Diet divergence in two sympatric congeneric butterflies: community or species level phenomenon?

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Summary

Two species of *Euphydryas* butterflies were studied in California, USA, and showed considerable diet overlap at the species level. They utilize many of the same plant genera for oviposition. However, *E. editha* is less likely to use woody perennials than is *E. chalcedona*.

Both butterfly species are known to specialize on different host plants in different populations, so species level divergence may not be a good predictor of community level divergence. Within five communities, *E. editha* and *E. chalcedona* showed no dietary overlap. A major component of the niche of *E. editha* in one community was occupied by *E. chalcedona* in a second community, even though both butterfly species occupied both communities. These resource use patterns indicate that community level interactions may affect diet divergence. The degree to which divergence within communities is greater (or less) than expected from a species level comparison may be used to provide a measure of community organization. Equations are given in the Appendix for calculating overlap probabilities from presence/absence types of data; in this study, presence is oviposition on a particular plant species, absence is no oviposition on that plant species. Given the various assumptions of the model, *E. editha* and *E. chalcedona* show significant community level components of their dietary divergence in the areas studied. However, in some other communities *E. editha* and *E. chalcedona* do share host plant species. Therefore, we could not demonstrate community level divergence conclusively, nor has this been demonstrated for any other pair of insect herbivore species. We do not know whether this is because the phenomenon is truly rare or just very hard to demonstrate.

Introduction

A problem facing community ecologists is to discern to what degree community 'organization' is due to ecological and evolutionary events taking place within each community, and to what degree community patterns are determined by the different phylogenetic histories of the species that make up each community. Unless the phylogenetic component of variation in resource use patterns can be factored out, it is not possible to appraise whether community structure really exists, let alone understand the ecological factors determining structure.

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Diet divergence in Euphydryas butterflies

One way to separate phylogenetic and community components of resource use is to compare divergence between species at two levels. Over their entire ranges, any overall divergence between sympatric species may be attributable to their different phylogenies. This phylogenetic divergence provides an expectation that when species co-occur they will differ in resource use to a certain degree. Community ecologists have used this expectation as a baseline against which to test for community level interactions (e.g. Strong et al., 1979; Case and Sidell, 1982; Harvey et al., 1983; Colwell and Winkler, 1984). Lesser (or greater) overlap in diet than expected from this species level divergence can then be used to deduce that divergence (or convergence) has taken place at the community level. Perhaps misleadingly, models to test for community level patterns in this way have been called 'null models'. They are not really null, but are attempts to factor out some of the consequences of events that took place (a) at a time before present communities existed, and (b) outside the particular communities being studied. We will term resource use patterns caused by events (a) and (b) 'species properties'.

For plant-feeding insects, phylogenetic events such as past coevolution with host plants can give rise to species properties and these events are thought to be important in determining the diets of insect herbivores (Brues, 1924; Ehrlich and Raven, 1965). Thus, entomologists studying insect herbivores have rarely dwelt on the possible importance of interactions with other members of the same trophic level as determinants of community level patterns of resource partitioning, but have concentrated instead on the importance of plant characters and natural enemies (e.g. cf. Strong et al., 1984; Zwölfer, 1977, 1979; Chew, 1981; Fritz et al., 1986). However, communities may contain several plant species that fall within the nutritionally acceptable limits that are set by phylogenetic constraints, and ecological factors are often thought to affect insect diet choice among these nutritionally adequate resources (e.g. Smiley, 1978; Gilbert, 1979). Therefore, direct or indirect interactions among members of the same trophic level might be expected to contribute to the choice of resources within communities that contain more than one potential resource type. At present, we know of no study that attempts a statistical analysis of community level resource use patterns of insect herbivores while controlling for, or factoring out, species properties.

In this paper we investigate species and community level divergence in two butterflies, Euphydryas editha and E. chalcedona (Lepidoptera: Nymphalidae). They are interesting in this regard because both species show great regional variation in diet. E. editha is well known for its tendency for different populations to oviposit on different host species (Singer, 1971; White and Singer, 1974). All hosts recorded for oviposition are in the plant families Scrophulariaceae and Plantaginaceae. Oviposition records for the state of California and the eastern slopes of the Sierra Nevada mountains in

Species level comparisons

Euphydryas editha has a scattered distribution throughout the western USA, with different populations utilizing different host plants (Singer, 1971; White and Singer, 1974). All hosts recorded for oviposition are in the plant families Scrophulariaceae and Plantaginaceae. Oviposition records for the state of California and the eastern slopes of the Sierra Nevada mountains in