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Terrestrial Arthropod Assemblages: Their Use in Conservation Planning

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Abstract: *Arthropods, the most diverse component of terrestrial ecosystems, occupy a tremendous variety of functional niches and microhabitats across a wide array of spatial and temporal scales. We propose that conservation biologists should take advantage of terrestrial arthropod diversity as a rich data source for conservation planning and management. For reserve selection and design, documentation of the microgeography of selected arthropod taxa can delineate distinct biogeographic zones, areas of endemism, community types, and centers of evolutionary radiation to improve the spatial resolution of conservation planning. For man-*

Asociaciones de artrópodos terrestres: Su uso en la planificación conservacionista

Resumen: *Los artrópodos, el componente más diverso de los ecosistemas terrestres, ocupa una tremenda variedad de nichos funcionales y microhábitats a lo largo de un amplio espectro de escalas espaciales y temporales. Nosotros proponemos que los biólogos de conservación deberían aprovechar la diversidad de los artrópodos terrestres como una rica fuente para el planeamiento y manejo conservacionista. La documentación de la microgeografía de ciertos taxones de artrópodos puede delinear zonas biogeográficas precisas, áreas de endemismo, tipos de comunidades, y centros de radiación evolutiva para mejorar la resolución espacial en el planeamiento conservacionista destinado a la selección y*

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agement of natural areas, monitoring of terrestrial arthropod indicators can provide early warnings of ecological changes, and can be used to assay the effects of further fragmentation on natural areas that no longer support vertebrate indicator species. Many arthropod indicators respond to environmental changes more rapidly than do vertebrate indicators, which may exhibit population responses that do not become evident until too late for proactive management. Not all arthropod taxa are equally effective as indicators for conservation planning, and the qualities of indicators can differ for purposes of inventory versus monitoring. Assemblages of arthropod taxa used as biogeographic probes in inventories should exhibit relatively high species diversity, high endemism, and encompass the geographic range of interest. For monitoring purposes, indicator assemblages should exhibit varying sensitivity to environmental perturbations and a diversity of life-history and ecological preferences.

Introduction

Whether measured by species, individuals, or biomass (Erwin 1982, 1988, 1991c; Wilson 1985, 1988; Stork 1988; Gaston 1991a, 1991b), arthropods dominate terrestrial ecosystems. Despite increased awareness of their importance to global conservation planning (Wilson 1988), relatively little attention has been devoted to the inventory and monitoring of terrestrial arthropods (Dourojeanni 1990; di Castri et al. 1992). The diversity and abundance of terrestrial arthropods can provide a rich base of information to aid efforts in the conservation of biodiversity and the planning and management of nature reserves (Pyle et al. 1981; Collins & Thomas 1991; Murphy 1992; Pearson & Cassola 1992). This paper, the synthesis of a workshop held in June 1991 is intended to encourage conservation biologists to develop methods for tapping this rich data source to improve inventory and monitoring for conservation planning.

Inventory and Monitoring: Definitions

Inventory and monitoring, two essential and interrelated activities necessary for scientific conservation planning, differ in their objectives and hence in the types of indicators useful to each activity. Inventory programs document the spatial distribution of biological elements—populations, species, guilds, communities, and ecosystems. For conservation planning, such information can be used (1) to select and design reserves (Usher 1986; Noss 1987; Scott et al. 1987; Margules et al. 1988; Margules & Stein 1989; McKenzie et al. 1989); (2) to assess the potential for sustainable use of natural

diseño de reservas. En cuanto al manejo de áreas naturales, el monitoreo de artrópodos terrestres puede proveer de avisos tempranos sobre cambios ecológicos y puede ser usado para investigar los efectos de la fragmentación subsecuente de áreas naturales que ya no mantienen especies de vertebrados indicadoras. Muchos artrópodos indicadores responden a los cambios ambientales mas rapidamente que vertebrados indicadores, los cuales pueden exhibir respuestas poblacionales que sólo se hacen evidentes cuando ya es muy tarde para el manejo proteccionista. No todos los taxones de artrópodos son igualmente efectivos como indicadores para el planeamiento conservacionista, y las calidades de los indicadores pueden variar dependiendo si su uso es con fines de inventario o de monitoreo. Las asociaciones de artrópodos usados como sondas en inventarios deberían exhibir diversidades específicas relativamente altas, alto endemismo y deberían abarcar el rango geográfico de interés. Si son usados con propósitos de monitoreo, las asociaciones de indicadores deberían exhibir diferentes sensibilidades a las perturbaciones ambientales, y diversidad en cuanto a historias de vida y preferencias ecológicas.

resources (Eisner 1991; Plotkin & Famolare 1992); (3) to strengthen the case for habitat conservation by documenting the distribution of threatened or endangered species (see Thomas et al. 1990; Reinthal & Stiasny 1991); and (4) to provide the basis for selecting indicator species or assemblages for ecological monitoring (Noss 1990; Spellerberg 1991; Kremen 1992).

In contrast, the goals of monitoring programs are to assess changes in ecosystem structure, composition, and function in response to natural factors, human disturbances, or management activities over time (Noss 1990; Spellerberg 1991). A challenge in monitoring is to separate variation in baseline conditions due to natural fluctuations from variation due to human disturbances. This challenge is met in part by monitoring control plots in "pristine" habitats, as well as plots subject to disturbance. The response of indicators to known environmental perturbations, including management activities, can then be used to suggest better management practices (Holling 1978; Murphy & Noon 1991).

In the conservation context, neither inventory nor monitoring programs can be exhaustive. Such programs must therefore rely on indicator species or indicator assemblages; that is, suites of species that respond readily to environmental change in ways that are easily measured or observed. Increasing attention is now being directed to the use of indicator species assemblages (Verner et al. 1986; Landres et al. 1988; Noss 1990; Karr 1991), which tend to improve both resolution and scale of inventory and monitoring programs (Kremen 1992, 1994). Use of species assemblages is especially appropriate for terrestrial arthropods, since many of their most valuable attributes as biological probes result from their extraordinary morphological and functional diver-

sity. For example, a monitoring program that includes assemblages of terrestrial arthropods representing a diversity of taxa and/or functional groups automatically broadens the scope of the environmental factors that can be perceived.

Indicator assemblages useful for reserve selection and design should allow planners to identify biogeographic zones, areas of endemism, evolutionary centers of radiation (Erwin 1991*b*), patterns of geographic replacement, and community types. Indicator assemblages appropriate for monitoring must be sensitive to anthropogenic disturbance and should be able to provide an early warning of ecological change. Given these different objectives, indicator assemblages to be used in inventory are not always the best ones for monitoring purposes, and vice versa.

Terrestrial Arthropods as Indicators for Inventory and Monitoring

Terrestrial arthropods have been referred to as “the little things that run the world” (Wilson 1988); they occupy the widest possible diversity of ecosystems, microhabitats, and niches, and they play many key ecological roles (Collins & Thomas 1991). Values of terrestrial vertebrate indicators have already been recognized and are generally accepted (Verner et al. 1986; Landres et al. 1988). In this discussion, we frequently compare terrestrial arthropods and vertebrates—not to insist that terrestrial arthropods universally serve as “better” indicators, but to illustrate circumstances in which their use might be particularly advantageous.

Terrestrial arthropods make up 93% of the total animal biomass in one hectare of Amazonian rain forest (Wilson 1987), a fact reflecting their ecological importance. In tropical and temperate settings, insect herbivores exert comparable or greater grazing pressures on plants than do their vertebrate counterparts (Broadhead 1958; Janzen 1981; Thornton 1985). Arthropod spatial and temporal distributions span the ranges occupied by many vertebrate and plant species, but they also include finer-grained patch sizes and geographic distributions, more complex seasonal and successional sequences, and patch dynamics with more rapid turnover (Shelford 1907; Callan 1964; Waloff 1968; Price 1973; Lawton 1978; Southwood 1978; Erwin & Scott 1980; Schoener 1986; Scott & Epstein 1986; Gaston & Lawton 1988; Wolda 1988; Usher & Jefferson 1991). Terrestrial arthropods exhibit a great range of body sizes, vagilities, and growth rates (Borner & DeLong 1971; Walker 1975; Duellman & Trued 1986; Tyrrell & Tyrrell 1990; M. J. Kaliszewski & D. Wagner, personal communication), and they span a great variety of ecological niches and distributional, population, and dispersal traits. In short, the diversity of arthropods provides a potentially wide

array of biogeographical and ecological probes for use in virtually any inventory or monitoring challenge.

Statistical rigor in inventory and monitoring programs is feasible for many terrestrial arthropod species, given the high diversity of species and their tendency to exhibit large population sizes. Terrestrial arthropods can be easier and less costly to survey than vertebrates. Passive survey methods can reliably sample large numbers of individuals over short time periods, and specimens can be processed in a fraction of the time necessary to handle equivalent numbers of vertebrate specimens. Fewer societal and ecological considerations constrain the collection of terrestrial arthropods during the course of inventory or monitoring studies. For these reasons, terrestrial arthropod species have been the preferred subjects of many basic and applied ecological studies, including some studies that would have been impossible to investigate using other taxa—for instance, Simberloff and Wilson's (1969) extirpation of the entomofauna of mangrove islands to test island biogeographic theory.

Reference collections of terrestrial arthropods can be maintained indefinitely and inexpensively for future and retrospective studies (for example, for molecular genetics); extensive holdings already exist in public and private collections. Terrestrial arthropods, rich in external morphological characteristics, are amenable to rapid species sorting, construction of taxonomic keys (Hammond 1990), and phylogenetic analysis. Phylogenetic systematics in turn can be valuable in assessing global conservation priorities (Humphries et al. 1991) and for detecting centers of radiation where speciation is occurring congruently in distinct lineages (Erwin 1991*b*). Although certain terrestrial arthropods (including some families of Lepidoptera, Coleoptera, Hymenoptera, and Odonata) are taxonomically well known in many geographic areas, the systematics of many other groups are poorly known. Terrestrial arthropods, nonetheless, can be used successfully for inventory or monitoring purposes if individuals can be accurately sorted to morphospecies. Increasingly, entomologists interested in applying their work to conservation and land management issues are taking this approach (Klein 1989; Andersen 1991; Erwin 1991*a*; Kremen 1992, 1994; McIver et al. 1992; Moldenke in press). In fact, in poorly surveyed regions such as many tropical moist forests, sorting to morphospecies for some arthropod taxa may be quicker and more reliable than for many plants and some vertebrates, a real advantage for inventory studies.

Training local assistants in the preparation and recognition of morphospecies is no more difficult or time consuming for terrestrial arthropod taxa than for vertebrate or plant taxa, provided appropriate target groups of terrestrial arthropods are chosen (groups in which morphospecies can be readily recognized) and training

is limited in taxonomic scope. Because specimens of terrestrial arthropods are generally collected (rather than observations alone being recorded), more opportunities exist for experts to supervise parataxonomists and ensure the accuracy of data collection.

Inventory of Arthropods

Because an explicit goal in establishing networks of reserves is to maximize protection of biotic diversity, it is logical to utilize the most diverse biotic elements as indicators in the assessment of land areas for their conservation value. Many terrestrial arthropod taxa not only are diverse but include suites of species that are endemic to highly localized areas and specific microhabitats (O'Neill 1967; Fellows & Heed 1972; Kaneshiro et al. 1973; Turner & Broadhead 1974; Freitag 1979; Savage 1982; Pearson & Cassola 1992). Erwin (1983), for instance, found that 83% of beetle species collected in four types of forest in the Brazilian Amazon were restricted to a single forest type. Inventories of such taxa could result in enhanced biogeographic resolution of communities, habitats, ecotones, and biotypes, as well as areas of endemism and centers of diversity (Kremen 1994), and thus could provide effective tools for conservation planning (Brown 1991; Greenslade & New 1991; see also Rytí 1992), particularly for determining reserve boundaries or identifying small reserves to capture unique remnant communities. For example, in temperate-zone grasslands, Erhardt and Thomas (1991) used their detailed understanding of the microhabitat requirements (microclimate, fine-scale habitat structure, and host-plant needs) of an assemblage of diurnal Lepidoptera to identify the minority of grassland sites that had histories of continuous traditional management over the past 3500–4000 years, arguing that a similar inventory of plant species would not be equally revealing. Such grasslands now constitute an important and diminishing biotic resource in Britain and continental Europe.

Conserving the habitats of charismatic megavertebrates that require large land areas for population persistence has been an effective strategy that also affords protection for organisms with lesser habitat requirements (Murphy & Wilcox 1986). Increasingly, however, invertebrates, other smaller animals, and plants that are able to persist in small habitat patches are becoming the umbrella species for the protection and management of tiny, remnant natural areas (Main 1987; Murphy et al. 1990; Samways 1990; Wilson 1991; Murphy 1992; Pearson & Cassola 1992; The Wilds and IUCN/SSC Captive Breeding Specialist Group 1992). Protection of the Oregon silverspot butterfly (*Speyeria zerene hippolyta*) under the Endangered Species Act, for example, will

ensure the conservation of several highly threatened native coastal grassland communities in Oregon (McIver et al. 1989). In the developed world, where few large natural areas remain to be protected, inventory of the terrestrial arthropod fauna of such patches is a critical priority to aid in establishing the potential conservation value of these areas, as well as legal mechanisms for their protection (Murphy 1991).

The inventory of arthropods can also contribute to assessments of the economic value of natural areas. Prospecting for unusual organic compounds used by arthropods for defense, communication, and reproduction may reveal lucrative new chemicals for medicine or industry and can result in benefits for conservation (Eisner 1991; Roberts 1992). Taxa likely to display such characteristics (such as spiders and certain beetle families) can be selected as the target assemblages for "chemical prospecting" inventories.

Inventory Strategies

To represent the biological diversity and ecological complexity present within a region, a conservation inventory (an inventory conducted for conservation planning) should strive to include a number of higher taxa with differing ecological functions, habitat and niche specializations, and distributional characteristics (di Castri et al. 1992). We therefore advocate that such inventories include several vertebrate, plant, and terrestrial arthropod taxa, at a minimum. Strategies for conducting terrestrial arthropod surveys within the context of team-conducted inventories are presented below. All taxa to be selected for inventories should be readily observed or collected, amenable to random and reproducible sampling, and relatively well-known taxonomically and/or ecologically.

In the first method, Coddington et al. (1991) stress reconciling the differences in taxonomic sampling practiced by traditional museum collectors and by community ecologists. Museum collectors efficiently generate relatively complete species lists at sites but rarely gather quantitative data on relative abundances. In contrast, community ecologists often concentrate on obtaining relative abundance estimates to the detriment of species lists. Using spiders as an example, Coddington et al. demonstrate that it is possible to do both, simply by developing time-limited sampling methods based on taxon-specific collecting procedures that can be replicated between sites. Quantitative between-site comparisons can then be drawn from data on relative abundances, community composition, and species diversity, and then can be used to aid in prioritizing sites for conservation planning.

In related work, Lamas et al. (1991) discuss the ad-

vantages and disadvantages of sampling with an intended bias to maximize the number of species collected, rather than sampling at random. This method can work only for taxa in which species can be readily recognized at the time of sampling (such as butterflies), such that species previously collected can be ignored or released. Such a protocol allows a much higher proportion of the focal taxon to be collected at a site in a shorter time period, without over-collecting the fauna or gathering a huge number of specimens that will then be expensive to process and curate.

A final method, target taxon analysis (Kremen 1994), is based on the concept of inventorying only "biogeographically informative" taxonomic assemblages that are likely to represent environmental patterns or the distributional patterns of species in other unrelated assemblages. Kremen hypothesized that taxonomic assemblages resulting from evolutionary radiations within a region will be biogeographically informative. Such taxa (usually of low taxonomic rank, such as genera or tribes, to be of relevance to regional conservation planning) can be preselected on the basis of their high species richness and endemism within a region. Assemblages with these characteristics frequently occur among terrestrial arthropods, especially in the tropics, and many groups are well-characterized enough for such target groups to be selected.

By focusing on a number of such narrowly-defined taxa representing a diversity of higher taxa, the time and cost devoted to sampling, sorting, and training are greatly reduced. Target taxon analysis lends itself to team survey work and, in fact, depends upon it. The following steps are recommended:

- (1) Five to ten higher taxa that are relatively well-characterized (a preliminary regional species list would be sufficient) are chosen—for example, bats, birds, frogs, certain families of vascular plants, butterflies, carabid (ground) beetles, dragonflies, wasps and bees, and dung beetles (see also Brown 1991; Sutton & Collins 1991). Each higher taxon chosen should include one or more low-ranking taxa with high diversity and endemism for testing as a target taxon.
- (2) For each taxon, specialists will select a target assemblage using the selection criteria (species-rich, high endemism), to the extent possible given available knowledge. When known, additional criteria should be used to select those taxon whose member species are collectively well distributed and abundant and display high *beta* or *gamma* diversity (Kremen 1994).
- (3) Using standard ecological sampling design (as in Coddington et al. 1991), the information value of target assemblages can be tested in a limited inventory across an obvious environmental gradient or dispersal barrier. Correlations can then be analyzed (1) between target taxa and environmental gradients, and (2) between the distributions of different taxonomic assemblages. The strength of resulting correlations provides the basis for accepting or rejecting target assemblages as biogeographic indicators.
- (4) Once target assemblages are chosen, the team can conduct larger-scale inventories of the entire region, including all major habitat types and environmental gradients. The information can then be used to identify areas of endemism (Brown 1982, 1991; Fa 1989; Cracraft 1991), to select a minimum number of sites by complementarity to represent the full range of species or habitat types (Margules et al. 1988), or to perform "gap analysis" (Scott et al. 1987). Alternatively, the relationship between distributional and environmental data can be used to predict the full range of a species or species assemblage, and the predicted ranges can then be used to select reserves or to evaluate protection afforded by existing reserve networks (Margules & Stein 1989; McKenzie et al. 1989).

Monitoring of Arthropod Indicator Assemblages

An effective monitoring program will utilize a variety of indicators to assess environmental responses at population, species, community, and ecosystem levels of organization (Noss 1990). Monitoring of terrestrial arthropods can fit into this scheme across a continuum from populations to communities. Indicator assemblages of arthropods might be chosen taxonomically (that is, by monitoring the presence/absence or relative abundance of all members of a taxonomic group or groups over time) or functionally (by monitoring sets of species representing different ecological roles in their habitats).

To reiterate, the advantage of considering arthropod indicators, either individual species or groups of species, as candidates for monitoring is that their tremendous ecological diversity provides a wide choice for designing appropriate assessment programs. The sensitivity of many terrestrial arthropod populations to environmental impact, including fragmentation, disturbance, habitat modification, ecological disruption, climate change, and chemical pollution, makes them potentially informative for scientifically based reserve design and management. For example, most previous studies of habitat fragmentation have focused on birds (see Diamond 1975; Thomas et al. 1990; Blake 1991; Newmark 1991) and other vertebrates (Burgess & Sharpe 1981; Shaffer 1981; Harris 1984; Newmark 1985, 1987;

Cutler 1991) and have shown the tremendous and far-reaching impact of fragmentation on the maintenance of ecological diversity and stability. It is far less widely recognized that habitat fragmentation also exerts considerable influence on terrestrial arthropod populations; those studies that do exist have shown striking area and isolation effects, particularly for species with limited dispersal capabilities. Turin and den Boer (1988) found that, over the past century, the most sedentary carabid beetle species no longer occupy many localities in which they were formerly found in the Netherlands, a pattern attributable to habitat fragmentation (see also den Boer 1990). Heathland spiders in Great Britain were also found to be restricted to the largest habitat patches, having disappeared from smaller patches (Hopkins & Webb 1984). Klein (1989) found that dung- and carrion-eating beetles of Brazilian rain forests would not cross even narrow clear-cut barriers (less than 350 m wide); species richness and abundances declined significantly in this group in response to decreasing patch area just several years after isolation. In the same study area, in patches isolated since 1980, forest-restricted butterflies of the subfamilies Morphinae, Brassolinae, Theclinae, and Riodininae showed dramatic declines in species richness with area (Brown 1991). Selected terrestrial arthropods thus can demonstrate strong responses to habitat fragmentation, and therefore can be effective indicators that will provide early warnings of the ecological consequences of fragmentation.

Monitoring the distributional and functional responses of terrestrial arthropods to fragmentation may also permit detection of ecological change at an appropriately fine spatial scale to permit improved reserve design and management. The reactions of terrestrial arthropods to microenvironmental gradients (such as temperature, humidity and wind) make them highly responsive both to edge effects (Brown 1991) and to the size of forest clearings (Shure & Phillips 1991). Fragmentation and habitat destruction influence not only the distribution and abundance of terrestrial arthropods (Desender & Turin 1989) but also their ecological functions. Jennersten (1988) demonstrated a disruption in insect pollinator services due to fragmentation, and Klein (1989) showed that dung decomposition in small, isolated patches of tropical moist forest declined with lowered diversity and abundance of dung-feeding beetles. Minimization of dysfunctions resulting from edge and area effects are of critical concern in reserve design and management (Noss 1983; Harris 1984), and further studies of area and edge impact on functional linkages are needed for a variety of taxa.

The ecological health of certain microhabitats may be best monitored using highly specific assemblages of terrestrial arthropods. For example, the terrestrial arthropod fauna of Pacific Northwest old-growth forest floors is comprised of highly characteristic assemblages

adapted to the narrow temperature and moisture ranges of these environments (McIver et al. 1990; Moldenke & Lattin 1990; Parsons et al. 1991; Lattin & Moldenke 1992). These assemblages include numerous species of oribatid mites, harvestmen, millipedes, centipedes, springtails, beetles, flies, wasps, crickets, and isopods. Many of the species inhabiting understory microhabitats are relatively sedentary (wingless or flightless). The dispersal of understory species is therefore limited by both distance and inhospitable terrain; consequently these assemblages are likely to be strongly affected by alteration of old-growth and mature forest environments (Moldenke & Lattin 1990; Olson 1992). Since many of these species are involved in litter decomposition and nutrient recycling, disruptions in the structure of these communities will have important functional implications for old-growth ecosystems.

One goal of the management of natural areas is to maintain the ecological stability and diversity found in "pristine" ecosystems. Gilbert (1980) noted the importance of "mobile-links"—species that pollinate or disperse the seeds of a wide variety of plants—in maintaining diversity and suggested that autecological and monitoring studies of representative mobile-link species be conducted. Mobile-link species, many of which are insects, support "keystone mutualist" plant species, which in turn provide critical resources (such as fruits, nectar, leaves, secondary chemical compounds, sites for mating and predator avoidance, and so forth) used by a wide variety of other organisms (Janzen 1981; Bawa 1990). The monitoring of mobile-link species would complement studies of two other functional groups critical to the maintenance of community diversity and stability: top predators (Terborgh 1988) and keystone-mutualist plants (Gilbert 1980; Terborgh 1986).

Paradoxically, these mobile-link species may include some of the more generalized taxa among terrestrial arthropods. A well-studied group of mobile links are the neotropical euglossine bees. Single species of euglossine bees can link plant species from all stages and strata of forests into systems of indirect mutualism. Many euglossine species rely on early successional patches and the plants that they support for larval food, and they are the obligate pollinators of plants restricted to late-successional forests. Females may travel long distances when foraging for pollen and thus may be critical to the reproductive success of plants that exist in low densities (Dobson 1966; Janzen 1971; Gilbert 1980). Monitoring euglossine populations thus indirectly allows assessment of the health of interacting habitat patches within ecosystems. Euglossines are easy to inventory and monitor because they are attracted to chemical scents, can be readily identified without collecting, and can be individually marked for population studies.

Many terrestrial arthropods have rapid population growth rates and short generation times, and therefore

can exhibit rapid responses to fluctuating environmental conditions (including local and regional changes in abundance, patch extinction and colonization, and range expansions and contractions—see Pollard 1979; Murphy & Weiss 1988*a*, 1988*b*, 1991; Murphy et al. 1990; Colwell & Naeem 1993). When such changes can be shown to be correlated across taxa, to be causally connected or strongly correlated with known environmental changes, or to occur as persistent population lows, highs, or extinctions, these changes may be recognized as early warnings of human-influenced ecosystem change. For example, declines in the abundance of temperate diurnal Lepidoptera species have heralded alterations in habitat structure well before those changes have become evident in populations of their host plants (Erhardt & Thomas 1991; Thomas 1991). The challenge in separating natural population fluctuations from those produced by anthropogenic perturbation holds for any indicator species, particularly when species demonstrate nonequilibrium population dynamics; recent analysis of available time-series data (Turchin & Taylor 1992) suggests that both insect and vertebrate populations “exhibit a similar spectrum of population dynamics,” ranging from no obvious regulation of population density to complex endogenous dynamics (damped oscillations, limit cycles, etc.).

The sensitivity of population growth rates and development of many arthropods to temperature, humidity, and rainfall (Wolda 1988), and the reliance of arthropod populations on narrowly defined microclimate niches (Dobkin 1985; Weiss et al. 1987, 1988; Erhardt & Thomas 1991; Murphy & Weiss 1988*b*, Britten et al. 1994) may make arthropods especially effective indicators of local and regional climate change (see Ehrlich et al. 1972; Murphy & Weiss 1992; see also Fajer 1989; Fajer et al. 1989; Dennis & Shreeve 1991; Britten et al. 1994). Fossil records of arthropod communities have been used to reconstruct climatic history (Atkinson et al. 1987).

Understanding the natural population dynamics of terrestrial arthropods has already proved important for managing arthropod pests in agroecosystems, such as the catastrophic cottony-cushion-scale outbreak in California in 1946, when DDT killed the natural enemy, vedalia beetles, of this citrus pest—see Anlow and Rosset (1990). Controlling agricultural disease vectors will become increasingly important as pest populations change in response to pesticide campaigns, climate change, and declines in the populations of their natural enemies (Schowalter 1985, 1989; Morris et al. 1991). When the environmental impact caused by pesticides is monitored, nonpest arthropods are natural subjects (Bracker & Bider 1982) because they are often the first organisms to be affected by phenomena that can later have severe consequences for rare mammals and birds, species at high trophic levels that may then require in-

tensive and costly recovery programs (for example, the peregrine falcon, Anderson & Hickey 1972; Cade 1988; Nisbet 1988). For example, honey bees are highly susceptible to DDT, dieldrin, carbaryl, malathion, and methyl parathion, and bee poisoning can be easily monitored by collecting dead bees at commercial hives (Johansen 1977).

Despite their relative merits, there has been little experience in utilizing terrestrial arthropod species or assemblages as indicators for inventory or monitoring related to conservation planning and management (but see Murphy et al. 1990; Brown 1991; Pearson & Cassola 1992). Instead, traditional management indicator species have been large vertebrates (Landres et al. 1988). The methodologies for utilizing terrestrial arthropod assemblages thus have yet to be fully developed and tested, and their constraints have not been identified.

Monitoring Strategy

To capitalize on the diversity of arthropods and their inherent potential for rapid ecological change, the goal is to select indicators that respond to human impact long before changes ramify through complex networks of ecological interactions to affect higher trophic levels and/or more long-lived organisms. Terrestrial arthropod assemblages could be selected to represent (1) a diversity of higher taxa; (2) a diversity of higher taxa and functional groups; or (3) a diversity of functional groups within the same higher taxon.

If monitoring is to be conducted to assess the effects of a suspected or known environmental impact, then the assemblages should comprise species responsive to the direct or indirect effects of that impact. The monitoring system will be potentially more sensitive if radically different functional elements can also be incorporated or metrics integrated from different taxonomic groups or levels of ecological organization (see the Index of Biological Integrity, Karr 1991). For example, in response to forest thinning (the proposed management strategy for the federal forest matrix outside of Habitat Conservation Areas in the Pacific Northwest), terrestrial arthropod populations might be expected to decline due to desiccation stresses, temperature increases, and wider ranges of variation for these factors (Majid & Jusoff 1987; Uhl & Kaufman 1990; Olson 1992). One might monitor the impact of such changes using assemblages of decomposers in the leaf litter and of predatory insects in the understory or canopy. The leaf-litter assemblage is composed of a high percentage of stenotopic species and will be highly responsive to changes in microclimate induced by the reduction of canopy cover. While the predaceous understory and canopy insects may be less narrowly adapted (Olson 1992) and therefore less responsive to the direct impact on microclimate, they

may respond indirectly to alterations in the densities of their prey populations. The sensitivity of these two assemblages can be tested in field trials (see also Kremen 1992).

If monitoring is instead more generalized (assessment of the status of biodiversity or "ecological health"), then a strategy that maximizes the representation of diverse higher taxa and functional groups would be preferred. Again, selection of indicator assemblages that are likely to respond in different ways to the same stress improves the sensitivity and robustness (Karr 1991) of monitoring, particularly in situations in which the relative importance of different effects is not known.

Monitoring of terrestrial arthropod assemblages could be conducted by (1) measuring the presence or absence of member species; (2) characterizing community structure by functional groups; (3) measuring the relative abundance of member species; or (4) carrying out population or autecological studies of member species. These techniques represent a gradient from least to most costly and difficult to implement. The second method, characterizing community structure by functional groups, potentially represents an efficient means of measuring biological responses to environmental changes using terrestrial arthropods. For example, the faunal assemblages of old-growth forests of the Pacific Northwest are distinct and contain predictable proportions of functional groups, including many herbivores, predators, and detritivores (Mispagel & Rose 1978; Voegtlin 1982; Schowalter et al. 1988; Schowalter 1990); in contrast, younger forests and monocultures are dominated by sap-sucking herbivores and a much less diverse array of predators (Schowalter 1989). Similar community shifts are observed in eastern deciduous forests with respect to natural or human-generated succession, leading to the conclusion that functional linkages are being altered in predictable ways in these different forest types (Schowalter 1989, 1990). Environmental impact could thus be reliably assessed by monitoring the functional structure of communities over time.

The functional approach integrates a huge amount of data (the responses of many, differently adapted organisms, see also Karr 1991) but is comparatively easy to implement because it relies on cataloging individuals or morphospecies by function rather than by taxonomic identity. For certain taxa (for example, Scarabaeidae), functional groupings can be readily assigned using morphological characteristics (for example, mouthparts) in combination with knowledge of the functional biology of higher taxa. Keys to the functional groups found within higher taxa can then be generated by specialists for use in assessment programs. Such methods would be particularly applicable in the tropics, where taxonomic identifications are frequently not feasible due to lack of knowledge of the diverse terrestrial arthropod fauna.

Conclusions

Terrestrial arthropods, because of their diversity of species and functional roles; wide range of body sizes, vagilities, and distributional characteristics; and propensity for rapid growth and evolutionary rates, offer certain exceptional characteristics as indicator groups for conservation inventory and monitoring programs. The unparalleled diversity of arthropods provides a rich data source that can improve the spatial resolution of biological inventories and hence the planning of natural-areas networks. Their capacity for exhibiting rapid responses to environmental change over both ecological and microevolutionary time makes them potential early warning indicators of environmental change.

To date, this rich data source remains largely untapped. In contrast, substantial experience exists in using aquatic arthropod communities for monitoring of water quality (Berkman et al. 1986; Karr 1991) and classification of aquatic habitats (Savage 1982; Johnson & Wiederholm 1989; Johnson et al. 1993). Some of this experience could be translated to terrestrial systems. An effort is needed on the part of conservation biologists, terrestrial arthropod ecologists, and systematists both to apply current knowledge and to develop new methodologies using terrestrial arthropods as indicators for conservation inventory and monitoring.

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Literature Cited

- Andersen, A. N. 1991. Responses of ground-foraging ant communities to three experimental fire regimes in a savanna forest of tropical Australia. *Biotropica* 23:575-585.
- Anderson, D. W., and J. J. Hickey. 1972. Eggshell changes in certain North American birds. Proceedings of the XVth International Ornithology Conference, Leiden, The Netherlands.

- Anlow, D. A., and P. M. Rosset. 1990. In C. R. Carroll, J. H. Vandermeer, and P. M. Rosset, editors. *Agroecology*. McGraw-Hill, San Francisco, California.
- Atkinson, T. C., K. R. Briffa, and G. R. Coope. 1987. Seasonal temperatures in Britain during the past 22,000 years, reconstructed using beetle remains. *Nature* 325:587–592.
- Bawa, K. S. 1990. Plant-pollinator interactions in tropical rain forests. *Annual Review of Ecology and Systematics* 21:299–422.
- Berkman, H. E., C. F. Rabeni, and T. P. Boyle. 1986. Biomonitoring of stream quality in agricultural areas: Fish versus invertebrates. *Environmental Management* 10:413–419.
- Blake, J. G. 1991. Nested subsets and the distribution of birds on isolated woodlots. *Conservation Biology* 5:58–66.
- Borror, D. J., and D. W. DeLong. 1971. *An introduction to the study of insects*. Holt, Rinehart, and Winston, New York.
- Bracker, G. A., and J. R. Bider. 1982. Changes in terrestrial animal activity of a forest community after application of aminocarb. *Canadian Journal of Zoology* 60:1981–1997.
- Britten, H. B., P. F. Brussard, and D. D. Murphy. The pending extinction of the Uncompahgre fritillary butterfly. *Conservation Biology*. In press.
- Broadhead, E. 1958. The psocid fauna of larch trees in northern England—an ecological study of mixed species populations exploiting a common resource. *Journal of Animal Ecology* 27:217–263.
- Brown, K. S. 1982. Paleocology and regional patterns of evolution in neotropical forest butterflies. Pages 255–308 in G. T. Prance, editor. *Biological diversification in the tropics*. Columbia University Press, New York.
- Brown, K. S. 1991. Conservation of neotropical environments: Insects as indicators. Pages 349–404 in N. M. Collins and J. A. Thomas, editors. *The conservation of insects and their habitats*. Academic Press, London, England.
- Burgess, R. L., and D. M. Sharpe, editors. 1981. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York.
- Cade, T. 1988. *Peregrine falcon populations: Their management and recovery*. The Peregrine Fund, Inc., Boise, Idaho.
- Callan, E. 1964. Ecology of sand dunes with special reference to the insect communities. *Monographs in Biology* 14:174–185.
- Coddington, J. A., C. E. Griswold, D. S. Dávila, E. Peñaranda, and S. F. Larcher. 1991. Designing and testing sampling protocols to estimate biodiversity in tropical ecosystems. Pages 10–48 in E. C. Dudley, editor. *The unity of evolutionary biology: Proceedings of the fourth international congress of systematic and evolutionary biology*. Dioscorides Press, Portland, Oregon.
- Collins, N. M., and J. A. Thomas, editors. 1991. *The conservation of insects and their habitats*. Academic Press, London, England.
- Colwell, R. K., and S. Naeem. 1993. Life history patterns of hummingbird flower mites in relation to host phenology and morphology. Pages 34–44 in M. A. Houck, editors. *Mites: Ecology and evolutionary analyses of life history patterns*. Chapman and Hall, New York.
- Cracraft, J. 1991. Patterns of diversification within continental biotas: Hierarchical congruence among the areas of endemism of Australian vertebrates. *Australian Systematic Botany* 4:211–227.
- Cutler, A. 1991. Nested faunas and extinction in fragmented habitats. *Conservation Biology* 5:496–505.
- den Boer, P. J. 1990. The survival value of dispersal in terrestrial arthropods. *Biological Conservation* 54:175–192.
- Dennis, R. L. H., and T. G. Shreeve. 1991. Climatic change and the British butterfly fauna: Opportunities and constraints. *Biological Conservation* 55:1–16.
- Desender, K., and H. Turin. 1989. Loss of habitats and changes in the composition of the ground and tiger beetle fauna in four west European countries since 1950 (Coleoptera: Carabidae, Cicindelidae). *Biological Conservation* 48:277–294.
- Diamond, J. M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural preserves. *Biological Conservation* 7:129–146.
- di Castri, F., J. R. Vernhes, and T. Younés. 1992. A proposal for an international network on inventorying and monitoring of biodiversity. *Biology International* 27:1–27.
- Dobkin, D. S. 1985. Heterogeneity of tropical floral microclimates and the response of hummingbird flower mites. *Ecology* 66:536–543.
- Dobson, C. H. 1966. Ethology of some bees of the tribe Eulglossini. *Journal of the Kansas Entomological Society* 39:607–629.
- Dourojeanni, M. J. 1990. Entomology and biodiversity conservation in Latin America. *American Entomologist* 36:88–92.
- Duellman, W. E., and L. Trueb. 1986. *Biology of the amphibians*. McGraw-Hill, New York.
- Ehrlich, P. R., D. E. Breedlove, P. F. Brussard, and M. A. Sharp. 1972. Weather and the “regulation” of subalpine populations. *Ecology* 53:243–247.
- Eisner, T. 1991. Chemical prospecting: A proposal for action. Pages 196–202 in F. H. Bormann, S. R. Kellert, editors. *Ecology, economics, ethics: The broken circle*. Yale University Press, New Haven, Connecticut.
- Erhardt, A., and J. A. Thomas. 1991. Lepidoptera as indicators of change in the seminatural grasslands of lowland and upland Europe. Pages 213–236 in N. M. Collins, J. A. Thomas, editors. *The conservation of insects and their habitats*. Academic Press, London, England.
- Erwin, T. L. 1982. Tropical forests: Their richness in Coleoptera and other arthropod species. *The Coleopterist's Bulletin* 36:7475.

- Erwin, T. L. 1983. Tropical forest canopies: The last biotic frontier. *Bulletin of the Ecological Society of America* 64:14–19.
- Erwin, T. L. 1988. The tropical forest canopy: The heart of biotic diversity. Pages 123–129 in E. O. Wilson, editor. *Biodiversity*. National Academy Press, Washington, D.C.
- Erwin, T. L. 1991a. Establishing a tropical species co-occurrence database. Part 1. A plan for developing consistent biotic inventories in temperate and tropical habitats. *Memorias del Museo de Historia Natural* 20:1–16.
- Erwin, T. L. 1991b. An evolutionary basis for conservation strategies. *Science* 253:750–752.
- Erwin, T. L. 1991c. How many species are there? Revisited. *Conservation Biology* 5:330–333.
- Erwin, T. L., and J. C. Scott. 1980. Seasonal and size patterns, trophic structure and richness of Coleoptera in the tropical arboreal ecosystem: The fauna of the tree *Lubea seemani triana* and *planch* in the canal zone of Panama. *The Coleopterist's Bulletin* 34:305–322.
- Fa, J. E. 1989. Conservation-motivated analysis of mammalian biogeography in the trans-Mexican neovolcanic belt. *National Geographic Research* 5:296–316.
- Fajer, E. D. 1989. How enriched carbon dioxide environments may alter biotic systems even in the absence of climatic changes. *Conservation Biology* 3:318–320.
- Fajer, E. D., M. D. Bowers, and F. A. Bazzaz. 1989. The effects of enriched carbon dioxide atmospheres on plant-insect herbivore interactions. *Science* 243:1198–1200.
- Fellows, D. P., and W. B. Heed. 1972. Factors affecting host plant selection in desert-adapted cactiphilic *Drosophila*. *Ecology* 53:850–858.
- Frietag, R. 1979. Carabid beetles and pollution. Pages 507–521 in T. L. Erwin, G. E. Ball, and D. R. Whitehead, editors. *Carabid beetles, their evolution, natural history and classification*. W. Junk, The Hague, The Netherlands.
- Gaston, K. J. 1991a. Estimates of the near-imponderable: A reply to Erwin. *Conservation Biology* 5:564–566.
- Gaston, K. J. 1991b. The magnitude of global insect species richness. *Conservation Biology* 5:283–296.
- Gaston, K. J., and J. H. Lawton. 1988. Patterns in the distribution and abundance of insect populations. *Nature* 331:709–712.
- Gilbert, L. E. 1980. Food web organization and the conservation of neotropical diversity. Pages 11–34 in M. E. Soulé, B. A. Wilcox, editors. *Conservation biology: An evolutionary-ecological perspective*. Sinauer Associates, Sunderland, Massachusetts.
- Greenslade, P., and T. R. New. 1991. Australia: Conservation of a continental insect fauna. Pages 33–70 in N. M. Collins, J. A. Thomas, editors. *The conservation of insects and their habitats*. Academic Press, London, England.
- Hammond, P. M. 1990. Insect abundance and diversity in the Dumoga-Bone National Park, N. Sulawesi, with special reference to the beetle fauna of lowland rain forest in the Toraut region. Pages x–343 in W. J. Knight, J. D. Holloway, editors. *Royal Entomological Society of London, London, England*.
- Harris, L. D. 1984. *The fragmented forest: Island biogeography theory and the preservation of biotic diversity*. University of Chicago Press, Chicago, Illinois.
- Holling, C. S. 1978. *International series on applied systems analysis: Adaptive environmental assessment and management*. Vol. 3. John Wiley and Sons, New York.
- Hopkins, P. J., and N. R. Webb. 1984. The composition of the beetle and spider faunas on fragmented heathlands. *Journal of Applied Ecology* 21:935–946.
- Humphries, C., D. Vane-Wright, and P. Williams. 1991. Biodiversity reserves: Setting new priorities for the conservation of wildlife. *Parks* 2:34–38.
- Janzen, D. H. 1971. Euglossine bees as long-distance pollinators of tropical plants. *Science* 171:203–205.
- Janzen, D. H. 1981. Food webs: Who eats what, why, how, and with what effects in a tropical forest? Pages 167–182 in F. B. Golley, editor. *Tropical rain forest ecosystems: Structure and function*. Vol. 1A. Elsevier Scientific, Amsterdam, The Netherlands.
- Jennersten, O. 1988. Pollination in *Dianthus deltooides* (Caryophyllaceae): Effects of habitat fragmentation on visitation and seed set. *Conservation Biology* 2:359–367.
- Johansen, C. A. 1977. Pesticides and pollinators. *Annual Review of Entomology* 22:177–192.
- Johnson, R. K., and T. Wiederholm. 1989. Classification and ordination of profundal communities of nutrient poor, oligomesohumic lakes in relation to environmental data. *Freshwater Biology* 21:375–386.
- Johnson, R. K., T. Wiederholm, and D. M. Rosenberg. 1993. Freshwater biomonitoring using individual organisms, population, and species assemblages of benthic macroinvertebrates. Pages 40–41 in D. M. Rosenberg, N. H. Resh, editors. *Freshwater biomonitoring and benthic macroinvertebrates*. Chapman and Hall, New York.
- Kaneshiro, K. Y., H. L. Carson, F. E. Clayton, and W. B. Heed. 1973. Niche separation in a pair of homosequential *Drosophila* species from the island of Hawaii. *The American Naturalist* 107:766–774.
- Karr, J. R. 1991. Biological integrity: A long-neglected aspect of water resource management. *Ecological Applications* 1:66–84.
- Klein, G. C. 1989. Effects of forest fragmentation on dung and carrion beetle communities in central Amazonia. *Ecology* 70:1715–1725.
- Kremen, C. 1992. Assessing the indicator properties of species assemblages for natural areas monitoring. *Ecological Applications* 2:203–217.

- Kremen, C. 1993. Biological inventory using target taxa: Case study of the butterflies of Madagascar. *Ecological Applications*.
- Lamas, G., R. K. Robbins, and D. J. Harvey. 1991. A preliminary survey of the butterfly fauna of Pakitza, Parque Nacional del Manu, Peru, with an estimate of its species richness. *Publicaciones del Museo de Historia Natural* 40:1–19.
- Landres, P. B., J. Verner, and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species: A critique. *Conservation Biology* 2:316–329.
- Lattin, J. D., and A. R. Moldenke. 1992. Ecologically sensitive invertebrate taxa of Pacific Northwest old-growth conifer forests. Report prepared for the Northern Spotted Owl Recovery Team, Other Species and Ecosystems Committee. Corvallis, Oregon.
- Lawton, J. H. 1978. Host-plant influences on insect diversity: The effects of space and time. Pages 105–125 in L. A. Mound and N. Walsff, editors. *Diversity of insect faunas*. Symposium of the Royal Entomological Society, London, England.
- Main, B. Y. 1987. Persistence of invertebrates in small areas: Case studies of trapdoor spiders in Western Australia. Pages 29–39 in D. A. Saunders, G. W. Arnold, A. A. Burbidge, and A. J. M. Hopkins, editors. *Nature conservation: The role of remnants of native vegetation*. Surrey Beatty, Chipping Norton, New South Wales, Australia.
- Majid, N. M., and K. Jusoff. 1987. The impact of logging on soil temperature in a low elevation forest of Malaysia. *Tropical Ecology* 28:35–44.
- Margules, C. R., and J. L. Stein. 1989. Patterns in the distributions of species and the selection of nature reserves: An example from *Eucalyptus* forests in southeastern New South Wales. *Biological Conservation* 50:219–238.
- Margules, C. R., A. O. Nicholls, and R. L. Pressey. 1988. Selecting networks of reserves to maximize biological diversity. *Biological Conservation* 43:63–76.
- McIver, J., S. Muttulingam, D. Pickering, and R. Van Buskirk. 1989. Population dynamics and habitat selection of the Oregon silverspot butterfly (*Speyeria zerene hippolyta*): A comparative study at four primary sites in Oregon. The Nature Conservancy, Portland, Oregon.
- McIver, J. D., A. R. Moldenke, and G. L. Parsons. 1990. Litter spiders as bio-indicators of recovery after clearcutting a western coniferous forest. *Northwest Environmental Journal* 6:410–412.
- McIver, J., G. Parson, and A. R. Moldenke. 1992. Litter spider succession after clearcutting in a western coniferous forest. *Canadian Journal of Forestry Research* 22:984–992.
- McKenzie, N. L., Belbin, C. R. Margules, and G. J. Keighery. 1989. Selecting representative reserve systems in remote areas: A case study in the Nullarbor Region, Australia. *Biological Conservation* 50:239–261.
- Mispagel, M. E., and S. D. Rose. 1978. Arthropods associated with various age stands of Douglas fir from foliar, ground and aerial strata. WS/IBP Coniferous Forest Biome, University of Washington, Seattle, Washington.
- Moldenke, A. R. Soil arthropods. In *Methods of soil analysis: Biochemical and microbiological properties*. Agronomy Handbook No. 9. Soil Society of America, Madison, Wisconsin. In press.
- Moldenke, A. R., and J. D. Lattin. 1990. Dispersal characteristics of old-growth soil arthropods: The potential for loss of diversity and biological function. *Northwest Environmental Journal* 6:408–409.
- Morris, M. G., N. M. Collins, R. I. Van-Wright, and J. Waage. 1991. The utilization and value of non-domesticated insects. Pages 319–347 in N. M. Collins and J. A. Thomas, editors. *The conservation of insects and their habitats*. Academic Press, London, England.
- Murphy, D. D. 1991. Invertebrate conservation. Pages 181–198 in K. A. Kohm, editor. *Balancing on the brink of extinction*. Island Press, Washington, D.C.
- Murphy, D. D. 1992. Invertebrates and the conservation challenge. Pages 4–7 in *Wings: Essays on invertebrate conservation*. The Xerces Society, Portland, Oregon.
- Murphy, D. D., and B. D. Noon. 1991. Coping with uncertainty in wildlife biology. *Journal of Wildlife Management* 55:773–782.
- Murphy, D. D., and S. B. Weiss 1988a. Ecological studies and the conservation of the Bay checkerspot butterfly, *Euphydryas editha bayensis*. *Biological Conservation* 46:183–200.
- Murphy, D. D., and S. B. Weiss. 1988b. A long-term monitoring plan for a threatened butterfly. *Conservation Biology* 2:367–374.
- Murphy, D. D., and S. B. Weiss. 1991. Monitoring the effects of regional climate change on biological diversity. *Science in Glacier National Park* 1990:4–6.
- Murphy, D. D., and S. B. Weiss. 1992. Predicting the effects of climate change on biological diversity in western North America: Species losses and mechanisms. Pages 355–368 in R. L. Peters and T. E. Lovejoy, editors. *Global warming and biological diversity*. Yale University Press, New Haven, Connecticut.
- Murphy, D. D., and B. A. Wilcox. 1986. Butterfly diversity in natural habitat fragments: A test of the validity of vertebrate-based management. Pages 287–292 in J. Verner, M. L. Morrison, and C. J. Ralph, editors. *Wildlife 2000, modeling habitat relationships of terrestrial vertebrates*. University of Wisconsin Press, Madison, Wisconsin.
- Murphy, D. D., K. E. Freas, and S. B. Weiss. 1990. An environment-metapopulation approach to population viability analysis for a threatened invertebrate. *Conservation Biology* 4:41–51.
- Newmark, W. D. 1985. Legal and biotic boundaries of western North American national parks: A problem of congruence. *Biological Conservation* 33:197–208.
- Newmark, W. D. 1987. A land-bridge island perspective on mammalian extinctions in western North American parks. *Nature* 325:430–432.
- Newmark, W. D. 1991. Tropical forest fragmentation and the local extinction of understory birds in the Eastern Usambara Mountains, Tanzania. *Conservation Biology* 5:67–78.

- Nisbet, I. C. T. 1988. The relative importance of DDE and dieldrin in the decline of Peregrine Falcons. Pages 351–376 in T. Cade, editor. Peregrine falcon populations: Their management and recovery. The Peregrine Fund, Inc., Boise, Idaho.
- Noss, R. F. 1983. A regional landscape approach to maintain diversity. *Bioscience* 33:700–706.
- Noss, R. F. 1987. Protecting natural areas in fragmented landscapes. *Natural Areas Journal* 7:2–13.
- Noss, R. F. 1990. Indicators for monitoring biodiversity: A hierarchical approach. *Conservation Biology* 4:355–364.
- Olson, D. O. 1992. The Northern Spotted Owl conservation strategy: Implications for Pacific Northwest forest invertebrates and associated ecosystem processes. Order no. 40-04HI-2-1650. U.S. Forest Service, Portland, Oregon.
- O'Neill, R. V. 1967. Niche segregation in seven species of diplopods. *Ecology* 48:983.
- Parsons, G. L., G. Cassis, A. R. Moldenke, J. D. Lattin, N. H. Anderson, J. C. Miller, P. Hammond, and T. D. Schowalter. 1991. Invertebrates of the H. J. Andrews experimental forest, western Cascade range, Oregon. V: An annotated list of insects and other arthropods. General technical report PNW-GTR-290. U.S. Department of Agriculture-Forest Service, Portland, Oregon.
- Pearson, D. L., and F. Cassola. 1992. World-wide species richness patterns of tiger beetles (*Coleoptera: Cincindelidae*): indicator taxon for biodiversity and conservation studies. *Conservation Biology* 6:376–391.
- Plotkin, M., and L. Famolare, editors. 1992. Sustainable harvest and marketing of rain forest products. Island Press, Washington, D.C.
- Pollard, E. 1979. Population ecology and change in range of the white admiral butterfly. *Ladoga camilla* L. in England. *Ecological Entomology* 4:61–74.
- Price, P. W. 1973. Parasitoid strategies and community organization. *Environmental Entomology* 2:623–626.
- Pyle, R., M. Bentzien, and P. Opler. 1981. Insect conservation. *Annual Review of Entomology* 26:233–258.
- Reinthal, P. N., and M. L. J. Stiassny. 1991. The freshwater fishes of Madagascar: A study of an endangered fauna with recommendations for a conservation strategy. *Conservation Biology* 5:231–243.
- Roberts, L. 1992. Chemical prospecting: Hope for vanishing ecosystems? *Science* 256:1142–1143.
- Ryti, R. T. 1992. Effect of the focal taxon on the selection of nature reserves. *Ecological Applications* 2:404–410.
- Samways, M. J. 1990. Land forms and winter habitat refugia in the conservation of montane grasshoppers in Southern Africa. *Conservation Biology* 4:375–382.
- Savage, A. A. 1982. Use of water boatmen (Corixidae) in the classification of lakes. *Biological Conservation* 23:55–70.
- Schoener, T. W. 1986. Overview: Kinds of ecological communities—ecology becomes pluralistic. Pages 467–479 in J. Diamond and T. J. Case, editors. *Community ecology*. Harper and Row, New York.
- Schowalter, T. D. 1985. Adaptations of insects to disturbance. Pages 235–252 in S. T. A. Pickett, P. S. White, editors. *The ecology of natural disturbance and patch dynamics*. Academic Press, San Diego, California.
- Schowalter, T. D. 1989. Canopy arthropod community structure and herbivory in old-growth and regenerating forests in western Oregon. *Canadian Journal of Forestry Research* 19:318–322.
- Schowalter, T. D. 1990. Invertebrate diversity in old-growth versus regenerating forest canopies. *Northwest Environmental Journal* 6:403–404.
- Schowalter, T. D., S. G. Stafford, and R. L. Slagle. 1988. Arboreal arthropod community structure in an early successional coniferous forest ecosystem in western Oregon. *Great Basin Naturalist* 48:327–333.
- Scott, J. A., and M. E. Epstein. 1986. Factors affecting phenology in a temperate insect community. *American Midland Naturalist* 117:103–118.
- Scott, J. M., B. Csuti, J. D. Jacobi, and J. E. Estes. 1987. A geographic approach to protecting future biological diversity. *BioScience* 37:782–788.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience* 31:131–134.
- Shelford, V. E. 1907. Preliminary note on the distribution of the tiger beetles (*Cincindela*) and its relation to plant succession. *Biology Bulletin* 14:9–14.
- Shure, D. J., and D. L. Phillips. 1991. Patch size of forest openings and arthropod populations. *Oecologia* 86:325–334.
- Simberloff, D. S., and E. O. Wilson. 1969. Experimental zoogeography of islands: The colonization of empty islands. *Ecology* 50:278–289.
- Southwood, T. R. E. 1978. The components of diversity. Pages 19–41 in L. A. Mound and N. Walsff, editors. *Symposium of the Royal Entomological Society: Diversity of insect faunas*. Blackwell Scientific, Oxford, England.
- Spellerberg, I. F. 1991. *Monitoring ecological change*. Cambridge University Press, Cambridge, England.
- Stork, N. E. 1988. Insect diversity: Facts, fiction and speculation. *Biological Journal of the Linnean Society* 35:321–337.
- Sutton, S. L., and N. M. Collins. 1991. Insects and tropical forest conservation. Pages 405–424 in N. M. Collins and J. A. Thomas, editors. *The conservation of insects and their habitats*. Academic Press, London, England.
- Terborgh, J. 1986. Keystone plant resources in the tropical forest. Pages 330–344 in M. E. Soulé, editor. *Conservation biology: The science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts.

- Terborgh, J. 1988. The big things that run the world—a sequel to E. O. Wilson. *Conservation Biology* 2:402–403.
- Thomas, J. A. 1991. Rare species conservation: Case studies of European butterflies. Pages 149–197 in I. F. Spellerberg, F. B. Goldsmith, and M. G. Morris, editors. 29th Symposium of the British Ecological Society: Scientific management of temperate communities. Blackwell Scientific Publications, Oxford, England.
- Thomas, J. W., E. D. Forsman, J. B. Lint, E. C. Meslow, B. R. Noon, and J. Verner. 1990. A conservation strategy for the Northern Spotted Owl. U.S. Department of Agriculture Forest Service, Portland, Oregon.
- Thornton, I. W. B. 1985. The geographical and ecological distribution of arboreal Psocoptera. *Annual Review of the Entomological Society* 30:175–196.
- Turchin, P., and A. D. Taylor. 1992. Complex dynamics in ecological time series. *Ecology* 73:289–305.
- Turin, H., and den Boer. 1988. Changes in the distribution of carabid beetles in the Netherlands since 1880. II. Isolation of habitats and long-term time trends in the occurrence of carabid species with different powers of dispersal (Coleoptera, Carabidae). *Biological Conservation* 44:179–200.
- Turner, B. D., and E. Broadhead. 1974. The diversity and distribution of psocid populations on *Mangifera indica* L. in Jamaica and their relationship to altitude and micro-epiphyte diversity. *Journal of Animal Ecology* 43:173–190.
- Tyrrell, E. Q., and R. A. Tyrrell. 1990. Hummingbirds of the Caribbean. Crown Publishers, New York.
- Uhl, C., and J. B. Kaufman. 1990. Deforestation, fire susceptibility, and the potential trees responses to fire in the eastern Amazon. *Ecology* 71:437–449.
- Usher, R. R. 1986. Wildlife conservation evaluation. Chapman and Hall, London, England.
- Usher, M. B., and R. G. Jefferson. 1991. Creating new and successional habitats for arthropods. Pages 263–291 in N. M. Collins and J. A. Thomas, editors. The conservation of insects and their habitats. Academic Press, London, England.
- Verner, J., M. L. Morrison, and C. J. Ralph, editors. 1986. Wildlife 2000: Modeling habitat relationships of terrestrial vertebrates. University of Wisconsin Press, Madison, Wisconsin.
- Voegtlin, D. 1982. Invertebrates of the H. J. Andrews Experimental Forest, Western Cascade Mountains, Oregon: A survey of arthropods associated with the canopy of old-growth *Pseudotsuga menziesii*. Special publication 4. Forest Research Laboratory, Oregon State University, Corvallis, Oregon.
- Walker, E. P. 1975. Mammals of the world. Johns Hopkins University Press, Baltimore, Maryland.
- Waloff, N. 1968. Studies on the insect fauna on scotch broom (*Sarothamnus scoparius*). *Advances in Ecological Research* 5:87–208.
- Weiss, S. B., R. R. White, D. D. Murphy, and P. R. Ehrlich. 1987. Growth and dispersal of larvae of the checkerspot butterfly *Euphydryas editha*. *Oikos* 50:161–166.
- Weiss, S. B., D. D. Murphy, and R. R. White. 1988. Sun, slope, and butterflies: Topographic determinants of habitat quality for *Euphydryas editha*. *Ecology* 69:1486–1496.
- The Wilds, and IUCN/SSC Captive Breeding Specialist Group. 1992. *Lycaeides melissa samuelis*, Karner Blue Butterfly, population and habitat viability assessment (PHVA) workshop. Captive Breeding Specialist Group, Zanesville, Ohio.
- Wilson, E. O. 1985. The biological diversity crisis. *Bioscience* 35:700–706.
- Wilson, E. O. 1987. The little things that run the world (the importance and conservation of invertebrates). *Conservation Biology* 1:344–346.
- Wilson, E. O. 1988. The current state of biological diversity. Pages 3–17 in E. O. Wilson, editor. Biodiversity. National Academy Press, Washington, D.C.
- Wilson, E. O. 1991. Ants' Wings: Essays on invertebrae conservation. 16:4–13. The Xerces Society, Portland, Oregon.
- Wolda, H. 1988. Insect seasonality: Why? *Annual Review of Ecology and Systematics* 19:1–18.

