

Disentangling the effects of primary productivity and host plant traits on arthropod communities

Gina M. Wimp¹  | Shannon M. Murphy² 

¹Department of Biology, Georgetown University, Washington, DC, USA

²Department of Biological Sciences, University of Denver, Denver, CO, USA

Correspondence

Gina M. Wimp

Email: gmw22@georgetown.edu

Funding information

National Science Foundation, Grant/Award Number: 1026000 and 1026067

Arthropods are one of the most diverse groups of organisms and depend, directly or indirectly, on autotroph primary production. Primary production along with plant traits such as nutritional quality, physical and chemical defences, all affect the performance of primary consumers. These bottom-up effects have a significant impact on measures of insect herbivore abundance and fitness that vary across herbivore guilds and diet breadth (Vidal & Murphy, 2018). It follows then that variability in plant quantity and quality should impact arthropod community composition.

Early models of food web structure predicted that enhanced primary productivity extends food-chain length and thus diversity (Oksanen et al., 1981; Polis et al., 1998), but this relationship has been debated extensively (Post, 2002). Empirical studies have found positive (Oksanen & Oksanen, 2000; Persson et al., 1992; Polis et al., 1998; Schoener, 1989; Thompson & Townsend, 2005), negative (Jepsen & Winemiller, 2002; Pimm & Kitching, 1987), or no relationship (Briand & Cohen, 1987; Post et al., 2000) between productivity and trophic diversity. Often these studies confound primary productivity with changes in plant community diversity. From a biodiversity perspective, enhanced productivity alone (plant species diversity effects controlled) should promote increased consumer diversity (e.g. Rosenzweig, 1995; Tilman, 1986). Enhanced primary productivity can promote consumer diversity by: a correlated rise in plant quality that allows nitrogen-sensitive species to persist (e.g. Huberty & Denno, 2006), increased plant biomass and architectural complexity (diversity and abundance of feeding niches) that supports additional consumer species (Haddad et al., 2000; Lawton, 1983; Moran, 1980; Siemann, 1998), and/or by indirectly enhancing prey resources for consumers at higher trophic levels (Abrams, 1995; Siemann, 1998). Alternatively, top predators may eliminate intraguild prey species under high-productivity conditions (Morin, 1999) offsetting increases in species richness arising from enhanced niche diversity (Moran, 1980; Siemann, 1998; Suding et al., 2005).

The first study to examine how food web structure is altered through trophic dynamics extending solely from changes in plant production, not plant community composition, was conducted by Wimp et al. (2010). They found that in *Spartina* marshes, increased primary production via fertilization alters arthropod community structure and composition across the entire food web, but higher trophic level species demonstrated the strongest responses (Wimp et al., 2010). However, even within a monoculture, plants and arthropods respond to fertilization differently. Murphy et al. (2012) found that plant quality increased with a minimal increase in biomass in a northern marsh whereas in a southern marsh plant biomass increased with a minimal increase in quality; consumers responded more readily to increases in plant quality than biomass. The impact of plant productivity on arthropod communities has been highly variable among and even within systems, perhaps because different plant traits likely vary simultaneously in productivity experiments, and different groups of arthropods may respond to particular traits or sets of correlated traits. Determining the independent effects of plant biomass versus leaf traits on the arthropod community is experimentally daunting.

In this issue of *Functional Ecology*, Lu et al. (2021) fill this knowledge gap by examining how arthropod communities are affected by productivity and plant traits. They conducted an impressive experiment to tease apart the separate and combined effects of plant biomass and leaf traits on arthropod diversity by replicating monocultures of 15 different plant species from 4 families. They found that above-ground net primary production (ANPP) positively affected arthropod species richness and abundance. Furthermore, after controlling for plant productivity, they found that arthropod species richness, but not abundance, was positively affected by enhanced plant quality. However, both arthropod species richness and abundance were negatively affected by declining plant quality. The effects of ANPP and plant quality on the arthropod community

may be driven by an increase in overall resources, which leads to greater arthropod abundance and thereby higher species richness. It is interesting that the impacts of declining plant quality more consistently impacted arthropod species richness and abundance. Importantly, the methods they used to separate quantity and quality can be employed by other researchers as they did not manipulate plant traits experimentally, they simply measured multiple plant traits during the course of their experiment and then teased apart the impact of plant traits on arthropod responses statistically.

Many studies examining arthropod communities give a general overview but do not break-down differences in feeding behaviour that may lead to variable responses among taxa. Notably, Lu et al. (2021) investigated the feeding behaviour of the arthropods in their community to make specific predictions about which groups would be most affected by plant biomass and leaf traits. The positive impacts of ANPP on arthropod species richness and abundance were driven by three orders (Diptera, Coleoptera and Neuroptera) because larvae require large amounts of plant resources or greater plant resources led to more prey for predators. Similarly, the positive impact of plant quality on arthropod species richness was also driven by Diptera and Coleoptera. However, the strong negative impact of low plant quality on arthropod diversity was driven by Hymenoptera and Hemiptera, perhaps because higher lignin content makes it more difficult for Hemipterans to pierce plant tissues. Differences in how taxa respond are important because the dominant taxa differ across systems (e.g. Orthoptera in grasslands, Hemiptera in salt marshes), which may explain variable responses across studies.

Lu et al. (2021) clearly demonstrate that researchers need to quantify leaf traits in addition to overall measures of biomass when examining the impacts of plant productivity on arthropod diversity. Furthermore, this article helps us to understand variable responses across systems. Because herbivores with different feeding behaviours (e.g., sucking vs. chewing) dominate different systems, we must consider which plant traits likely have the largest impact on herbivores in that system. It is also important to consider whether the dominant organisms in the system are generalists that are more versatile in their selection of different host plants compared to specialists. Thus, Lu et al. (2021) gives researchers examining the bottom-up effect of plants on arthropods a path forward for uniting seemingly disparate outcomes across systems and building theory.

ORCID

Gina M. Wimp  <https://orcid.org/0000-0002-6255-109X>

Shannon M. Murphy  <https://orcid.org/0000-0002-5746-6536>

REFERENCES

- Abrams, P. A. (1995). Monotonic or unimodal diversity-productivity gradients: What does competition theory predict? *Ecology*, *76*, 2019–2027. <https://doi.org/10.2307/1941677>
- Briand, F., & Cohen, J. E. (1987). Environmental correlates of food chain length. *Science*, *238*, 956–960. <https://doi.org/10.1126/science.3672136>
- Haddad, N. M., Haarstad, J., & Tilman, D. (2000). The effects of long-term nitrogen loading on grassland insect communities. *Oecologia*, *124*, 73–84. <https://doi.org/10.1007/s004420050026>
- Huberty, A. H., & Denno, R. F. (2006). Consequences of nitrogen and phosphorus limitation for the performance of two planthoppers with divergent life-history strategies. *Oecologia*, *149*, 444–455. <https://doi.org/10.1007/s00442-006-0462-8>
- Jepsen, D. B., & Winemiller, K. O. (2002). Structure of tropical river food webs revealed by stable isotope ratios. *Oikos*, *96*, 46–55. <https://doi.org/10.1034/j.1600-0706.2002.960105.x>
- Lawton, J. H. (1983). Plant architecture and the diversity of phytophagous insects. *Annual Review of Entomology*, *28*, 23–39. <https://doi.org/10.1146/annurev.en.28.010183.000323>
- Lu, X., Zhao, X., Tachibana, T., Uchida, K., Sasaki, T., & Bai, Y. (2021). Plant quantity and quality regulate the diversity of arthropod communities in a semi-arid grassland. *Functional Ecology*. <https://doi.org/10.1111/1365-2435.13742>
- Moran, V. C. (1980). Interaction between phytophagous insects and their *Opuntia* hosts. *Ecological Entomology*, *5*, 153–164.
- Morin, P. (1999). Productivity, intraguild predation, and population dynamics in experimental food webs. *Ecology*, *80*, 752–760.
- Murphy, S. M., Wimp, G. M., Lewis, D., & Denno, R. F. (2012). Nutrient presses and pulses differentially impact plants, herbivores, detritivores and their natural enemies. *PLoS ONE*, *7*(8), e43929.
- Oksanen, L., Fretwell, S. D., Arruda, J., & Niemelä, P. (1981). Exploitation ecosystems in gradients of primary productivity. *The American Naturalist*, *118*, 240–261. <https://doi.org/10.1086/283817>
- Oksanen, L., & Oksanen, T. (2000). The logic and realism of the hypothesis of exploitation ecosystems. *The American Naturalist*, *15*, 703–723. <https://doi.org/10.1086/303354>
- Persson, L., Diehl, S., Johansson, L., Anderson, G., & Hamrin, S. F. (1992). Trophic interactions in temperate lake ecosystems: A test of food chain theory. *The American Naturalist*, *140*, 59–84. <https://doi.org/10.1086/285403>
- Pimm, S. L., & Kitching, R. L. (1987). The determinants of food chain length. *Oikos*, *50*, 302–307.
- Polis, G. A., Hurd, S. D., Jackson, C. T., & Sanchez-Piñero, F. (1998). Multifactor population limitation: Variable spatial and temporal control of spiders on Gulf of California Islands. *Ecology*, *79*, 490–502.
- Post, D. M. (2002). The long and short of food-chain length. *Trends in Ecology & Evolution*, *17*, 269–277. [https://doi.org/10.1016/S0169-5347\(02\)02455-2](https://doi.org/10.1016/S0169-5347(02)02455-2)
- Post, D. M., Pace, M. L., & Hairston, N. G. Jr (2000). Ecosystem size determines food-chain length. *Nature*, *405*, 1047–1049.
- Rosenzweig, M. L. (1995). *Species diversity in space and time*. Cambridge University Press.
- Schoener, T. W. (1989). Food webs from large to small. *Ecology*, *70*, 1559–1589.
- Siemann, E. (1998). Experimental tests of effects of plant productivity and diversity on grassland arthropod diversity. *Ecology*, *79*, 2057–2070.
- Suding, K. N., Collins, S. L., Gough, L., Clark, C., Cleland, E. E., Gross, K. L., Milchunas, D. G., & Pennings, S. (2005). Functional- and abundance-based mechanisms explain diversity loss due to N fertilization. *Proceedings of the National Academy of Sciences of the United States of America*, *102*, 4387–4392. <https://doi.org/10.1073/pnas.0408648102>
- Thompson, R. M., & Townsend, C. R. (2005). Energy availability, spatial heterogeneity and ecosystem size predict food-web structure in streams. *Oikos*, *108*, 137–148.
- Tilman, D. J. (1986). A consumer-resource approach to community structure. *American Zoologist*, *26*, 5–22. <https://doi.org/10.1093/icb/26.1.5>
- Vidal, M. C., & Murphy, S. M. (2018). Bottom-up vs. top-down effects on terrestrial insect herbivores: A meta-analysis. *Ecology Letters*, *21*, 138–150.
- Wimp, G. M., Murphy, S. M., Finke, D. L., Huberty, A. F., & Denno, R. F. (2010). Increased primary production shifts the structure and composition of a terrestrial arthropod community. *Ecology*, *91*, 3303–3311. <https://doi.org/10.1890/09-1291.1>