

# Can latitudinal studies predict potential effects of global climate change on insect herbivore - host plant interactions?

Richard A. Niesenbaum\*

Biology Department, Muhlenberg College, Allentown, PA 18104, USA

## ABSTRACT

Broad scale ecological theory predicts that latitudinal variation in primary productivity will influence interactions between plants and their insect herbivores. Specifically, it has been hypothesized that herbivore-plant interactions are more intense and plant defenses are more developed at lower latitudes than at higher latitudes where productivity is lower. However, the ultimate outcome of insect-plant interactions may not be so easily predictable because it could be determined not only by plant traits at a particular location, but also by productivity driven trophic dynamics, insect population size, individual insect feeding rates, and other latitude specific ecological factors. In this paper, I review the prior work on how insects, plants, insect-plant interactions, and tri-trophic interactions with specific regard to insect herbivory vary with latitude. Because these latitudinal gradients encompass the range of temperatures expected with climate change, I use this prior work to predict how that change could influence complex ecological interactions between insects, host plants and insect predators. This led to the predictions that with warming, rates of herbivory will increase, there will be a lag in any concomitant increase in plant defense with these increases in herbivory, there should be a shift towards greater top-down control of herbivory, and specialist herbivores may be at greater risk. Insight on limitations of the predictive power of latitudinal studies and suggestions for future research in this area are offered.

**KEYWORDS:** climate change, herbivory, latitudinal effects, plant defense, tri-trophic interactions

## INTRODUCTION

The average surface temperature of the Earth is likely to increase by 1.1-6.4°C by the end of the 21st century and this increase is progressing faster than previously predicted [1]. One of the more challenging goals of ecological entomology is to predict how these changes in temperature will affect insect populations and communities. There has been much research on how climate change might influence the physiology of individual insects, insect population abundances, and community biodiversity [2]. It is also widely recognized that biological interactions involving insects such as pollination, herbivory, and predation play an important role in the maintenance of biodiversity and in the provision of ecosystem services [3]. These complex ecological interactions are greatly affected by the biophysical environment as well. Thus, to truly understand the potential impact of global climate change on individual insect species we must also understand how this change will impact the ecological interactions in which they participate [3-4]. However, the influence that climate change can have on complex ecological interactions is much more insidious and less frequently considered than the effects on individual species, thereby, limiting our predictive power of the impact of climate change on insect species.

One reason why the potential for climate change to influence ecological interactions of insects with other organisms is less frequently studied is that it is difficult to manipulate climatic variables

---

\*niesenba@muhlenberg.edu

over the scale of these interactions as they occur in the field. One proxy for the predicted temporal change in climatic factors, specifically warming temperature, is the gradual change of this factor over small spatial scales with latitude. The mean temperature at sea level ranges from 20°C to -10°C or about 1°C per 145 Km from the tropics through temperate zones (Fig. 1) [1]. Latitudinal studies of natural communities can directly address how they may respond to warming, and extrapolating from these studies may be the best available approach for predicting how global changes in temperature will influence ecological interactions in the future [5]. This is particularly true for wide ranging insect-plant associations.

The objective of this paper is to review latitudinal studies on terrestrial insects, plants and their interactions with specific regard to herbivory, and to assess the potential of this work to predict how these interactions might change as temperatures increase with global climate change. Although it is recognized that temperature is not the only global climate change driver that may affect biological interactions (e.g., increases in CO<sub>2</sub>) [4],

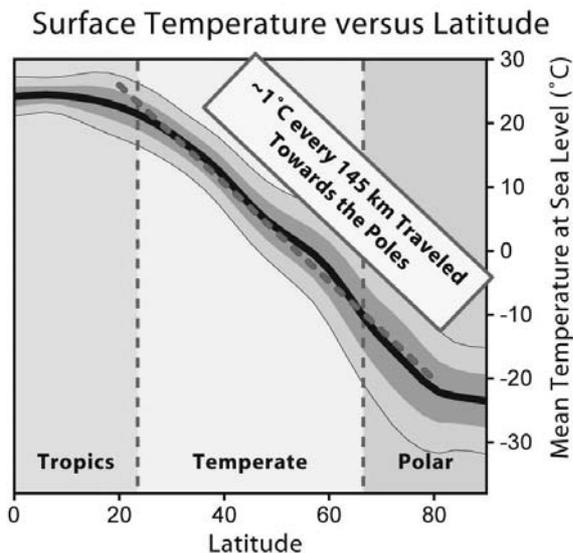
it is the single variable that changes with latitude at the same scale as that predicted with global climate change. Also, temperature has been reported as the dominant abiotic factor directly affecting herbivorous insects, it has been shown to affect their development, survival, range and abundance, and consumption rates of plants, and there is little evidence that CO<sub>2</sub> or UVB directly affect insect herbivores [4, 6]. However, the potential of these other climate change drivers to interact with changes in temperature to influence insect-plant interactions will also be addressed in this review.

### Latitudinal studies

Ecologists have long investigated latitudinal trends. This was initially driven by the desire to answer questions about why species diversity is higher at lower latitudes [7]. Other trends have also been observed with decreasing latitude including increased productivity, and length of growing or active season [8-10]. Numerous studies have also documented patterns of genetic diversity along latitudinal gradients; common patterns include a correlation between allelic frequencies and latitude [11-12], the loss of rare alleles along post-glacial colonization routes [13-14], and in some cases, a loss of genetic diversity at range limits resulting in greater diversity at mid-latitudes [14].

### Insects

Much of the latitudinal work on insects has focused on documenting that the latitudinal ranges of insects are generally smaller at lower than at higher latitudes (Rapoport's Rule). This has been shown to be due to the wider range of physiological tolerances at higher latitudes as a result of increases in climatic variation [15]. Other work has focused on latitudinal gradients in body size (Bergmann's Rule), though studies on various insect groups indicate that this varies greatly among taxonomic groups [16]. Long term studies of insect distributions have revealed shifts away from the equator and towards the poles for a variety of taxa [17-19]. Votivism, or the number of generations completed in one year in the field, has also been shown to increase with decreasing latitude for a variety of insect groups [20]. Life cycle stages such as the emergence of adults tend to be completed more rapidly at warmer, lower latitudes, but not all life-cycle stages show the



**Fig. 1.** This plot shows the variation in surface temperature as a function of latitude, after removing the effects of varying surface elevation. Farther from the equator, temperature falls off by approximately 1°C for every 145 km traveled North-South as indicated by the dashed line. Image created by Robert A. Rohde/Global Warming Art with land-sea surface temperature data [75-76].

same response [21]. Specialist insects which are dependent on specific seasonal plant resources may exhibit less of a response in voltinism to changing temperature. Diapause or the timing of emergence may be temperature dependent, but is more often driven more by photoperiod [22]. In some cases, temperature has the opposite than expected effect on diapause where higher temperatures slow diapause development and emergence occurs earlier at cooler sites because of limited time for emergent phases of the life-cycle [22-24]. Also, because termination of diapause is often a response to fluctuating abiotic cues, insects may be able to adjust as the abiotic conditions change, and thus the presence of winter diapause could moderate the effects of climatic warming because of this adjustment [22].

There is evidence that there is greater herbivory by insects at lower latitudes, possibly due to the fact that abiotic conditions are less severe and exert less control of insect populations, or because plant productivity is more predictable [25]. Independent of latitude, warmer temperature has been shown to increase consumption rates of leaves perhaps due to increased metabolism, and insect growth and development [2, 6] and latitudinal studies reflect this with higher herbivory rates at warmer/lower latitudes [21]. Temperature has been shown to be a more important factor for influencing lepidopteran species richness in northerly regions [26] while water availability is more limiting at lower latitudes [27].

### **Plants**

Latitudinal studies on plants show increased primary productivity, rates of photosynthesis, and length of growing season moving from the poles towards the tropics [8-10]. Plant growth rate, also greater at lower latitudes, may be a more significant determinant of insect herbivory than rates of production because fast growing plants have more nutrient content and less defensive chemistry, and tend to be more palatable than slower growing plants [8, 28-29]. One study, however, found differences in leaf toughness by latitude, but no difference in the carbon:nitrogen ratio [30]. A number of studies have demonstrated higher phenolics, tannins, a greater complexity of chemical constituents, greater mechanical defenses, greater

frequency of plants with alkaloids and latex, and reduced leaf protein content at lower latitudes [25, 31-33].

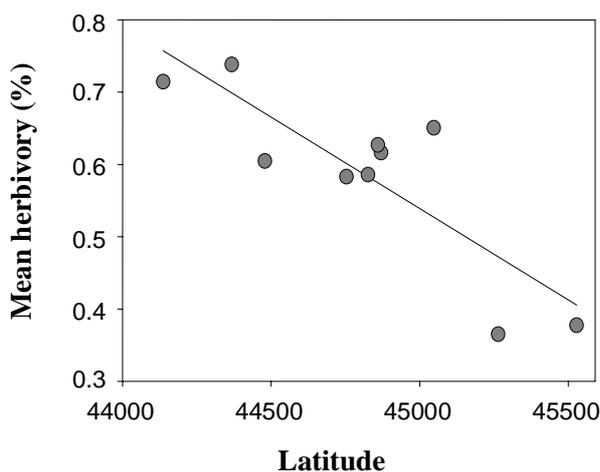
Latitudinal variation in traits such as toughness and variation in palatability and herbivory have been shown to persist when plants are reared in a common garden suggesting that this variation is constitutive and is likely under genetic control [25, 34]. These results suggest that greater herbivory pressure at lower, tropical latitudes may have provided selection for greater defense. Gene flow over large geographical distances can be limited and populations may be locally adapted, which could mute the relationship between abiotic conditions, leaf characteristics, herbivory, and herbivore predation [35]. Other traits that relate to plant-insect interactions like leaf N, carbon:nitrogen ratio, volatile release, and specific leaf area may not be under genetic control and are more closely tied to abiotic conditions rather than plant genotype [36].

### **Herbivory**

Given that host plant communities vary somewhat predictably in their diversity, structure, and composition across biogeographic zones and that insect herbivory is tied to productivity which varies with latitude, the strength of plant-insect interactions should vary predictably across these zones [37]. This is supported by a well studied, wide ranging insect-plant association that is composed of temperate salt marsh species [34, 38-39]. These studies are significant because they focused on multiple plant species at sites within high and low latitude locations. They consistently found that northern plants were eaten more by herbivorous insects than southern plants. These differences were driven by differences in per capita effects and or interaction strength among species, and not by insect diversity or abundance. Reduced herbivory at lower latitudes was attributed to higher leaf toughness, and lower concentrations of palatable polar extracts and leaf nitrogen [38]. These latitudinal differences are consistent with standard predictions that insect-plant interactions are more intense at lower latitudes and that plants have evolved greater leaf defense in response to this pressure. However, they also consider climate, length of growing season, salinity and other factors

as possible causes. In a pilot study of *Lindera benzoin* in 10 sites along a gradual latitudinal gradient, the mean proportion of leaves with herbivory decreased with increasing latitude (Fig. 2). Another study found that the rate of decrease of folivory with increasing latitude was greater in warmer regions suggesting the intensity of insect-plant interactions might be more susceptible to temperature change in warmer temperate climates [40]. One study, however found no significant differences in herbivory with latitude for insects from a diversity of feeding guilds, but only on a single host plant [30]. The latitudinal gradient in herbivory is further validated by the fossil record which shows a greater diversity of insect leaf feeding during warm climate intervals [41].

Another latitudinal pattern in herbivory is that at lower latitudes a larger proportion of the leaf consumption by insects is on younger leaves because older leaves are better defended than ephemeral younger leaves [25]. This pattern varies with the successional stage of the forest and small scale differences in productivity [25, 42]. Because insect herbivores must find not only a specific plant, but one at the appropriate developmental stage, the interaction is more tightly bound and any phenological changes caused by independent response of plants and insects to warming



**Fig. 2.** In a pilot study of *L. benzoin* at 10 sites along a continuous latitudinal gradient within PA. The mean proportion of leaves with herbivory significantly decreased as latitude increased. From: Mooney and Niesenbaum, Unpublished data.

could have significant impacts on herbivore-plant communities [43-44]. Although well documented at lower latitudes, study of this phenomenon is lacking in temperate zones.

### Tri-trophic control of insect herbivores

Herbivore populations are controlled by a combination of availability and quality of food resources (bottom-up) and predators and parasitoids (top-down). The relative importance of top-down and bottom-up controls has been disputed for decades [45-47]. More recently, it has been hypothesized that as productivity increases (high latitudes to low latitudes) there is a shift from bottom-up control to top-down control [8, 48-50]. Support for this has been found in aquatic systems and in several terrestrial systems [8, 42, 48-50], and in a meta-analysis comparing tri-trophic interactions in tropical versus temperate communities [51]. In addition to differences in primary productivity, higher insect, plant, and ecosystem structural diversity at lower latitudes may also be a cause of greater top-down control closer to the equator [40]. It should be noted that because insect parasitoids and their hosts have discrete generations, the timing of which often depends on temperature, climate change would likely disrupt the interaction [52].

### Predictions

Based on our current knowledge of latitudinal effects one can make the following predictions about how gradual increases in temperature with global climate change might influence plant-insect interactions:

#### 1. As temperate ecosystems warm, rates of herbivory will increase

Multiple factors may contribute to this. Populations of insects will be under reduced control by abiotic conditions. Also, because insects tend to be more vagile than plants, their migration northward should exceed that of local plant hosts which should increase both the diversity and abundance of insects in relation to plants. Warming has the potential to increase insect diversity particularly at higher latitudes [53]. There is already evidence of recent increases in insect outbreaks [54-55] and diversity [30] at northern latitudes. With warming there could be an increase in voltinism, and per

capita consumption rates. Warming will increase rates of primary production, plant growth rate, and the proportion of younger leaves all of which could lead to increased herbivory.

## **2. There will be a lag in any concomitant increase in plant defense with increases in herbivory**

Many aspects of plant defense are under genetic control, and higher levels of defense at lower latitudes are likely constitutive, evolved traits in response to higher levels of herbivory [25, 34, 56]. For many defensive traits, it may take generations for plants to exhibit any evolved response to increased pressure by herbivores. Induced responses and defense related volatile release, leaf C and N may respond more quickly as these are more closely tied to abiotic conditions. Plants, especially woody perennials, tend to have much longer generation times than insects further intensifying this lag. Many temperate zone herbivorous insect species have already shifted their distribution northward in response to recent warming [57-59]. Given their rapid generation time, insects have already begun to experience genetic change in response to recent climate change [55], which may allow them to adapt to northern host plants therefore intensifying herbivory during this lag.

## **3. There should be an eventual shift to greater top-down control of herbivory, but existing, more complicated tri-trophic interactions will be easily disrupted**

As productivity increases with warming, there theoretically should be a shift from greater bottom-up to more top-down control of herbivory. Even over small spatial scales, increases in productivity due to the formation of tree fall gaps, led to greater predator/parasitoid control of herbivory [42]. However, due to the greater complication of having three trophic levels that depend on one another's development time and other phenological characteristics, changing climate could disrupt such complex interactions. Alterations in seasonal synchrony among plants, insect herbivores, and their natural enemies in response to recent warming has already been observed and is resulting in higher levels of herbivory i.e. less top-down control [60], and range shifts may also result in a decoupling of tri-trophic interactions because of different rates of dispersal [61].

Furthermore, it has been argued that generalist natural enemies of host specific herbivores may restrict host-plant range (enemy free space hypothesis) [62]. Disruptions of these interactions may therefore indirectly influence the ranges of plants, herbivores, and their enemies. Tri-trophic interactions including host plant selection and cuing of herbivore predators and parasitoids rely on the release of plant volatile organic compounds (VOCs). Changes in temperature may disrupt VOC emission patterns by plants and their perception by insects thereby further disrupting these complex interactions [63]. Unfortunately, latitudinal studies of tri-trophic interactions and of VOC release by plants are few in number, particularly in temperate zones.

## **4. Specialist herbivores and their interactions with their host plants have greater potential to be altered or disrupted by climate warming**

Constrained ecological relationships like herbivores that specialize on one or a few plant host species may be more easily altered by migration and population changes that occur with climate change [64]. Species that exhibit highly evolved host plant interactions over narrow ranges or in "at-risk" microhabitats are in danger of extinction [65]. Specialist Lepidoptera species are declining in the United Kingdom, while generalist species are increasing [65-67]. The general consensus is that the greater redundancy in interactions exhibited by generalists leads to greater stability of that community; however, others have argued that climate variables will have a greater effect on generalists than on specialists which are more dependent on host plant diversity [68]. When insects not only specialize on a particular species, but also can only consume leaves of a specific age, the compounded effects of changes in phenology and host plant abundance with warming will severely impact those herbivore-plant interactions [42-43].

## **Limitations**

Using latitudinal studies to predict the effects of temperature rise on insect-plant interactions has many obvious limitations. One such limitation is that although they are helpful in predicting response to gradual temperature change, they do not readily take into account other climate change

drivers that either will interact with temperature or independently influence insect-plant interactions. Predicted increases in atmospheric CO<sub>2</sub> will most definitely impact the plant side of the interaction with potential increases in primary production, and shifts towards higher carbon:nitrogen ratios. This could result in increases in carbon based defenses such as phenolics and tannins [44] and decreases in alkaloid concentrations [69]. It has been shown that elevated CO<sub>2</sub> and O<sub>3</sub> decreased defense and increased levels of herbivory in Quaking Aspen [70]. Others predict that warmer temperatures will result in increased nitrogen availability and carbon-based secondary compounds are therefore expected to decrease [71]. Increases in CO<sub>2</sub> should not directly influence insect herbivores [2, 72]. Changes in nitrogen availability that may also occur with climate change [4] and would likely influence the carbon-nitrogen balance in plants which ultimately can determine rates of photosynthesis and allocation to defense [44].

Increased solar ultraviolet-B (UV-B) radiation reaching the earth's atmosphere, due to stratospheric ozone depletion is another consequence of climate change [73]. Although this is not expected to directly affect insects [2], it may indirectly affect them because plants often respond to increased UV-B radiation with the production of phenolics which also serve as deterrents to insect feeding. Other drivers such as increased cloud cover and changes in water balance could also influence productivity and allocation to defense which in turn may drive levels of herbivory. It is clear that multiple factors acting simultaneously will result in higher order effects and do present a challenge to predicting the future responses of ecological interactions and communities to global climate change [4].

Generalizations of results from where multiple populations are sampled only at extremes of a latitudinal gradient may be limited by the confounding influences of genetic relatedness, plasticity and latitude. Many herbivory-related traits in plants are genetically determined, and in any given species, populations at either end of a latitudinal distribution are likely to be more closely related as a result of local adaptation or common ancestry. Thus, plants from nearby sites at a particular latitude could share herbivory-related

traits because they are closely related. This could lead to the spurious appearance of latitude-driven differences in herbivory and herbivory related traits. Studies of wider ranging plant-insect interactions along a gradual gradient could alleviate this problem.

Many latitudinal studies of insect-plant interactions and host plant quality do not apply consistent methods, and have been limited in their geographic distribution resulting in inconsistent and contradictory results [74]. Results also appear to be ecosystem dependent so research from a diversity of ecosystems should be a priority [74]. Collaborative research agendas like the World Herbivory Project supported by the Australian Research Council, Macquarie University, the Australian Geographic and the Amazon Conservation Association ought to help mitigate this. Project participants are applying standard methods at approximately 100 sites around the world to study herbivory.

## CONCLUSIONS

To better predict the future distribution and abundance of insects, the possible effects of climate change must be considered from the perspective of multi-trophic interactions, and should consider differential responses of species at each trophic level. One way to do this may be to study these interactions over latitudinal clines in temperature using consistent methods that consider several traits simultaneously. Future work needs to consider insect herbivore and host plant phenotypic and genotypic flexibility and responses of each to climate change in concert [2]. We must consider climate change effects not only in terms of differential range expansion, but also with respect to habitat change, fragmentation and loss; and species invasion which are occurring concurrently with climate change. Despite the predicative potential of latitudinal studies especially when considered together with experimental variation of climate variables and local response to recent warming, actual impact on complex insect-plant interactions may unfortunately only become apparent in the long term.

## ACKNOWLEDGEMENTS

Amanda Meier, Erin Jo Tiedeken, Marten Edwards, and Beth Johnson provided insightful comments

in the development of this work. Many of the ideas from this paper came from a collaborative research project supported by NSF-DBI Award 0442049, and work and discussion with Emily Mooney, Norris Muth, Marten Edwards, and Christine Ingersoll.

## REFERENCES

1. Intergovernmental Panel on Climate Change. 2007, *Climate Change 2007 - The Physical Science Basis*, Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K. B., Tignor, M. and Miller, H. L. (Eds.), Cambridge University Press, Cambridge, 996.
2. Bale, J. S., Masters, G. J., Hodkinson, I. D., Awmack, C., Bezemer, T. M., Brown, V. K., Butterfield, J., Buse, A., Coulson, J. C., Farrar, J., Good, J. E. G., Harrington, R., Hartley, S., Jones, T. H., Lindroth, R. L., Press, M. C., Symrnioudis, I., Watt, A. D. and Whittaker, J. B. 2002, *Glob. Change Biol.*, 8, 1.
3. Gilman, S. E., Urban, M. C., Tewksbury, J., Gilchrist G. W. and Holt, R. D. 2010, *Trends Ecol. Evol.*, 25, 325.
4. Tylianakis, J. M., Didham, R. K., Bascombe, J. and Wardles, D. A. 2008, *Ecol. Lett.*, 11, 1351-1363.
5. Pennings, S. and Bertness, M. D. 1999, *Curr. Topics Wetland Biogeochem.*, 3, 100.
6. Niesenbaum, R. A. and Kluger, E. C. 2006, *Environ. Entomol.*, 35, 600.
7. Ricklefs, R. E. 2004. *Ecol. Lett.*, 7, 1.
8. Fraser, L. H. and Grime, P. J. 1997, *Oikos.*, 80, 499.
9. Benowicz, A., L'Hirondelle, S. and El-Kassaby, Y. 2001, *Forest Ecol. Manag.*, 154, 23.
10. Pärtel, M., Laanisto, L. and Zobel, M. 2007, *Ecol.*, 88, 1091.
11. Gauthier, P., Gouesnard, B., Dallard, J., Redaelli, R., Rebourg, C., Charcosset, A. and Boyat, A. 2002, *Theor. Appl. Genet.*, 105, 91.
12. Nason, J. D., Hamrick, J. L. and Fleming, T. H. 2002, *Evol.*, 56, 2214.
13. Williams, J. H. and Arnold, M. L. 2001, *Int. J. Plant Sci.*, 162, 1097.
14. Grivet, D. and Petit, R. J. 2002, *Mol. Ecol.*, 8, 1351.
15. Addo-Bediako, A., Chown, S. L. and Gaston, K. J. 2000, *Proc. R. Soc. Lond. B.*, 267, 739.
16. Hawkins, B. A. and Lawton, J. H. 1995, *Oecol.*, 102, 31.
17. Crozier, L. 2002, *Wildlife Response to Climate Change*, Root, T. L. and Schneider, S. H. (Eds.), Island Press, Washington DC, 57.
18. Karban, R. and Strauss, S. Y. 2004, *Ecol. Entomol.*, 29, 251.
19. Parmesan, C. and Yohe, G. 2003, *Nature*, 421, 37.
20. Corbet, P. S., Suhling, F. and Soendgerath, D. 2005, *Int. J. Odonat.*, 9, 1
21. Fiedling, C. A., Whittaker, J. B., Butterfield, J. E. L. and Coulson, J. C. 1999, *Funct. Ecol.*, 13, 65.
22. Corbet, P. S. 2003, *J. Entomol. Soc. Brit. Columbia*, 100, 3.
23. Tauber, M. J., Tauber, C. A. and Masaki, S. 1986, *Seasonal Adaptations of Insects*, Oxford University Press, Oxford.
24. Lee, R. E., Chen, C. P. and Denlinger, D. L. 1987, *Science*, 238, 1415.
25. Coley, P. D. and Aide, T. M. 1991, *Plant-Animal Interactions: Evolutionary Ecology in Tropical and Temperate Regions*, Price, P. W., Lewinsohn, T. M., Fernandes, G. W. and Benson, W. W. (Eds.), Wiley & Sons, NY, 25.
26. Turner, J. R. G., Gatehouse, C. M. and Corey, C. A. 1987, *Oikos.*, 48, 195.
27. Stefanescu, C., Peñuelas, J. and Filella, I., 2003, *Global Change Biol.*, 9, 1494.
28. Cebrian, J. and Duarte, C. M. 1994, *Funct. Ecol.*, 8, 518.
29. Coley, P. D., Bryant, J. P. and Chapin III, F. S. 1985, *Science*, 230, 895.
30. Andrew, N. R. and Hughs, L. 2005, *Oikos.*, 108, 176.
31. Lewinsohn, T. M. 1991, *Chemoecol.*, 2, 64.
32. Basset, Y. 1994, *Acta Oecol.*, 15, 181.
33. Hallam, A. and Read, J. 2006, *J. Trop. Ecol.*, 22, 41.
34. Salgado, C. S. and Pennings, S. C. 2005, *Ecol.*, 86, 1571.
35. Pennings, S. C., Selig, E. R., Houser, L. T. and Bertness, M. D. 2003, *Ecol.*, 84, 1527.
36. Muth, N. Z., Kluger, E. C., Levy, J. H., Edwards, M. J. and Niesenbaum, R. A. 2008, *Ecosci.*, 15, 182.

37. Agrawal, A. A., Lau, J. A. and Hambäck, P. A. 2006, *Quart. Rev. Biol.*, 81, 349.
38. Siska, E. L., Pennings, S. C., Buck, T. L. and Hanisak, M. 2002, *Ecol.*, 83, 3369.
39. Pennings, S. C., Siska, E. L. and Bertness, M. D. 2001, *Ecol.*, 82, 1344.
40. Zhang, Y., Adams, J. and Zhao, D. 2011, *Ecol. Res.*, 26, 377.
41. Adams, J. M., Brusa, A., Soyeong, A. and Ainuddin, A. N. 2010, *Rev. Palaeobot. Palyno.*, 162, 63.
42. Richards, L. A. and Coley, P. D. 2007, *Oikos*, 116, 31.
43. Aide, T. M. and Londoño, E. C. 1989, *Oikos*, 55, 56.
44. Ayres, M. P. 1993, *Biotic interactions and global change*. Kareiva, P. M., Kingsolver, J. G. and Huey, R. B. (Eds.), Sinauer, Sunderland, MA, 75.
45. Rosenzweig, M. 1971, *Science*, 171, 385.
46. Fretwell, S. 1977, *Perspect. Biol. Med.*, 20, 169.
47. Oksanen, L., Fretwell, S. D. Arruda, J. and Niemelä, P. 1981, *Am. Nat.*, 118, 240.
48. Carpenter, S. R., Kitchell, J. F. and Hodgson, J. R. 1985, *BioSci.*, 35, 634.
49. Wootton, J. T. and Power, M. E. 1993, *Proc. Nat. Acad. Sci. USA*, 90, 1384.
50. Forkner, R. E. and Hunter, M. D. 2000, *Ecol.*, 81, 1588.
51. Dyer, L. A. and Coley, P. D. 2001, *Multitrophic Level Interactions*. Tscharrntke, T. and Hawkins, B. A. (Eds.), Cambridge University Press, Cambridge, 67.
52. Hassel, M. P. and Pacala, S. W. 1990, *Philos. T. Roy. Soc. B*, 330, 203.
53. Turner, J. R. G., Gatehouse, C. M. and Corey, C. A. 1987, *Oikos*, 48, 195.
54. Esper, J., Büntgen, U., Frank, D. C., Nievergelt, D. and Liebhold, A. 2007, *Proc. R. Soc. B*, 274, 671.
55. Régnière, J. 2009, *Unasylva.*, 60, 37.
56. Basset, Y. 1994, *Acta Oecol.*, 15, 181.
57. Battisti, A., Stastny, M., Buffo, E. and Larson, S. 2006, *Glob. Change Biol.*, 12, 662
58. Jepsen, J. U., Hagen, S. B., Ims, R. A. and Yoccoz, N. Z. 2008, *Oecol.*, 134, 95.
59. Tran, J. K., Ylioja, T., Billings, R. F., Régnière, J. and Ayers, M. P. 2007, *Ecol. App.*, 17, 882.
60. Stireman III, J. O., Dyer, L. A., Janzen, D. H., Singer, M. S., Lill, J. T., Marquis, J. R., Ricklefs, R. E., Gentry, G. L., Hallwachs, W., Coley, P. D., Barone, J. A., Greemey, H. F., Connahs, H., Barbosa, P., Morais, H. C. and Diniz, I. R. 2005, *Proc. Nat. Acad. Sci. USA*, 102, 17384.
61. Van der Putten, W. H., Marcel, M. and Visser, M. E. 2010, *Phil. Trans. R. Soc. B*. 365, 2025.
62. Stamp, N. 2001, *Oecol.*, 128, 153.
63. Yuan, J. S., Himanen, D. J., Holopainen, J. K., Chen, F. and Stewart, C. N. 2009, *Trends Ecol. Evol.*, 24, 323.
64. Scriber, J. M. 2002, *Eur. J. Entomol.*, 99, 225.
65. Lewis, S. L. 2006, *Phil. Trans. R. Soc. B.*, 361, 195.
66. Thomas, J. A. 2005, *Phil. Trans. R. Soc. B.*, 360, 339.
67. Franco, A. M. A., Hill, J. K., Kitschke, C., Collingham, Y. C., Roy, D. B., Fox, R., Huntley, B. and Thomas, C. D. 2006, *Glob. Change Biol.*, 12, 1545.
68. Menéndez, R. 2007, *Tijdschr. Entomol.*, 150, 355.
69. Ziska, L. H., Emche, S. D., Johnson, E. L., George, K., Reed, D. R. and Sicher, R. C. 2005, *Glob. Change Biol.*, 11, 1798.
70. Kopper, B. J. and Lindroth, R. L. 2003, *Oecol.*, 134, 95.
71. Peñuelas, J., Gordon, C., Llorens, L., Nielsen, T., Tietema, A., Beier, C., Bruna, P., Emmett, B., Estiarte, M. and Gorissen, A. 2004, *Ecosyst.*, 7, 598
72. Fajer, E. D., Bowers, M. D. and Bazzaz, F. A. 1991, *Oecol.*, 87, 37.
73. Manning, W. J. and Tiedemann, V. 1995, *Envir. Poll.*, 88, 219.
74. Moles, A. T., Bonser, S. P., Poore, A. G. B., Willis, I. R. and Foley, W. J. 2010, *Funct. Ecol.*, 25, 380.
75. New, M., Lister, D., Hulme, M. and Makin, I. 2000, *Climate Res.*, 21, 1.
76. Reynolds, R. W., Rayner, N. A., Smith, T. M., Stokes, D. C. and Wang, W. 2002, *J. Climate*, 15, 1609.