



INSECTS ON PLANTS: Diversity of Herbivore Assemblages Revisited

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■ **Abstract** The diversity and composition of herbivore assemblages was a favored theme for community ecology in the 1970s and culminated in 1984 with *Insects on Plants* by Strong, Lawton and Southwood. We scrutinize findings since then, considering analyses of country-wide insect-host catalogs, field studies of local herbivore communities, and comparative studies at different spatial scales. Studies in tropical forests have advanced significantly and offer new insights into stratification and host specialization of herbivores. Comparative and long-term data sets are still scarce, which limits assessment of general patterns in herbivore richness and assemblage structure. Methods of community phylogenetic analysis, complex networks, spatial and among-host diversity partitioning, and metacommunity models represent promising approaches for future work.

INTRODUCTION

Seldom in the history of science is an unmistakable cornerstone laid for a new subject, but Southwood (1961) was undoubtedly the first to consider insect herbivore richness and its variation among host-plant species a phenomenon worthy of explanation. Southwood's inaugural papers remained largely unappreciated until MacArthur & Wilson (1967) presented their theory of island biogeography and Janzen (1968) proposed that its theoretical framework could be applied to the diversity of herbivores on host plants. Within a decade or so, sufficient evidence had been gathered on the diversity of herbivorous insects associated with various host plants to allow inferences on the role of various causative processes, and in 1984 this became the leading theme of the book *Insects on Plants* (Strong et al. 1984).

Insect-plant interactions grew into a research domain in its own right, but its emphasis has shifted toward population-level processes and interactions, and to

phylogenetic analyses of herbivore and plant lineages (e.g., Futuyma & Mitter 1996, Herrera & Pellmyr 2002, Schoonhoven et al. 1998). Thus, despite their importance in the 1970s and 1980s, the size of herbivore-host communities and their determinants has seemingly drifted from attention.

Twenty years after the publication of *Insects on Plants*, the time seemed opportune to consider further developments on its leading questions, which remain as relevant as before. We thus set out to evaluate the extent to which subsequent work has produced (a) major data sets that support earlier findings and hypotheses, (b) new empirical results that lead to novel insights, and (c) substantial advances in theory or explanatory models.

Our concern here is the size, structure, and composition of herbivore assemblages on particular plant species as well as the processes or factors that determine their variation. We do not consider the effects of herbivores on their hosts or on plant communities.

Three fairly distinct approaches can be recognized in studies of host-associated herbivore assemblages; these approaches often address different questions (see Denno et al. 1995, Strong et al. 1984). Accordingly, we focus first on analyses of data sets compiled from country-wide or regional catalogs of insect records. Next, we review observational and experimental field studies of local herbivore communities. We then consider studies conducted across several sites or at different spatial scales. In the final sections, we concentrate on evolutionary and dynamic aspects of herbivore assemblages, and then highlight certain lines of enquiry that promise new insights into patterns of herbivore diversity on plants and their determinants.

INSECT-HOST LISTS

Species Richness on Different Hosts

Insects recorded on British trees formed one of the data sets that inaugurated the entire subject (Southwood 1961), and since then it has been amended and repeatedly reanalyzed. Thus, Kennedy & Southwood (1984) estimated host area from their occurrence both in 10 km × 10 km and 2 km × 2 km grid units. This combined variable accounted for 58% of variation in insect species numbers. Further variables in their multiple-regression model were historical (length of time a host has been present in Britain), phenological (deciduousness), evolutionary (taxonomic relatedness, the size of the host's order in Britain), and structural (host average height and leaf length). All variables contributed significantly to the multiple-regression model, which explained 82% of variation, but their correlation structure was not investigated.

Kelly & Southwood (1999) incorporated phylogenetic relationships among British host trees into the foregoing model. The independent contrasts analysis returned only a statistically nonsignificant improvement in the variance explained by host area, compared with species analyzed as independent entities. Host phylogeny,

thus, evinced no effect on herbivore richness, although this finding may be partly due to the recent (i.e., postglacial) establishment of the British biota. They also reexamined the separate explanatory contributions of host frequency at the local (2-km units) and the regional scale and found that host frequency at the smaller scale was a far better predictor than was host regional range. This result concurs with Straw & Ludlow (1994), who showed that host local biomass is a better predictor of the regional number of herbivore species of British trees than either their smaller-scale or larger-scale frequency in the United Kingdom.

Few other data sets have lent themselves to equivalent exercises. In British Rosaceae, host geographic range, growth form (herbs to trees), and architecture (a function of plant height times leaf length) correlate with the numbers of herbivores (Leather 1986). For German tree genera, host area, size, and postglacial age of establishment explained 88% of variation in herbivore richness (Brändle & Brandl 2001), whereas taxonomic relatedness did not contribute to the multiple-regression model. Furthermore, the genera shared by Britain and Germany had highly correlated assemblage sizes in these countries; on average, more associated herbivores were listed in Germany. As found by Kelly & Southwood (1999), host phylogeny entailed no significant improvement to the model.

Frenzel & Brandl (1998) analyzed a data set of insects on Brassicaceae in Poland. Unlike other studies, this data set derives from a set of host records obtained in five custom "collection gardens," combined with occurrences in natural populations. Sampling effort was the main predictor for species richness of generalist but not of specialist insects; however, because effort was correlated with plant distribution and presumably with the number of sites where each host species was inspected, sampling effort may reflect differences in beta-diversity among these herbivore groups (see below). No other factor explained variation in herbivore richness. Thus, these studies mostly reinforce findings from early analyses of herbivore/host catalogs.

Taxonomic Composition and Guild Structure

Assemblages can be evaluated on their taxonomic or functional composition; the latter is often characterized by guilds. The proportions of different taxa or guilds can be estimated either for herbivore species or for individuals. Two simple descriptors used for herbivore assemblages are the specialist to generalist ratio, and the ratio of ectophages to endophages (feeding on versus within the plant), which is a minimalistic guild classification. These descriptors are correlated, because endophages tend to be more specialized than ectophages (Gaston et al. 1992).

A central concern here is whether the relative richness and abundance of guilds is determined by the available plant resources, competitively partitioned up by individual guilds or by relative sizes of regional species pools for individual guilds that serve as sources for plant colonization. The latter alternative seems more likely because no compensation between guilds (i.e., negative correlation between their species richness or abundance across plant species) has been found for tropical

(Basset & Novotny 1999) or temperate (Cornell & Kahn 1989) guilds. Likewise, variable guild composition on the same host across different geographic areas (Lawton et al. 1993) points to the importance of regional species pools for assemblage composition of local communities.

Cornell & Kahn (1989) explored the insects on British trees for regularities in size or proportion of different guilds. Except for a positive correlation of sap-suckers and chewers, guild sizes varied independently. They were also not influenced by the host traits used to predict total herbivore numbers (see above). The lack of predictable and general features in feeding guilds—especially relative size and taxonomic composition—across different hosts led Cornell & Kahn (1989) to propose that the British herbivore fauna reflects idiosyncratic histories of the herbivores on each host, despite the predictability of their total richness.

Constant taxonomic and guild composition among tree species may simply reflect regional or global differences in relative species richness of herbivore taxa. For example, the relative species richness of various hemipteran families in the tropics is virtually constant across continents (Hodkinson & Casson 1991). Guild structure may nonetheless differ among distinct plant lineages. For instance, nitrogen-fixing Fabaceae appear to be particularly important for xylem-suckers (Young 1984).

Differences in patterns conveyed by these simple descriptors suggest that the functional or taxonomic composition of herbivore assemblages is hardly explainable by immediate ecological factors, without consideration of the regional biotic history and phylogenetic constraints of the implicated plant and herbivore lineages.

COMPARATIVE AND EXPERIMENTAL FIELD STUDIES

Sampling Effort and Rarity: Pervasive Problems

A problem that besets all field studies is that observed species richness is correlated with sampling intensity. Within highly diverse assemblages that contain many rare species (Novotny & Basset 2000, Price et al. 1995), even very large samples fail to reach an asymptote. For example, Basset & Novotny (1999) with aggregate samples collected from 15 *Ficus* species in Papua New Guinea, were unable to establish clear asymptotes from circa 13,000 leaf-chewer and 45,000 sap-sucker individuals.

To overcome this predicament, richness in different-sized samples can be statistically standardized, usually through a rarefaction procedure. Otherwise, total richness can be estimated for each herbivore assemblage through various parametric and nonparametric estimators (Gotelli & Colwell 2001). Sampling effort can be factored out before the statistical effects of proposed causative factors are assessed (e.g., Frenzel & Brandl 1998). However, in spatially extensive samples, sampling intensity often correlates with geographical range so that, by factoring out sample size or number, the effect of geographic range cannot be fully assessed. At the local level, a rarefaction procedure yields standardized richness estimates independent of local sampling intensity (Lewinsohn 1991). At the regional scale,

the entire set of recorded herbivores is performed the basis for assessment of regional richness and the contribution of beta-diversity to it, which can be teased out, for instance, through path analysis (Lewinsohn 1991).

Many rare species are not trophically associated with the plants on which they were collected, especially in mass samples. These species have to be excluded from community analyses by *in situ* feeding observations or laboratory feeding experiments. However, many rare species prove to be associated with studied hosts, hence, infrequent interactions form a substantial part of plant-herbivore assemblages (Novotny & Basset 2000, Price et al. 1995). Quantitative insect-host records enable analyses that deemphasize rare interactions and correct potential bias (e.g., Godfray et al. 1999).

Plant Traits and Local Assemblages

Plant size and architecture affect the number of associated herbivore species (Strong et al. 1984). In some local studies, larger plant individuals (Cytrynowicz 1991) or species (Marquis 1991) were shown to support more herbivore species, whereas in other studies, no such effect was found (Basset 1996). In general, plant size effects *per se* are hard to evaluate because other factors are correlated with size, such as density, life stage, phenology, and architecture. Recent studies have focused on intraspecific differences between host growth stages (see below).

Architecture itself has no agreed-upon definition or measure. It can signify life stage (Fowler 1985), growth form of different species (Strong et al. 1984), size or number of structures (Haysom & Coulson 1998), or some combination of these (Strong et al. 1984). Thus, its effects on herbivore assemblages, whether significant or not, are difficult to compare among different studies.

Few studies have examined effects of chemical differences among host species on local herbivore assemblages. In Florida, each one of six oak species supported a distinctive cynipid gall-former assemblage whose composition was strongly related to certain chemical constituents (Abrahamson et al. 2003); this set of highly specialized herbivores thus differentiates its hosts at the species level. Likewise, many studies have investigated adaptive responses of certain insects to particular physical defenses and anatomical traits, but very few have extended to herbivore assemblages. For instance, Ezcurra et al. (1987) showed that glabrous plants supported higher densities of leaf-chewers and galls than did their pilose conspecifics, on which, however, sap-suckers were more abundant. Peeters (2002) found that herbivore guild composition was more influenced by leaf structural traits than by leaf nitrogen, fiber, or water content.

Succession

Herbivore assemblages on different successional stages have been mostly studied by mass sampling in vegetation plots (e.g., sweep-netting or vacuuming). Overall insect species richness or guild structure can then be compared against total plant richness or vegetation structure. Earlier studies (see Strong et al. 1984) had shown

that total richness increases with succession, in accord with plant richness. Higher total herbivore richness can be driven by (a) increased richness per host (herbivore species density), (b) higher average host specificity, (c) higher host diversity, or a combination of these. Aggregate insect samples are unsuitable for discriminating among these effects, however.

Though pioneer hosts support higher densities of herbivores and experience more damage compared with late successional plant species, herbivore richness per host does not seem to differ between pioneer and climax plant species, either in temperate or tropical vegetation (Basset 1996, Leps et al. 2001, Marquis 1991, Novotny 1994). An overall increase in herbivore species richness from early successional to mature vegetation would, therefore, be caused either by insect richness tracking the changes in plant-species richness or by higher average host specialization.

In tropical forests, the limited data available suggest that herbivore host specificity does not change noticeably during succession (Basset 1996, Leps et al. 2001, Marquis 1991), probably because, in contrast to temperate vegetation, tropical succession is often dominated by woody plants from the onset.

Tropical Forests

Early studies of tropical forests relied on mass trapping methods (reviewed in Basset 2001b), especially fogging, which produced large series of insects from canopies (Stork et al. 1997). However, particularly in tropical forests, the spatial distribution of individual insects is a poor indicator of herbivore niches and host ranges, because highly mobile insects circulate freely within a botanically diverse forest canopy [including lianas (Ødegaard 2000)] rather than being limited to their hosts. Canopy fogging studies are, therefore, being superseded by studies that combine in situ feeding observations, experimental feeding tests, and rearing of immatures (Basset et al. 2003, Marquis 1991).

Tropical studies are mostly local, directed at particular insect communities, whose comparison or analysis at the regional level is hampered by the many unnamed species they usually contain, so that specimens rather than names must be cross-checked (Kitching 1993). Furthermore, the asymptotic species richness of host-associated herbivore communities is difficult to estimate because of the large number of rare species. Hence, there are more studies on herbivore host specificity than on their species richness (Novotny & Basset 2005). The few comprehensive studies to date suggest that local factors, especially the availability of resources such as young foliage or overall plant biomass, or the pressure of ants and other enemies, may be more important in the determination of local herbivore richness than are historical or regional plant traits (Basset 1996, Basset & Novotny 1999, Marquis 1991), although these factors require further investigation.

Studies of arthropod stratification in rainforests represent a relatively recent field, facilitated by improvements in canopy access. Stratification studies either compare mass samples among strata without regard to hosts (see Basset et al. 2003) or compare the fauna of mature trees with that of conspecific seedlings

or saplings (e.g., Barrios 2003, Basset 2001a). Both approaches indicate that the abundance and diversity of herbivorous taxa tend to be higher in the upper canopy than in the understory [with the possible exception of galls (Cuevas-Reyes et al. 2004, Price et al. 1998)] and that the faunal similarity between the understory and the upper canopy is low. Differences among conspecific plants from different strata include nutritional quality, complexity, and resource quantity, compounded by environmental differences in temperature, light, and exposure to rain and wind.

The higher and less variable supply of young foliage in the upper canopy may be a significant determinant of herbivore stratification. Lowman et al. (1993) suggested that the upper canopy of temperate forests has proportionally fewer niches than does the tropical forest canopy. This proposition may help explain the pronounced vertical stratification of tropical forest herbivores, compared with temperate forest herbivores.

LARGER-SCALE PATTERNS

Diversity Across Spatial Scales

The straightforward comparison of herbivore assemblages that feed on the same plant species at different sites and under contrasting ecological conditions (Lawton et al. 1993) has been used surprisingly rarely to test the effect of environmental variables such as altitude (Novotny et al. 2005) or climate (Andrew & Hughes 2004). Forestry and agriculture are potentially rich sources for data on spatial variability of herbivore communities on economically important hosts, but these sources have been scarcely looked into by ecologists (but see Lill et al. 2002, Strong et al. 1977).

The limits to extraction of general inferences on diversity patterns from studies that pertain exclusively to the local or to the regional scale are obvious. In studies that combine local and regional sets, regional diversity can be partitioned into spatial components, such as alpha-diversity and beta-diversity; these components can be assessed in an additive ANOVA model (Lande 1996).

The relationship between local-community diversity and the size of the regional species pool can elucidate the process of community assembly from the regional set of species (Ricklefs 2004). Most studies (e.g., Cornell & Lawton 1992) report a linear increase of local diversity with regional diversity, which suggests that local communities are proportional samples of regional species pools, from which, presumably, their component species are drawn independently (although not necessarily randomly, as they may still be subject to assembly rules). These results were viewed as evidence for the nonsaturation of local herbivore assemblages; that is, their resource space is not fully occupied by existing species (Cornell 1985, Cornell & Lawton 1992, but see Loreau 2000).

Local communities may depend on regional pools, but the converse causal direction is also plausible: communities are assembled through local dynamics and amalgamated into regional pools rather than determined by them. Zwölfer (1987)

took this approach with thistle flowerheads in Europe, whereas Straw & Ludlow (1994) proposed a model that derives regional species-area relations from local dynamics, in which local host biomass is the key driver, and applied it successfully to British tree and European thistle data. Lewinsohn (1991) examined both the regional-to-local causal model and its reverse in herbivore assemblages on flower heads of Brazilian Asteraceae. Both studies found a strong correlation of local and regional herbivore richness, as well as substantial turnover among sites. Thus, the higher herbivore richness of widespread plants was caused both by higher alpha-diversity and by higher beta-diversity.

Fernandes & Price (1991) found no relationship between gall richness and host distribution, whereas Blanche & Westoby (1996) showed that host-plant range influenced regional, but not local, richness of gallers on *Eucalyptus* species in Australia. Blanche & Westoby (1996) also demonstrated consistent differences among host subgenera, which highlighted that some host taxa or lineages bear a greater galling diversity than do others. In fact, regional diversity patterns may be essentially driven by the spatial turnover of certain host taxa that support high gall richness (Fernandes & Price 1991, Price et al. 1998).

Geographical Variation of Host Associations

Herbivorous insects are often oligophages, whose hosts belong to a species group (e.g., Becerra 1997), a genus, or subtribe (Prado & Lewinsohn 2004). However, host affiliations can vary geographically (Fox & Morrow 1981), both in specialized (Thompson 1999) and in generalist (Sword & Dopman 1999) insects. Insect ranges can either be smaller than that of host plants (Strong et al. 1984) or extend beyond limits of their individual host species (Scriber 1988). Thus, spatial turnover among herbivore assemblages may be produced either by plant or by insect change, or by shifting interactions among different sites. Sword & Dopman (1999) demonstrated geographical shifts in food plants among *Schistocerca emarginata* populations, together with ontogenetic shifts: nymphs were more specialized than adults and on different plants as well.

Historical processes can explain geographical differentiation of local assemblages. Sobhian & Zwölfer (1985) found that herbivorous assemblages on *Centaurea solstitialis* L. (Asteraceae) decreased from the Balkans, the plant's center of origin, towards Spain, mostly through loss of specialists, so that smaller Western assemblages consisted largely of polyphages. A similar pattern was found in pine-feeding Hemiptera in Central Europe (Brändle & Rieger 1999). However, on *Onopordum* thistles, specialists tracked their hosts across the Mediterranean, and polyphages were responsible for most of the spatial turnover in their herbivore assemblages (Briese et al. 1994).

Even though additional studies are needed, evidence seems to indicate that the "regional species pool" is, in fact, a variable assortment of specialists and generalists that have different probabilities of pertaining to local communities, according to conditions such as host abundance and predictability.

Plant introductions can be viewed as large-scale manipulative experiments with controls, represented by the alien's herbivore assemblage in its own native range (Memmott et al. 2000, Strong et al. 1977, Zwölfer 1988) or by assemblages on native plants in the alien's area of introduction (Leather 1986). Early studies showed that ectophagous herbivores can assemble rapidly on novel hosts (Kennedy & Southwood 1984, Strong et al. 1977), whereas endophages may be slower colonizers (Strong et al. 1984), and specialized guilds, such as seed-feeders, may be missing on recently arrived plant species (Memmott et al. 2000, Zwölfer 1988). Herbivores are quicker to colonize alien plants with native close relatives (Burki & Nentwig 1997).

Geographical Trends in Herbivore Richness

Regional diversity of almost all taxa of insect herbivores is known to be highest in the tropics; aphids are a notable exception (Dixon et al. 1987). However, the diversity of herbivore communities that feed on particular plant species appears to be similar between tropical and temperate forests (Basset & Novotny 1999, Janzen 1988). The ratio of butterfly to plant species also shows no major difference among regions (Gaston 1992). Flowerhead-feeders on Asteraceae do seem to have a higher local richness per host species in the neotropics than in Europe, after richness is adjusted for sampling effort; however, different plant tribes were studied in each region (Lewinsohn 1991, Zwölfer 1987). Thus, the considerable increase in regional diversity of insect herbivores from temperate to tropical areas appears driven largely by increasing plant diversity, but higher turnover among sites (beta-diversity) or among hosts (i.e., higher specialization) can contribute to this effect as well. However, in California, the simple correlation of butterfly richness with plant richness disappeared from more comprehensive models that included elevational range and actual evapotranspiration as explanatory variables; therefore, in this case, herbivore richness cannot be said to respond to host diversity per se (Hawkins & Porter 2003).

Rapid local censuses of gall-maker diversity, based on their morphologically distinct galls, produced for numerous sites around the world, suggest a richness gradient that peaks around 25° to 38° latitude (Price et al. 1998), whose interpretation is hindered by unequal distribution of samples and interaction of local factors (e.g., climate and soil). Within regions, the positive relationship between host and gall richness was confirmed in the South African Fynbos (Wright & Samways 1998), in Mexican dry forest (Cuevas-Reyes et al. 2004), and in the western United States and southeast Brazil (Fernandes & Price 1991, who mistakenly dismissed it as a spurious effect of other variables).

The altitudinal trend in herbivore richness is controversial, particularly in the tropics. Maximum species richness has been reported at lowland or at midmontane elevations (Fernandes & Price 1991, Lees et al. 1999, McCoy 1990). Furthermore, at least one study found species richness of the entire moth community constant with elevation, in seeming contrast to host diversity (Brehm et al. 2003). Another

study reported constant species richness of moths per plant species (Novotny et al. 2005).

Steep altitudinal gradients of climate and biotic factors, such as vegetation structure or ant predation, foster high herbivore beta-diversity. Altitudinal gradients are also subject to spatial constraints that, on purely geometrical grounds, can establish either a monotonic decrease in species richness with elevation because of diminishing area or a peak in species richness at mid elevations (Lees et al. 1999). Furthermore, few studies (e.g., Hawkins & Porter 2003) verify whether variables are spatially autocorrelated.

The extraordinarily high local diversity of insects in tropical forests was extrapolated by Erwin (1982) to a global diversity estimate of 30 million insect species. This estimate assumed that herbivores are extremely host specific and, therefore, exhibit high turnover among tree species. Further studies (Basset et al. 1996, Novotny et al. 2002a, Ødegaard et al. 2000, Thomas 1990) have not confirmed this key assumption and revised insect diversity estimates to approximately 5 to 7 million species. Other studies (Orr & Häuser 1996) indicate that local assemblages may represent a large proportion of the regional species pool in tropical forests; hence, beta-diversity would also be lower than supposed in the initial estimates. However, this suggestion needs substantiation.

HERBIVORE ASSEMBLAGES AS EVOLUTIONARY DYNAMIC SYSTEMS

Herbivores and Host Phylogeny

Only a small, although growing, number of studies consider the phylogeny of host plants or herbivores when analyzing their assemblage size or structure. Methods for analyzing phylogenetic effects in communities are in the process of development, and some issues are still contentious (Losos 1996, Ricklefs 1996). Thus, despite the manifest importance of phylogeny, to what extent new analyses of assemblages in phylogenetic context change our understanding of community structure remains to be seen. For instance, reanalyses of regional species richness on British trees by use of phylogenetically independent contrasts still identified plant local frequency and distribution as their main determinants (Brändle & Brandl 2001, Kelly & Southwood 1999).

The lack of adequate species-level phylogenies is often limiting, especially in highly diverse tropical plant groups. Analyses of host specificity have mostly approximated phylogenetic relationships between host-plant species by their supraspecific taxonomic ranks that, however, are not commensurate across plant lineages (Losos 1996). New phylogenetic measures of host specificity and breadth (Symons & Beccaloni 1999, Webb et al. 2002) have not yet been widely applied (but see Weiblen et al. 2005). Phylogenetic constraints on host-plant selection may be also examined as a relationship of species turnover between herbivore communities and the phylogenetic distance of their host-plant species (Novotny et al. 2002a).

The interpretation of community composition requires understanding the evolutionary dynamics of host affiliation by herbivores. Increasingly powerful phylogenetic analyses enable tests for congruence between plant and herbivore phylogenies (Lopez-Vaamonde et al. 2003, Weiblen & Bush 2002) as well as for the effect of plant traits, such as secondary metabolites, on plant colonization by herbivores (Becerra 1997). These studies indicate that strict cospeciation between herbivores and plants is rare, although it is found in insect herbivores that also serve as specialized pollinators (Kato et al. 2003, Weiblen & Bush 2002). In other herbivores, even those intimately associated with host plants, such as leaf-miners, multiple colonizations of host lineages are common (Lopez-Vaamonde et al. 2003, Jermy & Szentesi 2003). This finding does not mean that the pattern of host use is random, as closely related herbivore species often feed on closely related plants (Futuyma & Mitter 1996).

Given the importance of plant chemistry in mediating plant–insect associations and their evolution (Becerra 1997, Berenbaum 2001), surprisingly few studies have attempted to investigate how it affects insect diversity. In British umbellifers, chemical uniqueness was unrelated to insect richness, whereas chemical diversity had a positive but slight effect (Jones & Lawton 1991). This observation lends only modest support to the hypothesis that chemically more diverse plants share more chemicals with other species, which, therefore, would facilitate host switches and, thus, increase herbivore richness.

Are more diverse communities especially rich in specialists or generalists, or is species richness independent from host specificity? So far, only a few cases have been studied. For instance, higher species richness of herbivorous chalcid wasps in Germany compared with wasps in Britain was solely caused by a higher number of generalists (Tschamtkke et al. 2001). Herbivore communities on alien plants often reach the same species richness as those on native plants, but these species include higher proportions of generalists (Novotny et al. 2003, Zwölfer 1988).

Herbivory appears to be conducive to speciation, given that herbivore lineages tend to be more diverse than other modes of life. Most phytophagous beetles belong to radiations provoked by new angiosperm lineages (Farrell 1998).

Are assemblages more similar on phylogenetically closer hosts? The general answer to this question, as expected, is yes. Herbivore similarity may decrease gradually at increasing taxonomic levels of their host plants (comparisons among host genera, families, etc.) or may decrease sharply at one particular level, which in turn signals two attributes: (a) the taxonomic level at which insects recognize plants as equivalent or distinct hosts and (b) an upper threshold within which insects can shift more easily among host species (Futuyma & Mitter 1996, Jermy & Szentesi 2003). Thus, many herbivores respond similarly to congeneric plants but discriminate allogeneric plants, whereas their responses to confamilial compared with allofamilial plants are less distinct (Novotny & Basset 2005).

The degree of similarity also differs among guilds, depending on their host specialization. It should be lower for specialists than for generalists and, therefore, lower for endophages than for ectophages. Frenzel & Brandl (2001) found that

endophages were consistently less similar than ectophagous assemblages among different Brassicaceae but not among Cynaroideae hosts. Furthermore, overall herbivore assemblage similarity was substantially lower among host species in the Cynaroideae than in Brassicaceae. This example indicates the vast potential for studies of lineage-specific differences in herbivore assemblages across plant phylogenies (Futuyma & Mitter 1996).

Interactions: Competition and Facilitation

A number of early observational studies searched herbivore assemblages on host plants for evidence of resource partitioning, as expected from theory (Denno et al. 1995). Failure to find such evidence established herbivorous insects as prime evidence against the proposition of interspecific competition as a major organizing force in communities (Denno et al. 1995, Lawton & Strong 1981, Strong et al. 1984).

A reassessment of studies on interspecific competition among herbivorous insects (Denno et al. 1995) revealed that it was detected in 76% of the investigated pairwise interactions. It was less common only among external leaf-chewers—precisely the guild on which previous assessments and generalizations had been based (Lawton & Strong 1981).

The commonness of interspecific competition is not necessarily commensurate with its intensity or net effect (Denno et al. 1995). Thus, the effects of interspecific interactions on species richness and assemblage structure remain to be assessed. Indeed, analyses of co-occurrences and experimental studies both show a number of instances in which some herbivore species facilitate the presence of others by providing entry points, shelter, or otherwise modifying the host (Lill & Marquis 2003, Martinsen et al. 2000, Waltz & Whitham 1997).

Herbivore community studies can be further complicated by numerous indirect and diffuse effects (Strauss & Irwin 2004) mediated by their predators (Romero & Vasconcellos-Neto 2004) or shared parasitoids [apparent competition (e.g., Morris et al. 2004)]. Particularly in the tropics, ant-tending promotes the occurrence of certain sap-sucking and folivorous groups but reduces the presence of other external feeders (Dyer & Letourneau 1999). The herbivore guild composition is, thus, affected by ants, but we are not aware of any evaluation of their effect on herbivore species richness. Most studies of indirect interactions assess demographic responses of particular species (Strauss & Irwin 2004) rather than effects on community attributes.

Insect-Plant Arrays

The diversity of entire local plant–herbivore assemblages can be partitioned into within-host and among-host diversity (Lewinsohn et al. 2001, Summerville et al. 2003). Turnover among hosts in this case is an alternative sense of beta-diversity and an inverse measure of host specialization. Partitions of diversity within hosts, compared with diversity among host species, can be evaluated with ANOVA-like

models (Lande 1996) or randomization procedures (Summerville et al. 2003). For caterpillars that feed on four temperate-forest tree species (three of them coniferal), beta-diversity among hosts was only occasionally different from chance expectations, because of low host specialization (Summerville et al. 2003), although differentiation among hosts increased seasonally.

Alternatively, comprehensive host–insect arrays can be analyzed as interaction matrices to ascertain properties such as nestedness or compartmentation, two ways in which such matrices can show nonrandom structure (Lewinsohn et al. 2005). Nestedness has long been probed in biogeographic studies and recently has been found to characterize many mutualistic assemblages (Jordano et al. 2005); however, it has scarcely been sought in plant–herbivore arrays. A nested structure means that specialists should accumulate on hosts with the most diverse assemblages, whereas hosts with poorer assemblages should only be associated with generalist herbivores (Lewinsohn et al. 2005); this situation could result, for instance, from source–sink dynamics among co-occurring host species.

Compartments are sets of densely linked plants and insects, whose outer boundaries are set by evolutionary processes, whereas their inner patterns can reflect more immediate ecological conditions. Compartmentation has been predicted to be uncommon in food webs on theoretical grounds but was demonstrated through multivariate and randomization procedures in an assemblage of specialized endophages on closely related hosts (Prado & Lewinsohn 2004). In a tropical secondary forest, Novotny et al. (2004) showed that most Lepidoptera, although not strictly monophagous, concentrate locally on a single host, and that the entire assemblage is highly compartmented.

Assembly Rules for Herbivore Communities

Herbivore assemblages that feed on bracken fern on different continents (Lawton et al. 1993) are quite dissimilar in guild, niche, and taxonomic composition. Although comparable studies on other plants are required, this finding demonstrates the importance of regional herbivore species pools for the composition of local assemblages.

The predictability of the process of community assembly from a particular regional species pool remains controversial. In tropical forests, spatially and temporally replicated fogging samples of herbivorous assemblages, particularly of adult beetles, differ widely and unpredictably in composition on the same host-plant species or even individual (Floren & Linsenmair 1998, Mawdsley & Stork 1997). These assemblages may represent nonequilibrium stochastic communities; on the other hand, unpredictability can be a sampling artifact, derived from tourist species that do not feed on the sampled hosts and from the large numbers of rare species characteristic of tropical assemblages (Novotny & Basset 2000, Price et al. 1995). The latter alternative is supported by higher constancy in tropical vegetation of the species composition and abundance of locally common, feeding herbivores (Novotny et al. 2002b). Community assembly rules are amenable

to experimental study in artificially defaunated vegetation (Floren & Linsenmair 1998).

PERSPECTIVES

New Theoretical Approaches

Various theoretical avenues may provide further understanding of the determinants of diversity and organization of herbivore assemblages. We deem the following especially worthy of attention.

MECHANISTIC MODELS The distribution of plant species within extensive vegetation, such as lowland tropical forest, has been tested against predictions under the assumptions of uniform distribution, random but spatially autocorrelated distribution caused by dispersal limitation, and patchy, environmentally determined distribution (reviewed in Chave 2004). Such neutral models can be adapted to test spatial changes in herbivorous communities on particular plant species.

Straw & Ludlow (1994) proposed a mechanistic model in which herbivore richness can be derived from host abundance and availability, combined with insect-resource appropriation efficiencies. This model deserves further empirical tests, although the necessary data are laborious to obtain.

PARTITIONING HERBIVORE DIVERSITY Partitioning of diversity into either spatial components or within-host and among-host components has been discussed before. Further advances are possible if both of these partitioning modes are combined into an integrated framework, outlined by Lewinsohn et al. (2001), that extends earlier hierarchical schemes (Routledge 1984; also see Couteron & Pélissier 2004). This framework can be envisioned as a three-way table whose entries are the herbivores found on a given host in a site, which then are aggregated by locality and by host; two turnover components (among-site and among-host beta-diversity), plus their potential interaction, are thus factored into total herbivore richness.

Diversity-partitioning models provide promising means of separating herbivore turnover among hosts from spatial turnover and, therefore, can be useful in clarifying the apportionment of total diversity. A comparison of this apportionment in different geographical regions or biomes would be of high interest. Components of diversity are also potentially useful in monitoring changes over time in systems of particular concern.

HERBIVORE ASSEMBLAGES AS METACOMMUNITIES Extension of metapopulation theory to metacommunities is fairly incipient, but Hugueny & Cornell (2000) proposed a patch-occupancy model to predict local numbers of species drawn independently from a regional pool; this model agreed well with cynipid galls on oaks. The herbivore assemblage on ragwort, *Senecio jacobaea* L., was studied

experimentally in a metapopulation framework by Harrison et al. (1995), who found, however, that the theoretical assumptions were met only in part by the herbivores. Herbivore assemblages offer useful testing grounds for metacommunity theory and also for models of communities in spatially structured landscapes (see Tschamtké & Brandl 2004).

COMPLEX-NETWORK THEORY The bloom of complex-network theory has had a strong impact on food-web studies. It has been fruitfully applied to the investigation of structural and dynamic properties of mutualistic assemblages, especially of plants with pollinators or frugivores (Jordano et al. 2005). Plant–herbivore assemblages can be similarly represented as bipartite networks; that is, as an array of interactions between elements of two distinct sets (Lewinsohn et al. 2005). Among properties of interest that can be explored through this approach are, for instance, the asymmetry of trophic-link distribution among species, and the effects of random or directed species loss on the structure and dynamics of the entire plant–herbivore assemblage.

PHYLOGENY AND COMMUNITY STRUCTURE Recent exponential increase in molecular data and improved cladistic methods for their analysis provide rapidly expanding opportunities for community-wide studies that incorporate phylogeny (Webb et al. 2002). The introduction of a phylogenetic perspective is one of the most significant recent advances in community ecology, although it still needs specific models and agreement on procedures (Ricklefs 1996).

The relatedness of coexisting plant species and the distribution of their life-history traits have been compared through resampling procedures and yielded a null expectation based on random draws from their regional species pool (Webb et al. 2002). This approach holds promise for the study of herbivore species coexisting on a particular host species.

Long-Term and Spatially Extensive Studies

Some of the open questions on herbivore assemblages can only be answered with an increase of temporally and spatially extensive studies. Far too few geographically extensive studies of assemblages have been sampled in a large number of localities, and even fewer studies (e.g., Barbosa et al. 2000, Root & Cappuccino 1992) have followed local communities over several years. Both kinds of studies are essential to elucidate the organization of local communities and their relations to regional assemblages.

A potential opportunity for long-term studies is offered by permanent study plots established primarily to study vegetation structure and dynamics. The intercontinental network of 50-ha forest plots, whose vegetation is regularly censused (Losos & Leigh 2004), and extensive networks of replicated experiments on plant communities (e.g., Van der Putten et al. 2000), exemplify systems in which herbivore assemblages and their host associations could be recorded regularly to assess

variation across seasons and years, track longer-term changes, or compare different geographic regions.

The major difficulty for sound cross-latitudinal comparisons is the lack of rigorously comparable data. Temperate field studies can resort to catalogs and atlases for complementary information on regional lists, host distribution, and herbivore-host ranges. Such information is usually lacking for tropical areas. Conversely, extensive surveys of tropical communities (Janzen 1988, Novotny et al. 2002a) often do not have matching counterparts in temperate communities. Paradoxically, the best short-term strategy for broader comparisons, thus, seems to be the production of inventories in temperate regions with the same procedures and under the same restrictions that apply in tropical settings, rather than the reverse (Novotny & Basset 2005).

Response to Global Changes

Given that herbivorous insects are the largest single contingent of terrestrial biodiversity (Schoonhoven et al. 1998) and have a variety of effects on food plants, their response to global warming and other large-scale changes are of high interest (Wilf & Labandeira 1999). Paleontological evidence indicates that the intensity of herbivory as well as average per-host diversity of herbivores increased during the Cenozoic warming that peaked 53 mya (Wilf & Labandeira 1999). This finding raises the possibility that global warming may promote long-term increases in herbivore assemblages and in herbivory levels in temperate ecosystems. In tropical and subtropical regions, reverse effects are conceivable; more insects will be forced past their tolerance limits. In either case, effects will also depend on changes in humidity and precipitation. Other consequences of climate change, already detectable by now (Walther et al. 2002), include shifts in geographical distribution and in timing and synchronization of phenological events; all of these changes will necessarily affect herbivores both directly and by way of their host plants. Changes in local and regional assemblage size and structure are inescapable but harder to predict than those of single species or pairwise interactions, although at least as important. Few experiments (e.g., Hartley & Jones 2003) as yet attempt to assess effects of global changes on herbivore assemblages.

Labandeira et al. (2002) show that specialized herbivore-plant interactions were at greater risk and had lower rates of recovery than did generalist interactions from past catastrophic events. An overall loss of specialists and specialized links would simplify interaction webs, increase overlap among host assemblages, and diminish compartmentation. However, stochastic assortment and idiosyncratic local conditions could still enlarge differences among local assemblages and, therefore, increase the relative weight of beta-diversity in total diversity.

Global climate changes do not occur independently from other worldwide alterations, especially species introductions and landscape changes, such as fragmentation and habitat loss. Introductions are expected to homogenize biotas among world regions, so that total diversity would be reduced while local and regional

diversity would increase (Rosenzweig 2001). However, habitat loss, especially in megadiverse tropical areas, is by far the major and most immediate menace to biotic diversity (Myers et al. 2000, Rosenzweig 2001).

CONCLUSIONS

In this review we have endeavored to highlight several themes on which the study of insect assemblages on plants made progress over the past two decades.

The description and understanding of herbivore assemblages at different spatial scales has seen substantial development. Beta-diversity is clearly a key component in the understanding of the spatial organization of such assemblages and is instrumental in the refinement of specific explanatory hypotheses and predictions.

Phylogenetic analyses have emerged as an important perspective for separation of the imprint of plant phylogenetic relationships from contemporaneous ecological effects and are successful in explaining the evolution of host affiliation in herbivorous insects. Similar progress may be expected in finding explanations for the assembly of herbivore communities on plants.

Finally, studies of tropical communities, particularly their host specificity and stratification in forests, have emerged as an active area of research.

To return then to our initial questions: Twenty years after the seminal book by Strong et al. (1984), are more or better data available for the same explanatory factors? Are models improved, and have noticeable theoretical advances occurred? What is the current contribution of plant–herbivore assemblages to the general understanding of terrestrial species diversity?

Most early studies made use of data obtained for purposes other than the questions they posed, so that testing the factors of interest with such data demanded substantial ingeniousness. Given the gradual shift to studies actually designed to investigate patterns of insect richness on plants, the same factors could be more rigorously evaluated; plant structural, historical, or distributional variables, although nominally the same, are in general more strictly defined and can thus be better assessed. Hence, with regard to our first question, there are now better data for the same models, and these data span a more diverse set of taxa, geographical regions, and biomes.

As for analytical models, prevailing practice has incorporated some improvements but made no major advances; thus far, few studies recognize or deal with structural or spatial correlation among explanatory variables. We have also indicated some theoretical directions, such as phylogenetic analysis or complex network theory, that can be expected to offer new insights but whose expanded application is still in process.

The current contribution of insect–herbivore assemblages to a general perspective of terrestrial diversity is not commensurate with their diversity or importance. We have seen fewer advances in the production of broader evaluations of proposed patterns, and few generalizations can be safely established. Although underlying

theoretical impediments may exist, at this stage, generalizations are unquestionably limited by the extent and nature of the data at hand. In natural habitats, especially in the tropics, with few exceptions, only local data are available, and these data sets cover as yet far too few taxa, habitats, and localities, mostly in forest settings. For temperate areas, many studies are on smaller plants in open and modified habitats, combined with further explorations of extensive host catalogs and atlases. Our current version of comparing apples and oranges is comparing herbivore assemblages on collards or oaks in temperate settings with assemblages on fig trees in tropical rainforests.

Advances in the immediate future can be fostered in two ways: First, we need to increase the number of comprehensive studies of plant–insect arrays in which individual trophic interactions are tested and quantified. These studies will produce improved descriptions of the structure of herbivore assemblages and better tests of hypotheses on their spatial and functional organization. Second, we must have wide-ranging comparative studies. The broader questions on which this field of enquiry was inaugurated cannot be resolved without large-scale comparative and collaborative work.

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