

Insect natural history, multi-species interactions and biodiversity in ecosystems

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The composition and dynamics of ecosystems are influenced by insects serving as providers, eliminators and facilitators across multiple trophic levels. The role of insects in ecosystems may be documented by manipulative field studies involving exclusion techniques applied to species that are decomposers, herbivores or predators. The presence or absence of insects is important to the distribution, abundance and diversity of plants and vertebrates, which typically are the premier species in conservation efforts. Thus, policy-making in environmental management programmes should consider the role of insects in ecosystems when establishing objectives and procedures for species conservation and biodiversity.

Keywords: insects; ecosystem; exclusion; environmental management

Introduction

The species composition of ecosystems is fundamentally dynamic and in part driven by forces of disturbance (Holland, 1986; Pickett and White, 1985; Cohen and Newman, 1991). If a certain set of plant or animal species is the desired goal for a given conservation effort then an active environmental management programme involving habitat manipulation may be required. If active intervention in management of the habitat-ecosystem is not conducted, then the existing set of species and communities will likely change and the initial goal of the conservation effort will not be achieved. An example of this philosophy was presented by Diamond (1992) in an observation that passive management does not translate into maintaining the status quo of ecosystems but may result in undesirable changes in the habitat being held for preservation. The challenge for environmental management policy-makers and the scientific community is to establish appropriate practices for achieving conservation of special habitat, and/or maintaining biodiversity.

The central theme of this paper is the proposition that information on functional relationships among species gained via disturbance or exclusion studies can enhance management of selected habitats for species conservation and biodiversity. This proposition is illustrated and supported by examples based on the natural history of insects, including ripple effects on plants and vertebrates. Westman (1990) concluded a discourse on managing for biodiversity with the following statement

“If we can come to a better understanding of the existence and role of keystone and critical-link species, we may find that we can model the role of particular species in biospheric

function and thereby enhance both understanding of the globe and of the critical role that some species play in its maintenance."

This statement is underscored by Seastedt and Crossley (1984) in their observation that arthropod detritivores exhibited a major influence on ecosystem functions based on a study that measured arthropod impact on nutrient cycling of potassium, nitrogen, phosphorus and calcium as well as on the standing crop of decaying vegetation. Also, Janzen (1987) noted that insects played nonreplacement roles in pollination, defoliation and as providers of food for carnivores. He further argued that conservation of insects should not be viewed as a byproduct of plant and vertebrate conservation efforts but as a goal unto itself. Morris (1987) also argued that habitat management for insect conservation and biodiversity should be a primary goal. The inevitable element of human disturbance was the focus of Samways (1989) in his discussion of how insects are sensitive to habitat/climate change and how certain insect populations exhibit an ability to recover. Focusing on population recovery, Schowalter (1985) presented a synthesis on adaptations of insects to disturbance. A common concern to each of these studies was the question of how do we identify, acquire and maintain appropriate habitat for species conservation and biodiversity.

Ecosystem management involves: (1) establishing objectives; (2) implementing practices to attain the objectives; (3) documentation of the impact to judge the practices. Assuming that the objectives and management practices for a given habitat are established, the remaining issue concerns how to document the current state of the habitat and any ensuing change. The classical approach is to inventory the species. A count of the flora and fauna could result in data on the number of individuals, species richness, species evenness and species diversity. Additional measurements on standing crop, expressed as biomass and energy flow, expressed in kcal, may be taken. While such data are valuable for assessing ecosystem composition at any given point in time and space, three important issues remain.

- (1) Which species (or combination of species) indicate the condition (perhaps the state of succession) of the ecosystem?
- (2) At what range in numbers per unit of habitat do various species occur?
- (3) What numbers of individuals and species are critical to predicting ecosystem dynamics?

The answers to these questions may be acquired with an approach to ecosystem studies that focuses on determining functional relationships between the species. This approach is particularly valuable for connecting population dynamics of various species across multiple trophic levels and going beyond units of related species.

The relevance of this approach for species conservation and biodiversity becomes apparent when the relationships among species within a defined community are understood (see Johnson, 1984). Impacts resulting from a change in the numbers of one species may, or may not, ripple through multiple trophic levels affecting dozens of species. There are three key questions.

- (1) How do interactions between certain species influence ecosystem composition?
- (2) What happens when certain individual species, or groups of species, are removed?
- (3) What happens when new species are added to the ecosystem?

As mentioned earlier, the 'what happens' aspect of these questions may be measured in units, such as species lists, species richness, species diversity, biomass and energy flow. In

one of the conclusions to this paper it is suggested that functional relationships among species and impacts on populations need to be assessed across multiple trophic levels involving a multitude of species not taxonomically related. As the subject at hand focuses on insects, a brief account of natural history from an entomological point of view is in order.

Insect natural history

How and when does the presence of an insect result in 'obvious' ecosystem impacts? At least four conditions contribute to the more apparent impacts: (1) colonization by exotic species of an environment with suitable climate and food resources and devoid of natural enemies, such as, the gypsy moth; (2) population outbreaks in native species resulting in epizootics or plagues, such as grasshoppers and bark beetles; (3) population outbreaks following disturbances, natural or human caused, such as air or water pollution, pesticide use, or floods; or (4) consequences of management practices inhibiting fire or planting vegetation in areas not appropriate for growth of particular species. A more intriguing question is how and when does the absence of an insect result in 'obvious' ecosystem impacts? This question relates directly to species conservation and biodiversity because one goal of environmental management is to prevent the loss of certain species.

The diversity of insect species and the abundance of individuals is reflected in the wide array of life history patterns exhibited by insects (Thompson, 1984). Insects participate in the functioning of all trophic levels except primary producers. Thousands of species and billions of individuals play influential roles in the processing of organic matter as decomposers, herbivores and carnivores up to at least the quaternary consumer level. A perspective different from the trophic level approach is to note how insects interact with other organisms in three categories: providers, eliminators and facilitators.

Insects may serve a role as providers in communities and ecosystems. Various insects are providers for other species, including plants and non-insect animals, by serving as food or as hosts for carnivorous plants, predacious animals and parasites. Insects also produce byproducts, such as, honeydew, frass and cadavers that sustain other species.

Insects may serve a role as eliminators in communities and ecosystems. The role of eliminator is achieved by removing waste products and dead organisms (decomposers and detritivores), consuming and recycling live plant material (herbivores) and eating other animals (carnivores).

Insects may serve the role of facilitator for interspecific interactions in communities and ecosystems. Insects facilitate other organisms by phoresy, vectoring pathogenic organisms (which may result in lowering the fitness of the recipient), pollination, seed dispersal and microhabitat development (tunnels and nests which other organisms use for a home).

The three functions (provider, eliminator and facilitator) should not be viewed as mutually exclusive when determining the roles of insects in an ecosystem. In fact, an opposite view should be encouraged, that of perceiving each function occurring in concert. As species are viewed in this perspective the network of a foodweb becomes immediately apparent (see Schoenley *et al.*, 1991 for an expansion of this theory). Impacts from disruption of the foodweb are a major concern of those who contemplate and study such matters. For instance, the functional roles can be incorporated into a scenario for ecosystem dynamics such as the one presented by Schowalter (1981) which

may consider the types of ripple effects caused by disturbance, in particular the loss of species.

The impact on an ecosystem following the loss of all resident immature Lepidoptera (caterpillars), which are all herbivores, can be superimposed on Schowalter's scheme of ecosystem dynamics with the following hypothetical scenario. Removal of caterpillars which, in part, act as eliminators of foliage (ca 80% reduction in abundance of all individuals over 100s of hectares can occur, e.g. Miller, 1990, 1992), could result in less leaf tissue processed during spring and summer. This could create a situation for an increase in population density of non-lepidopteran herbivores. Fewer caterpillars would be available as food (providers) for carnivores that prefer caterpillars (including birds, rodents, other insects and spiders). A change in defoliation could also alter intra- and inter-specific competition among plants (McEvoy *et al.*, 1991). A change in the composition of the flora could result in a different microclimate that could change the soil microbiota which in turn could alter the health of the plants upon which the Lepidoptera should be feeding. This hypothetical scenario does not judge the effects as positive or negative, rather the lesson is that some degree of change from the original 'dynamic trajectory' of the ecosystem will occur. A shift from this hypothetical scenario to empirical data is in order.

Plant and animal tissues, as well as animal excrement, are decomposed in part by insects. If detritivore, carrion and dung-feeding insects that serve as providers, eliminators and facilitators, have an influence on the composition of the existing community-ecosystem, then their removal should result in measurable changes. Houston (1987) excluded ants from carrion and observed a significant increase in maggots which decreased the amount of time the carrion was available to vultures. He hypothesized that the presence or absence of ants at carrion may have a functional relationship with vultures. Another example that focuses on decomposition concerns the addition of species rather than their removal and involves bovine dung beetles, pasture flora, dung flies and predaceous mites. The introduction of dung-burying beetles into areas where they did not occur naturally changes the condition (density and height of grasses) of the pasture flora and suppresses populations of dung-breeding flies. Furthermore, phoretic mites that are transported by the beetles are predators of flies (Krantz, 1983). Note that the mite induced suppression of flies (mites are eliminators) conserves resources (dung) for the beetles (mites are facilitators).

Living plants are intensively exploited by insects, particularly by means of herbivory. Nearly all plant species have a few species of insects associated with them as consumers of their leaves, roots, stems, flowers or seeds. The style of feeding includes juices, mining certain tissues, chewing small pits into the plant or eating entire plant parts. The herbivores may be considered as a guild within which interspecific competition contributes to the composition of the ecosystem. In some cases the guild of insect herbivores may consist of 50–100 species or more. The plant may be pollinated by insects and the plant may provide a place of refuge, pollen and nectar for many insect species.

If herbivorous insects that serve as providers, eliminators and facilitators have an influence on the composition of the existing community-ecosystem, then their removal should result in measurable changes. For example, when Brown *et al.* (1988) excluded insects from a five-year-old field they found a significant change in the perennial grasses and lower plant diversity after two years. Thus, the removal of insects demonstrated measurable change. If a habitat dominated by perennial grasses was a presumed goal of a

given conservation effort, then such results could be considered good. The impact of herbivore presence or absence on plant distribution and abundance is well documented in the literature on biological control of weeds (Johnson, 1984). Also, the relationship between seed feeding animals, namely insect-vertebrate interactions, will affect plant dispersal and fitness (Sallabanks and Courtney, 1992).

The impact of insect herbivores on plant populations is mediated by the presence of natural enemies acting as predators and parasitoids. Each herbivore species may have numerous species of natural enemies: predators, parasitoids and pathogens. So for every herbivore species there may be 10 or more natural enemies (Ehler and Miller, 1978; Miller, 1980), some of which will be generalist and others specialist or host specific obligate natural enemies. An increase in species richness of herbivores and natural enemies may occur with the addition of plant species (Strong *et al.*, 1984). Thus, the food chain becomes a web of species interdependent upon one another to varying degrees.

If carnivorous insects that serve as providers, eliminators and facilitators have an influence on the composition of the existing community and ecosystem, then their removal too should result in measurable changes. Risch and Carroll (1982) observed an increase in abundance in 24 species and a decline in 3 species when a certain species of ant was excluded from corn and squash fields. The ants were acting as a keystone species by being generalist predators (eliminators) and serving as guardians (facilitators) of aphids. The impact of carnivore presence-absence on herbivore distribution and abundance is well documented in the literature concerning the biological control of plant pests (MacKauer *et al.*, 1990).

Interactions among carnivores mediated by competition and/or predation may influence species at other trophic levels. Buskirk (1988) observed an increase in *Bufo* tadpoles, while the number of *Hyla* and *Pseudaxia* tadpoles decreased, accompanied by minor changes in zooplankton, when two species of nymphal dragonflies were excluded from ponds. Also, using an aquatic system, Morin *et al.* (1988) noted a significant change in the composition of zooplankton and periphyton populations due to differences in anuran populations resulting from the exclusion of aquatic insects from ponds.

All of the preceding examples illustrated that population dynamics of various species may be altered when certain species are added or removed from the local environment. The shift in abundance is due to altered interactions involving individuals (species) roles as providers, eliminators and facilitators. These roles act in concert as factors influencing population dynamics of species across many trophic levels.

Issues in ecosystem management

Conceptual models and empirical data all suggest that the disruption of multi-species interactions will result in an altered ecosystem. The revelation about such change are not necessarily judged as positive or negative until we superimpose the objectives of a given environmental management plan. In this context this paper ends with brief statements concerning five issues of importance regarding species conservation, biodiversity and ecosystem management and how insects relate to the theme of each issue.

Issue 1: documentation of ecosystem disturbance and recovery

Insects are suitable subjects for assessing the impact of disturbance on ecosystem composition and dynamics (Schowalter, 1985). Insects may serve as excellent 'test

organisms' for comparison of disturbed and undisturbed habitats because of the functional relationships among species (including non-insects as previously documented) and the levels of high abundance in many taxa.

Issue 2: ecosystem management practices on how best to reestablish selected flora and fauna in disturbed environments and to maintain existing environments at a desired state

The essence of this issue is to what degree do prescribed management practices manipulate the habitat. For instance, following the eruption of a volcano should fallen trees be removed for industrial use or should they remain in the habitat for insects and fungi to decompose for enhancement of the carbon and nitrogen cycles in the soil and water? Economic and political philosophies contribute to the solution to such issues but the scientific contribution must be developed on fundamental principles derived from empirical observation and models. The questions asked during the studies of observation and modelling must reach beyond documentation of impact (see *Issue 1* above) and be designed to understand mechanisms, namely competition, predation and facilitation, among species at the community and ecosystem level.

Issue 3: climate/global warming

As regional and world-wide shifts in climate occur (due to natural causes, such as El Nino; or human induced changes resulting from 'greenhouse gases') the distribution and abundance of organisms, including insects, will also occur. Such shifts will likely result in significant change in the species composition of affected ecosystems because functional relationships among species will become altered.

Issue 4: toxins

The presence of lethal and subacute toxins in the soil, air and water is another issue that results from management decisions balancing the social, political and scientific philosophies of various cultures. In particular, many environmental toxins are waste products from industry manufacturing goods for society as a whole. On the other hand, many of the most notorious environmental toxins are not waste products, but are intentionally applied chemicals, such as, pesticides, used to control insect pests. Insects serve as the target species for such treatments but an array of nontarget effects may follow: biomagnification of toxins, secondary outbreaks of populations of nontarget species, resurgence in the pest population and contamination of soil, air and water. All of these impacts are generally considered undesirable in the context of community and ecosystem dynamics.

Issue 5: organism and manipulation

The fifth, and final issue concerns the practices that result from the intentional and unintentional introduction of species. For instance, the importation of materials for industry may result in the accidental introduction of undesirable species. The accidental importation of a herbivore could result in the presence of a new pest. Conversely, the intentional introduction of a herbivore may help in the biological control of a weed, thereby mitigating the effects that occurred when the weed species was introduced. Similarly, the intentional introduction of natural enemies (predators and parasitoids) is a well documented practice for biological control of insect pests. Currently, introduction of genetically altered organisms for climatic tolerance, yield improvement, pest resistance and production of certain molecules (i.e. medicine) is a component of this issue.

Final comments

A number of messages emerge from a consideration of insect natural history and a concern for maintaining biodiversity that are germane to ecosystem sustainability and the conservation of species.

- (1) Conservation of certain species may require reduced species diversity and considerable habitat disturbance.
- (2) Species that are common may require detailed conservation plans and employment of appropriate management practices as do rare and endangered species.
- (3) Documentation of the type and degree of disturbance needs to be conducted via manipulative experiments under field conditions. Furthermore, observations on impacts need to include multiple (at least three) trophic levels and continue for an extended period of time (5–10 years).
- (4) Compensatory actions among species may buffer the impacts of single species losses or gains.
- (5) The impacts on ecosystem dynamics due to the loss or gain of a guild will likely be much more dramatic than the loss or gain of a similar number of species that are not associated in the same guild.
- (6) The role of rare and endangered species in ecosystem dynamics is not easily studied because changes may have already occurred for years as the species declined in numbers. We are left with the ethical dilemma of further decline in the population if manipulative experiments are conducted.
- (7) The impact of reducing (rather than totally excluding) certain species population levels needs to be studied as a condition that may occur prior to or in the process of becoming (locally) extinct.
- (8) The importance for conservation of insects might gain higher attention by documenting functional relationships between insects and vertebrates. This suggestion is based on the socio-political reality of the relatively high profile vertebrate conservation ethic that presently exists.
- (9) The public needs to be informed, in lay-terms but with scientific credibility, about the relationship between population dynamics, ecosystem dynamics and the trade-offs of various management practices and how the conservation of species relates to environmental quality.
- (10) Biodiversity is not a mechanism with ecological force that controls stability or change. Instead, species relationships provide a measurable product that we call biodiversity.
- (11) Imagine the role of humans in the ecosystem as providers, eliminators and facilitators. The functional relationship between humans and certain organisms illustrates our role as providers; the need to manage habitats for conservation illustrates our capacity as eliminators; the ability to manage habitats for conservation illustrates our potential as facilitators.

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