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Case Studies of Arthropod Diversity and Distribution

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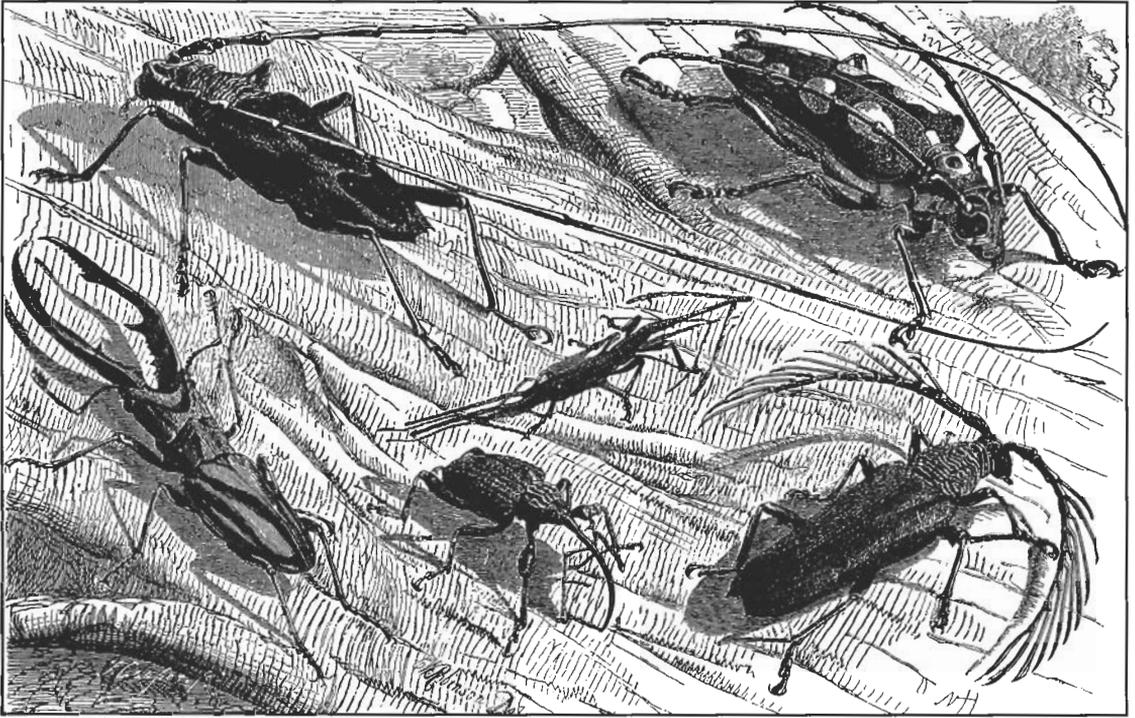
Because insects and other arthropods exhibit such striking diversity in the tropics, these taxa have provided models for the development of many key topics in tropical biology. Some of these topics are emphasized elsewhere in this book, including parts 3, 5 (mimicry and pollination), 4 (plant-herbivore relations), and 10 (ecosystem ecology). This part highlights three papers that helped fuel major discussions of both pattern and process in the diversity of tropical arthropods and other organisms. Erwin (1982; paper 28) laid out a set of testable hypotheses that led to major reinterpretation of the magnitude of tropical diversity. The series of studies in Haddow, Corbet, and Gillett (1961; paper 27) were an early and elegant view of vertical stratification of insects in tropical forests. Wilson (1958; paper 26) wrote the first in a series of papers based on observations of ants in Papua New Guinea that led to major discussions of heterogeneity, ant mosaics, and taxon cycles. The discussion below will show that these are still important topics in tropical biology.

How Many Species Are There?

For most of the twentieth century, the total number of insects in the world was assumed to be around 2 million. For example, Sharp (1895) and Frost (1942) gave estimates of 2.5 million and 2 million, respectively. Sabrosky (1952) reviewed knowledge of insect diversity at that time and said “workers in the division of insect identification of the [United States] Department of Agriculture estimate that [by] 1948 approximately 686,000 different species of insects” had been described in the world (1952, 1). For the total including undescribed species, Sabrosky (1952) stated “recent guesses vary from 2,500,000 to 10,000,000 different kinds” and “[t]he final roll call may be far short of 10 million but it seems sure to be somewhere in the millions” (1952, 2).

Some twenty years ago, in an ingenious and visionary paper, Erwin (1982) suggested that there may be as many as thirty million species of insects, instead of the previously estimated two or so million species. His conclusions were

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Remarkable beetles found at Simunjon, Borneo. From Wallace (1869)

based on beetles sampled in insecticidal fogging of nineteen individuals of the tree *Luehea seemanii* in Panama (Erwin and Scott 1980; see Basset et al. 1996 for a table summarizing the assumptions and steps in the estimate). Subsequently, Erwin (1988) admitted that he was surprised by the attention that his calculations received and the controversy they generated, stating that he had simply advanced a hypothesis that could be tested rigorously, and suggested that this "must begin by refining of our knowledge about host specificity of insects in tropical forests" (1988, 123).

Although many papers have debated Erwin's conclusion, very few have actually attempted to test his assumptions, in particular the proportion of host-specific insect herbivores associated with different species of tropical trees (e.g., Stork 1988; Erwin 1988; May 1988, 1990, 2000; Thomas 1990a; Hammond 1992; Gaston 1991; Hodkinson and Casson 1991; Basset et al. 1996). Erwin's paper raised many questions regarding how to properly assess the number of host-specific arthropod species in general, and in the tropics in particular. One issue is the problem of transient species that are dispersing from tree species not under direct study (Janzen 1976; Stork 1993). Specialist species may be collected on other tree species besides their normal hosts. With greater diversity of plant species within the study site, more transient species are likely to be collected on the foliage of study trees (Basset 1999; Novotny and Basset 2000).

Another issue is the varying degree of host specificity observed among taxonomic groups. For example, wood-eating guilds of beetles rarely feed on living tissues and are therefore often much less host specific in the tropics than leaf-feeding beetles (Basset 1992). Studies of herbivorous insects associated with single plant genera in the Neotropics have recognized 30 percent monophagous (single-host-feeding) species on *Passiflora* (Thomas 1990b) and 10 percent monophagous geometrid moths and 26 percent monophagous species of weevils on *Piper* (Marquis 1991). But several recent studies have found much lower host specificity

across broader assemblages of hosts. In a study of leaf-chewing insects on ten tree species in Papua New Guinea, Basset et al. (1996) found 4.3 percent of the beetles were restricted to one of the ten tree species. In a much larger study of host specialization of leaf-chewing insects on sixty-two species of woody rain forest plants, Novotny, Basset, and Miller (in preparation) found that most herbivore species had wide host plant ranges within plant genera, but were restricted to only a few genera. A similar pattern has been found for tropical mites that feed on nectar in hummingbird-pollinated flowers (Naskrecki and Colwell 1998). Because speciose plant genera (such as *Ficus* and *Psychotria*) are a characteristic feature of tropical floras, the large overlap among herbivore communities on congeneric plants means that the total number of herbivores is lower than might otherwise be expected. Similar low host specificity at the plant species level was found by Wagner (1998) from canopy fogging in Uganda, and Tavakilian et al. (1997) in rearing cerambycid beetles from trees in French Guiana.

Moreover, tropical tree species may support very different ratios of specialist species, varying with host plant, forest characteristics, and geographic locations (Basset 1992, 1999). For example, chrysomelid beetle samples obtained in Panama (Erwin and Scott 1980) and the Peruvian Amazon (Farrell and Erwin 1988) were dominated by Alticinae, whereas in chrysomelid samples from Papua New Guinea (Basset and Samuelson 1996) and Borneo (Stork 1991) Eumolpinae dominated. Since Alticinae are often more host specific than Eumolpinae (e.g., Jolivet 1988), the overall proportions of specialists on particular tree species in the Neotropics may be higher than these in the Old World tropics.

Aside from differences in taxonomic composition of the overall fauna, tropical regions also differ in overall diversity. Although data on regional diversity are too poor for comparisons among most beetle taxa, it is well known that butterfly faunas differ markedly across regions. Within equal-sized areas, species richness of butterflies in the Oriental region is about

half that in the Neotropics (Robbins 1993). Finally, the relative diversity of canopy versus soil faunas remains a subject of conjecture (Stork 1988; Hammond 1992; André, Lebrun, and Noti 1992). Much more work is needed on soil biota (see also the discussion of Fittkau and Klinge 1973 [paper 45]).

As illustrated by the papers cited above, vigorous discussion of how to predict the global number of arthropods continues. Current evidence from the major museum collections of sorted and labeled insect species, whether described or undescribed, does not support the larger estimates, and insect taxonomists broadly concur from this that although there may be up to five million species of insects in the world, there are probably less than ten million (Nielsen and Mound 2000). In a recent review, May (2000) settled on a "best guess" of four million species.

Although the magnitude of undescribed insects in the Andean region may be extremely high, this does not appear to be the case in other regions. Scholtz and Chown (1995) analyzed taxonomic knowledge of insects in southern Africa and considered "a doubling in [species] numbers to be the upper limit of the increase in species richness" in the region (125). In a detailed review of present knowledge of ants (Hymenoptera: Formicidae) of tropical Africa, Robertson (2000) suggests that about half the species of ants have been described—a figure that concurs approximately with these recent world insect diversity estimates.

Several factors contributed to the influence of Erwin's paper. First, his study suggested that there are many more insect species than previously thought, even if the magnitude of the number is still not agreed. Second, this was part of the first comprehensive quantitative analysis of fogging samples to the morphospecies level. Third, Erwin was the first to articulate a set of quantitative assumptions about global insect species richness in a sequence that could be discussed and tested. This step, in addition to the unexpected magnitude of the result, gained the attention not only of insect taxonomists, but also the broader scientific community and

ultimately conservationists. But sadly, this discussion also points out two other features of tropical insect research—the low availability of data and how slowly the gaps are being filled.

Vertical Patterns of Species Distribution

A large body of literature focuses on arthropod samples obtained from the forest "canopy," usually referring to samples obtained fifteen meters or more above the ground, with various methods (reviewed in Basset 2001). Most entomological studies, either with insecticidal fogging (e.g., Erwin 1995), with light traps (e.g., Sutton, Ash, and Grundy 1983; Wolda, O'Brien, and Stockwell 1998), or by felling trees (Amedegnato 1997; Basset, Charles, and Novotny 1999), cannot sample the upper canopy selectively. Recently, entomologists have been able to sample selectively the upper canopy either with fixed canopy cranes (Wright and Colley 1994) or a mobile canopy raft and sledge (Hallé and Blanc 1990), offering the promise of deeper biological understanding. These studies have generally found significant differences in composition and abundance of arthropods at different vertical levels in the canopy, but questions of what is actually being sampled and lack of understanding of the biology of the organisms has limited the conclusions that can be made. Some studies find greater abundance at higher levels (e.g., Basset, Aberlenc, and Delvare 1992), while others find greater abundance at lower levels (e.g., Wolda, O'Brien, and Stockwell 1998) or no significant differences are observed (e.g., Intachat and Holloway 2000).

Much of this recent ecological literature would leave the reader with the impression that the study of vertical stratification was invented only in the 1970s. On the contrary, there is a diverse literature, much of it in medical entomology journals, on much earlier efforts to study vertical stratification of biting flies and other economically important insects (e.g., Bates 1944; Mattingly 1949). Early efforts to study stratification outside of medical entomology included those of Allee (1926) on

Barro Colorado Island, Panama, Hingston (1930) and associates in Guyana, and Paulian (1947) in Ivory Coast. The methods may have been primitive by today's standards, but the logistic scale of samples taken on various kinds of platforms suspended in trees remains impressive.

Here we highlight one of the more impressive efforts of Haddow, Corbet, and Gillett (1961) in Africa—a 120-foot (36-m) tower, originally built at Mpanga, Uganda, in 1958 for mosquito studies. The tower was moved to a nearby site at Zika in 1960, and has been in more or less continuous use up to the present. The Zika site is near Entebbe, in a small forest fringing Lake Victoria. Zika has been the site of fairly intensive biodiversity research since 1946, including studies of vegetation, biting flies, dragonflies, other insects, birds, and mammals (Buxton 1952; Davenport, Howard, and Dickinson 1996). This was the first time that a fixed tower was used as a long-term research platform in a tropical forest. When it was built, the tower represented the same kind of leap forward in the application of technology as the new generation of canopy cranes when they were developed in the 1990s. Studies on the tower stratified samples in multiple ways—around the clock, through the seasons, and vertically through the forest and above the canopy.

Haddow's team found that values of some climatic parameters showed little variation vertically (temperature and saturation deficiency, a measure of humidity), whereas others did (wind and light). Vertical stratification was observed in breeding sites of mosquitoes. Patterns of stratification varied among different insect groups, and in some groups, males and females exhibited different patterns. Because of the cycles involved in flight patterns, some kinds of traps gave biased views of overall population activities. Haddow's group also published some of the first detailed observations of insect behavior above the canopy, noting especially the swarming activities of mosquitoes. The data were used in broader discussions of interactions between endogenous (genetic) and exogenous (environmental) components in determining insect behavior patterns (Corbet 1966).

Many abiotic and biotic characteristics of the upper canopy are different from other forest layers below. Irradiance, air temperature, wind, fluctuation of relative humidity, and dew formation at night are notably higher in the upper canopy than in the understory (Parker 1995). Leaf area density and the abundance of young leaves, flowers, and seeds are also usually higher in the upper canopy than lower levels (Parker 1995). For example, in a rain forest in Cameroon, the environmental and biophysical conditions characteristic of the top canopy layer are more like those of chaparral shrub vegetation than of the rain forest ground-layer vegetation. The implications for the distribution of insect herbivores along vertical gradients in tropical rain forests may be significant. Insect herbivores foraging and feeding in the upper canopy encounter serious hygrothermal stress during day and water condensation at night. Conversely, the supply of young leaves available to them is greater than in the lower forest strata. As discussed by Basset et al. (2001) this suggests several possible strategies for coping with this apparently conflicting situation: (1) a specialized and distinct fauna, well adapted to the extreme microclimatic conditions of the upper canopy; (2) interchanges of fauna between the upper canopy and lower layers, e.g., individuals resting in lower layers by day and moving up to feed at night, perhaps taking advantage of air movements (Sutton 1989); or (3) both strategies above.

In a study of abundance, activity, and species richness of arthropods in the upper canopy and understory of a lowland rain forest using the "canopy raft" in Gabon, Basset et al. (2001) found that the density and abundance of many arthropod higher taxa and species were significantly higher in the upper canopy than in the understory. Arthropod activity was also higher during day than night. In particular, insect herbivores were more than twice as abundant and twice as speciose in the upper canopy as in the understory, probably responding to higher and more diverse food resources. Faunal overlap between the upper canopy and understory was low. Herbivore turnover between day and night

was rather high in the upper canopy and no strong influx of insect herbivores from lower foliage to the upper canopy was detected during night. This suggests that insect herbivores of the upper canopy may be resident and well adapted to environmental conditions there.

It is premature to draw general conclusions about the vertical distribution of insects in tropical forests. We simply do not have enough data yet. Long-term studies, such as that of Roubik (1993), suggest that temporal movements up and down in response to changes in the environment (food and nectar sources, as well as microclimate) and the insect populations (mating behaviors, for example) are of critical importance and can be seen and understood only with long-term observations. Regular vertical movements of insects reach an extreme in seasonally inundated forests (Adis 1984). May (1999) points out that most ecological research is still relatively short term, often limited by the length of Ph.D. programs and research grants.

Patchy Distributions of Ant Species

Based on extensive fieldwork in Papua New Guinea in 1955, Wilson published a series of papers documenting the taxonomy, ecology, speciation patterns, and biogeography of the Melanesian ant fauna. The paper we reprint here (Wilson 1958) dealt with the patchiness, or heterogeneity, of the local distribution of ant species. Leston (1973), building on the concept of ants being discontinuously distributed through the three-dimensional space as described by Wilson (1958), Greenslade (1971), Schneirla (1971), and others, characterized ant "mosaics" in cocoa plantations and forests in West Africa. Leston's concept of ant mosaic includes dominant species being distributed in a three-dimensional pattern, with lacunae in which less dominant species are able to persist, although other dominant species are excluded from the territory. Dominant species are usually nonnomadic, arboreal, multinested, sugar-loving, and predatory, practicing mutualism with Homoptera (such as scale insects), and with the potential for rapid population growth.

Aside from the ecological interest, manipulation of such mosaics in plantation crops could have practical applications in pest control. The distribution of arboreal ants in both plantations and natural forests has now been studied in West Africa, Brazil, Borneo, New Guinea, Solomon Islands, and Australia (Dejean et al. 2000; Floren and Linsenmair 2000; Greenslade 1971; Majer 1993; Room 1975). Although many aspects of Leston's description hold true, all the elements are not always present and the complex factors effecting community organization are not fully understood. Thus, although the concept is useful (Dejean et al. 2000), it needs further study before it is widely accepted. One element that remains clear is the overwhelming ability of ants to dominate their environment (Wilson 1990).

The taxon cycle. Wilson (1959b) provided a more formal description of the ecological diversification and stratification of the ant fauna. Insular species evolve through a series of stages from newly arrived colonists, indistinguishable from their mainland relatives, to highly differentiated endemics, which ultimately become extinct. Wilson (1959a) described patterns of speciation, adaptive radiation, and dispersal of Melanesian ants, and characterized a "cyclical pattern of expansion, diversification, and contraction . . . account[ing] for later evolutionary events following initial dispersal" (143). This cyclical pattern was further characterized and named the taxon cycle in a subsequent paper (Wilson 1961). Wilson later extended some of the concepts further, including composition and dominance in local ant faunas (Wilson 1976). A related taxon pulse was characterized by Erwin (1979).

Both concepts are based on common assumptions: (1) habitat specialization is largely irreversible in a lineage, (2) ecological specializations arise in a center of origin, and (3) dispersal events leading to current distributions can be ascertained (see Liebherr and Hajek 1990 for further discussion and comparison). The taxon cycle concept has been applied with success to staphylinid beetles in the Solomon

Islands (Greenslade 1972a, 1972b, later expanded into discussion of adversity selection in Greenslade 1983), West Indian birds (Ricklefs and Bermingham 1999), *Anolis* lizards (Miles and Dunham 1996), and fishes in the Lake Victoria region (Kaufman 1997), but unsuccessfully to West Indian ground beetles (Liebherr and Hajek 1990). As noted by Brown and Lomolino (1998), "given its ability to integrate distributional, ecological, and evolutionary phenomena, Wilson's theory of taxon cycles merits far more attention and more rigorous assessment" (447). In turn, the taxon cycle inspired the more expansive taxon pulse hypothesis (Erwin 1979, 1998), which has been little tested beyond ground beetles (see Liebherr and Hajek 1990 for comparison of taxon cycle and taxon pulse). Rigorous tests of the taxon cycle and the pulse hypothesis require accurate cladistic taxonomies, which are still only rarely available for tropical arthropods (see Liebherr and Hajek 1990 for further discussion).

Both Wilson (see his autobiographical note—Wilson 1985) and Erwin were influenced by the earlier notions of faunal dominance of P. J. Darlington (Darlington 1957, 1971). It is also interesting to note the importance of carabid beetles and ants in the development of ideas by Darlington, Wilson, Erwin, and many others (Ball 1985). Wilson's studies, along with subsequent papers (Wilson and Taylor 1967a, 1967b), remain among of the most comprehensive biogeographical studies of any insects in the Pacific Basin (Miller 1996) and also provided the background for the equilibrium theory of island biogeography (MacArthur and Wilson 1967).

Conclusion

Elegant and testable hypotheses laid out many years ago remain poorly tested and provide clear evidence that much interesting work remains to be done in the evolutionary biology of

tropical insects. Forty years ago, Wilson laid out the taxon cycle model, and also contributed the foundation for Leston's proposal, thirty years ago, of the ant mosaic model. Twenty years ago, Erwin made a chain of hypotheses about insect diversity. While Erwin's conclusions fueled discussions about the scale and conservation of biological diversity, the underlying assumptions remain poorly tested. Although Haddow, Corbet, and colleagues did not contribute explicit hypotheses about insect stratification, their bold experiments in the forests of Uganda challenged existing assumptions that remain inadequately tested forty years later. This commentary also shows that it is indeed difficult to identify single seminal papers because of the cumulative growth of theories, and data to test them, over time. Much of tropical insect ecology remains in the case study phase, and generalizations across continents are still difficult to make for most topics. New techniques of sampling, analysis, and information management (e.g., Longino and Colwell 1997; Basset et al. 2000) are facilitating a new generation of long-term research accumulating large data sets that should help fill these gaps.

Reprinted Selections

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