BUTTERFLIES

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GLOSSARY

aposematic Describing an organism that is rendered less susceptible to predation by advertising its obvious unpalatability.

Batesian mimicry A form of mimicry in which the target organism is rendered less susceptible to predation by its resemblance in morphology or coloration to a different species that is unpalatable.

cryptic Describing an organism that is concealed or obscured by the similarity of its appearance to the surrounding environment.

Müllerian mimicry A form of mimicry in which two or more unpalatable species resemble each other, with the effect that predators are more likely to avoid any species with this appearance.

myrmecophily Ability to form symbiotic associations with ants.

vibratory papillae Mobile, grooved, rod-like appendages arising from the distal edge of the first thoracic segment, used for communicating.

BUTTERFLIES LIKELY REPRESENT the most familiar and best known group of all insects. Within the context of human society, butterflies serve as centerpieces in educational media, they are used extensively in the arts, including nature and commercial advertising, and they are used as symbols for religious and social groups. Within the field of biology, studies on butterflies have been fundamental to the development of biogeography, behavior, coevolution, conservation, development, ecological genetics, evolution, global warming, mimicry, population ecology, sexual selection, speciation, symbiotic associations, and systematics. In summary, butterflies have been important to how we perceive biodiversity.

I. OVERVIEW OF BUTTERFLY TAXONOMIC DIVERSITY

Although butterflies may be the best known group of insects, our understanding of their taxonomic diversity has two fundamental weaknesses. The first regards the recent decline of professional butterfly taxonomists and species level revisions in the past 50 years. This requires most species diversity estimates (from family to genus) to be derived from a literature that is out-of-date. The second is that the number of families and subfamilies of butterflies varies among classifications because, despite current interest in phylogenetic systematic methods and analyses, the relationships within the major groups are unresolved, particularly within Nymphalidae and Lycaenidae. Such is the state of butterfly taxonomy. Nevertheless, the "true" butterflies (superfamily Papilionoidea) may be placed conservatively into four families (Papilionidae, Pieridae, Nymphalidae, and Lycaenidae) that together include between 12,900 and 15,819 species. One useful framework for organizing butterfly taxonomic diversity is P. R. Ackery's (1984) synthesis of butterfly classification, which forms the basis of the following synopsis:

Family Papilionidae (Swallowtails, Fig. 1): a group of 500–600 species in three subfamilies, distributed worldwide but with most species being tropical; adults medium to large sized, both sexes have six walking legs bearing nonbifid tarsal claws; most are brightly colored, may be Batesian or Müllerian mimics, all feed on flower nectar, and males drink at wet soil (Fig. 1); caterpillars are herbivores, body smooth without hardened spines, and possess extrusible glands (osmeteria) that are unique among butterflies; pupa typically with a silk girdle at third thoracic segment.

Subfamily Baroniinae: one species (*Baronia brevicornis*) endemic to Mexico; caterpillars unique among the family by feeding on Fabaceae.

Subfamily Parnassinae: 40–50 species, mainly in north temperate mountains; host plant families include Crassulaceae, Fumariaceae, and Zygophyllaceae.

Subfamily Papilioninae (Fig. 1): more than 500 species placed into three or more tribes; distributed worldwide; most species are tropical. Many species with long hindwing tails; many with sexes strongly dimorphic; many involved in mimicry; species range from palatable mimics (*Papilio* and *Eurytides*) to unpal-

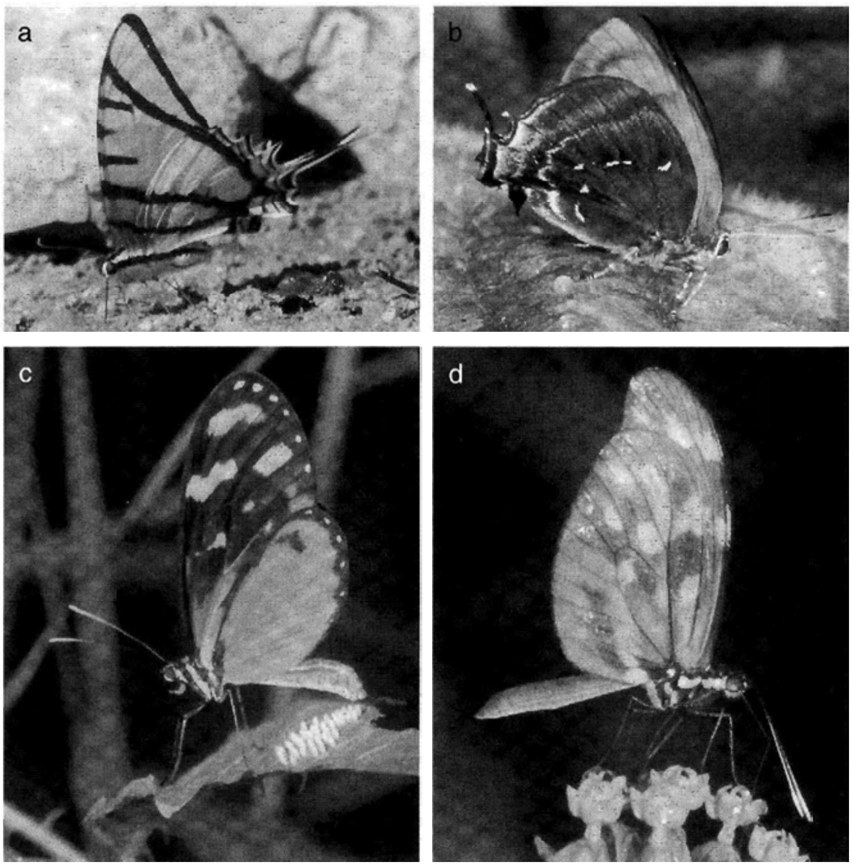

FIGURE 1 Adult butterflies. Clockwise from upper left: (a) newly eclosed male *Eurytides protesilaus* (Papilionidae) drinking from wet soil; (b) male *Theritas* nr. *hemon* (Lycaenidae: Theclinae) perching on a leaf; (c) male *Dismorphia amphiona* (Pieridae: Dismorphinae) visiting flowers; (d) female *Mechanitis isthmia* (Nymphalidae: Ithomiinae) ovipositing a cluster of eggs. [All photos copyright P. J. DeVries.]

atable models (*Parides, Pachliopta*, and *Troides*), and some are among the largest butterflies (*Trogonoptera* and *Ornithoptera*); host plant families include Annonaceae, Apiaceae, Aristolochiaceae, Fumariaceae, Hernandicaeae, Lauraceae, Magnoliaceae, Rosaceae, and Rutaceae.

Family Pieridae (whites, sulphurs, jezebels, cabbage butterflies; Fig. 1): a group of more than 1100 species in four subfamilies; adults small to medium-sized, both sexes have six walking legs and distinctly bifid claws; most species are white or yellow or orange (or combinations thereof) derived from pterin pigments, some with red and black patterning; adults feed on flower nectar (Fig. 1), and males visit wet soil; caterpillars are herbivores, body smooth without hardened spines, often covered in granulations; pupa suspended at 45° angle from substrate with silk girdle at the first abdominal segment.

Subfamily Pseudopontinae: one species (*Pseudopontia paradoxa*) endemic to West Africa; early stage biology unknown.

Subfamily Dismorphiinae: approximately 100 species, nearly all Neotropical. Most *Dismorphia* (Fig. 1) are astonishingly precise mimics of certain aposematic Nymphalidae (*Heliconius, Mechanitis*, and *Oleria*), and represent the original example from which Batesian mimicry theory was derived; host plants are in the Fabaceae.

Subfamily Pierinae (whites, jezebel, and cabbage butterflies): approximately 700 mostly tropical species, especially in Africa and Asia; some species have spectacularly bright, contrasting colors of white, red, and black (e.g., *Delias, Mylothris, Pereute*, and allies) suggesting unpalatability and warning coloration; some groups with dimorphic sexes in which females resemble unpalatable nymphalids and papilionids; some species undergo spectacular mass migrations (e.g., *Ascia, Appias*, and *Belenois*), and a few species are crop pests (*Pieris*); host plant families include Capparidaceae, Brassicaceae, Santalaceae, and Loranthaceae.

Subfamily Coliadinae (sulphurs): 400–600 species well represented in temperate and subtropical regions; generally yellow or white with short, thickly scaled antennae; common in open areas, some migrate in large numbers and have been recorded out at sea far from land (*Colias, Phoebis, Catopsilia, Aphrissa*, and *Eurema*); many species with patterns visible only in the ultraviolet.

Family *Lycaenidae* (hairstreaks, blues, coppers, and metal marks; Fig. 1): a group of 6000–6500 mostly tropical species in 10 subfamilies (the total number may change with future study), and accounts for nearly 50% of all butterflies; most species are small to very small, both sexes have six walking legs (except Riodininae), and frequently with alternating black and white bands on the antennae; the group displays a tremendous diversity of form, color, and life histories; adults feed on flower nectar, fruits, carrion, and honeydew, and a few species do not feed as adults; some African and Southeast Asian groups are involved in mimicry complexes; caterpillars most often slug-like, without hard spines or projections, but the Riodininae shows an extensive variety of form; as a group, lycaenids have the widest diet breadth of all butterflies, and depending on the group caterpillars may feed on plants, other insects, or insect secretions; many caterpillars form intimate and complex symbiotic associations with ants and produce acoustical calls similar to ant calls, secretions that are harvested by ants, and chemicals that alter ant behaviors; pupae are typically round, seed-shaped, unadorned with projections, and may produce clicking or whirring sounds when stimulated.

Subfamily Riodininae (metalmarks): 1200–1400 species that are almost exclusively Neotropical; arguably the most diverse of all lycaenoid groups with respect to adult and larval forms, and they are often treated as a distinct family (Riodinidae) divided into five subfamilies; adults feed primarily on flower nectar, some drink at wet soil, others at carrion; overall their life histories are poorly known, but as a group riodinid caterpillars appear to be mainly herbivores (*Euselasia, Mesosemia, Ancyluris, Metacharis, Mesene, Symmachia, Emesis, Anteros*, and *Helicopis*), with a few carnivorous species on Homoptera (*Alesa* and *Setabis*); about one-third of the riodinids form symbioses with ants and have vibratory papillae as sound producing organs [*Thisbe, Audre, Lemonias, Synargis, Nymphidium*, and *Setabis* (Fig. 2)]; riodinid myrmecophily is entirely Neotropical; host plant families include Araceae, Asteraceae, Bromeliaceae, Bombacaceae, Cecropiaceae, Clusiaceae, Dilleniaceae, Euphorbiaceae, Fabaceae, Lecythidaceae, Loranthaceae, Malpighiaceae, Marantaceae, Melastomataceae, Myrtaceae, Orchidaceae, Rubiaceae, Sapindaceae, and Zingiberaceae plus mosses, liverworts, and lichens.

Subfamily Styginae: one enigmatic species (*Styx infernalis*) that is endemic to the Peruvian high Andes; the early stage biology is unknown.

Subfamily Lipteninae: a small African group of 30–40 species; some are Batesian mimics of aposematic nymphalids (*Mimacraea* and *Ornipholidotos*); caterpillars feed on lichens and microscopic fungi (*Durbania* and *Deloneura*).

Subfamily Poritiinae: a small group restricted to the Oriental regions; caterpillars may be gregarious, feed

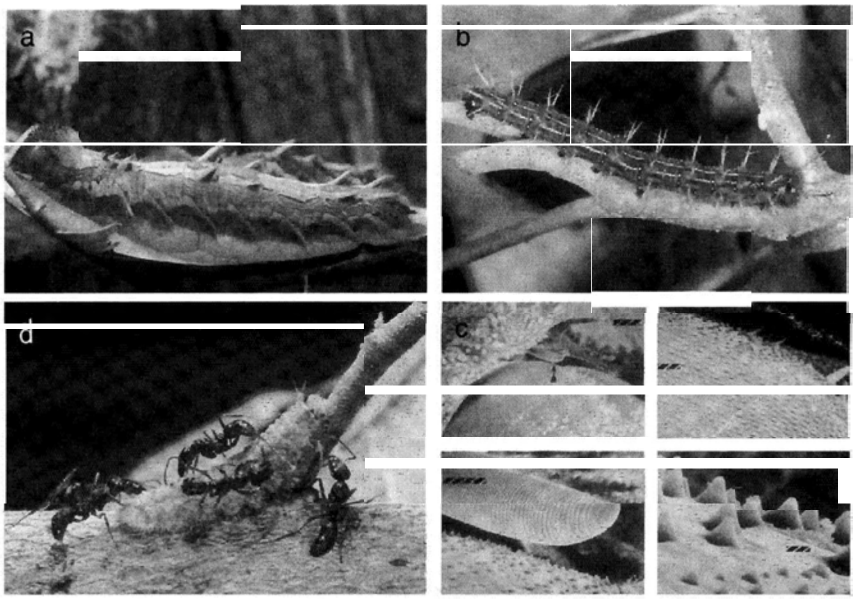

FIGURE 2 Butterfly caterpillars. Clockwise from upper left: (a) final instar caterpillar of *Morpho achilles* (Nymphalidae: Morphinae); (b) final instar caterpillar of *Tigridia acesta* (Nymphalidae: Nymphalinae); (c) Four frames showing details of the call production mechanism of *Thisbe irenea* (Lycaenidae: Riodininae). Upper left—top of caterpillar head, a vibratory papilla (arrow) and anterior margin of first thoracic segment. Upper right—granulations on top of caterpillar head. Lower left—detail of vibratory papilla. Lower right—head granulations at high magnification; (d) final instar caterpillar of *Thisbe irenea* (Lycaenidae: Riodininae) being tended by ants. [All photos copyright P. J. DeVries.]

on plants in the Fagaceae (*Poritia*), and may not associate with ants.

Subfamily Liphyrinae: a small group found in Africa, Australia, and Asia; adults have the proboscis partly or entirely atrophied; depending on the species, caterpillars feed entirely on insects (Homoptera) or on ant brood within ant nests (*Liphyra* and *Aslauga*).

Subfamily Miletinae: a moderate-sized group with most species in tropical Africa and the Orient and one in North America; caterpillars mainly feed on nymphs of Homoptera (*Feniseca, Spalgis*, and *Allotinus*), with a few species feeding on secretions of Homoptera (*Allotinus*) or ant regurgitations (*Thestor*); adults feed mainly on honeydew secretions of Homoptera.

Subfamily Curetinae: approximately 40 species restricted mainly to tropical Asia, all in the genus *Curetis*; caterpillars with tentacle organs as conspicuous, rigid cylindrical tubes; caterpillars feed on Fabaceae and have loose associations with ants.

Subfamily Theclinae (hairstreaks; Fig. 1): this very large and diverse group is found worldwide, but most species are tropical; caterpillars are mainly herbivores, some carnivores on Homoptera, and many associate with ants, but the life histories of most species remain unknown; host plant families include Anacardiaceae, Annonaceae, Asteraceae, Bromeliaceae, Clusiaceae, Cycadaceae, Euphorbiaceae, Fabaceae, Fagaceae, Geraniaceae, Lecythidaceae, Loranthaceae, Malpighiaceae, Malvaceae, Melastomataceae, Meliaceae, Myrtaceae, Oleaceae, Orchidaceae, Sapindaceae, Sapotaceae, Solanaceae, Sterculiaceae, Ulmaceae, and Verbenaceae.

Subfamily Lycaeninae (coppers): a group of 20–40 species found mainly in temperate regions, a few are tropical; caterpillars are herbivores on Polygonaceae, and some form loose associations with ants.

Subfamily Polyommatinae (blues): a large group with a worldwide distribution, most are pale, reflective blue above; caterpillars appear to always associate with ants, and their diets range from herbivores to carnivores, and some (*Maculinea*) feed on ant larvae and are clearly complex parasites and predators within ant nests; host plant families include Crassulaceae, Euphorbiaceae, Fabaceae, Lamiaceae, Myrsinaceae, Oxalidaceae, Primulaceae, Rhamnaceae, Rutaceae, Santalaceae, Sapindaceae, Saxifragaceae, Selaginaceae, Sterculiaceae, Verbenaceae, Zingiberaceae, and Zygophyllaceae.

Family Nymphalidae (brush-footed butterflies; Figs. 1 and 2): a group of 4800–6000 species in 14 subfamilies embracing a prodigious variety of forms and sizes, with both sexes having four walking legs; the forelegs are greatly reduced (hence "brush-footed"); adults may be dull brown (Satyrinae and Nymphalinae), brightly colored (Nymphalinae and Brassolinae), brilliantly iridescent due to physical properties of the wing scales (Morphinae and Apaturinae), or transparent (Ithomiinae and Satyrinae); some groups are entirely palatable, others highly distasteful, and some (Danainae, Ithomiinae, Heliconiinae, and Acraeinae) are extremely important mimetic models; some species (Charaxinae and Nymphalinae) mainly inhabit tropical forest canopies; adults may feed on flower nectar, pollen, rotting fruits, carrion, or do not feed at all; the caterpillars may bear many spines on the body, some also have head spines, whereas others are devoid of spines (Fig. 2); caterpillars are entirely herbivorous, and the particular groups exhibit strong associations with particular plant families; the pupae are typically suspended.

Subfamily Charaxinae: a group of 350–400 mainly tropical species; adults fly very fast with robust bodies; underside of wings typically camouflaged and leaf-like, some with brilliantly colored upperside (*Agrias*, *Prepona*, and *Charaxes*); all are palatable, with few Batesian mimics (*Consul* and *Euxanthe*); adults feed primarily on juices of rotting fruit, dung, and/or carrion (rarely flower nectar), and most inhabit the forest canopy; caterpillars have smooth bodies, often bearing a corona of head spines or projections; host plant families include Annonaceae, Celastraceae, Convolvulaceae, Euphorbiaceae, Fabaceae, Flacourtiaceae, Lauraceae, Myrtaceae, Piperaceae, Poaceae, Rhamnaceae, Rutaceae, Santalaceae, and Sapindaceae.

Subfamily Apaturinae: a small group of medium to large species that are mainly tropical (often placed within the Nymphalinae); males often with brilliant iridescence on wing upperside, the Neotropical species (*Doxocopa*) with proboscis and forelegs lime-green; adults are strong fliers and feed entirely on carrion and putrefying fruits; caterpillars are herbivores on Ulmaceae and have a smooth body, bifid tail, and head with a pair of strong horns.

Subfamily Satyrinae (satyrs, wood nymphs, and browns): a cosmopolitan group of 1500–2000 mainly tropical species that are generally dull brown (some notable exceptions) with well-developed eyespots on the wings; most feed on juices of rotting fruits, some on fungi, and some on flower nectar in temperate regions; all are palatable, with only few clear examples of Batesian mimicry from Asia (*Penthema*, *Zethera*, and *Elymnias*); caterpillars are smooth with bifid tails, and some bear paired head projections; host plant families include Arecaceae, Araceae, Cyperaceae, Heliconiaceae, Poaceae, and Selaginellaceae.

Subfamily Brassolinae (owls): 70–80 entirely Neotropical species ranging from medium to some of the largest butterflies known (*Caligo*) that fly at dawn and dusk, most with characteristic, large eyespots on the hindwing underside, and they are common in butterfly conservatories; most species feed entirely on rotting fruit juices, but a few with a strongly reduced proboscis (*Brassolis* and *Dynastor*) may not feed; caterpillars have smooth bodies, often with dorsal pseudospines, bifid tails, and multiple horn-like projections on the head; host plant families include Arecaceae, Bromeliaceae, Heliconiaceae, Musaceae, and Poaceae, and they can be pests in banana and palm plantations.

Subfamily Amathusiinae (fauns and duffers): an Indo-Australian group of approximately 80 species (sometimes placed in Brassolinae or Morphinae); medium to large butterflies that fly at dawn and dusk and feed on rotting fruit juices; the group is palatable (except for perhaps *Taenaris*) and shows little or no mimicry; caterpillars have smooth bodies, some with long, downy setae, bifid tails, often with paired head horns; host plant families include Arecaceae, Musaceae, Poaceae, and Smilacaceae.

Subfamily Morphinae (morphos; Fig. 2): a group of 40–50 Neotropical species of medium to very large butterflies; the large reflective blue species (*Morpho*) are immediately noticeably in nature and in butterfly conservatories, but others that fly in the forest understory (*Antirrhea* and *Caerois*) are seldom observed; all feed on rotting fruits, none are considered to be unpalatable, and none are mimics; a favorite of collectors and butterfly conservatories, surprisingly little is known of their natural history; caterpillars are covered with red, yellow, and green patterns, bear tufts of dorsal and lateral setae, possess bifid tails, and bear short, paired projections on the head (Fig. 2); host plant families include Arecaceae, Bignoniaceae, Fabaceae, Menispermaceae, Poaceae, and Sapindaceae.

Subfamily Calinaginae: a group represented by two to five species in the genus *Calinaga* restricted to the Himalayan regions; it is apparent that *Calinaga* forms mimicry complexes with *Parantica* (Danainae), but it is not clear if it is Batesian or Müllerian mimicry; caterpillars are smooth with short bifid tails and stout head horns and feed on Moraceae.

Subfamily Nymphalinae: a diverse, cosmopolitan group of more than 3000 species (sometimes split into Limenitinae and Nymphalinae) containing a tremendous range of size and color patterns; some are migratory (*Vanessa*, *Eunica*, and *Sallya*), some are unpalatable models, some are palatable mimics, some show tremendous seasonal polymorphism (*Junonia*), some feed on flower nectar, others feed on rotting fruits and carrion; some groups inhabit tropical forest canopies (*Euphaedra, Cymothoe, Panacea, Epiphile*, and *Baeotus*), some pass north temperate zone winters as adults (*Nymphalis*); caterpillars usually covered in spines, many with well-developed pairs of head spines (Fig. 2); pupa often with bifid projections on head; host plant families include Acanthaceae, Caprifoliaceae, Convolvulaceae, Euphorbiaceae, Fagaceae, Flacourtiaceae, Lamiaceae, Loranthaceae, Moraceae, Plantaginaceae, Poaceae, Rubiaceae, Rutaceae, Salicaceae, Sapindaceae, Scrophulariaceae, Urticaceae, and Verbenaceae.

Subfamily Acraeinae: a group of approximately 250 tropical African species, with a few in Asia and the neotropics; ranging from small to large, all are slow-flying unpalatable species that contain cyanogenic compounds, forming aposematic models for a variety of other groups, and are involved in Müllerian mimicry (*Acraea, Bematistes*, and *Actinote*); one species (*Acraea encedon*) is almost entirely female and reproduces via parthenogenesis; caterpillars (many which feed gregariously in communal nests) are densely covered in spines, but lack head spines; host plant families include Asteraceae, Passifloraceae, Sterculiaceae, Tiliaceae, and Urticaceae.

Subfamily Heliconiinae (passionflower butterflies): a group of 70–80 mainly Neotropical species with a few in Asia; most with well-developed eyes that are wider than the thorax, elongate forewings, and most serve as models in Batesian and Müllerian mimicry complexes; they feed on flower nectar, and some on pollen (*Heliconius* and *Laparus*) from which they can derive some of their unpalatability; caterpillars are densely spiny, bear paired head spines, and feed entirely upon plants in the Passifloraceae and allies—hence the name passionflower butterflies.

Subfamily Danainae (milkweed butterflies, tigers, and crows): a cosmopolitan group of approximately 150 species, with most in tropical Africa and Asia; ranging from medium to large size, most are slow flying, conspicuously colored, and models in mimicry complexes (*Danaus, Amauris, Idea, Tirumala*, and *Parantica*); their distasteful nature derives from feeding as caterpillars on milkweeds, but they also acquire other chemical defenses by feeding as adults on flowers and wounds in certain plants containing particular alkaloids; males often have well-developed, brush-like scent hairs they use during courtship; caterpillars are smooth, often patterned with alternating bands of black, white, and yellow, and many have dorsal pairs of fleshy tubercles; the pupae are frequently reflective gold or silver; host plant families include Apocynaceae, Asclepidaceae, and Moraceae.

Subfamily Ithomiinae (ithomiines and glass wings; Fig. 1): approximately 300 entirely Neotropical species; adults typically with a very small head, elongate wings, and species vary in color from transparent (*Greta, Ithomia*, and *Pteronymia*) to bright tiger-striped patterns [*Mechanitis, Tithorea*, and *Melinaea* (see Fig. 1)]; they are involved in both Müllerian and Batesian mimicry, representing unpalatable models for many other groups; their unpalatable properties derive from larval host plants and chemicals acquired by adult feeding, and males typically possess a tuft of scent hairs between the wings that disseminate pheromones; caterpillars are smooth, often with fleshy tubercles, and may be brightly colored or cryptic; The pupa is often reflective gold or silver and squat; host plant families include Apocynaceae, Gesneriaceae, and Solanaceae.

Subfamily Tellervinae: a group of 6–10 Australasian species all in the genus *Tellervo;* they serve as a models for nymphaline and satyrine Batesian mimics; this group has been included within the Ithomiinae; the caterpillars resemble some Danainae and feed on Apocynaceae.

Subfamily Libytheinae (beaks and snout butterflies): a cosmopolitan group of approximately 10 species recognized by the large erect palpi that form a "snout"; most species are well-known to periodically undergo spectacular migrations; the caterpillars somewhat resemble those of the Pieridae, and all feed on Ulmaceae.

II. EARLY STAGES AND HOST RELATIONSHIPS

Like all members of Lepidoptera, butterflies have four discrete stages in the life cycle (egg, caterpillar, pupa, and the adult), each with particular characteristics, behaviors, and requirements. Furthermore, to complete their life cycle, butterflies require a plant or insect host to feed on.

A. Egg

Butterfly eggs are laid either singly or in small to large clusters, either on or off the host, and the location where the egg is laid is typically important (Fig. 2). The eggshell frequently has an elaborate sculpturing that plays a role in respiration, and each major group of butterfly has its own form of egg.

B. Caterpillars

Depending on the group, the appearance of butterfly caterpillars may range from cryptic to aposematic, they may be covered with spines and/or hairs or appear to be naked, and their diets may include plant tissue or the flesh of other insects or they may feed entirely on secretions produced by other insects (Fig. 2). All caterpillars consist of three major sections: the head, thorax, and abdomen. The hardened head houses mandibles that function to shear off bites from their food. The head bears a gland that lays down silk that is grasped as the caterpillar moves forward, helping the caterpillar grip the substrate and also to secure rolled leaves in which they may shelter. Each thoracic segment bears a pair of true legs, whereas the 10 abdominal segments form the bulk of the body, housing the long gut. Caterpillars walk by using the prolegs (segments 3–6 and segment 10), and these function by hydraulic pressure and muscles. Segments 1–8 bear the external ring-like orifices (spiracles) that allow gas exchange with the atmosphere.

After reaching a particular size each caterpillar instar stops eating and undergoes a molt to the next instar; this is how caterpillars grow. Generally, but not always, there are five larval instars followed by a molt to the pupa, or chrysalis. Caterpillar growth is not a steady increase in weight from first to final instar; rather, there is a dramatic fluctuation of weight between each molt. Newly molted caterpillars may weigh about the same as or even less than previous instars, but their weight will quickly increase and exceed that of previous instars.

Caterpillar feeding behavior often differs among instars. In many groups, late-instar caterpillars may stop feeding during the day and then feed entirely at night. Alternatively, some lycaenid caterpillars may start life feeding on plants and, after molting to a later instar, they fall off the plant, are picked up by ants, and are carried into their nest where the caterpillars feed as carnivores on ant brood.

C. Pupa

When the final-instar caterpillar is fully grown, it stops eating and enters its molt to the pupa, or chrysalis. Within the pupa the caterpillar tissues are reconstructed into the adult by the process known as metamorphosis. The pupa attaches to a substrate by a series of hooks on the last segment (cremaster), and major groups typically have characteristic manners of pupation. For example, pupating with the head downward attached only by the cremaster is typical of Nymphalidae, but pupae of Papilionidae and some Pieridae attach by the cremaster with head upward and are restrained by a silk girdle. Pupae of Lycaenidae produce a whirring, clicking, or buzzing sound with a rasp and file system on the abdomen that may be a defense against predators. Sound production is also known in some nymphalid pupae.

When mature, the pupa splits along its dorsal surface, and the adult ecloses. After eclosion, the adult normally hangs from the pupal shell or nearby with the wings suspended downward so that it can expand and dry its wings. If dried in a crumpled manner the wings are useless for flying, and the butterfly is effectively dead. As a rule, female butterflies are mated soon after or even before eclosion, exemplifying one the most potent laws of evolution—nature abhors a virgin.

D. Adult

The adult butterfly (Fig. 1) is incapable of additional growth but is capable of flight, mating, and reproduction. Like all insects, the butterfly body is composed of the head, thorax, and abdomen.

The most obvious features of the butterfly head are the large compound eyes composed of numerous facets (ommatidia) that cannot focus but are sensitive to movement, light, and certain colors. A pair of distally thickened antennae arise from between the eyes that vary in shape according to the group. The antennae function as sensory organs for finding food, mating, and balance during flight and are sensitive to volatile chemicals. Between the eyes there is a pair of appendages called labial palpi, and between them lie the proboscis, a hollow tube composed of two interlocking halves that is coiled like a watch spring when not in use and can be extended for feeding. By virtue of having a proboscis, butterflies are restricted to a liquid diet that may include flower nectar, the juices of rotting fruit, carrion, dung, or semidigested pollen. Proboscis length may vary according to the group; in some species it is nearly vestigial, thus precluding feeding as adults (*Brassolis* and *Liphyra*), whereas in others the proboscis measures more than 1.5 times the length of the body (*Eurybia*), allowing them to take nectar from a wide range of flowers.

The thorax is composed of three fused segments bearing the wings and legs, and it contains the muscles for locomotion and various internal organs. As in all insects, the adult butterfly has six legs, one pair per segment. Butterflies have four wings (two forewings and two hindwings) typically covered in scales that give butterflies their characteristic colors and patterns. The color patterns of butterflies result mainly from the covering of scales that are arranged like overlapping roof tiles. There are three notable types of scales. The pigmentary scales are colored by the deposition of melanin, pterins, or other chemicals. Structural scales generate blue, violet, copper, or green colors by reflecting particular wave lengths of incident light. Androconial scales store and disseminate chemical odors (pheromones) that are used in mating, and some of these scales may be physically transferred to the female during mating.

The abdomen houses the digestive and reproductive tracts, terminating in the reproductive organs (genitalia). Except for segments housing the genitalia, the abdomen can stretch when the gut becomes filled with food, and abdominal distention may be considerable in groups feeding on rotting fruits (Charaxinae). The penultimate abdominal segment of males bears two appendages (claspers) that open to expose the aedeagus (penis) and serve to grip the female's abdomen during mating. The female abdomen terminates in three openings: the anus, egg pore, and copulatory pore. The configuration of genitalia is used extensively in butterfly taxonomy.

E. Host Relationships

An important aspect in the butterfly life cycle is the ability of ovipositing females to find, and caterpillars to feed on, particular plants. The liaison with plants is so strong that many groups of butterflies only associate with particular taxonomic groups of plants; other plants are unacceptable to both caterpillars and ovipositing females. In the Lycaenidae this association may extend to particular species of ants or Homoptera. For example, caterpillars of milkweed butterflies (Danainae) only feed on plant families containing milky latex, and those of the Heliconiinae use plants in the Passifloraceae. Such patterns of host association in butterflies gave rise to Ehrlich and Raven's classic paper that developed the concept of coevolution. On the whole, host association records for the Papilionidae, Pieridae, and Nymphalidae are much more complete than for the Lycaenidae.

III. BUTTERFLY–ANT SYMBIOSES

The ability to form symbiotic associations with ants (myrmecophily) occurs only within the Lycaenidae. Here, caterpillars provide food secretions to ants in exchange for protection against insect predators such as social and parasitic wasps. To form these symbioses, caterpillars have a suite of unique adaptations that may include organs (collectively known as ant-organs) to produce food secretions, volatile chemicals, and sound, all of which work in concert to modify ant behavior and enhance the protective attitude of ants toward caterpillars. Recent studies on ant-organs indicate that myrmecophily evolved at least twice in the butterflies: once in the Riodininae and independently in other lycaenid subfamilies.

The widespread trait of myrmecophily within the Lycaenidae and the fact that lycaenids account for approximately 50% of all butterfly species led Pierce (1984) to suggest that myrmecophily has amplified speciation rates in this group. Indeed, the diversity of life histories in myrmecophilous butterflies can be exceedingly complex, encompassing herbivores, carnivores, and those that feed as caterpillars only on secretions, and the associations with ants range from mutualistic to completely parasitic or predatory.

A. Food Secretions

Ants pay close attention to particular abdominal segments bearing ant-organs that produce food secretions, which in some species are known to have high concentrations of amino acids and sugars. In some Riodininae, these consist of a pair of organs (tentacle nectary organs) on the eighth abdominal segment that can be extruded individually or simultaneously. In all other lycaenid subfamilies, this organ is a single dorsal pore on segment 7 (dorsal nectary organ). Ants are so intent on obtaining the secretions that they constantly antennate the caterpillar to solicit more, and in many cases, this is a good example of a general rule among participants in symbiotic associations— "you scratch my back and I'll scratch yours."

B. Semiochemical Production

Myrmecophilous caterpillars may have extrusible glands that seem to produce volatile chemicals (semiochemicals or pheromones) that alter the behaviors of attending ants. Some Riodininae have a pair of extrusible glands on the third thoracic (anterior tentacle organs), whereas other lycaenids have a pair of glands on the eighth abdominal segment (tentacle organs). In both cases, when extruded from the body these organs do not produce a liquid secretion but rather the tip is modified with spines that gives the appearance of a tiny feather duster. These spines likely provide a larger surface area to disseminate volatile chemicals that may be similar to ant alarm pheromones. Instead of anterior tentacle organs, a small group of Riodininae caterpillars (*Theope*) possess a corona of inflated setae around the head that appear to disseminate semiochemicals.

C. Call Production

The idea that caterpillars produce acoustic calls might seem unlikely. We now know, however, that myrmecophilous caterpillars produce substrate-borne calls that function in the formation and enhancement of their symbioses with ants, and these calls bear similarities to those produced by ants for communicating among themselves. In most Riodininae caterpillars calls are produced by a pair of mobile, grooved, rod-like appendages (vibratory papillae) arising from the distal edge of the first thoracic segment. An acoustical signal is produced when the grooves on the vibratory papillae grate against head granulations (Fig. 2). In other lycaenid caterpillars the call is produced by thickened bumps located ventrally between abdominal segments. Most concepts of insect communication suggest that acoustical calls evolved in a sexual context. However, caterpillar calls provide an example showing that, by forming symbiotic associations, the call of one species may evolve to attract another, unrelated species.

D. Ants and Caterpillar Associations

In general, myrmecophily in caterpillars occurs with a particular type of ant. A basic element among myrmecophilous caterpillars is that they typically form symbioses only with ant species that depend heavily on secretions as food—ants that also form symbioses with Homoptera and plants. Therefore, secretion-harvesting ants likely played a key role in the evolution of myrmecophily, whereas those ants that are predators or herbivores did not. An ecological consequence of the evolution with secretion-harvesting ants is that in any suitable contemporary habitat, a suite of caterpillar, plant, and Homoptera species all share the same species of ant symbionts.

Among myrmecophilous caterpillars there are two main categories of ant association. The most widespread category comprises an association in which a particular caterpillar species may be tended by a suite of secretion-harvesting ant species. The other category comprises an association in which a caterpillar has an obligate association with a single species of ant. In this case, female butterflies may require the presence of a particular ant species to lay their eggs since caterpillars are unable to form symbioses with any other ant species. Furthermore, it is in these types of associations in which some caterpillars are adopted by the ants, taken into the nest, and become parasites or predators of their hosts.

IV. BUTTERFLY MIMICRY AND DIVERSITY

When several species of butterflies share conspicuously bright color patterns and fly together in the same habitat, this is called mimicry—a widespread and important antipredator defense. Fundamentally, mimicry occurs when one species closely resembles another species, and based on outward appearance one or both are avoided by predators. Virtually all major taxonomic groups of butterflies exhibit mimicry, but the warningly colored (aposematic) models are found predominately in particular groups of Papilionidae, Pieridae, and Nymphalidae, whose caterpillars feed on poisonous plants. Mimicry is a complex and subtle topic, but there are two basic types of mimicry in butterflies, both involving species that advertise conspicuous color pattern to predators: Batesian and Müllerian mimicry.

A. Batesian Mimicry

This is the phenomenon whereby one or more palatable species resemble one or more unpalatable model species, and the palatable species gain protection by duping predators. Here, predators avoid mimics because they resemble unpalatable models. The best known basic example of Batesian mimicry involves the palatable viceroy (*Limenitis archippus*) and the unpalatable monarch butterfly (*Danaus plexippus*) in North America. However, Batesian mimicry occurs in all biogeographic regions, and one of the most intriguing examples involves the sex-limited mimicry of the wide-ranging African swallowtail, *Papilio dardanus*. Here, only the females are mimics. In this case, females are polymorphic with respect to their appearance, and their color patterns change geographically when flying with different model species. In other words, *P. dardanus* females from Kenya may look entirely different from those from Zaire or elsewhere, and in each instance they precisely mimic a different unpalatable model species. Thus, the type of female color pattern evolves in response to and depends on the local community diversity of the model species.

B. Müllerian Mimicry

This is the phenomenon whereby several unpalatable species (co-mimics) fly in the same area and share the same color pattern. In this case, the association of similarly patterned unpalatable species is thought to reinforce the nasty experience predators have when eating butterflies of such a color pattern, thus educating predators to avoid it.

C. Mimicry and Diversity

Aposematic species are an important element of butterfly diversity, particularly in the tropics. For example, approximately 20–25% of all Papilionidae, Pieridae, and Nymphalidae in Costa Rica and Kenya are clearly aposematic models. Although accounting for a large percentage of all butterfly species, there are few documented examples of aposematic Lycaenidae.

Müllerian mimicry is primarily a tropical phenomenon and is an important part of tropical faunal diversity. This can be appreciated by considering the diversity of color patterns shown by many co-mimetic species and races of ithomiine and heliconiine butterflies (plus many co-mimic moths and other butterfly groups) that converge across large areas of the neotropics. Even when the tightly overlapping distribution of only two co-mimetic species of *Heliconius* and their many precisely convergent color patterns are mapped over the Neotropical region, one cannot doubt the power mimicry plays in the evolution, organization, and diversification of tropical butterfly faunas. The numerous co-mimetic species of Acraeinae butterflies throughout the African region also serve as another potent example of the influence of mimicry on the diversity of butterfly communities. It is clear that butterfly mimicry evolved in the context of multispecies interactions which involved butterflies, their predators, and the plant and insect hosts they feed on as adults and caterpillars. Thus, mimicry serves to remind us that habitat disturbance and/or destruction may have important implications for the continued survival and future evolution of interacting species.

V. GEOGRAPHICAL PATTERNS OF BUTTERFLY DIVERSITY

One of the most frequently asked questions about butterflies is the following: How many are there? The answer is thought to be between 12,900 and 15,819 species. This is hardly a satisfying answer since the question has little biological context. In contrast, questions framed by comparing different geographical areas impart a sense of dynamics to butterfly diversity. For example, one might ask: Does butterfly species diversity change with respect to latitude? or How do different areas of Africa compare with respect to numbers of butterfly species? Indeed, comparing species numbers among areas shows that latitude, biogeographical region, area size, and taxonomic affinity all contribute to global butterfly species diversity. A caveat is in order about comparative species numbers: Sampling effort is almost always unequal among different areas, and the taxonomic accuracy of species counts or lists often varies among sites. Thus, it is prudent to use care when interpreting the generality of species diversity patterns among areas.

A. Latitudinal Gradients of Species Diversity

As is the case for most groups of terrestrial organisms, butterfly species diversity increases toward the equator. Comparing the North American and Neotropical faunas suggests that the neotropics has an estimated 10–12 times more butterfly species compared to North America (Table I). Comparing site diversity at different latitudes, however, provides a richer perspective of this phenomenon. A latitudinal transect using five well-known sites from the Americas makes it obvious that species numbers increase when moving from the north latitudes toward the equator (Table II), even though the smallest areas being compared are at the equator. The dramatic equatorial increase in species is exemplified by the fact that a mere 500 ha of lowland Ecuadorian forest has more butterfly species than all of North America.

The relative contribution of each butterfly family to site diversity also varies with latitude. From Table II, it is evident that the relative contribution of Papilionidae and Pieridae to total species diversity is about the same regardless of latitude, but the contributions of Nymphalidae and Lycaenidae increase dramatically between 20 and 0° latitude (Fig. 3). The increase in species

TABLE I
Approximate Numbers of American and World Butterfly Species

	North America	Neotropics	World
Papillionidae	35	169	621–645
Pieridae	63	347	1086–1105
Lycaenidae	171	2300–3000	6000–6900
Nymphalidae	202	1850–2500	5175–5975

TABLE II
Latitudinal Transect Showing Changes in American Butterfly Species Diversity

Site	Latitude	Area	Family				Total species
			Papilionidae	Pieridae	Nymphalidae	Lycaenidae	
H. J. Andrews Forest, Oregon	44°14′	6400 ha	5	7	27	23	62
Los Angeles Basin, California	34°4′	>1 million ha	6	15	26	32	79
Estacion Los Tuxlas Mexico	18°35′	700 ha	14	19	113	66	212
La Selva, Costa Rica	10°26′	1000 ha	16	26	219	181	442
Garza Cocha, Ecuador	0°29′	500 ha	24	25	314	312	676

of Nymphalidae is accounted for by subfamilies that reach their greatest diversity in the Amazon (Morphinae, Brassolinae, Charaxinae, Satyrinae, and Ithomiine), whereas the increased contribution of Lycaenidae is due mainly to the subfamily Riodininae, which is also an Amazonian group.

B. Variation among Neotropical Sites

Species diversity is not equal among Neotropical forest sites. Nine well-known sites that have many species in common vary strongly in numbers of species and in the contribution of each family to species diversity (Table III). Here, species numbers may range from 212 in Mexico to 1199 at one Brazilian site. Among six Amazonian sites, numbers range from 676 to 1199 species. When averaged over the entire Table III, the contribution of each family to species diversity is as follows: Papilionidae, 3.8%; Pieridae, 4.8%; Nymphalidae, 45.2%; and Lycaenidae, 46.1%. It may be significant that these proportions approximately reflect those observed when comparing latitude (Fig. 3).

Comparisons among sites from the Americas point to the general relationship of the higher species richness that occurs at lower latitudes and to the marked variation among sites that share many species in common. These examples also show that the relative contribution of each family to species richness is not equal; the proportion of nymphalid and lycaenid species increases toward the equator, but the proportion of papilionid and pierid species appears relatively constant. At this point, we might ask if there are similar patterns outside the neotropics.

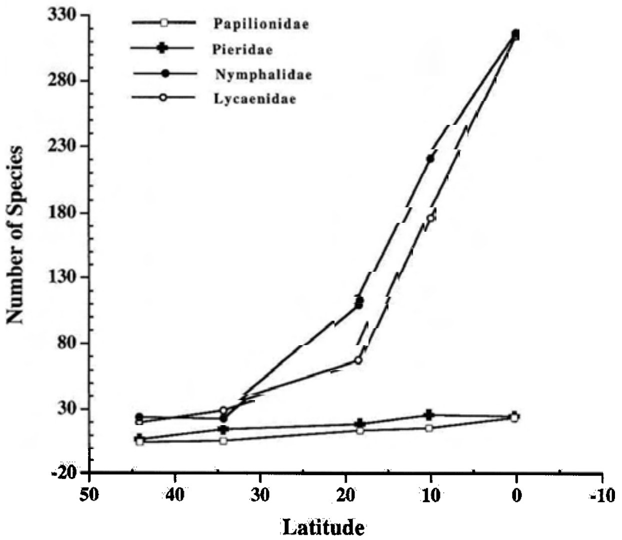

FIGURE 3 Latitudinal Gradient of American Butterfly Species Diversity. Each line represents species numbers per family contributed to five sites distributed from 44° north to the equator.

C. Regional Patterns of Species Diversity

Although most butterfly species are tropical, the number of species is not distributed equally among tropical regions (Table IV). As one might expect, those areas closest to the equator have a greater number of species, but there is also an effect of size on species diversity (Table IV). In this comparison, the continent of Africa has by far the most species, but it also encompasses the greatest geographical area and habitat types (deserts, mountains, forests, and savannas) of any area. Within Africa there are more species in Zaire than in Kenya or Southern Africa, highlighting the ecological diversity in African climate and habitat types. Thus, the entire continent of Africa should contain more species than a geographic subset.

As in the neotropics, the relative contributions of families to total species numbers differ among areas of Africa (Table IV). Here, the Papilionidae and Nymphalidae contribute equally to total richness of both Kenya

TABLE III

Comparative Diversity among Neotropical Sites[a]

Site	Family				Total species	Total area (ha)
	Papilionidae	Pieridae	Nymphalidae	Lycaenidae		
Estacion Los Tuxlas Mexico	14 (6.6)	19 (8.9)	113 (53.3)	66 (31.1)	212	700
Finca La Selva, Costa Rica	16 (3.6)	26 (5.8)	219 (49.5)	181 (40.9)	442	1,000
Garza Cocha, Ecuador	24 (3.5)	25 (3.7)	315 (46.6)	312 (46.1)	676	500
Jatun Sacha, Ecuador	25 (3.6)	23 (3.2)	306 (43.7)	345 (49.3)	699	600
Paquitza, Manu, Peru	25 (2.9)	31 (3.6)	369 (43.3)	427 (50.1)	852	3,900
Tambopata, Peru	25 (3.1)	26 (3.3)	337 (42.3)	409 (51.3)	797	>2000
Cacaulandia, Brazil	30 (2.5)	31 (2.6)	423 (35.3)	715 (59.6)	1199	2,000
Alto Jurua, Brazil	38 (3.7)	37 (3.6)	467 (45.0)	496 (47.8)	1038	>500
Cerro do Japi, Brazil	19 (4.7)	36 (8.9)	193 (47.8)	156 (38.6)	404	>400

[a] The percentage of the total species at a particular site is in parenthesis.

and Zaire, but Kenya shows an increased proportion of Pieridae and a decreased proportion of Lycaenidae. On the other hand, the proportional contributions of Papilionidae and Pieridae are reversed in the Zaire fauna. The Papilionidae and Nymphalidae in the Southern African fauna contribute less to the total than other mainland African areas, but nearly 55% of all Southern African butterflies are Lycaenidae. Overall, these proportional differences (Table IV) may reflect the ecological responses of taxonomic groups to differences in habitat types and/or the differences among regional taxonomists. Finally, in comparison to mainland Africa the fauna of Madagascar is interesting. Here, only 17% of all butterflies are lycaenids, but nymphalids constitute 67% of the total fauna, most of which are Satyrinae (i.e., 42% of all the butterflies). This example demonstrates how historical colonization and subsequent radiation of an island by one group can produce a fauna distinctly different in composition from that of the mainland.

Only a broad-brush comparison among areas of different sizes and regions is necessary to appreciate that, overall, butterfly diversity is highest in the neotropics (Table I–Table V). Despite the great disparity in geo-

TABLE IV

Variation in the Contribution of Each Family to Species Richness among Different Faunas[a]

Fauna	Family				Total
	Papilionidae	Pieridae	Nymphalidae	Lycaenidae	
All of Africa	80 (2.9)	145 (5.3)	1107 (40.6)	1397 (51.2)	2729
Zaire	48 (3.7)	100 (7.6)	607 (46.5)	551 (42.2)	1306
Kenya	27 (3.7)	87 (12.1)	335 (46.5)	271 (37.6)	720
Southern Africa	17 (2.3)	54 (7.2)	265 (35.6)	409 (54.9)	745
Madagascar	13 (4.9)	28 (10.7)	175 (66.8)	46 (17.5)	262
Australia	18 (6.5)	35 (12.6)	85 (30.6)	140 (50.3)	278
New Guinea	41 (5.2)	146 (18.6)	222 (28.3)	376 (47.9)	785
Malaysia	44 (5.8)	44 (5.8)	273 (35.9)	400 (52.5)	761
Costa Rica	42 (4.0)	71 (6.8)	438 (41.9)	493 (47.2)	1044

[a] The percentage of total faunal richness by each family is given in parentheses.

TABLE V

Percentage of World Species by Geographical Region[a]

	Region						
	North America	Neotropics	Costa Rica	Africa	Australia	New Guinea	Maylasia
Total species	471	5341	1044	2729	278	785	761
% World fauna	3.4	38.8	7.6	19.8	2.0	5.7	5.5

[a] Total number of butterfly species for world fauna (13, 753.5) and the neotropical region (5341) represent averages.

graphical area in the comparison, the small country of Costa Rica has a greater percentage of the world's butterfly species than does North America, Australia, New Guinea, or the peninsula of Malaysia (Table V). Since our taxonomic understanding of African, Australian, and Oriental butterflies is more thorough than that of the neotropics, it is likely that the total Neotropical butterfly species count will increase in the future.

D. Species Diversity in Space and Time

When estimating species diversity in any habitat, the variables of time, space, and sample size can be profoundly important. For example, consider two samples taken in the same Wisconsin prairie—one for 7 days in mid-July and the other for 7 days in mid-January. Despite equal sampling effort, the number of species tallied in January would certainly be zero because no butterfly is known to fly in a prairie during midwinter. Here, it is easy to see that time of sampling is important for estimating species diversity.

The problem of sampling in space and time becomes more important in forest areas, especially tropical ones. Consider a recent study of fruit-feeding nymphalid butterflies conducted on 600 ha of lowland Ecuadorian rain forest that investigated how species were distributed in space and time. To ensure equal sampling, butterflies were simultaneously trapped in the canopy and understory for the first week of every month for a period of 1 year. The results showed that both time of sampling (month) and position of trap (canopy or understory) were extremely important in estimating species diversity at this site (Fig. 4). In other words, had the study sampled for only a few months, or only in the understory, species diversity would have been greatly underestimated. A similar study from a different site in Ecuador also demonstrated that a significant proportion of species diversity was accounted for by time of sampling and the forest canopy fauna. This study further showed that species diversity varied significantly over short distances within the same, seemingly uniform rain forest, and it highlights the importance of sample size in comparisons of species diversity (Fig. 5). Such studies illustrate the critical nature of sampling methods, space, time, and sample sizes in comparisons of butterfly diversity.

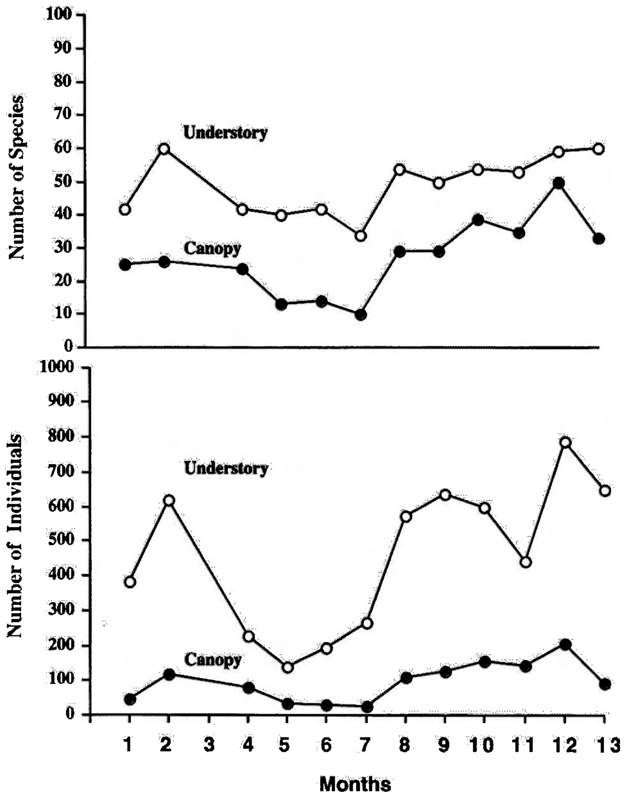

FIGURE 4 Monthly variation in species richness (top) and abundance (bottom) of fruit-feeding Nymphalidae in forest canopy and understory (from DeVries *et al.*, 1997).

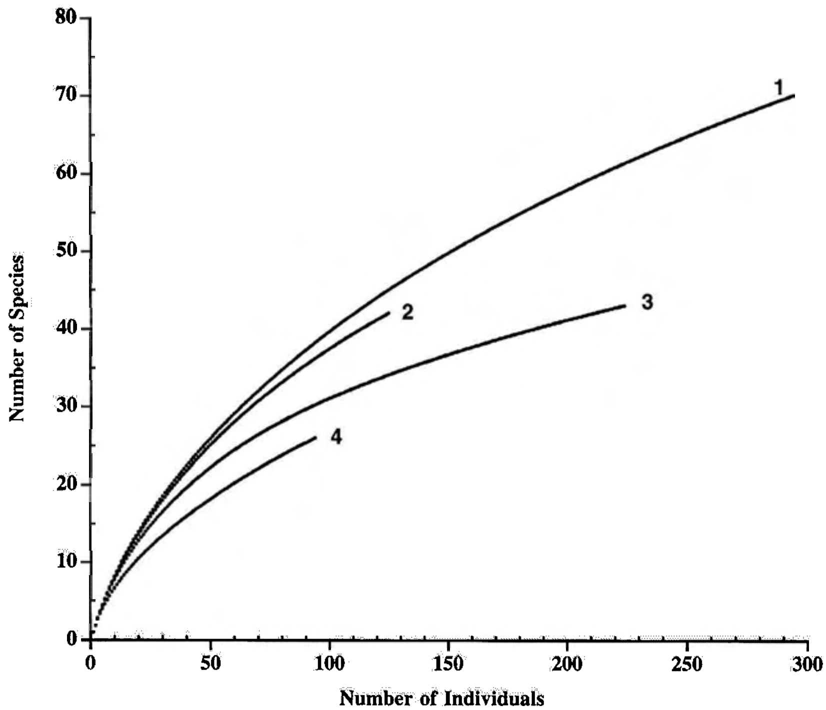

FIGURE 5 Species diversity of fruit-feeding Nymphalidae showing the relationship to space and sample-size. Each numbered line represents a plot sampled from within a single tract of continuous rainforest (from DeVries *et al.*, 1999).

VI. BUTTERFLY DIVERSITY AND HABITAT DESTRUCTION

It is obvious that the evolution of butterfly diversity is based on historical and contemporary interactions with many species. These biological interactions include plant and/or insect hosts, co-mimics in Batesian and Müllerian mimicry complexes, predators, and parasites. Butterflies have also evolved within and adapted to a great many biomes, habitats, and microhabitats, ranging from the multilevels within lush tropical rain forests to starkly dry deserts and subarctic tundra.

Habitat destruction always has profound effects on the biological communities that inhabit them, and butterflies are no exception. Like all organisms, butterflies live, evolve, and diversify within dynamic biological systems, and as such they cannot be studied as art objects or protected as inventoried stock. To date, butterflies have served as tools for understanding the diversification of life on Earth and the fundamental interactions among species. However, our future understanding of butterfly diversity will depend on a renewed interest in studying them in the natural world and valuing the habitats in which they occur.

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See Also the Following Articles

HYMENOPTERA • INSECTS, OVERVIEW • MOTH • SPECIES COEXISTENCE

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