

Insect herbivory along environmental gradients

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ABSTRACT

There is a general assumption in the literature that insect herbivory increases towards the tropics, but decreases with increasing altitude. Similar generalities have been identified along other environmental gradients, such as resource, temperature, climatic and biotic gradients. However there is growing evidence in the scientific literature that such generalities are not consistent. This could be due to a number of reasons including the lack of consistency in the way herbivory is assessed such as different methodologies used by researchers, or fundamental differences in leaf damage caused by different types of insect herbivores. Here we assess 61 publications researching insect herbivory along a range of environmental gradients (both biotic and abiotic) and review the methods that researchers have used to collect their data. We found leaf chewing from samples collected in North America dominated the field and most studies assessed herbivory on a single host plant species. Thirty three percent of the studies assessed latitudinal gradients, while 10% assessed altitudinal gradients. Insect herbivory was most commonly expressed as percentage leaf damage using point herbivory. Fewer studies measured a range of different types of herbivory (such as sap sucking, leaf mining, galling, and root feeding) as leaves aged. From our synthesis, we hope that future research into insect herbivory along environmental gradients will take into account herbivory other than just leaf chewing, such as sap sucking, which may cause more damage to plants. Future research should also assess herbivory as a rate, rather than just a single point in time as damage to a young leaf may be more costly to a plant than damage to a mature or senescing leaf. Measurements of plant traits will also assist in comparing herbivory across habitats, plant species, and within species physiological variation. The

true impacts that insects have on plants via herbivory along environmental gradients are still poorly understood.

Keywords: Insect Herbivory; Gradients, Leaf Chewing; Sap Sucking; Galling; Root Feeding

1. INTRODUCTION

There is a general assumption in the literature that herbivory increases towards the tropics, but decreases with increasing altitude. However there is growing evidence that such generalities are not consistent across space, time and interacting resource gradients. These inconsistencies may be due to a variety of different methodologies used by researchers, or fundamental differences in leaf damage caused by different types of herbivores. Here we assess the current state of the literature and determine whether the study of insect herbivory along environmental gradients measuring different insect taxa can be compared across space, time and research methodologies. We also examine the biases in the type of herbivory collections that have been undertaken and advocate the use of more consistent methods that can be reproduced in all ecosystems.

Since Coley and Aide published their seminal work finding that herbivory was higher in the tropics compared to the temperate zones [1], there has been a suite of papers citing this research but not actually testing its assumptions. Researchers citing this work have failed to acknowledge the problems of using a small number of sites at each zone or the ability to compare herbivory in one habitat as a surrogate for another at similar latitudes both north and south of the equator. For example, the northern hemisphere is not a mirror image of the southern hemisphere [2] with substantial asymmetry between hemispheres leading to very different plant and animal species and associated interactions.

Another major issue with assessing insect herbivory along environmental gradients is the variation among plant species sampled within the gradient. Different plant species are found across all gradients, especially those covering tropical and temperate zones, lowlands to al-

pine areas, and coastal to inland desert regions. Along smaller gradients plants have different evolutionary relationships, different interactions with other species, and are under different competitive and symbiotic pressures both within and across species. From a structural point of view, plants have a suite of different aged leaves, with different chemical compositions [3], so measuring leaf herbivory using a “consistent” leaf structure along a gradient can be difficult when morphological and chemical aspects have not been controlled for [4-7].

Here we compare literature that has been published on insect herbivory along a range of gradients (including latitudinal, altitudinal, temperature, successional and architectural among others) and assess the methods that they have used to carry out their herbivory measurements.

2. METHODS

In this review we assessed how insect herbivory has been measured across a range of studies. We have collected information on study location, the type of insect herbivory measured, plant species, gradient, and how herbivory was measured, either as a single point in time, or measured as a rate (either over leaf lifespan or between two points in time).

A literature search was conducted in Scopus for literature with the keywords: “herbivory and insect”, “herbivory and [each of the insect order names]”. Citations and abstracts were downloaded and assessed. Each article was then assessed to determine if it was appropriate for further assessment, and a reprint was downloaded. It is known that Scopus also lists keywords in addition to the author’s keywords, with many articles not actually referring to herbivory, in any part of their paper. If herbivory (or equivalent term) was not referred to in the paper (abstract or main body) it was not included in the assessment.

3. RESULTS AND DISCUSSION

Of the 61 studies assessed over 30 years between 1982 and 2012 (**Table 1**), 28 datasets were collected from North America, eight from Europe, six from South America, five from Australia and Central America, three were from multiple regions/worldwide, and one from China. A bias towards North America is common for many research areas, but such a strong dominance was unexpected. This bias in the literature towards northern hemisphere studies is particularly problematic when attempting to make generalisations across space, time and resource gradients. North American temperate climate is very different to that found in the southern hemisphere, so direct comparisons with similar latitudes in the south can be misleading [2]. Northern Hemisphere forests are

more deciduous than those in the tropics and the southern hemisphere [8] making direct comparisons of herbivory difficult especially when using different collection and assessment techniques across the plant and insect phylogeny. Plants in deciduous forests will transfer up to 50% of leaf nitrogen and phosphorous back into the plant [9] seasonally, so insect herbivores such as aphids and sap suckers that can exploit this resource movement will capitalize on this. Chewing herbivory is also reduced by deciduousness with early autumnal coloration onset in the previous season reducing chewing damage in the next growing season [10]. This relatively high publication of studies from North America and Europe is obvious as it is where most researchers who publish in western scientific journals reside and carry out their research. Papers published in languages other than English are biased against in terms of having access to English speaking audiences, and especially Asian research journals were not identified in the literature search. This could be due to a high rejection rate of manuscripts from non native English speaking countries [11], reducing the ability of research from countries such as China and India to be exposed to a wider audience.

In the 61 studies reviewed, the type of herbivory assessed was also biased. Thirty one studies assessed leaf chewing herbivory. Only nine studies assessed sap sucking herbivory, and a further nine studies assessed a range of herbivory types. Six studies did not assess a specific herbivory type and four were reviews. Other studies assessed a range of herbivory types as well as pit, mining and galling herbivory separately. Even though chewing herbivory is the most obvious and easiest type of herbivory to measure, other herbivory types, such as sap-sucking into phloem and xylem can be more damaging to a plant. For example sap-sucking psyllids on Eucalypts in Australia can reduce sap flow by 50% and reduce leaf mass by 20% from necrotic tissue loss [12]. In addition, the mirid bug herbivore, *Capsodes infuscatus* significantly reduced the flower nectar yield of a Mediterranean geophyte, *Asphodelus aestivus* by 40% when insect herbivore density treatments were carried out [13]. A meta-analysis based on 52 papers assessing the effects of sap feeding on growth photosynthesis and reproduction of woody plants, compared to folivory (chewing damage) found that sap-feeders impose a more severe overall negative impact on plant performance than do defoliators [14]. By concentrating research efforts on one type of herbivore, particularly chewing herbivores, there may in fact be an under estimation of the true impact of all types of insect herbivory across environmental gradients.

Of the studies assessed, most were carried out on a single tree species ($n = 14$), followed by single native shrub species ($n = 11$), multiple native tree species ($n = 9$), single herb/grass species ($n = 8$), multiple native

Table 1. Review of literature assessing herbivory across a range of environmental gradients. Table includes region where data was collected, herbivory type assessed, number of plant species that data was collected from, gradient assessed, how herbivory was measured, and if it was a rate or point measurement, with major findings of the paper that were directly related to herbivory.

Author	Date	Region	Herbivory type	Plant species	Gradient	Damage measurement	Point Rate Herbivory measured	Major findings
Louda [30]	1982	North America	Gall/Mine	Multiple native shrubs	Altitude	Area damaged	Point	Predation of seeds by insects caused decline in plant population along the gradient
Louda [31]	1983	North America	Chew/Gall/Mine	Native shrub	Climatic	Percentage	Rate	Seed destruction due to herbivores significantly greater at the coastal sites then further inland.
Lincoln & Mooney [32]	1984	North America	Chewing	Native shrub	Light	Percentage	NS	With increased exposure to light there was an increase in herbivory.
Koptur [33]	1985	South America	Chewing	Native tree	Altitude	Percentage	Point	Greater herbivory at higher elevations, though insect abundance did not vary.
Collinge & Louda [34]	1988	North America	Mining	Native herb	Light	Area damaged	Point	Those plants artificially shaded had significantly more area mined. This is unusual as plants exposed to the sun are more prone to higher levels of herbivory.
Morrow & Fox [35]	1989	Australia North America	NS	Multiple native trees	Latitude	Area damaged	NS	Southern hemisphere species more damaged than Northern hemisphere species tested
Galen [36]	1990	North America	Sucking	Native herb	Altitude	NA	NS	Aphids more frequently found on plants at lower elevations, significantly lower than at higher elevations.
Coley & Aide [1]	1991	NA	NS	Metanalysis	Latitude	NA	Point	Herbivory higher in the tropics
Louda & Collinge [37]	1992	North America	Range	Native herb	Climatic	Area damaged	Rate	Increased plant stress led to increase in herbivory by chewers and leaf-miners, but not sap-feeders
Stone & Bacon [38]	1994	Australia	Chew/Suck/Mine	Native tree	Moisture	Area damaged	NS	Leaf area lost via insect herbivory increased with increasing distance from floodwater. In moisture-stressed trees, increased herbivory related to smaller leaf size.
Aizen & Patterson [39]	1995	North America	Rasping	Native shrub	Temperature	Percentage	Point	Herbivory higher in cooler temperatures
Landsberg & Gillieson [40]	1995	Australia	Chew/Mine	Multiple native trees	Climatic	Area damaged	Rate	Rates of herbivory increased with increasing site productivity and associated changes in soil, vegetation and foliar properties. No evidence to support models relating high herbivory to low-resource environment and plant stress.

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Louda & Rodman [41]	1996	North America	Chew/Suck /Mine	Native herb	Temperature	Area damaged	Rate	Shade removal increased herbivory. Insect abundances higher in the sun.
Feller & Mathis [42]	1997	Central America	Chewing	Native tree	Tree architecture	Percentage	Point	Herbivory highest in tall trees
Kelly [43]	1998	North America	Sucking	Native shrub	Altitude	NA	NS	At higher elevations there were fewer flowering shoots infested with aphids.
Uriarte & Schmitz [44]	1998	North America	Chew/Suck	Native shrub	Succession	Area damaged	Rate	Herbivores only decreased goldenrod shoot biomass in the late successional stage.
Maron [45]	1998	North America	Chew/Roots	Native shrub	Tree architecture	Area damaged	Point	No significant interaction between herbivory above or below ground.
McEvoy & Coombs [46]	1999	Worldwide	Range	Native herb	Disturbance	Modelling	NS	Herbivory by insects controlled ragwort when habitat was disturbed.
Alonso [47]	1999	Europe	Chewing	Native tree	Altitude	Area damaged	Rate	Increased in herbivory in warmer areas closes to sea level.
Fagan & Bishop [48]	2000	North America	NS	Native herb	Succession	Percentage	Rate	Removing insect herbivores increased growth of lupine at the edge region, but not in the core region.
Pennings <i>et al.</i> [49]	2001	North America	Chewing	Multiple native shrubs	Latitude	Area damaged	Rate	Evidence of latitudinal gradient in plant palatability, with herbivores showing a significant or marginally significant preference for northern plants.
Rand [50]	2002	North America	Chewing	Native shrub	Salinity	Percentage	Rate	Herbivory highest at mid-levels.
Bale <i>et al.</i> [51]	2002	N/A	Review	Review	Temperature	NA	NS	Intensity of herbivory increases with rising temperatures at constant latitude. Seed predation was lower on clipped (artificial browsing) plants at higher elevations as clipping delayed blooming and reduced the length of the growing season.
Freeman <i>et al.</i> [52]	2003	North America	Chewing	Native shrub	Altitude	Area damaged	Point	Defoliation intensity shows a significant association with previous warm winters.
Hodar & Zamora [53]	2004	Europe	Chewing	Native tree	Altitude	Percentage	Rate	Low frequency and density of galling insects on fertile soils
Cuevas-Reyes [54]	2004	Central America	Galling	Multiple trees and shrubs	Soil fertility	Galling	NS	Population dynamics of holly leaf-miner across its geographical range is complex. Mortality relates to varying host plant quality.
Gaston <i>et al.</i> [55]	2004	Europe	Mining	Native shrub	Latitude	NA	NS	No significant difference across gradient.
Andrew & Hughes [22]	2005	Australia	Chew/Suck /Mine	Native shrub	Latitude	Percentage	Rate	

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Novotny & Basset [56]	2005	NA	Review	Review	Latitude	NA	NS	Host specificity between temperate and tropical forests are difficult to assess due to differences in collection methods.
Knight & Holt [57]	2005	North America	Pit feed	Multiple trees and shrubs	Disturbance	Percentage	Rate	Insect abundance at the edge of burned areas, greater than in the interior. Herbivory greater at edge than in the interior of burned sites.
Pennings & Silliman [58]	2005	North America	Chewing	Multiple native shrubs	Latitude	Percentage	Point	High latitude plants more palatable to herbivores than low latitude plants. Low latitude plants experienced greater levels of leaf damage from consumers than did high latitude plants. If herbivores introduced early on during the invasion of a pest species, they can act as an effective biocontrol agent, with the model suggesting that the more established plants are fed on less extremely.
Fagan <i>et al.</i> [59]	2005	North America	Chewing	Native herb	Succession	Modelling	NS	Mean herbivory levels correlated negatively with plant species richness
Unsicker <i>et al.</i> [60]	2006	Europe	Chewing	Multiple native shrubs	Plant species richness	Area damaged	Point	Tallow trees that had been growing for the longest had lower levels of herbivory. Noted that there is variation in the "magnitude of herbivory" across a variety of environmental gradients, though claim most studies needed to be more robust.
Siemann <i>et al.</i> [61]	2006	North America	NS	Native tree	Succession	Area damaged	Point	High latitude plants more palatable to herbivores than low latitude plants. Plants at low latitude field sites experience greater levels of herbivore pressure than plants at high latitude sites.
Maron & Crone [62]	2006	Worldwide	Review	Review	Range	NA	NS	No significant difference across gradient.
Pennings <i>et al.</i> [63]	2007	Europe	Chewing	Multiple native shrubs	Latitude	Percentage	Point	Free living herbivory decreases with height, gall diversity increases with height.
Andrew & Hughes [24]	2007	Australia	Chew/Suck/Mine	Multiple trees and shrubs	Latitude	Percentage	Rate	Leaf herbivory decreased with height, galling increased with height.
Pontes Ribiero & Basset [64]	2007	Central America	Chew/Gall	Native tree	Tree architecture	Percentage	Point	Leaf damage decreased with latitude.
Ribeiro & Basset [64]	2007	Central America	Chew/Gall	Multiple trees and shrubs	Tree architecture	Percentage	Point	No significant difference across gradient.
Kozlov [65]	2008	Europe	Chew/Mine	Native tree	Latitude	Percentage	Point	
Sinclair & Hughes [66]	2008	Australia	Mining	Multiple native trees	Rainfall	NA	Point	

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Wolf <i>et al.</i> [67]	2008	Europe	Chewing	Native tree	Latitude/Altitude	Modelling	Point	A decrease of insect impact towards the north and higher up in the mountains.
Adams & Zhang [68]	2009	North America	Range	Multiple native trees	Latitude	Percentage	Point	Less percentage area damage per leaf in lower latitude areas of eastern North America.
Adams <i>et al.</i> [69]	2009	North America	Range	Multiple native trees	Latitude	Percentage	Point	No significant latitudinal trend in herbivory, condensed and hydrolyzable tannins, or total phenolics. Findings contradict the theory that low latitude plants are better defended.
Adams & Zhang [70]	2009	North America	Range	Multiple native trees	Latitude	Area damaged	Point	Percentage area damage per leaf was significantly less in lower latitude areas.
Adams <i>et al.</i> [69]	2009	North America/Asia	Range	Multiple native trees	Latitude	Area damaged	NS	Lowland tropical forest has significantly higher leaf herbivory than temperate forest. Used different index, which suggested different results-Percent damage "per unit time of growing season" is calculated based on an estimate of leaf lifetime, tropical lowland herbivory damage is less than temperate zone. Intensity of herbivory on leaves per unit of time, the opposite trend occurs.
Sobek <i>et al.</i> [71]	2009	Europe	Chew/Mine/Gall	Multiple native trees	Plant species richness	Percentage	Point	Only one species (Beech) showed a decline in damage due to leaf-chewing herbivores across the tree diversity gradient. No significant patterns for galls and mines.
Miller <i>et al.</i> [72]	2009	North America	Chew/Suck/Mine	Native shrub	Altitude	Percentage	Rate	Insect abundance and damage by insects decreased with increasing elevation.
del-Val & Armesto [73]	2010	South America	NS	Native tree	Latitude	Percentage	Rate	Invertebrate herbivory greater in temperate forests.
O'Neill <i>et al.</i> [74]	2010	North America	Chew/Suck/Skel	Agricultural species	CO ₂	Variable	NS	Concentration of plant compounds higher in plants grown under elevated levels of CO ₂ . Leaf skeletonizers the main cause of leaf damage.
Schuldt <i>et al.</i> [75]	2010	China	Chew/Mine/Gall	Multiple trees and shrubs	Plant Sp Rich	Area damaged	Point	Herbivory was greater with greater plant diversity.
Ballhorn <i>et al.</i> [76]	2011	Central America	Chewing	Multiple native shrubs	CO ₂ /Leaf age	Area damaged	Point	Highest herbivore damage in mature leaves under natural CO ₂ to highest damage of young leaves under elevated CO ₂

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Zhang <i>et al.</i> [77]	2011	North America	Range	Multiple native trees	Latitude	Area damaged	Rate	Leaf damage greater in warmer, lower latitude areas of eastern North America
Bjorkman <i>et al.</i> [78]	2011	NA	Review	Review	Latitude	NA	NS	Higher predator pressure in warmer climates.
Cornelissen & Stiling [79]	2011	North America	Mine/Gall	Multiple native shrubs	Salinity	NA	Rate	Positive relationship between leaf asymmetry and herbivory rates.
Garibaldi <i>et al.</i> [80]	2011	South America	Range	Native tree	Altitude	Percentage	Point	Leaf damage higher on plants from low altitude origin.
Garibaldi <i>et al.</i> [81]	2011	South America	Range	Native tree	Latitude	Percentage	Point	Leaf damage decreased with latitude.
Moles <i>et al.</i> [19]	2011	Worldwide	NS	Metanalysis	Latitude	Variable	NS	Leaf damage increases with latitude.
Blue <i>et al.</i> [82]	2011	North America	NS	Native herb	Nutrients	Area damaged	Point	Nitrogen did not influence herbivory though there were still minor effects to biomass due to insect herbivory.
Silva <i>et al.</i> [83]	2012	South America	Chewing	Native tree	Succession	Area damaged	Point	Herbivory decreased as rainy season progressed.
Silva <i>et al.</i> [83]	2012	South America	Chew/Suck	Native tree	Succession	Percentage	Rate	Herbivore diversity highest in early stage succession. Herbivory rates highest in intermediate and late stage succession.

shrub species ($n = 7$) or multiple native tree/shrub species ($n = 5$). For studies along gradients, restricting the analyses to a single host plant species can be problematic as the gradient length is also constrained by the host plant distribution, but it is the simplest way to constrain host plant variables between species. However, even within host plant species, leaf chemistry and physiological traits can be substantially different. These differences may include variation across plant genotypes and geographical ranges, leaf chemical and physiological variation across different aged leaves, localized soil and microclimatic conditions, and previous herbivore feeding on plant tissue and plant viruses [15-18]. Assessing traits enables direct analysis of herbivory in relation to not only a range of plants, but to leaves at different ages and plants at different ages. For example Moles *et al.* [19] assessed a range of plant traits and herbivory across 301 plant species from 75 sites world-wide. These traits included leaf toughness and size, polyethylene glycol-binding capacity, nitrogen digestibility, lipid concentration, ash content, force of fracture, specific leaf area, C:N ratio, delayed greening, spines, hair on mature leaves, and cyanogenesis. Therefore assessing plant trait differ-

ences along gradients would be much more informative [20], and measurements across large scale gradients at multiple sites could be more comparable.

Insect herbivory along latitudinal gradients were the most studied environmental gradient ($n = 20$) followed by altitudinal gradients ($n = 10$), with 6 studies along successional gradients, and three along climatic, and host plant architectural gradients. Coley and Aide's seminal 1991 paper [1] was one of the crucial synthesis of information to give future researchers the testable hypotheses that there is more herbivory in the tropics versus the temperate zones. It is now also becoming recognized from trends in the literature that altitudinal gradients are not just smaller scale latitudinal gradients-both have their own unique differences, and thus are both equally important to assess. Climatic gradients are also becoming a more useful way to assess potential impacts of climate change [21]. They incorporate both variation in temperature and rainfall, rather than just assessing changes in herbivory along latitudinal gradients [22] which is usually a surrogate for changes in temperature and is particularly important for understanding the impacts of climate change on insect/plant interactions.

Percentage damage of leaf tissue was more widely measured than amount of leaf tissue damage per size of leaf (24 studies versus 19 studies). By using percentage herbivory data, researchers commonly arcsin transform their data to “normalize” it for standard univariate statistical analysis. This analysis of proportional data after arcsine square root transformation should not be used [23]. Instead, logistic regression and logit transformation of actual tissue area damaged (normalized by total leaf area) has greater interpretability and higher power than proportional data that has been arcsin transformed [23] and enables data to be analysed and interpreted correctly.

Assessing herbivory from leaf emergence to leaf senescence can be difficult to compare changes along gradients. Here we found 27 studies used point herbivory, while 18 used rate of herbivory, and 16 studies were non-specific in how herbivory was assessed. The importance of using consistent methods can be illustrated by Andrew and Hughes [22]. In 2005, they did the first broad-scale test for a latitudinal gradient in herbivory made with consistent methods, in similar habitat type, over the entire lifespan of leaves (phyllodes). They assessed different types of leaf damage (chewing, sap-sucking and mining herbivory) along the entire coastal latitudinal range of a single host plant, *Acacia falcata*. Even though the range was relatively short (1150 km) it did go from a temperate zone into a sub-tropical zone of Australia. With these consistent methods they found no significant differences in the rate of herbivory among latitudes sampled. Andrew and Hughes also assessed herbivory along this gradient and compared it to herbivory on the same host plant transplanted to a warmer climate [24] and found that rates of herbivory did not significantly differ between the transplanted individuals and plants endemic to the sites within the natural range. This suggests that the methods used to compare herbivory along gradients, whether they be latitudinal, altitudinal, climatic, or environmental, need to be consistent, and assessing the rate of herbivory is crucial to such comparisons [25]. Low-man [25] found that rates of herbivory were fourfold higher when using herbivory assessed over time compared to point sampled herbivory demonstrating that rates of herbivory were far more informative than simply measuring herbivory as a snap-shot in time.

Insect herbivory was most commonly assessed as leaf chewing herbivory at a single point in time (**Table 1**). The amount of leaf tissue missing was measured as obvious leaf feeding damage with most studies not recording a range of important observations relating to true damage to the plant. Leaf longevity of evergreen tree species ranges from under 100 days to over 12 years [4-6] and this has huge consequences for plant investment into leaf tissue. There is a trade-off between leaf longevity, construction costs for the plant producing the leaf, and

photosynthetic rates [7]. Measurement of leaf damage by insect herbivores should consider leaf age and lifespan. This can only be done via measuring rates of herbivory across the leaf lifespan, and not done via point assessments, unless the leaves are deciduous and the leaf lifespan is easily calculated.

General trends in how insect herbivory may change along biotic or abiotic gradients for different trophic groups is still unclear. For classic gradients, such as those done at different latitudes, the method used to assess herbivory plays a crucial role in the results found. The amount of herbivory has generally been reported as being higher in the tropics than at more temperate latitudes [15,26]. Coley and Aide's [1] and Coley and Barone's [26] generalizations have been widely accepted (Coley and Barone paper cited 525 times as of April 2012: Scopus database). However, these generalizations are based on literature compilations comparing studies that used a variety of methodologies, performed under a range of environmental conditions, and using plant species from a variety of phylogenies with different chemical and mechanical properties [1,27,28]. The type of herbivory measured also plays a particularly important role, for example leaf chewing herbivores will have very different impacts to sap suckers, galls and leaf miners. Leaf age will also play an important role in determining the herbivore damage seen on plants.

4. CONCLUSION

Most studies assessing insect herbivory along environmental gradients have concentrated on latitudinal gradients with a bias toward chewing herbivores in the Northern Hemisphere. Future research into insect herbivory along gradients should assess herbivory caused by different types of herbivores rather than concentrate on chewers which are much easier to assess in the field but do not give a complete picture with regard to the impact of total insect herbivory on plant species. Future studies should also assess herbivory as a rate, rather than just a single point in time. This could be done by assessing herbivory across the leaf lifespan, or as a rate of herbivory that can be directly compared between host plant species and sample sites. Ideally knowing leaf life span and measuring herbivory at known leaf ages is also important, particularly for leaves that live for more than a single growing season. Assessing herbivory in relation to plant and leaf trait changes is also crucial as this will allow within and between species comparisons across a variety of environmental gradients. Plant traits (morphological and chemical) can act as defences against herbivores both by reducing herbivore performance directly and attracting natural enemies [29]. Such incorporation of more specific and comparable functional plants traits

and how they change with different types of herbivory will become invaluable in assessing if generalizations can be made to assess insect herbivory across environmental gradients.

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