

Resource-driven terrestrial interaction webs

PETER W. PRICE*

*Department of Biological Sciences, Northern Arizona University, Flagstaff, Arizona
86011-5640, USA*

Terrestrial food webs based on living plants may well represent 75% of global terrestrial biodiversity. The majority of component species are specialists and a large proportion is parasitic as herbivores and carnivores, with consequences for high sensitivity to heterogeneity on a variety of scales. Relatively large primary producers support relatively small insect herbivores and carnivores, with plants providing both food and habitat, making resource-driven effects very strong. Complexity of resources provided by plants, with influences up the food web, is generated by at least seven major factors: (i) plants as food; (ii) plants as habitat; (iii) the physical traits of plants such as size, toughness and trichomes; (iv) traits of plants that require evolutionary responses by herbivores in terms of crypsis, phenological synchrony, life history and behavioral adaptations; (v) the constitutive chemicals in plants; (vi) the induced changes in plants caused by herbivory; and (vii) landscape and biogeographic variation in vegetation types and food web richness. No other trophic level has such a wide-ranging impact on other trophic levels. But such broad impact makes the term 'food web' overly narrow and inadequate. The term 'interaction web' is preferable, aiding recognition of the many kinds of interactions that pass up food webs from living plants. Any claim that top-down impact is stronger than bottom-up influences is necessarily couched in a narrow sense of biomass or numbers reduction.

Key words: bottom-up influences; insect herbivores; living plants; parasitoids.

THE SPECIAL NATURE OF PLANT-BASED FOOD WEBS

Terrestrial food webs based on living plants include a high proportion of global biodiversity. Incorporating worldwide an estimated 310 000 plant species, 360 000 phytophagous insects and 400 000 carnivorous insects, the resulting food webs contribute about 75% or more of global terrestrial biodiversity. Yet, not a single food web, out of the thousands available for study, is understood in terms of the mechanistic explanation of distribution, abundance and dynamics of all components. Thus, this conference on 'Food web dynamics in spatial heterogeneity under multiple disturbances' is the beginning of a major challenge to ecologists worldwide. In terrestrial food webs

based on plants there are three major points to keep in mind:

- (1) The sources of heterogeneity.
- (2) The size and specificity of the component species.
- (3) The relative strengths of connections between bottom-up and top-down influences. These will be discussed briefly in turn.

The sources of heterogeneity

Heterogeneity originates for many different reasons and at many different scales. As heterogeneity is likely to be linked to the size of the organisms that experience the variation and their specificity, these two points are obviously tightly associated. Heterogeneity becomes extreme for small, specialized organisms and extreme heterogeneity forms an important basis for understanding high species richness: an inevitable lock-step association when the first trophic level is living plants. A cycle of reciprocating intensity

*Author to whom correspondence should be addressed. Email: peter.price@nau.edu

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builds through the trophic system when species interact in specific ways, for the interactions create their own kind of heterogeneity.

Large-scale heterogeneity starts with steep gradients of latitude, altitude, precipitation and temperature on which broad vegetation categories can be mapped. Within such vegetation types landscape dynamics create rivers, lakes, valleys, slopes, mountains, swamps, bogs and marshes. In this variable landscape plant species grow in zones and patches depending on soil type, moisture, aspect and many biotic influences such as competition, herbivory, mutualism and parasitism. The 'habitat templet', as Southwood (1977) called it, is complex and rich in heterogeneity.

In the first trophic level of plants, the herbaceous species are the most diverse and the most specific in their ecological requirements, and they have speciated rapidly. This cause-and-effect interaction of specificity, heterogeneity and species richness is very clear. Shrubs and trees have slower speciation rates and are less diverse than herbs and grasses (Levin & Wilson 1976). Nevertheless, the plants in one area provide a very rich set of resources as host plants providing food and shelter for insect herbivores.

Plant species add an enormous heterogeneity of their own, relative to insect herbivores. First, there are varying mixtures of plants over a landscape, some of them food plants, some of them not. Second, each plant species provides many habitats and food items such as leaves, stems, flowers, seeds, fruits and roots, as well as bark and wood in woody plants. Third, there are wide ranges in size and chemistry of these plant parts making certain plants or modules vary relative to the herbivores' needs from high-quality habitat and/or food to low quality, or even completely inhospitable.

The size and specificity of the component species

Such plant heterogeneity becomes extreme and understandable when we appreciate the size relationships in plant-based terrestrial food webs. Plants are generally large and the insect herbivores are small. Taking an oak tree as an example, the individual tree may weigh many metric tons whereas an individual herbivore may weigh a few milligrams. A difference in length of five orders of

magnitude may exist. So the tree provides many different kinds of places to live and feed, and many species can coexist and exploit such a multiplicity of resources. Consequently, an oak tree species can support about 300 species of insect herbivore (Southwood 1961).

These insect herbivores also provide heterogeneity for the carnivore trophic level. Many carnivores, probably the majority, are smaller than the herbivores, for the larvae feed as parasites on or in the host, and these parasitoids are again specialists on an insect species and on a certain life stage of the insect: eggs, young larvae, grown larvae or pupae. Host insects may live in sun or shade or in moist or dry sites, and parasitoids and arthropod predators respond to this kind of heterogeneity also. Each herbivore species may be attacked by five to 15 or more parasitoid species as well as many small arthropod predators such as spiders and insects. However, the system as a whole is dominated in number of species by those with a parasitic way of life, feeding in or on another living organism. This applies to insect herbivores and their parasitoids, and parasites generally evolve to be very specialized in their host relationships (Price 1980).

Emphasizing the size relations in terrestrial food webs with plants and insects, and the inherent specificity of most components, makes the contrast with other food webs clear. In aquatic systems, be they freshwater lakes or rivers or marine, primary producers are very small, in the form of phytoplankton, and organismal sizes increase up the trophic system to zooplankton, small fish and larger fish. Hence, a single primary producer has virtually no impact up the trophic web, but large fish have strong impact down the system. Trophic cascades are commonly observed (e.g. Carpenter *et al.* 1985). These systems are dominated by predation, with large organisms eating small and, of necessity, being generalized in what they eat. Even in grazing systems, common in lakes and rivers, very few specialists exist in terms of what they eat. In other food webs with vertebrate herbivores, grazing and browsing is usual, with large herbivores eating small grasses and herbs in many cases, and generalized diets prevail. Other terrestrial systems not based on living plants as habitat and food are also dominated by generalist feeders, with much omnivory, cannibalism and predation,

as exemplified in Polis's (1991) studies on the desert community of the Coachella Valley, California. Detritivore food webs are similar.

Thus, while terrestrial food webs with plants, insect herbivores and parasitoids may be viewed as unusual, or even unique, relative to other types, they are by far the most common in terms of numbers of species involved. This is not a paradox, nor is it unexpected. Yet, I feel that most ecologists are not aware of the magnitude of difference between the types of food webs discussed above, and the consequences for the scales of heterogeneity we must appreciate and understand for each food web type.

The relative strengths of connections between bottom-up and top-down influences

Another consequence of large plants supporting food webs composed largely of parasites is that bottom-up effects through the trophic system are likely to be very strong. The plant is the habitat and food for the herbivores, and it is also the habitat for the carnivores. Most insect herbivores are relatively sedentary as immatures and many live on a single plant, acting as true parasites. Every herbivore must eat food, so food plants, their quality variation and heterogeneity impact every individual of every species and these, in turn, impact the carnivores. Being largely specialists we should anticipate many detailed interactions, mediated not so much by sight and rapacious predatory acts, but by subtle aromas, body odors, chemical signals and stealthy interactions. We move into a world that is strange to us and hard to fathom. As dominant large omnivores on this planet we are particularly ill suited as students of this world of specialists, extreme heterogeneity and enormous subtlety.

Because the primary producers are plants, relatively large organisms compared to insect herbivores and carnivores, and because they provide both food and habitat for higher trophic levels, they have an inordinately strong impact up the trophic system. We could remove carnivores or herbivores in many cases and hardly observe an effect on plant numbers. But remove the plants and, of course, the whole food web collapses (Hunter & Price 1992). Thus, I use the term

'resource-driven webs' in the title of this paper intentionally to indicate that bottom-up effects are profound, persistent and overbearing on numbers of individuals in a species and numbers of species in a community. The strengths of connections up the food web are much stronger than the influence down.

COMPLEXITY OF RESOURCES AND HABITATS

The constitutive chemicals in plants are composed of nutrients, structural materials that provide strength and resilience to soft tissues and metabolites that act towards herbivores as attractants, repellents, toxins or digestibility reducers. All these affect herbivores in many ways, too many to discuss in one short paper, but one figure summarizes many of the interactions (Fig. 1). The effects move either directly or indirectly up the trophic system. Many chemicals are volatile and act as body odor, which attracts some herbivores and

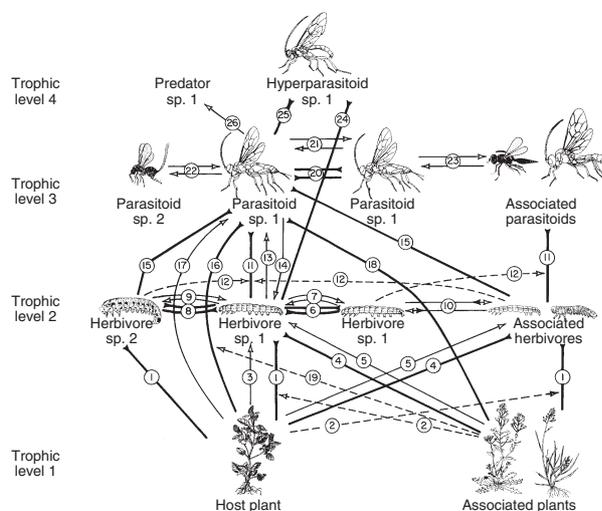


Fig. 1. Examples of chemically mediated interactions known to occur in plant–insect herbivore–parasitoid communities. Specific examples of interactions 1–26 are provided in Price (1981). Arrows are placed against the responding organism. Thick solid lines and solid arrows illustrate attraction to a stimulus (e.g. 1, 4, 11, 24). Thin solid lines and open arrows illustrate repulsion (e.g. 3, 13, 17, 26). Thin dashed lines show indirect effects such as interference with another response (e.g. 2, 12, 19). From Price (1981).

carnivores and repels others, just as humans are attracted or repelled by certain phytochemicals. Then, in turn, herbivores may emit odors that attract or repel enemies, and carnivores may be attracted to plant volatiles as a mechanism for finding hosts or prey.

Thus, the term 'food web' oversimplifies what really is a web of multiple interactions in the case of communities based on terrestrial plants. The web involves habitat, food, and other chemicals affecting components of the web in multiple ways. If we forget the complexity of these multiple components of such interactive webs, we cannot possibly appreciate the dynamics, heterogeneity and the role of disturbance in such communities.

Living plants, as food and habitat, are not passive in the interactions but they react to herbivory by releasing chemicals and changing defensive metabolites in many cases (e.g. Dicke 1988; Dicke *et al.* 1990; Karban & Baldwin 1997). Carnivores are attracted to damaged plants, such that the plants influence directly the numbers of individuals in a herbivore species and their predators (e.g. Turlings *et al.* 1990; Turlings & Benrey 1998; Turlings & Fritzsche 1999). Damaged plants can even become repellent to insects other than the species causing damage (Bernasconi *et al.* 1998). This means that the community richness is depleted relative to one based on a non-reactive food source. Thus, plants increase heterogeneity in response to herbivore damage within individuals and within populations. Individuals may show locally induced responses to damage-induced defenses and induced chemical emissions; and individuals in a population are likely to vary in the presence and intensity of induction. Effects pass up the trophic system.

Physical characteristics of plants also play important roles in food webs, not just on herbivores but also on carnivores, both directly and indirectly (e.g. Norris & Kogan 1980). Trichomes commonly interfere with foraging by small herbivores and carnivores alike. They may even change evolved herbivore behavior significantly, which influences the herbivore–carnivore interaction. For example, trichome structure influences leaf-mining behavior, which changes vulnerability to parasitoids (Gross & Price 1988). Tissue toughness, surface waxes and silica bodies all contribute to plant resistance and heterogeneity and effects

pass up the trophic system. As an example, tough tissues are less digestible so that herbivores must feed longer in the short term and also take longer to maturity, making them more vulnerable to carnivore attack (e.g. Feeny 1975, 1976). Also, the growth of plants, from small to large, from seedling to maturity, changes habitat structure enormously and the suitability of plants for herbivores and carnivores (e.g. Price 1976, 1992). In addition, as plants become larger at maturity, from herbs to shrubs to trees, so the number of associated insect herbivore species increases (Lawton & Schröder 1977), as must also the carnivores. As geographic range or patch size of plants increases so do the number of associated herbivores (Strong 1974, 1979; Price 1997).

Plants clearly impact evolved characters of insect herbivores including the obvious adaptations of physiology and biochemistry involved with digestion of food, but also evolutionary responses to feeding, behaviors relating to oviposition, life-history evolution that favors synchrony with high-quality food, and the evolution of crypsis, camouflage or aposematic coloration relative to the plants' background pattern. These evolved characters of insect herbivores in relation to plant traits have been treated in a huge amount of literature, so only some general references will be provided here (Bernays & Chapman 1994; Price 1997; Speight *et al.* 1999).

LANDSCAPE AND GEOGRAPHIC VARIATION

For specialized insect herbivores, host plant density varies over a landscape and geographically, with concomitant change in habitats for herbivores and carnivores alike. Interactions will change over these scales also because each species on each trophic level has individualistic adaptations and requirements; the interaction with a herbivore or carnivore species is only one of many aspects of the life of the individual. For example, parasitoids may feed for several weeks in one habitat and then move to another to find host species. The juxtaposition of resources in a landscape is significant for many species components of food webs, a fact well understood in agriculture where crop field and fallow ground are best left in close proximity. Food web

components are not necessarily fixed in one place but move over a landscape seeking out their individual and extensive needs.

Food web structure changes dramatically over the geographic range of species. For example, one parasitoid species, *Hoplismenus morulus*, is distributed over most of the USA (Price 1981). In the northwest, one host herbivore is available which feeds on 10 plant species in six families, all in mesic woodland. In the northeast, three host insects are available which feed on 21 plant species in 12 families, again all in mesic woodland. In the southwest, three host herbivore species are also available but are spread over 44 plant species in 17 families and in three habitats: chaparral, mesic woodland and mesic herbaceous vegetation. Clearly, the variation in heterogeneity and interactions is extreme, the complexity of food web structure changes dramatically even for one parasitoid species and then there are many other components that vary as much but in different ways. Comparative studies on such varying food webs would be rewarding.

On an even larger geographic scale, vegetation types influence herbivore distribution significantly. One example is the bottom-up influence from plant type to local insect herbivore richness of gall-inducing species (Price *et al.* 1998). Sclerophyllous components of vegetation appear to favor the evolution and persistence of gall-inducing species, with their usually very rich parasitoid members of the food web. Thus, in vegetations around the world dominated by sclerophyll or xerophyll vegetation, local species richness increases dramatically at the herbivore and carnivore trophic levels. Such vegetation types include campina, chaparral, cerrado, fynbos, Kwongan, matorral, maquis and other Mediterranean-type vegetations. Similar effects are seen in all vegetation types in relation to certain kinds of insect herbivores and carnivores.

Specialized insects and other herbivores such as fungi, bacteria and viruses, will also be influenced profoundly by genetic variation in plants at all scales, from individuals to geographic distributions and such plant variation drives genetic variation in herbivores. The 'geographic mosaic of evolving interactions' is Thompson's (1994) phrase for this interaction among genotypes, which may well result in coevolution among tightly associated

trophic levels such as plants and specialist insect and fungal herbivores (e.g. Thompson 1999 and associated papers). One example of the profound effect of plant genotype on insects and higher trophic levels involves hybrid swarms of cottonwoods (*Populus angustifolia* × *fremontii*), gall-inducing aphids, fungi and birds (e.g. Whitham 1989; Dickson & Whitham 1996).

THE MULTIFACETED INTERACTION WEB

Very briefly, I have addressed seven factors that are basic to food webs founded on living plants, all illustrating the very strong and overriding influences from the bottom up in these resource-driven food webs (Table 1). (i) Plants as food; (ii) plants as habitat; (iii) physical properties of plants; (iv) adaptation of insects to the plant habitat and food; (v) chemical constituents of plants; (vi) induced chemical reactions of plants; and (vii) landscape and biogeographic variation in vegetation types and food web richness. Can we claim that any other trophic level has such a multifaceted influence on the other two or more trophic levels? The answer is clearly 'no', for terrestrial food webs based on living plants in which the majority of components are usually specialized in host use. When we argue that there is a top-down influence it is used in a very narrow sense, of biomass or number reduction by a higher trophic level, while forgetting all the other influences moving up the interaction web.

I use the term 'interaction web' advisedly, because the term 'food web' is much too narrow a term. Thompson's (1997) term of 'interaction biodiversity' carries a similar emphasis on the increasing complexity of interactions as life diversifies. If we are to understand food webs we must understand all facets of the interaction web, with at least seven major factors involved, as noted above. From the perspective presented here, interaction webs based on living plants are clearly dominated by bottom-up, resource-driven processes.

Thompson (1982) emphasized 'the interaction structure of communities' in the last chapter of his book, noting that knowing the species structure of a community or food web tells us little more than a telephone directory informs us about a city. It is the nature of the interactions that shape

Table 1 Bottom-up, resource-driven factors dominating the interaction web based on terrestrial plants

A	The sources of heterogeneity
	1. Plants as food
	2. Plants as habitat
B	The size and specificity of the component species
	3. The physical traits of plants such as relatively large size, toughness, trichomes
	4. Traits of plants that require evolutionary responses by herbivores such as crypsis, phenological synchrony, life history and behavioral adaptations
C	The relative strengths of connections between bottom-up and top-down influences
D	Complexity of resources and habitats
	5. The constitutive chemicals of plants
	6. The induced changes in plants caused by herbivory
E	Landscape and geographic variation
	7. Landscape and biogeographic variation in vegetation types and food web richness

community components, and those components providing the most interactive mechanisms will have the most profound effects. As Hunter (2001) has implored, if we are to be clear in conveying ecological ideas our terminology should be exact and explicit. In this sense, the term 'food web' grossly oversimplifies our meaning, our interest and our study of what really are 'interaction webs'.

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REFERENCES

- BERNASCONI M. L., TURLINGS T. C. J., AMBROSETTI L., BASSETTI P. & DORN S. (1998) Herbivore-induced emissions of maize volatiles repel the corn leaf aphid, *Rhopalosiphum maidis*. *Entomologia Experimentalis et Applicata* **87**: 133–142.
- BERNAYS E. A. & CHAPMAN R. F. (1994) *Host-Plant Selection by Phytophagous Insects*. Chapman & Hall, New York.
- CARPENTER S. R., KITCHELL J. F. & HODGSON J. R. (1985) Cascading trophic interactions and lake productivity. *Bioscience* **35**: 634–639.
- DICKE M. (1988) *Infochemicals in Trophic Interactions*. PhD thesis, Agricultural University, Wageningen.
- DICKE M., VAN LENTEREN J. C., MINKS A. K. & SCHOONHOVEN L. M., eds. (1990) Proceedings of the international symposium: Semiochemicals and pest control – prospects for new applications. *Journal of Chemical Ecology* **16**, 3017–3212.
- DICKSON L. L. & WHITHAM T. G. (1996) Genetically-based plant resistance traits affect arthropods, fungi, and birds. *Oecologia* **106**: 400–406.
- FEENY P. P. (1975) Biochemical coevolution between plants and their insect herbivores. In: *Coevolution in Animals and Plants* (eds L. E. Gilbert & P. H. Raven), pp. 3–19. University of Texas Press, Austin.
- FEENY P. P. (1976) Plant apparency and chemical defense. In: *Biochemical Interaction Between Plants and Insects* (eds J. W. Wallace & R. L. Mansell), pp. 1–40. Plenum, New York.
- GROSS P. & PRICE P. W. (1988) Plant influences on parasitism of two leafminers: A test of enemy-free space. *Ecology* **69**: 1506–1516.
- HUNTER M. D. (2001) Multiple approaches to estimating the relative importance of top-down and bottom-up forces on insect populations: Experiments, life tables, and time-series analysis. *Basic and Applied Ecology* (in press).
- HUNTER M. D. & PRICE P. W. (1992) Playing chutes and ladders: Heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* **73**: 724–732.
- KARBAN R. & BALDWIN I. T. (1997) *Induced Responses to Herbivory*. University of Chicago Press, Chicago.

- LAWTON J. H. & SCHRÖDER D. (1977) Effects of plant type, size of geographical range and taxonomic isolation on number of insect species associated with British plants. *Nature* 265: 137–140.
- LEVIN D. A. & WILSON A. C. (1976) Rates of evolution in seed plants: Net increase in diversity of chromosome numbers and species numbers through time. *Proceedings of the National Academy of Sciences USA* 73: 2086–2090.
- NORRIS D. M. & KOGAN M. (1980) Biochemical and morphological bases of resistance. In: *Breeding Plants Resistant to Insects* (eds F. G. Maxwell & P. R. Jennings), pp. 22–61. Wiley, New York.
- POLIS G. A. (1991) Food webs in desert communities: Complexity via diversity and omnivory. In: *The Ecology of Desert Communities* (ed. G. A. Polis), pp. 383–437. University of Arizona Press, Tucson.
- PRICE P. W. (1976) Colonization of crops by arthropods: Non-equilibrium communities in soybean fields. *Environmental Entomology* 5: 605–611.
- PRICE P. W. (1980) *Evolutionary Biology of Parasites*. Princeton University Press, Princeton.
- PRICE P. W. (1981) Semiochemicals in evolutionary time. In: *Semiochemicals: Their Role in Pest Control* (eds D. A. Nordlund, R. L. Jones & W. J. Lewis), pp. 251–279. Wiley, New York.
- PRICE P. W. (1992) Evolutionary perspectives on host plants and their parasites. *Advances in Plant Pathology* 8: 1–30.
- PRICE P. W. (1997) *Insect Ecology*, 3rd edn. Wiley, New York.
- PRICE P. W., FERNANDES G. W., LARA A. C. F. *et al.* (1998) Global patterns in local number of insect galling species. *Journal of Biogeography* 25: 581–591.
- SOUTHWOOD T. R. E. (1961) The number of species of insect associated with various trees. *Journal of Animal Ecology* 30: 1–8.
- SOUTHWOOD T. R. E. (1977) Habitat, the templet for ecological strategies? *Journal of Animal Ecology* 46: 337–365.
- SPEIGHT M. R., HUNTER M. D. & WATT A. D. (1999) *Ecology of Insects: Concepts and Applications*. Blackwell Science, Oxford.
- STRONG D. R. (1974) Nonasymptotic species richness models and the insects of British trees. *Proceedings of the National Academy of Sciences USA* 71: 2766–2769.
- STRONG D. R. (1979) Biogeographic dynamics of insect-host plant communities. *Annual Review of Entomology* 24: 89–119.
- THOMPSON J. N. (1982) *Interaction and Coevolution*. Wiley, New York.
- THOMPSON J. N. (1994) *The Coevolutionary Process*. University of Chicago Press, Chicago.
- THOMPSON J. N. (1997) Conserving interaction diversity. In: *The Ecological Basis of Conservation* (eds S. T. A. Pickett, R. S. Ostfeld, M. Shachak & G. E. Likens), pp. 285–293. Chapman & Hall, New York.
- THOMPSON J. N. (1999) Specific hypotheses on the geographic mosaic of coevolution. *American Naturalist* 153 (Suppl.): S1–S14.
- TURLINGS T. C. J. & BENREY B. (1998) Effects of plant metabolites on the behavior and development of parasitic wasps. *Ecoscience* 5: 321–333.
- TURLINGS T. C. J. & FRITZSHE M. E. (1999) Attraction of parasitic wasps by caterpillar damaged plants. In: *Insect-Plant Interactions and Induced Plant Defence* (eds D. J. Chadwick & J. A. Goode), pp. 21–38. Wiley, Chichester.
- TURLINGS T. C. J., TUMLINSON J. H. & LEWIS W. J. (1990) Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. *Science* 250: 1251–1253.
- WHITHAM T. G. (1989) Plant hybrid zones as sinks for pests. *Science* 244: 1490–1493.