CONSERVATION BIOLOGY AND BIODIVERSITY

Comparison of the Biodiversity of Lepidoptera Within Three Forested Ecosystems

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ABSTRACT Lepidopterans function in the dynamics of forested ecosystems by serving as defoliators, decomposers, prey or hosts to carnivores, and pollinators. The biodiversity of Lepidoptera is thus linked into the ecosystem by influencing nutrient cycling, plant population dynamics, and predator-prey population dynamics. Two important measures of biodiversity are species richness and abundance of individuals. However, values for these measures require an ecosystem context for insightful interpretation of ecological function. We propose that such an ecosystem context is gained by an assessment of host resource requirements; in the case of Lepidoptera, this means larval host plants. The flora that contributes to the biodiversity of Lepidoptera can be grouped into 3 major vegetation types: (1) conifers, (2) hardwood trees and shrubs, and (3) herbs and grasses. We compared the macrolepidopteran biodiversity of 3 forested ecosystems: (1) western Oregon, (2) eastern Oregon, and (3) West Virginia. In respective order of the above locations, totals of 463, 385, and 475 species were found. Conifers supported 9, 10, and 1% of the species richness. By contrast, hardwoods supported 57, 45, and 61% of the species richness, whereas herbs and grasses supported 31, 42, and 31% of the species richness. The patterns in abundance of individual moths were different from species richness of moths and butterflies considered together. Comparisons of moth abundance showed conifers supported 18, 5, and 1%; hardwoods supported 69, 39, and 77%; and herbs and grasses supported 11, 55, and 8%. Practices involved in the management of forested ecosystems are discussed in the context of how Lepidoptera may be used as an indicator taxon for the assessment of land management practices, and how biodiversity of Lepidoptera could be considered in plans for habitat restoration with a specific focus on food web relationships.

KEY WORDS Lepidoptera, abundance, biodiversity, food webs, forest ecosystem, species richness

INSECT BIODIVERSITY INFLUENCES ecosystem dynamics through numerous mechanisms, such as decomposition of litter, pollination, suppression of plant growth, and serving as prey for carnivores (Seastedt and Crossley 1984). In general, these functions may be placed into 3 categories of roles in ecosystem dynamics: (1) exploiter, in the role of herbivore, parasite, or predator; (2) provider, serving as host or prey for a predator or parasite; and (3) facilitator, performing functions such as pollination, phoresy, or vector of a pathogen (Miller 1993). Furthermore, quantitative measures of species and individual abundance provide standardized comparative values for evaluation of various habitats, communities, and ecosystems.

In this article, we examined forest biodiversity with a focus on the interrelationships of the Lepidoptera and their larval food plants. This relationship is part of the foundation upon which available prey resources in the form of caterpillars, pupae, and adult moths and butterflies are linked to invertebrate and vertebrate carnivores. We conducted the study to determine the basis of Lepidoptera biodiversity among general categories of vegetation types within forested ecosystems. We also included data on abundance (moths only), which is a 2nd component of biodiversity important in assessing food web relationships (Kempton 1979, Hammond 1995).

We are conducting research regarding Lepidoptera biodiversity in forested ecosystems because current interests within the management needs of western coniferous forest biomes involve the documentation of species richness and function among insects at various trophic levels (USFS 1994). Examples of the types of studies occurring in western coniferous forests are the compilation of the biodiversity of plants and animals occurring on the west slope of the Cascade Mountains at the H. J. Andrews Experimental Forest, Oregon. Franklin and Dyrness (1971) listed 475 species of vascular plants, including 21 species of sporophytes, 16 species of conifers, 58 species of woody angiosperms, and 380 species of herbs and grasses. Parsons et al. (1991) listed 3,402 species of arthropods, including 492 species of Lepidoptera. The food web relationships involving Lepidoptera are further documented by the listing of 100 species of small vertebrates in the Cascade Range that may consume or be dependent upon carnivorous species that prey upon Lepidoptera (USFS 1991). The list included 70 species of birds, 20 species of insectivores and rodents, and 12 species of bats.

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Materials and Methods

Species richness and abundance of the macrolepidoptera fauna were compared among 3 sites. Each site was located in a distinct ecogeographic region in North America: western Oregon, northeastern Oregon, and West Virginia.

The Sites. The 2 Oregon sites, the H. J. Andrews Experimental Forest in the Cascade Mountains of western Oregon and the Starkey Experimental Forest in the Blue Mountains of northeastern Oregon, are in forests dominated by conifers. The H. J. Andrews Experimental Forest is in Lane and Linn counties, 100 km east of Eugene, situated between 800 and 1,500 m elevation on the west slope of the Cascade Mountains within the Willamette National Forest. In the Cascades, the most abundant conifer species are Douglasfir, Pseudotsuga menziesii; western hemlock, Tsuga heterophylla; noble fir, Abies procera; Pacific silver fir, Abies amabilis; and western red cedar, Thuja plicata. The hardwood component of the forest flora also contains a few dominant trees, such as big-leaf maple, Acer macrophyllum, and alders, Alnus spp. However, most of the hardwood species are small trees and shrubs, such as mainzanita, Arctostaphylos spp.; willow, Salix spp.; blueberry, Vaccinium spp.; hazelnut, Corylus cornuta; alders, Alnus spp.; and chinquapin, Chrysolepis chrysophylla. The western Cascade fauna occurs in a zone of high annual precipitation (≈230 cm/yr). The forest floor contains a relatively dense cover comprising the shrubs and small trees mentioned above. Additional site descriptions can be found in Parsons et al. (1991).

The northeastern Oregon site was the Starkey Experimental Forest in the Blue Mountains, situated in the Wallowa-Whitman and Umatilla National Forests, Union and Umatilla counties, between LaGrande and Ukiah, at an elevation of 1,200–1,800 m on the eastern and western slopes of the Blue Mountains. The Starkey Experimental Forest occurs in a relatively dry zone (65 cm/yr) dominated by Ponderosa pine, *Pinus ponderosa*; western larch, *Larix occidentalis*; grand fir, *Abies grandis*; and Douglas-fir. The forest floor is relatively open, with a high diversity of herbaceous and graminaceous vegetation. Additional site descriptions can be found in Grimble et al. (1992).

The West Virginia site was located at Cooper's Rock State Forest, in Preston and Monongalia counties, 32km east of Morgantown, situated at an elevation of 561 m. In contrast to the 2 Oregon sites, the Cooper's Rock State Forest is located in an area with a moist hardwood forest (125 cm/yr) dominated by oaks, *Quercus* spp.; maples, *Acer* spp.; and birches, *Betula* spp. Species of conifers are relatively uncommon and are primarily eastern white pine, *Pinus strobus*, and eastern hemlock, *Tsuga canadensis*. Additional site descriptions can be found in Butler and Kondo (1991).

Species Lists and Abundance. Compilation of species lists and individual abundance was conducted by various means depending on site and taxon. We conducted a survey of butterflies and moths at the 2 Oregon sites. At the H. J. Andrews Experimental ForTable 1. Proportion of macrolepidoptera (butterflies and moths) species (with known foodplants) using major foodplant groups in forested ecosystems

Feeding habits	Site ^a						
	Western Oregon		Eastern Oregon		West Virginia		
	n	%	n	%	n	%	
Hardwood	237	57	139	45	265	61	
Herb-grass	128	31	131	42	132	31	
Conifer	35	9	31	10	5	1	
Mixed	9	2	6	2	8	2	
Lichen-detritus	3	1	2	1	22	5	
Total	412	100	309	100	432	100	

^a Data from Parsons et al. (1991) for western Oregon; Grimble et al. (1992) for eastern Oregon; Butler and Kondo (1991) and Opler (1983) for West Virginia.

est, moths were collected with UV light traps operated 2 consecutive nights per week every week from May 1986 through September 1987. At the Starkey Experimental Forest, moths were collected with UV light traps operated 3 consecutive nights per week every week from May into the middle of October 1992. Details of methods were reported in Grimble et al. (1992). All moth collections were assessed for abundance of individuals of each species. The butterflies of the H. J. Andrews Experimental Forest and Starkey Experimental Forest were collected in aerial nets during visual searches conducted on a routine weekly basis; only species were listed, abundance data were not tabulated. The moth data for Cooper's Rock State Forest were obtained from a single UV light trap operated 1 night per week from mid-March to late October 1984. Additional details were reported in Butler and Kondo (1991). The checklist of butterflies of the Cooper's Rock State Forest site was obtained from Opler (1983). We considered these 3 particular studies because moths were collected through most of 1 complete flight season. However, because the moth trapping protocols were slightly different and the butterfly data a mixed visual and literature based survey, we emphasized comparisons of data expressed as percentages rather than absolute numerical values.

We established the following 5 categories for Lepidoptera feeding habits: (1) conifers, (2) hardwoods, (3) mixed (both conifer and hardwood), (4) herbgrass, and (5) lichen-detritivore. Information on feeding habits was obtained from Tietz (1972), Covell (1984), and our own records. Species with unknown hosts were not included in the analysis.

Results and Discussion

Species Richness. The total number of species of macrolepidoptera observed in the western Oregon and West Virginia studies was very similar—463 and 475, respectively (Table 1). The eastern Oregon site contained $\approx 25\%$ fewer species, 385. At each of the 3 sites the highest proportion of species, 45–61%, was associated with hardwoods. As would be expected based on the floral composition of the forest, the West

Table 2. Proportion of moth species (with known foodplants) using major foodplant groups in forested ecosystems

Feeding habits	Site ^a						
	Western Oregon		Eastern Oregon		West Virginia		
	n	%	n	%	n	%	
Hardwood	147	66	131	52	202	68	
Herb-grass	44	20	84	33	61	21	
Conifer	23	10	29	12	4	1	
Mixed	6	3	6	2	8	3	
Lichen-detritus	2	1	2	1	20	7	
Total	222	100	252	100	295	100	

^a Data from Parsons et al. (1991) for western Oregon; Grimble et al. (1992) for eastern Oregon; Butler and Kondo (1991) for West Virginia.

Virginia site ranked 1st in total number (n = 265) and percentage (61%) of species associated with hardwoods. However, the richness and proportion of species feeding on hardwoods was only slightly lower (n = 237, 57%) at the western Oregon site. Only 45% of the macrolepidoptera fauna was associated with hardwoods at the Blue Mountain site.

Herb-grass feeders were the second highest category, 31-42%, among all 3 forests (Table 1). The number of species in the herb-grass feeding category was very similar for the 3 sites. However, the highest proportion (42%) of herb-grass feeders occurred at the eastern Oregon site, where the more xeric conditions favor a rich and abundant herb-grass flora.

In the 2 Oregon forests, 9–10% of the macrolepidoptera species were associated with conifers, whereas only 1% of the Appalachian macrolepidoptera feed on conifers. The small number of species associated with conifers would be expected for the Appalachian site because of the relative paucity of conifer species. However, the relatively low percentage of species associated with conifers at the 2 Oregon sites is contrary to what might be predicted on the basis of canopy cover and biomass of foliage within the ecosystem (Waring and Franklin 1979). In a plant community different from a coniferous forest, Futuyma and Gould (1979) likewise noted a lack of correlation between the abundance of a particular floral type and richness of Lepidoptera.

Among the other feeding categories of the macrolepidoptera, only 2% of the species were classified as mixed feeders and only 1–5% were associated with lichen-detritus. The percentage of mixed feeders was identical among the 3 sites, but the species richness of lichen-detritus feeding species (n = 22, 5%) was highest at the West Virginia site.

A comparison of only the moth species, excluding the butterflies, in each feeding category resulted in a slightly different profile in the proportion of species associated with respective plant types (Table 2). Because many butterfly species feed on herbs and grasses, the proportion of hardwood-feeding species increased when we considered the moths separately. Nevertheless, herb-grass feeding species constituted a relatively high proportion of the moth fauna at the Table 3. Proportion of moth abundance (with known foodplants) using major foodplant groups occurring in forested ecosystems

Feeding habits	Site ^a							
	Western Oregon		Eastern Oregon		West Virginia			
	n	%	n	%	n	%		
Hardwood	3,878	69	5,442	39	8,166	77		
Ierb-grass	611	11	7,678	55	824	8		
Conifer	1,021	18	669	5	95	1		
Mixed	141	2	102	1	395	3		
ichen-detritus	8	<1	5	<1	1,171	11		
Total	5,659	100	13,896	100	10,651	100		

" Unpublished data of authors for western Oregon; Grimble et al. (1992) for eastern Oregon; Butler and Kondo (1991) for West Virginia.

Blue Mountain site. Overall, 66 and 52% of the moth species in western and eastern Oregon, respectively, feed on hardwoods. Hardwood-feeding species were 68% of the moth fauna at the West Virginia site. Herbgrass feeders were 20 and 33% of the moth fauna in western and eastern Oregon, respectively, and 21% in West Virginia. The proportion of moth species that were conifer feeders, 12%, was highest at the eastern Oregon site, 10% at the western Oregon site, and only 1% at the West Virginia site.

Abundance. An assessment of moth abundance provided an indication of the number of individuals generated from each of the host plant groups (Table 3). Overall, the lichen-detritus and mixed feeders were not abundant at the Oregon sites, but the lichendetritus-feeding species were relatively more abundant (11%) at the West Virginia site. The most apparent difference between the 2 Oregon sites is in the proportion of individuals associated with an herbgrass feeding habit. The number of moths at the Blue Mountain site was dominated (55%) by individuals that feed on herbs and grasses. Only 11% of moth abundance in the western Cascades was associated with herbs-grasses. The herb- and grass-feeding species represented 8% of moth abundance in West Virginia. The abundance of moths was dominated by hardwood-feeding species at the western Oregon site (69%) and the West Virginia site (77%). Also, the proportion of individuals associated with conifers was highest at the western Oregon site (18%) compared with 5% at the eastern Oregon site and only 1% at the West Virginia site.

The low percentage of moths associated with conifers at the West Virginia site would be predicted on the basis of the relative paucity of conifer species in southern Appalachian forests. The overall dominance of conifers in the pine and Douglas-fir forests of western North America would suggest the possibility of a relatively abundant fauna of moths feeding on conifers. This was not the case for moth abundance and, as previously mentioned, this was not true for species richness. However, a relatively low abundance of moths among the conifer-feeding species would be predicted if the most abundant trees had recently been subjected to an epizootic. In fact, a multiyear outbreak of the spruce budworm, *Choristoneura occidentalis* Freeman, had just subsided when our study took place at the eastern Oregon site. The effect of the budworm epizootic on the overall moth fauna is unknown. However, the circumstance of a budworm outbreak stimulates the hypothesis that an epizootic of a conifer-feeding caterpillar may decrease the abundance of other conifer-feeding species whereas at the same time enhance the abundance of hardwood and herb-grass-feeding species (Wickman et al. 1992). Additional studies are needed to address this hypothesis.

Conservation Implications. The larvae of butterflies and moths are major herbivores (exploiters) in most terrestrial ecosystems and often are the primary insect herbivores in temperate forest ecosystems (Furniss and Carolin 1977, Schowalter et al. 1986, Stamp and Casey 1993). Witkowski and Borusiewicz (1984) estimated that 2-8 million caterpillars occurred within 1 ha of a European forest. Acting in the role of exploiters, the gypsy moth and the western spruce budworm may consume a high percentage of the foliage in respective forest canopies, which in turn affects microclimate, plant mortality, and competition within and among plants (Brookes et al. 1987, Elkinton and Liebhold 1990, Campbell 1993). Thus, the Lepidoptera may play an important role in plant population dynamics and community organization (Gange and Brown 1989, Huntly 1991).

The relationship between plant species and the number of Lepidoptera species that they host has been well documented in numerous studies. For instance, a study of Lepidoptera associated with British trees showed that up to 106 species of macrolepidoptera were associated with 1 genus of plant (Southwood 1961). On a smaller geographic scale, >45 species of Lepidoptera were documented feeding on the foliage of Oregon white oak, Quercus garryana, in a study plot of 2,000 ha in western Oregon (Miller 1990). Thus, as species richness in plants changes during succession, the species richness in Lepidoptera probably exhibits a coincident change. To our knowledge no data exist that illustrate such a relationship. However, studies such as that conducted by Schoonmaker and McKee (1988) documented that plant species richness peaked at a mean of ≈58 species 20 yr after clear-cutting. We suggest that Lepidoptera species richness changes with such change in the vegetation. However, without information on the richness of Lepidoptera associated with respective plant species, we cannot predict the pattern of biodiversity within the Lepidoptera fauna that in turn supports higher trophic levels.

Species richness and diversity among herbivores and carnivores is based on plants as primary producers. In western coniferous forests, most of the vascular plants are angiosperms: hardwoods, herbs, and grasses. Coniferous species comprise $\approx 3\%$ of the vascular flora (Franklin and Dyrness 1971). Consequently, nearly 90% of the macrolepidoptera species within a forest ecosystem depend upon the presence of angiosperms as their host plants. Similarly, >80% of the overall abundance of macrolepidoptera is dependent upon angiosperms. These moths and butterflies, in turn, support or at least provide linkages in the food webs of predaceous animals such as arthropod predators, passerine birds, small mammals, and bats (Whitaker et al. 1977). Thus, the food chains within coniferous forests depend in a large measure upon the diversity of angiosperms; in particular, hardwoods, herbs, and grasses.

Serving in the role of provider, Lepidoptera convert plant biomass into animal biomass, which in turn supports 1st order carnivores such as arthropod predators, parasitoids, amphibians and reptiles, passerine birds, bats, and other small mammals (Pyle et al. 1981, Witkowski and Borusiewicz 1984). Examples of Lepidoptera in the food webs of forest ecosystems demonstrate their utility as prey for vertebrates. In temperate climates, small vertebrates often require a high dietary intake of protein when rearing offspring during spring and early summer (Welty 1975), precisely the time when Lepidoptera larvae are most abundant. Migratory passerine birds, such as warblers, depend upon larval Lepidoptera as their primary food source (Graber and Graber 1983). Also, Graber and Graber (1983) observed that in the spring 75-98% of the invertebrates on leaves in eastern hardwood forests were larval Lepidoptera and that warblers ate 1.2-1.7 times their weight in larvae per day. Mortality of larval Lepidoptera by bird predation ranged from 18 to 63% in the understory of eastern forests (Holmes et al. 1979).

The importance of Lepidoptera in the diet of insectivores may depend, in part, on season, life stage, and diurnal patterns of activity. Moths and butterflies differ in their circadian behavior. Butterflies are predominately diurnal, whereas moths are mostly nocturnal. The different flight habits affect the type of animal that might use one or the other as food. For instance, bats fly at night and therefore are not likely to feed on adult butterflies. Likewise, a day-flying bird will not encounter many flying moths but may search for perched moths as well as larvae and pupae. Burrowing mammals (i.e., moles) and wood-excavating birds (i.e., woodpeckers) may consume pupae of Lepidoptera. Second-order vertebrate predators, such as hawks, owls, coyotes, and bobcats also may depend indirectly on Lepidoptera to some degree. For example, Forsman et al. (1984) found that the northern spotted owl feeds primarily on the northern flying squirrel. The squirrel, in turn, is insectivorous and probably feeds extensively on caterpillars in the spring and early summer when young squirrels are being reared (Cahalane 1961, Larrison 1976). Thus, the reproductive success of the spotted owl is linked to the success of squirrels, which in turn is linked to the availability of Lepidoptera.

Previous studies of defoliating forest species, such as the western spruce budworm, suggest that generalist predators (i.e., ants, birds, and spiders) are important regulators of population abundance and contribute to maintaining herbivore numbers at endemic levels (Brookes et al. 1987, Campbell 1993). Our study suggests that such predators probably are supported by lepidopterans in the ecosystem because of the richness and abundance of angiosperms. We found that hardwood trees and shrubs are very important in the production of the moth biomass available to predators within the moist, forested site of the Cascade Mountains. Similarly, herbs and grasses growing on the forest floor are responsible for much of the moth biomass available to predators in the drier eastern Oregon site in the Blue Mountains. Consequently, we predict that forest management practices involving the elimination of angiosperms, and therefore the associated fauna of Lepidoptera, also will reduce the species richness and abundance of predators that rely on Lepidoptera. A coniferous forest possessing an imbalance in the numbers of insectivorous predators may be even more vulnerable to epizootic episodes in the population dynamics of conifer-feeding species such as the western spruce budworm and the Douglas-fir tussock moth, Orgyia pseudotsugata (McDunnough).

Our study focused on the species richness and abundance of Lepidoptera, but we suggest that the relationships extend to other taxa as well. Therefore, if maintenance of a certain level of diversity is a primary objective in the management of a given forest, then practices must be followed that promote diversity among the angiosperms (Hansen et al. 1991, Kuusipalo and Kanjas 1994). Six practices might include the following: (1) avoidance of herbicides that suppress brush recolonization and growth during reforestation projects; (2) prescribed use of fire in small local patches to improve growing conditions for herbs and grasses on the forest floor; (3) maintenance of natural open areas such as meadows and prairies within the forest habitat; (4) limitations on grazing by domestic livestock, namely cattle and sheep, in the herb-grass plant communities; (5) protection of vegetation along riparian zones, an area where certain angiosperms may be limited in their distribution; and (6) multispecies plantings of hardwood trees and shrubs in forest restoration projects. These measures are suggested as means to maintain, attain, or retain a diverse biota for enhancement of food webs and species biodiversity.

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