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# Tritrophic niches of insect herbivores in an era of rapid environmental change

John O Stireman III[a] and Michael S Singer[b]

A multi-trophic perspective improves understanding of the ecological and evolutionary consequences of rapid environmental change on insect herbivores. Loss of specialized enemies due to human impacts is predicted to dramatically reduce the number of tritrophic niches of herbivores compared to a bitrophic niche perspective. Habitat fragmentation and climate change promote the loss of both specialist enemies and herbivores, favoring ecological generalism across trophic levels. Species invasion can fundamentally alter trophic interactions toward various outcomes and contributes to ecological homogenization. Adaptive evolution on ecological timescales is expected to dampen tritrophic instabilities and diversify niches, yet its ability to compensate for tritrophic niche losses in the short term is unclear.

**Addresses**
[a] Department of Biological Sciences, Wright State University, Dayton, OH 45435, USA
[b] Department of Biology, Wesleyan University, Middletown, CT 06459, USA

Corresponding author: Stireman, John O (john.stireman@wright.edu)

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## Introduction

The role of natural enemies in controlling herbivore populations fundamentally informs the structure and dynamics of ecological systems, underlying such basic observations as the relative 'greenness' of the (terrestrial) world [1] and providing the theoretical underpinning for biological control. Indeed, top-down effects of predators and parasitoids on insect herbivore fitness may be as important as bottom-up factors of plants and habitats [2]. Less broadly appreciated are the evolutionary consequences of top-down dimensions of the niches of herbivorous insects. From an evolutionary perspective, selection from enemies is an additional, complementary axis of niche differentiation upon which the process of adaptive radiation can drive diversification [3]. Importantly, direct and indirect interactions between enemies and plants create evolutionary opportunities for adaptation, divergence, and niche partitioning that underlie the enormous diversity of phytophagous insects [4].

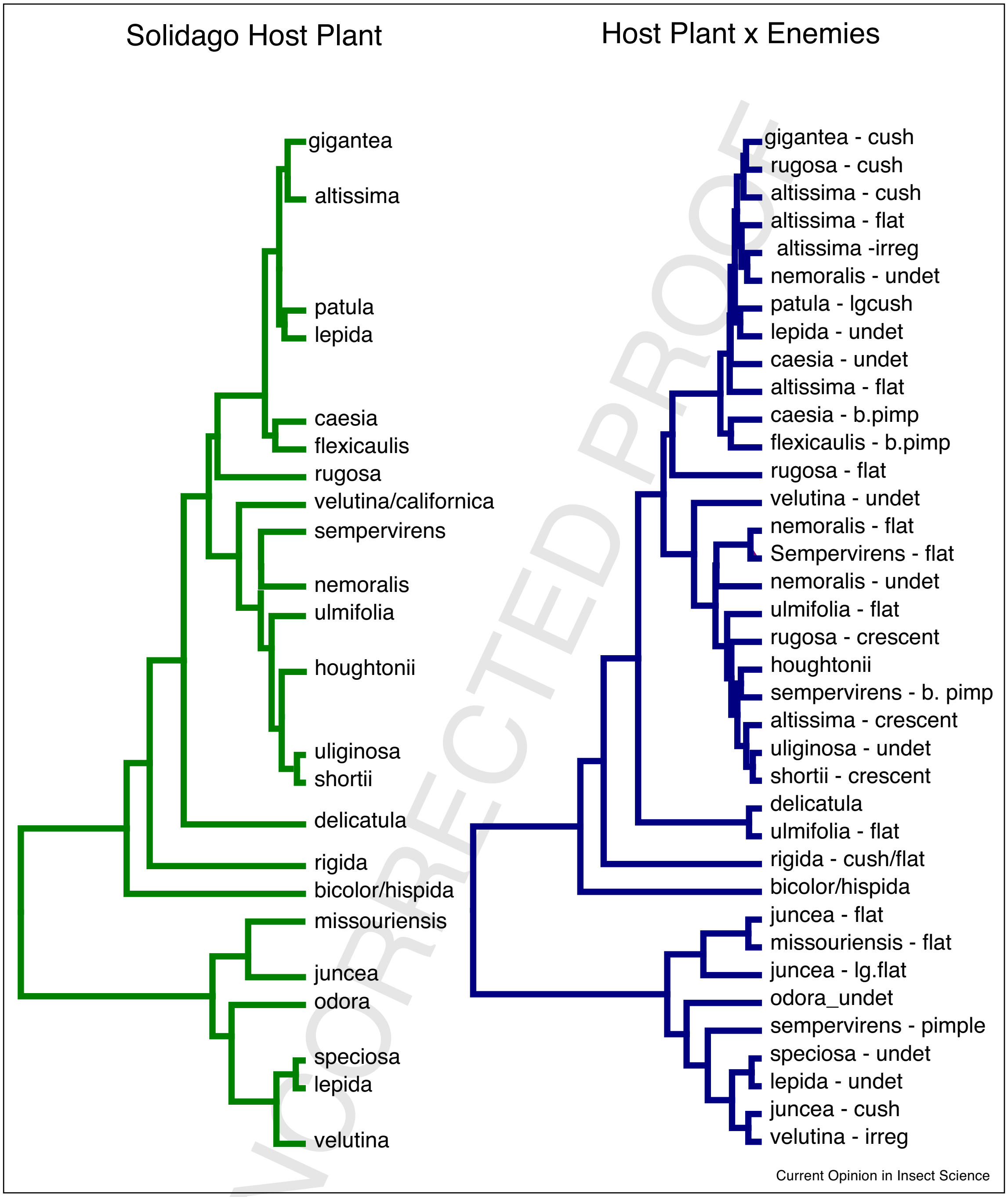
Ecological communities and their multitrophic networks are experiencing some of the most dramatic environmental changes in Earth's history. Anthropogenic environmental changes including habitat fragmentation and loss, climate change, and alien species invasion are fundamentally reshaping ecological communities and altering ecological interactions. Here we aim to review the tritrophic niche concept for phytophagous insects and its implications for understanding herbivore niches, evaluate how tritrophic communities and interactions are being affected by anthropogenic environmental impacts, and predict ecological and evolutionary consequences of these changes.

## The tritrophic niche

Inherent in the tritrophic niche concept is the view that ecological niches are neither a property of individual species nor of particular environments, but of ecological communities. Thus, their quantity and quality are determined critically by species interactions in addition to the abiotic environment. The value of a tritrophic perspective in understanding ecological niches of phytophagous insects has long been recognized if not stated explicitly [5,6]. Adoption of this view has led to the development of such influential concepts as enemy-free space (EFS; [7]), apparent competition [8], the slow-growth-high-mortality hypothesis (SGHM; [9]), and the 'tritrophic interactions hypothesis' [8]. Multitrophic perspectives can also illuminate adaptive evolutionary diversification of insect lineages [3,11] (Figure 1). As more studies explicitly consider both top-down and bottom-up factors, it is increasingly apparent that this broad perspective is necessary to understand the evolution and structure of herbivore communities.

Recent evidence for the tritrophic nature of herbivore niches comes from a variety of insect-plant systems. For example, niches of *Timema* walking sticks, a model for ecological speciation, are defined by their color patterns, host plants, and predation by birds [12]. Mismatches in these three components result not only in reduced *Timema* fitness, but also affect community diversity and processes [13]. Likewise, divergent host-plant specialization of pea aphid races is reinforced

**Figure 1**




An illustration of the multiplicative effects of host-plants and enemies in creating niches and driving adaptive diversification using *Asteromyia* gall midges on goldenrods (*Solidago* spp.). On the left is phylogenetic structure that can be attributed to differences host plant use (i.e. each lineage occupies a different host), on the right is phylogenetic structure attributable to the interaction between host-plants and enemies manifested by gall morphotypes (i.e. each lineage comprises a population defined by a particular host-plant and defensive gall morph combination). Gall morphotypes are indicated to the right, for example, cush = cushion, irreg = irregular, lg = large, pimp = pimple, undet = undefined. See Stireman *et al*. [11] for a more detailed examination of these patterns.



by escape from natural enemies [14•]. Perhaps most elegantly illustrating the tritrophic niche concept are *Blepharoneura* fruit flies that have radiated extensively into highly specific niches defined by host species, host plant part, and invulnerability to all but select specialized parasitoids [4] (Box 1). Although most studies have shown that enemies favor narrower host-plant niches in herbivores, several studies also point to enemies as a



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