rbcL* sequence from NCBI's GenBank (www.ncbi.nlm.nih.gov/genbank), which was available for 487 out of 1058

species. For another 202 species we were able to obtain sequence data from congeners (hereafter"placeholder" species).

We aligned sequences using BioEdit v.7.1.3 [37] and excluded sequences shorter than 500 121 nucleotides. Using the family-level tree as a constraint we reconstructed phylogenetic relationships 122 using maximum likelihood (ML) assuming a general time reversible model with 25 rate categories 123 in RAxML v7.3.1 [38, 39]. We made the branch lengths of the tree proportional to time using 124 Pathd8 v1.0 (http://www2.math.su.se/PATHd8/) and fossil calibrations (table S2). Finally, we 125 generated a posterior distribution of dated trees using BEAST v1.7.4 [http://beast.bio.ed.ac.uk; 126 127 40], using the ML topology as a constraint and allowing branch lengths to vary assuming a general time reversible model of DNA evolution, as selected as the best fit model by jModelTest v2.1.1 128 [41]. We used a log-normal relaxed clock to estimate substitution rate variation and time calibrated 129 130 the analysis using 19 fossil dates (table S2) as log-normal priors. We ran six BEAST analyses each lasting 33 to 72 million generations, where the first 8 to 15 million generations were discarded as 131 132 burn-in. Each of the separate post-burn-in runs was then concatenated, and the maximum clade 133 credibility values were extracted using TreeAnnotator. Phylogenetic inference was conducted on CIPRES (www.phylo.org). 134 Species for which no sequence data was available (367 species) were included as polytomies at 135

the least inclusive node, mostly at the level of genus, although 27 species had to be added at their
family node (the Nexus formatted script of the unresolved phylogeny is available as a
supplementary material). We then resolved polytomies using a Bayesian approach that fits a birth-

death diversification model, generating 1000 fully resolved trees [42].

140

141 (d) Phylogenetic comparative analysis

We used phylogenetic comparative methods to analyse differences in leaf herbivory across plant taxa and to characterize the evolutionary model that best explained variation in herbivory across lineages of vascular plants. First, we assessed the fit of a Brownian Motion (BM) model of stochastic evolution (Equation 1);

146

$$dX(t) = \sigma dB(t) \tag{1}$$

This equation describes the amount of change in trait (X) over a short time period (t). The term (dB(t)) are normal random variables with a mean of zero and variance of ($\sigma^2 dt$). The rate of stochastic evolution is thus (σ^2)[43, 44]. Second, we compared the fit of the Hansen model [45, 46] that assumes an Ornstein-Uhlenbeck (OU) process in which traits evolve toward an evolutionary optimum in a way that is consistent with evolution by stabilizing selection, while genetic drift causes traits to evolve away from this optima in a stochastic manner [43, 44]. This model is represented by equation 2:

154

$$dX(t) = \alpha \left[\theta - X(t)\right]dt + \sigma dB(t)$$
⁽²⁾

155 The additional term represents stabilizing selection, where (α) is the strength of selection 156 pulling the trait value towards the optimum trait value (θ).

157 We compared the fit of alternative models using sample-size corrected Akaike information criteria (AICc) scores [47]. First we compared the fit of simple OU and BM models ('OU1' and 158 159 'BM1') where all branches in the phylogeny had a fixed evolutionary optimum (θ , OU1 model) and rate of stochastic evolution (σ^2 , OU1 and BM1 models). Second, we allowed evolutionary 160 parameters to vary with plant traits. Complex models assumed multiple rates of stochastic 161 162 evolution (BMS) or multiple evolutionary optima (OUM) using the following trait categories: 1) life-history variation – annual, intermediate, and perennial, 2) woodiness – woody and non-woody, 163 and 3) growth form – tree, vine, shrub, graminoid, and forb. Multi-optima and multi-rate models 164 require information on expected trait values for each fitted clade. For this purpose, ancestral state 165

166 estimates were inferred from extant tip data using the *make.simmap* function in *phytools* package [48] in R [49] that simulates stochastic character mapping using a continuous-time reversible 167 Markov chain process. More complex models, that permitted variation in (σ^2) , (θ_i) , and (α) 168 simultaneously [44], would not convergence on stable ML estimates. 169 Analyses were conducted on natural log-transformed leaf herbivory rates (x + 1) using the 170 OUwie v.1.33 package [44] in R v.3.0 [49]. Because large differences in herbivory between major 171 lineages, it was not possible to run complex models across the entire phylogeny, we thus analysed 172 each major taxonomic group separately. Basal angiosperms, basal eudicots, and basal coreeudicots 173 were grouped into a single paraphyletic clade referred to as 'other angiosperms' since these 174 species did not fit as monophyletic groupings with other major lineages (see Fig. 2B for the 175 number of species within each lineage). 176

178 Supplemental tables

- 179 **Table S1.** Mean annual percent leaf tissue consumption as measured by four unpublished studies with taxonomic information and trait
- data. Study (A): data collected by R.M. Godfrey in Trinidad in 2011. Study (B): collected M.T.J. Johnson and G.T. Broadhead in
- 181 Eastern U.S.A. in 2009. Study (C): collected by M.T.J. Johnson in Eastern Canada and U.S.A. in 2012. Study (D): collected by C.J.M.
- 182 Thomsen in Ontario Canada in 2012.

atudu	species	sunonum	taxonomic	woodinoss	growth	life-history	mean leaf
study		synonym	lineage	wooumess	form	me-mstory	damage (%)
А	Asclepias curassavica		Asterids	Non-Woody	Shrub	Perennial	0.80
A	Bidens pilosa		Asterids	Non-Woody	Forb	Annual	0.40
А	Cassia fruticosa		Rosids	Woody	Tree	Perennial	5.00
А	Chrysothemis pulchella		Asterids	Non-Woody	Forb	Perennial	2.17
А	Lantana camara		Asterids	Woody	Vine	Perennial	5.58
A	Laurentia longiflora	Hippobroma longiflora	Asterids	Non-Woody	Forb	Perennial	0.20

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186

			taxonomic		growth	life-history	mean leaf
study	species	synonym	lineage	woodiness	form		damage (%)
А	Mimosa pudica		Rosids	Non-Woody	Forb	Intermediate	2.27
A	Psiguria umbrosa	Anguria umbrosa; Citrullus umbrosa	Rosids	Woody	Vine	Perennial	0.67
А	Spermacoce assurgens		Asterids	Non-Woody	Shrub	Intermediate	2.20
A	Stachytarpheta jamaicensis	,	Asterids	Non-Woody	Forb	Intermediate	8.33
A	Trimezia martinicensis		Monocots	Non-Woody	Forb	Perennial	0.20
В	Ambrosia artemisiifolia		Asterids	Non-Woody	Forb	Annual	1.15
В	Aquilegia canadensis		Other Angiosperms	Non-Woody	Forb	Perennial	1.43
В	Asclepias incarnata		Asterids	Non-Woody	Forb	Perennial	0.88
В	Asclepias syriaca		Asterids	Non-Woody	Forb	Perennial	2.68
В	Borrichia frutescens		Asterids	Woody	Shrub	Perennial	0.54
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188

	species		taxonomic		growth	1.6 1.4	mean leaf
study		synonym	lineage	woodiness	form	life-history	damage (%)
В	Campanula americanum		Asterids	Non-Woody	Forb	Annual	0.73
В	Capsella bursa-pastoris		Rosids	Non-Woody	Forb	Annual	0.10
В	Carduus nutans		Asterids	Non-Woody	Forb	Perennial	7.05
В	Cassia fasciculata		Rosids	Non-Woody	Forb	Annual	3.19
В	Datura stramonium		Asterids	Non-Woody	Forb	Annual	0.24
В	Decodon verticillatus		Rosids	Woody	Shrub	Perennial	1.21
В	Erigeron annuus		Asterids	Non-Woody	Forb	Annual	2.39
В	Hordeum vulgare		Monocots	Non-Woody	Graminoid	Annual	0.00
В	Hypericum perforatum		Rosids	Non-Woody	Forb	Perennial	2.81
В	Impatiens capensis		Asterids	Non-Woody	Forb	Annual	2.01
В	Ipomoea hederacea		Asterids	Non-Woody	Vine	Annual	12.49
В	Ipomoea purpurea		Asterids	Non-Woody	Vine	Annual	3.94
						T 11	7

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			taxonomic		growth	life-history	mean leaf
study	species	synonym	lineage	woodiness	form		damage (%)
В	Juglans nigra		Rosids	Woody	Tree	Perennial	7.78
В	Kalmia latifolia		Asterids	Woody	Shrub	Perennial	1.81
В	Lathyrus latifolius		Rosids	Non-Woody	Vine	Perennial	0.91
В	Liriodendron tulipifera		Magnoliids	Woody	Tree	Perennial	3.90
В	Lobelia cardinalis		Asterids	Non-Woody	Forb	Perennial	1.13
В	Lolium multiflorum		Monocots	Non-Woody	Graminoid	Annual	0.07
В	Mimulus ringens		Asterids	Non-Woody	Forb	Perennial	1.55
В	Oenothera biennis		Rosids	Non-Woody	Forb	Intermediate	6.29
В	Oenothera humifusa		Rosids	Non-Woody	Forb	Perennial	1.10
В	Oenothera laciniata		Rosids	Non-Woody	Forb	Annual	0.56
В	Phlox drummondii		Asterids	Non-Woody	Forb	Annual	0.07
В	Picea rubens		Gymnosperms	Woody	Tree	Perennial	0.00
						Table continues	on the next pag

192

			taxonomic		growth		mean leaf
study	species	synonym	lineage	woodiness	form	life-history	damage (%)
В	Polystichum acrostichoides		Ferns	Non-Woody	Forb	Perennial	2.31
В	Rhus glabra		Rosids	Woody	Shrub	Perennial	4.55
В	Rhus typhina		Rosids	Woody	Shrub	Perennial	0.75
В	Robinia pseudoacacia		Rosids	Woody	Tree	Perennial	7.34
В	Rumex acetosella		Other Angiosperms	Non-Woody	Forb	Perennial	3.23
В	Rumex hastatulus		Other Angiosperms	Non-Woody	Forb	Perennial	1.82
В	Sabatia angularis		Asterids	Non-Woody	Forb	Annual	4.08
В	Senecio vulgaris		Asterids	Non-Woody	Forb	Annual	2.44
В	Solanum carolinense		Asterids	Non-Woody	Forb	Perennial	3.05
В	Solanum ptychanthum		Asterids	Non-Woody	Forb	Annual	8.86
						Table continues	an the next nee

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- 4 J	species		taxonomic		growth	1.0 1.	mean leaf
study		synonym	lineage	woodiness	form	life-history	damage (%)
В	Solidago sempervirens		Asterids	Non-Woody	Forb	Perennial	1.62
В	Spartina alterniflora		Monocots	Non-Woody	Graminoid	Perennial	0.04
В	Taraxacum officinale		Asterids	Non-Woody	Forb	Annual	1.58
В	Trillium erectum		Monocots	Non-Woody	Forb	Perennial	5.23
В	Trillium grandiflorum		Monocots	Non-Woody	Forb	Perennial	0.00
В	Lorinseria areolata	Woodwardia areolata	Ferns	Non-Woody	Forb	Perennial	1.70
В	Yucca filamentosa		Monocots	Woody	Shrub	Perennial	0.11
С	Abies balsamea	Abies balsamifera	Gymnosperms	Woody	Tree	Perennial	3.40
С	Asplenium platyneuron		Ferns	Non-Woody	Forb	Perennial	2.28
C	Brasenia schreberi		Other Angiosperms	Non-Woody	Forb	Perennial	2.36

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196

			taxonomic		growth		mean leaf
study	species	synonym	m lineage	woodiness	form	life-history	damage (%)
С	Cystopteris fragilis		Ferns	Non-Woody	Forb	Perennial	6.90
С	Gymnocarpium dryopteris		Ferns	Non-Woody	Forb	Perennial	4.85
С	Juniperus communis		Gymnosperms	Woody	Tree	Perennial	0.30
С	Larix americana		Gymnosperms	Woody	Tree	Perennial	6.52
С	Nuphar variegatum		Other Angiosperms	Non-Woody	Forb	Perennial	6.03
С	Nymphaea odorata		Other Angiosperms	Non-Woody	Forb	Perennial	9.77
С	Osmunda claytoniana		Ferns	Non-Woody	Forb	Perennial	1.30
С	Phegopteris connectilis		Ferns	Non-Woody	Forb	Perennial	11.55
С	Phegopteris dryopteris		Ferns	Non-Woody	Forb	Perennial	1.97
С	Picea glauca		Gymnosperms	Woody	Tree	Perennial	2.03
						Table continue	s on the next near

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	species		taxonomic		growth		mean leaf
study		synonym	lineage	woodiness	form	life-history	damage (%)
С	Picea mariana		Gymnosperms	Woody	Tree	Perennial	0.00
С	Pinus banksiana		Gymnosperms	Woody	Tree	Perennial	0.60
С	Pinus resinosa		Gymnosperms	Woody	Tree	Perennial	4.27
С	Polypodium virginianum		Ferns	Non-Woody	Forb	Perennial	0.74
С	Taxus canadensis		Gymnosperms	Woody	Shrub	Perennial	0.04
С	Thuja occidentalis		Gymnosperms	Woody	Tree	Perennial	1.91
D	Larix laricina		Gymnosperms	Woody	Tree	Perennial	0.60
D	Picea abies		Gymnosperms	Woody	Tree	Perennial	0.06
D	Pinus strobus		Gymnosperms	Woody	Tree	Perennial	0.28
D	Pontederia cordata		Monocots	Non-Woody	Forb	Perennial	1.88
D	Sagittaria latifolia		Monocots	Non-Woody	Forb	Perennial	1.01
D	Tsuga canadensis		Gymnosperms	Woody	Tree	Perennial	0.88

node	node year (mya)		year (mya)
Lamiales	44.3	Malpighiales	49
Angiosperms	131.0	Myrtales	88.2
Bignoniaceae	35	Pandanales	65.0
Caprifoliaceae	36	Poales	68.1
Caryophyllales	83.5	Proteales	98.0
Cornales	86.0	Sapindales	65
Dilleniaceae	51.9	Solanales	44.3
Ericales	91.2	Vitaceae	57.9
Fabales	59.9	Zingiberales	83.5
Gymnosperms	310		

Table S2. Nineteen fossil ages modelled as log-normal priors. Means of priors were set to 0 with a
standard error of 1 and an offset value as listed in the table [dates were gathered from 50, 51].

203 Supplemental tables

204 Table S3. Comparison of evolutionary model fits for each major lineage. Top values represent median Akaike Information Criterion

- values corrected for sample size (AICc) from comparative analyses performed on the distribution of phylogenetic trees. Below these
- values we report the proportion of trees that show strong support for each model ($\Delta AICc \leq 4$). Models with the strongest support
- 207 ($\Delta AICc \le 4$) are shown in bold. Models include: Brownian Motion models of stochastic evolution with either a single rate of evolution
- 208 (BM1) or multiple rates for different traits (BMS), and Ornstein-Uhlenbeck models of stabilizing selection with either a single
- evolutionary optimum (OU1) or multiple optima for different traits (OUM). Up to three different multi-rate and multi-optima models
- are possible for each lineage base on plant traits: life-history (annual, intermediate, and perennial), woodiness (woody, non-woody),
- and growth form (tree, shrub, vine, forb, and graminoid). The "other angiosperms" lineage represents a paraphyletic grouping of species
- not contained as monophyletic groups of species in the other major lineages and includes basal angiosperms, basal eudicots, and basal
- 213 coreeudicots.
- 214
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220 Ta	able S3
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1.	DM1		BMS		011		OUM	
lineage	BMI	growth form	woodiness	life-history	- 001	growth form	woodiness	life-history
Forns	106.79				82.56			
rerns	0.045				1.000			
Cumposporms	57.82	•			40.28	•		
Gymnosperms	0.000				1.000			
Magnaliida	89.43	89.91			77.39	79.16		
wiagnomus	0.047	0.022			0.992	0.961		
Monocots	474.14	443.58	458.10	474.52	352.95	344.11	354.54	354.19
Withocots	0.000	0.000	0.000	0.000	0.061	0.923	0.015	0.011
Rosids	2333.1	2283.77	2307.06	2321.3	1401.5	1400.54	1390.57	1403.4
KUSIUS	0.000	0.000	0.000	0.000	0.006	0.000	0.810	0.000
Astorida	1083.7	1026.10	1068.28	1055.1	649.55	638.78	635.41	652.15
Asterius	0.000	0.000	0.000	0.000	0.001	0.799	0.859	0.000
Other	338.88	318.27	334.17	337.54	190.55	193.34	188.80	192.96
Angiosperms	0.000	0.000	0.000	0.000	0.935	0.047	0.937	0.559

222	Table S4. Parameter estimates for the stabilizing selection models. Maximum likelihood (ML) parameter estimates for each major
223	lineage for the Ornstein-Uhlenbeck models. See table S5 for the parameters of the poorly fitting BM models. Models include the single
224	evolutionary optimum (OU1) and the multiple optima models for different traits (OUM). Up to three different multi-rate models are
225	possible for each lineage base on plant traits: life-history (annual, intermediate, and perennial), woodiness (woody, non-woody), and
226	growth form (tree, shrub, vine, forb, and graminoid). Estimates are median parameter values of the ML optima value across 1000
227	phylogenetic trees. Values in parentheses are median 95% confidence intervals that were calculated for each tree and thus incorporate
228	both phylogenetic uncertainty and uncertainty in the maximum likelihood estimates. Parameters include the rate of stochastic evolution
229	σ^{2} , the strength of stabilizing selection α , and the ML evolutionary optimum θ , which is a phylogenetically informed estimate of the
230	rate of herbivory for each group [43, 44].
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Table S4

linoago		OU1		OUM Life-History					
nneage	α	σ^2	θ	α	σ^2	θ-Annuals	θ – Interm.	θ – Per.	
Ferns	1.13 (1.13- 1.18)	1.7 (0.82-2.64)	5.83 (4.01-8.3)						
Gymnosperms	0.14 (-0.07- 0.36)	0.13 (-0.06-0.33)	0.87 (0.42-1.47)						
Magnoliids	0.09 (-0.05- 0.25)	0.12 (-0.04-0.32)	8.44 (5.47-12.18)	-					
Monocots	1.05 (0.03- 2.64)	3 (0.07-7.2)	3.11 (2.25-4.01)	1.12 (0.03-2.64)	3.37 (0.07-7.14)	1.85 (-0.19-5.26)		3.17 (2.3-4.14)	
Rosids	2.99 (2.99 - 3)	4.58 (4.03-5.2)	8.16 (7.5-8.86)	2.99 (2.99-3)	4.57 (4.02-5.2)	6.61 (3.87-10.8)	5.43 (2.3-11.4)	8.25 (7.57-8.97)	
Asterids	3.21 (3.2-3.25)	5.35 (4.38-6.52)	4.31 (3.73-4.97)	3.2 (3.2-3.25)	5.31 (4.33-6.51)	3.09 (1.48-5.71)	3.75 (2.1-6.3)	4.44 (3.8-5.16)	
Other Angiosperms	2.04 (2.04- 2.06)	3.19 (2.13-4.44)	6.16 (4.8-7.81)	2.03 (2.03-2.06)	3.09 (2.07-4.26)	8.9 (1.94-2.29)	2.05 (-0.15-9.3)	6.27 (4.87-7.98)	

Table continues on the next page

lineage	α	σ^2	θ-Non- Woody	θ- Woody	α	σ^2	θ- Shrub	θ-Tree	θ- Forb	θ-Vine	θ- Graminoid
Ferns											
Gymnosperms	-										
	-				0.16	0.2 (-	12.12	7.58	_		
Magnoliids					(-0.12-	0.13-	(5.75-	(4.77-			
					0.5)	0.6)	23.38)	11.05)			
-	1.2	3.51	2.99	3.77	1.25	2.95	2.43	5.21	5.03	3.07	1.52
Monocots	(0.03-	(0.07-	(2.12-	(1.75-	(0.04-	(0.08-	(0.53-	(2.08-	(3.5-	(0.99-	(0.86-
	2.64)	7.17)	3.94)	6.93)	2.65)	6.24)	6.61)	11.64)	6.94)	6.71)	2.46)
	2.99	4.49	5.48	8.63	2.99	4.54	8.63	8.49	5.97	7.43	
Rosids	(2.99-	(3.95-	(4.28-	(7.9-	(2.99-	(3.99-	(6.82-	(7.7-	(4.58-	(4.92-	
	3)	5.08)	6.94)	9.42)	3)	5.17)	10.85)	9.35)	7.7)	10.94)	
	3.21	5.02	3.08	5.55	3.21	4.99	5.02	5.94	3.02	4.3	-
Asterids	(3.21-	(4.11-	(2.45-	(4.63-	(3.21-	(4.07-	(3.75-	(4.671-	(2.36-	(2.3-	
	3.25)	6.14)	3.83)	6.61)	3.24)	6.07)	6.59)	7.468)	3.79)	7.44)	
Other	2.04	3.01	4.76	7.72	2.04	3.01	7.23	8.21	4.71	8.16	-
Angiosnorms	(2.04-	(2.01-	(3.29-	(5.55-	(2.04-	(2.01-	(4.56-	(4.79-	(3.23-	(2.94-	
Angiosperms	2.06)	4.35)	6.7)	10.55)	2.06)	4.33)	11.09)	13.42)	6.67)	20.4)	

Table S5. Parameter estimates for the stochastic evolution models: Maximum likelihood parameter estimates for each major lineage for the243Brownian Motion models of stochastic evolution with either a single rate of evolution (BM1) or multiple rates for different traits (BMS). Up to three244different multi-optima models are possible for each lineage base on plant traits: life-history (annual, intermediate, and perennial), woodiness245(woody, non-woody), and growth form (tree, shrub, vine, forb, and graminoid). Estimates are median parameter values of the ML optima value246across 1000 phylogenetic trees. Values in parentheses are median 95% confidence intervals that were calculated for each tree and thus incorporate247both phylogenetic uncertainty and uncertainty in the maximum likelihood estimates. Parameters include the rate of stochastic evolution ' σ^2 ' and the248ML evolutionary optimum ' θ ', which is a phylogenetically informed estimate of the rate of herbivory for each group [43, 44].

]	BM1		BMS Life-History					
lineage	~ ²	Δ	σ^{2-}	σ^{2-}	σ^{2-}	Δ			
	0	0	Annual	Intermediate	Perennial	0			
Forms	0.03	5.52							
F CI IIS	(0.01-0.04)	(-0.74-131.24)							
Cumnasnamms	0.03	0.71	-						
Gymnosperms	(0.01-0.05)	(-0.97-107.03)							
Magnaliida	0.04	8.78	_						
magnomus	(0.02-0.05)	(0.58-55.47)							
Monocots	0.12	3.61	0.07	-	0.11	3.62			
wonocous	(0.09-0.15)	(-0.78-85.84)	(-0.06-0.22)		(0.08-0.14)	(-0.77-81.7)			
Rosids	0.28	6.71	0.16 (0.02-	0.05	0.27	6.76			
Rosius	(0.24-0.31)	(-0.82-301.21)	0.3)	(-0.05-0.17)	(0.24-0.3)	(-0.8-270.7)			
Astorids	0.23	4.18	0.29	0.4	0.17	4.17			
Asterius	(0.19-0.27)	(-0.8-107.64)	(-0.04-0.7)	(0-0.85)	(0.13-0.2)	(-0.69-67.2)			
Other	0.2	6.38	0.001	0.22	0.18	6.42			
Angiosperms	(0.14-0.27)	(-0.97-1451.3)	(-0.002-0.005)	(-0.28-0.76)	(0.12-0.25)	(-0.96-1138.1)			

Table continues on the next page

	BN	IS Woodin	ess		BMS Growth Form					
lineage	σ ²⁻ Non- Woody	σ^{2-} Woody	θ	σ ²⁻ Shrub	σ ²⁻ Tree	σ ²⁻ Forb	σ^{2-} Vine	σ ²⁻ Graminoid	θ	
Ferns										
Gymnosperms										
				0.02	0.04			-	8.89	
Magnoliids				(-0.01-	(0.02-				(0.76-	
				0.06)	0.06)				52.07)	
	0.1	0.11	3.62	0.03	0.14	0.06	0.1	0.1	3.63	
Monocots	(0.07-	(0.03-	(-0.69-	(-0.01-	(0.01-	(0.03-	(-0.01-	(0.06-	(-0.47-	
	0.12)	0.19)	66.6)	0.09)	0.27)	0.08)	0.2)	0.14)	32.37)	
	0.11	0.28	6.58	0.25	0.27	0.11	0.09		6.76	
Rosids	(0.07-	(0.25-	(-0.79 -	(0.12, 0.28)	(0.27)	(0.07-	(0.02-		(-0.68-	
	0.15)	0.32)	247)	(0.13-0.38)	(0.23-0.3)	0.16)	0.17)		190.27	
	0.23	0.16	4.19	0.04	0.17	0.23	0.16		3.96	
Asterids	(0.17-	(0.12-	(-0.67-	0.04	(0.12-	(0.16-	(0.03-		(-0.23-	
	0.3)	0.2)	68.1)	(0.02-0.00)	0.22)	0.29)	0.3)		26.56)	
Other	0.21	0.15	6.4	0.26	0.01	0.2	0.04		6.2	
	(0.11-	(0.08-	(-0.94-	(0.1.0.42)	(-0.00-	(0.11-	(-0.01-		(-0.63-	
Angiosperms	0.31)	0.21)	850)	(0.1-0.42)	0.01)	0.29)	0.09)		128.8)	

254 Supplemental figures

255 Supplemental figure legends

Figure S1. Evolutionary parameters for the best fitting model. Comparison of the evolutionary parameters estimated from the best fitting macroevolutionary model for each major plant lineage. $'\alpha'$ represents the strength of stabilizing selection and $'\sigma^2'$ is the rate of stochastic evolution [43]. Values represent median estimates and median 95% confidence intervals over the distribution of 1000 phylogenies.

261

Figure S2. Relationship between herbivory and life-history variation. Percent leaf herbivory for
lineages that vary in life-history strategy, which represent the evolutionary optima from the
stabilizing selection model (OUM – Life-History). Values represent median percent leaf herbivory
and median 95% confidence intervals over the distribution of 1000 phylogenies. Number of
species for each group is found within data points. Annual 'other angiosperms' were poorly
sampled and has a wide 95% confidence interval (1.9% – 32.3%) that extended beyond the bounds
of the figure.

269





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