

Introduction

I. WHERE TO FIND BUTTERFLIES

BUTTERFLY RANGES

To observe butterflies in the field, we first need to locate them. This task is often not easy, as any experienced observer knows. A few abundant species, such as Cabbage Whites and American Ladies, can literally be found almost anywhere—roadsides, gardens, parks, even vacant city lots. But most others require at least some degree of specific knowledge to locate. And a surprisingly large number of East Coast species—more than a quarter, by our count—reside in limited areas within our region, some with just a few known sites or colonies. To further complicate matters, butterfly ranges are not static. A dozen or more East Coast species have experienced significant range reductions in recent decades, often without clear reason (e.g., Grizzled Skipper and Regal Fritillary). And a smaller number of species, sometimes just as unaccountably, have undergone pronounced extensions (e.g., Common Ringlet and Red-banded Hairstreak). Even species with stable ranges may repeatedly extend their boundaries northward in mild years, only to be pushed back when a harsh winter intervenes (e.g., Shapiro, 1991).

A range, stated most simply, is the geographical region in which a species *usually* lives or occurs. Some variant of this simple definition is the starting point for even the most sophisticated computer models that simulate distribution patterns (e.g., Rapoport, 1982, p. 3). Most ordinary butterfly books (including this one) illustrate ranges as color blocks on a standardized map, each with well-defined boundaries. Such drawings can easily create the impression that butterflies are dispersed uniformly through the designated area, as if in a giant corral. This approach is useful as a means of visually condensing a great deal of complex information; but it can easily mask underlying biological dynamics, limiting our ability to appreciate the ecological forces that shape a species' distribution.

Researchers suggest that butterfly populations exist in constant flux. This may seem to overstate the case somewhat, from an observer's perspective, since we know of many stable colonies that persist for decades in one location. Yet population densities do regularly vary within butterfly ranges, often from year to year, and the precise loca-

tion of the edge of a distribution, which is important to know, can be vague and shifting.

In recent years, *metapopulation theory* has been invoked to explain the range dynamics of many butterfly species. First articulated in the 1950s, metapopulation theory holds that many organisms live in a series of largely isolated local populations, linked only by periodic dispersals, or cross-migrations (*see* Hanski, 1999). The fate of a species in any area depends on a set of key factors, including the viability of individual colonies, the rate of successful cross-dispersal, the "patchiness" of the environment, etc. Individual colonies may become extinct, but if conditions are favorable an area may later be recolonized (Ehrlich, 1985). As one author has phrased it, individual colonies blink off and on over time, "like lights on a Christmas tree" (Douglas, 1989, p. 100).

This is all a bit theoretical, however, if our main purpose is to locate butterfly populations in the field. For this, we need to focus on more tangible factors. With respect to butterflies, three key influences predominate: hostplants, habitats, and climate. These factors are not fully independent, to be sure, as climate affects the distribution of habitats, habitats define the range of hostplants, and hostplants (in large numbers) can modify climates. Still, each element has independent effects that can be explored separately.

CLIMATE

For cold-blooded (*exothermic*) creatures such as butterflies, temperature is the most critical aspect of climate, followed closely by precipitation. Species living in the North naturally require physiological adaptations to survive regular hard freezes. But other, less obvious effects are also apparent. In the South, for instance, longer flight seasons and faster caterpillar growth rates combine to increase the average number of yearly broods. (Arctic species, by comparison, may require two or more full summers as a caterpillar to reach adult status.) Climate can even affect subtle traits such as wing size: it has been proposed that medium-sized butterflies have a selective advantage in northern climates, regardless of family. The reasons for this interesting fact are discussed below.

The influence of climate is sufficiently pervasive that entire biological communities can be identified in climate-

specific terms—such as *bolarctic* plants and animals, found in northern territories around the world. In our mostly temperate region, though, no single family (and only a few subfamily groups or tribes) can be described as “climate specialists.” Instead, most groups have representatives scattered across the various climate zones. Climate does remain a significant component of *habitat*, on the other hand, and is discussed in that connection. For the moment, however, we proceed to a second factor—the most important single determinant of butterfly distributions, as well as many other aspects of their lives—specifically, hostplants.

HOSTPLANTS

Caterpillars are highly fussy about the foods they will accept, and adult female butterflies are even choosier in selecting target plants on which to lay eggs (*oviposit*). Evolution has been refining these preferences for tens of millions of years. Disagreement remains as to whether or not butterflies and hostplants *co-evolved*—with new defensive plant capabilities met by improved methods of caterpillar exploitation, prompting additional plant defenses, and so on (*see* Ehrlich & Raven, 1964; *but* Courtney & Chew, 1987; Scoble, 1995, pp. 174–76). Whatever the case, we know that present-day interrelationships between hostplants and butterflies are very close indeed. Scientists and observers alike try to make sense of these complicated interconnections.

Let us start at the tangible end of the process—the act of egg-laying by a female butterfly. This is among the most subtle and intricate of butterfly behaviors. Accurate oviposition is critical because the resulting caterpillar has little capacity to recover from a parental mistake. Even if caterpillars were more mobile, they would still lack the sensory apparatus and intelligence to seek out a suitable host over any significant distance. It is true that in some species females lay eggs on surfaces *near* the hostplant, rather than directly on it, seemingly to reduce predation; but in these situations hostplants are within the “crawl range” of instinctually guided hatchlings (e.g., Gannon, 1986, Brown, 1981; MacNeill, 1964).

Adult females select hostplants methodically. The initial contact is usually visual, based on leaf shape or various other specialized cues. Some species prefer isolated hostplants, or hostplants of a particular size or shape (*see*, e.g., Douglas, 1989, p. 180, Chew & Robbins, 1985, pp. 71–72). Approaching the target host, the female lands and tastes or smells the leaf with chemical sensors on her feet. Often, she drums at the leaf surface, evidently to dislodge chemicals for sampling (or to detect roughness). The chemical

cues that induce egg-laying are often highly specific (e.g., *see* Haribal et al., 1998). And some chemicals deter ovipositing rather than induce it.

Butterflies are exquisite taxonomists. They can often locate and identify plant species more reliably than trained human botanists. Naturalist Roger Hammer tells of the day he followed a female Polydamas Swallowtail around Elliot Key (in Biscayne Bay off Florida), until she led him to an endangered Marsh’s Dutchman’s-Pipe (*Aristolochia pentandra*) that he had been unable to find himself, despite diligent searching. Female butterflies do make oviposition errors, especially early in an egg-laying session (Stanton, 1984), though it is difficult to rule out the possibility that some of these errors may be part of a genetically programmed strategy for sampling alternate hostplants, or, as already noted, a strategy to avoid placing eggs in predictable locations that predators can target. Perhaps for this reason, caterpillars can often survive on a wider range of hosts than females are prone to lay on (Janz, 2003).

Having located a proper hostplant, the females of some species next check the plant for existing eggs, to avoid overcrowding or cannibalism on the part of another female’s earlier-hatched larvae (Raucher, 1979).¹ In some groups, such as checkerspots, eggs are laid communally. Here, the female may actually *seek out* existing eggs rather than avoid them. Finally, in *myrmecophilous* (ant-loving) lycaenids—certain blues and hairstreaks whose young are protected by ants in exchange for producing sweet secretions—the female may refuse to oviposit unless ants of the appropriate species are present. Females actually touched by these ants are prone to lay the most eggs (Douglas, 1989, p. 134).

The ovipositing female often lays only on particular portions of the hostplant. The concealed underside of a leaf may be selected rather than the exposed upper surface. Or, in species whose caterpillars feed on flowers, the female may lay only on unopened buds. Greater fritillaries lay eggs near the base of the hostplant in the fall, so that young caterpillars will not have far to look for a sprouting hostplant come spring. Females often lay eggs near the site of newly emerging foliage, which may offer desired concentrations of certain chemicals (either very low or very high, depending on the objective), or which may simply be more tender, and thus easier for newly hatched caterpillars to chew. Whatever determinations a female needs to make prior to ovipositing must be concluded quickly, in any case, as the moment of egg-laying is a vulnerable one for her (Hanski, 1999, p. 212).

In sulphurs, egg-laying begins as soon as a day or two after emergence and persists for up to two weeks. Female

¹ Few caterpillars are carnivorous per se, but many larvae will eat others of their own species that they happen to encounter. The purpose of larval cannibalism may be territorial more than nutritional, but this subtlety is largely immaterial to the victim.



I-1. In Florida, trees that shed their leaves during the winter drought refoliate in the spring. Here, a female Ruddy Daggerwing lays her eggs near the newly emerging leaves of a Strangler Fig, which will provide newly hatched caterpillars with a tender meal.

sulphurs lay an average of 700 eggs in laboratory conditions, though probably a fraction of this number in the wild. Other species are estimated to lay roughly between 200 and 1,000 eggs, occasionally more. Only a few of these need to reach adulthood in any locality for the species to persist.

HOSTPLANT USE: STRATEGIES AND PATTERNS

All these details beg a fundamental question. How did female butterflies acquire the genetic programming to seek out and identify specific hostplants in the first place? Unfortunately, it may be impossible to reconstruct the exact origins of early plant associations, since they were formed millions of years ago, when plants and butterflies were both still quite different. Some intelligent guesswork has been done to reconstruct these early events (e.g., Scott, 1986, p. 64), but it is still most practical for the moment to understand present-day circumstances from a functional perspective.

Researchers pay attention to the number of hostplants a butterfly species utilizes. Is there a single hostplant per species (*monophagy*), a limited number (*oligophagy*), or many (*polyphagy*), and are the hosts closely related? Polyphagous species may use multiple hostplants across their range, or they may be polyphagous at the population level only, keeping to a single host at any one location. Or, they may go through polyphagous episodes while shifting host-plant use. Much remains to be learned here.

Another approach is to analyze the hostplants used by all the butterfly species in a *particular region*. Table I lists 62 plant families with known primary butterfly associations

in our area (excluding some incidental uses). This list includes a wide variety of plant types, but what may be most telling is the large number of common plant families that are *not* included—maples (Aceraceae), mints (Lamiaceae), lilies (Lilaceae), orchids (Orchidaceae), and, for the most part, conifers (just two species feed on pines, another two on cedars). Even composites (Asteraceae) are rather modestly represented if we consider the size of the family and the large number of butterflies that use this family for nectar. Moth larvae, by comparison, have relatively diverse tastes, consuming fungi, lichens, nonvascular plants (moss/liverworts), algae, and ferns, as well as flowering plants in many families. Butterflies outside our region also use some of these additional food types, but Table I shows plainly that the process of hostplant selection among East Coast butterflies is not random. On the contrary, our species have made some very specific choices in affiliating themselves with particular hostplant families over time.

The hostplant choices of East Coast butterflies can be assigned to a concise set of descriptive categories, which we will call *hostplant-related lifestyles*. See p. 4. For the most part, these lifestyles amount to nothing more—nor less—than a suite of integrated adaptations that enhance the survival prospects of species using a particular class of food plant.

One common lifestyle strategy involves concentrating on a set of nutritious and digestible hostplants, exploiting them aggressively to achieve a high reproductive rate. This strategy may enable a species to outpace the many mor-

Table I. Hostplant Families Used by East Coast Butterfly Species

| # of Butterflies Using Family for Principal Hostplants | Hostplant Family |
|--|--|
| 15 or more | Grass (56), Pea (31), Sedge (16). |
| 10–14 | Aster (Composite) (11), Beech (10), Violet (10), Willow (10). |
| 6–9 | Birch (9), Rose (9), Cassia (8), Elm (7), Heath (7), Mustard (Crucifer) (7). |
| 4–5 | Mallow (5), Nettle (5), Acanthus (4), Buckwheat (4), Mimosa (4), Passionflower (4), Rue (4), Spurge (4). |
| 2–3 | Goosefoot (3), Figwort (3), Milkweed (3), Quassia (3), Cashew (3), Laurel (3), Verbain (3), Agave (2), Amaranth (2), Bayberry (2), Birthwort (2), Buckthorn (2), Buttercup (Crowfoot) (2), Cedar (2), Currant (Gooseberry) (2), Holly (2), Olive (2), Palm (2), Plantain (2), Pine (2), Saltwort (2), Soapberry (2), Walnut (2). |
| 1 | Arrowroot, Black Mangrove, Bursera, Cacao, Caltrop, Canna, Caper, Custard-Apple, Cycad, Dogwood, Flax, Hemp, Honeysuckle, Leadwort, Locustberry, Magnolia, Mistletoe, Mulberry, Parsley (Carrot), Red Mangrove, Sweetleaf. |
| 0 [No principal hosts] | Examples: Arum, Cactus, Evening-Primrose, Gentian, Geranium, Iris, Lily, Maple, Milkwort, Mint, Morning-Glory/Bindweed, Nightshade, Orchid, Saxifrage, St. John's-Wort, Sycamore, all lower plants & ferns. |

Note: "Plant Family" listings include number of butterflies using the family.

tality factors that beset butterfly populations. Nonwoody vascular plants (*herbs* in botanical parlance) are often well-suited to this strategy. Scott believes that primitive butterflies pursued an “herbal” lifestyle built around early members of the pea family (Scott, 1986, p. 64; *compare* Janz et al., 2001). A drawback to specializing on easily exploited herbs is that many such plants are ephemeral, growing in disturbed or transitional habitats. This injects an element of uncertainty, especially in prehistoric times, when these preferences evolved, since disturbed habitats were probably rarer in those times than human activity has made them today.

It was most likely the stable, widespread availability of two other plant groups, trees and grasses, that placed them at the center of their own strategic lifestyles—this despite their sophisticated chemical defenses, frequent indigestibility, and inconsistent nutritional content. A different set of factors would be required to account for the origins of root-feeding, as engaged in by giant-skipper, or the development of a newly acquired taste for flower parts, which is thought to have sparked the evolution of lycaenids (blues and hairstreaks) as a separate taxonomic group (Scott, 1986, p. 99).

Nutrition alone is not the sole basis for defining host-plant strategies, however, often not even the primary basis. Butterflies use hostplants as a source of diverse chemical substances, employed in defense, mating, synthesis of wing and body pigments, and other special life functions (Brower, 1985). Examples include alkaloids, cardenolides, flavonoids, glucosides, tannins, coumarins, organic cyanides, and many others. The main function of these so-called secondary plant chemicals seems to be the deterrence of herbivores, in one way or another. Some are actively toxic, others may simply be unpleasant, causing rejection because of bitter taste or unfamiliarity. A number of hostplants that are described in plant books as “aromatic” or “medicinal” may fall into this category. Some defensive plant chemicals, lastly, may protect butterflies indirectly, by making them hard to digest. There is experimental evidence that nestling birds fed on caterpillars with high tannin concentrations develop more slowly than chicks fed on caterpillars low in tannin (Brower, 1985, p. 121).

Ironically, secondary plant chemicals—once tamed—become primary targets for ovipositing female butterflies, especially those that can be extracted while feeding, thereby conferring toxicity during the butterfly’s life cycle. In some cases, particular defensive chemicals occur in a number of unrelated plant families, and this can result in unlikely seeming hostplant combinations. Cabbage and Great Southern Whites, e.g., feed on plants in four genera (three related, one not), but all contain mustard oils, or *glucosides* (Scott, 1986, p. 65). Similarly, Dorcas Coppers feed across families and genera (docks, smartweeds, and

Major East Coast Butterfly Lifestyles Based on Hostplant Use: An Overview

| Hostplant Type | General Strategy Factors |
|--|---|
| Vascular Plants (“Herbs”) | <ul style="list-style-type: none"> • Relatively easy to digest, offer ready nutrition • Fast caterpillar growth, numerous broods • Transient lifestyle, since many herbs are ephemeral • May be difficult for predators to target shifting populations |
| Grass | <ul style="list-style-type: none"> • Hostplants widespread and abundant, available throughout warm season • But often difficult to digest, nutritionally incomplete • Slow caterpillar growth, fewer broods per year (or smaller individuals, e.g., grass skippers) • Difficult for predators to target in large feeding areas • Hostplants not toxic, so adults are often cryptic (satyrs) or evasive (skippers) • Caterpillars often live in protective leaf rolls, feeding at night |
| Woody Plants (Trees, Shrubs & Woody Vines) | <ul style="list-style-type: none"> • Many trees have well-developed chemical defenses, with leaves hard to digest • Seasonally targeted broods may coincide with “leaf out” periods • Some caterpillars can detoxify a range of defensive chemicals (tannins, etc.) • But this slows development, reducing average brood frequency (one per year in <i>Satyrion</i> hairstreaks) • Tree feeders are often polyphagous, and may use a number of hostplant families • Exposure exists to arboreal predators, “false heads” are common |
| Flowers | <ul style="list-style-type: none"> • Flower parts and fruits relatively easy to digest; eaten by certain blue and hairstreak larvae • Seasonally targeted broods coincide with peak flower periods • Flower parts may lack strong defensive chemicals found in leaves; allows use of unrelated hostplants • Caterpillars cryptic and nocturnal, may hide or burrow in flower heads • Caterpillars often ant-tended |
| Insectivorous | <ul style="list-style-type: none"> • Harvester caterpillars eat Woolly Aphids; some blues eat ant larvae • Available nutrition from insect protein is relatively high • Cycle time short; from egg to adult just 3 weeks in Harvester • Adult Harvesters feed on “honeydew” secreted by aphids |
| Roots | <ul style="list-style-type: none"> • Hostplant for two giant-skipper species only • Yucca root is a rich food supply for burrowing caterpillars • But highly difficult to digest • Slow larval development, food energy stored as fat • Concealed lifestyle limits exposure to predation • Adults do not feed |
| Toxic Plants | <ul style="list-style-type: none"> • Some species sequester noxious chemicals ingested by caterpillars, rendering them unpalatable. • Bright, aposematic colors deter predators • This strategy can overlap with others above; much remains to be learned about the use of plant toxins by butterflies |

cinquefoils), but all contain a specific flavonoid that stimulates egg-laying in the female (Douglas, 1989, pp. 178–79). In such cases, defensive chemical considerations in host-plant selection may outweigh nutritional ones.

USING HOSTPLANTS TO LOCATE BUTTERFLIES

In locating butterflies, we have noted the importance of hostplant associations. Equally important, however, is the recognition that hostplants *themselves* have specialized ranges, often local and patchy. In some cases, hostplants are a strong and immediate indicator of a butterfly's likely presence, making it worthwhile to begin searching whenever the plant is found, even if no local colony is known. For example, Coinvine (*Dalbergia ecastophyllum*) is tightly associated with Statiras in southern Florida, Dutchman's Pipes (*Aristolochia*) with *Battus* swallowtails (Pipevine and Polydamas), and hackberries (*Celtis*) with American Snout and emperors.

This approach is heartening when it succeeds. On a birding "big day" in 1995, the first author paused to inspect a patch of Wild Indigo (*Baptisia tinctoria*) in a pinewoods clearing in southern New Jersey, and was excited to find a previously unknown colony of Frosted Elfins. (His birding companions, more impatient than enthused, were puzzled at this sudden loss of focus on warbler chirps.) Elsewhere, in an awe-inspiring display of serendipity, West Virginia state biologist Tom Allen happened to notice some tiny, near-invisible eggs on the underside of Dwarf Cinquefoil (*Potentilla canadensis*) leaves while doing fieldwork in the late 1990s. Returning the next April, he was rewarded with a colony of Appalachian Grizzled Skippers, among the rarest of East Coast butterflies.

Associations between butterflies and hostplants are not always obvious in the field, although with practice many subtle links will become apparent. Zebra Swallowtails, for instance, range widely in their habitats, seldom lingering in the immediate vicinity of pawpaws, except when ovipositing. Yet it is rare to see the swallowtail more than a few hundred yards from some pawpaw species. When everyday butterfly walks are redefined to include routine observation of local flora (including potential hostplants), new vistas materialize.

Changes in butterfly distribution can sometimes be linked to shifts in hostplant use. This is not especially common, since the ranges of most hostplants are well-established and a majority of hostplant-butterfly associations date back many millennia. But abrupt shifts do occur, often in connection with introduced plant species. In recent decades, Wild Indigo Duskywings have "jumped" from Wild Indigo (*Baptisia tinctoria*)

to Crown Vetch (*Coronilla varia*), an invasive member of the pea family that is widely planted on interstate right-of-ways to control erosion. Likewise, it has been suggested that the range of Hayhurst's Scallopwing extended north from its original boundaries because of Lamb's Quarters (*Chenopodium album*), an alien weed whose range exceeds those of the Hayhurst's native hosts (Opler & Krizek, 1984).

Not all exploitations of non-native hostplants lead to range expansion, however. In one of nature's more perverse gambits, some introduced hostplants are (1) attractive to native species, yet (2) fatally toxic to their caterpillars (e.g., Chew, 1975). The rapid decline of West Virginia Whites in the northeastern United States in recent decades has been linked to a fatal attraction on the part of female whites to chemical markers in the highly invasive European weed, Garlic Mustard (*Alliaria petiolata*).²

Occasionally, hostplant analysis provides unexpected insights into butterfly ecology. In conducting their classic studies of the Edith's Checkerspots in California, Paul Ehrlich and his students made a curious observation: checkerspot colonies at the Jasper Ridge site, near Stanford, were found only on serpentine soil, even though the primary hostplant (*Plantago erecta*) also grew on sandstone-based soils nearby. Subsequent research found that many caterpillars starve in dry years, when *Plantago* dries out before caterpillars finish feeding (Singer, 1972; Douglas, 1989, p. 102). In these years, populations survived by using a backup hostplant, Owl's Clover (*Orthocarpus densiflorus*). It so happens that Owl's Clover lives only on serpentine soils, explaining the checkerspots' limited distribution. Similar discoveries undoubtedly can be made regarding East Coast species.

But before striding into the field, flush with newfound confidence, we must acknowledge that using hostplants to locate butterflies is not always easy. Sometimes the hostplant is difficult to locate, such as Virginia Snakeroot (*Aristolochia serentaria*), a widely distributed but elusive native hostplant of Pipevine Swallowtails, or various northern currants (*Ribes* spp.), hostplants for the northern Gray and Hoary commas.

At other times, a hostplant is too common to be of much use in narrowing our search. This is especially likely with widespread trees and grasses. Or, a particular species may use a number of host species in a particular family (e.g., the Pea Family, Fabaceae), all of which may be found locally. Finally, there are cases in which the range of the hostplant extends well beyond that of the butterfly. Examples include Dusky Azure, 'Appalachian' Grizzled Skipper and Milbert's Tortoiseshell. Why this discrepancy should exist is a difficult question to be explored at another time.

² Garlic Mustard is toxic to caterpillars of both West Virginia and Mustard Whites, usually in the 1st or 2nd instar (Bowden, 1971). But one population of Mustard White (a species that eats Garlic Mustard in Europe) is apparently already becoming

acclimated to the new host (Courant et al., 1994). The ultimate fate of West Virginia White remains uncertain, but recent population declines are foreboding. See also Casagrande and Dacey, 2001 (Monarchs and Black Swallowwort).

We are far from having a complete understanding of all hostplant associations, even for East Coast butterflies, which are comparatively well-studied. Much information in the literature comes from informal trial-and-error testing, in which captive-reared caterpillars were offered a variety of different food plants. Such studies are most conclusive when a particular plant is firmly rejected, or when it is eaten but ends up being toxic. Otherwise, caution must be advised, since the number of plants accepted in captivity frequently exceeds the number chosen voluntarily in the wild (Scott, 1986, pp. 60–61).

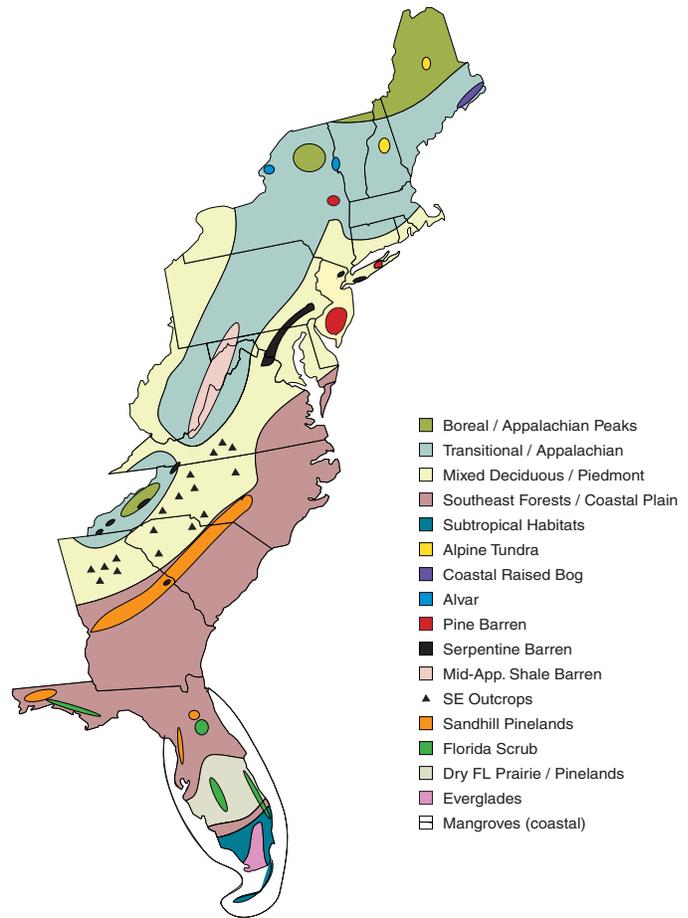
Opportunities abound for individual observers to make new discoveries. In the spring of 1999, for instance, natural history educator Alana Edwards noted that Gulf Fritillaries in a Lake Worth, Florida, nursery greatly preferred a native herb, *Piriqueta* (*Piriqueta caroliniana*), to nearby passionvines, the universally cited hostplant. An herbaceous member of the *Turnera* Family (*Turneraceae*), *Piriqueta* is closely related to passionvines (*Passifloraceae*). And, like passionvines, *Turneras* contain cyanogenic glucosides (Olafsdottir et al., 1990). Edwards suspects that use of *Piriqueta* is related to their dense arrangement in nursery beds (vs. a widely dispersed growth pattern in the field), and possibly to the fact that the female did not detect hostile ants on the *Piriqueta*, which can deter ovipositing on the passionvines.

HABITATS

No one doubts the importance of habitat in determining where butterflies live. But apart from being a nursery for specific hostplants, what *direct* role does habitat play in defining butterfly ranges? Quite a significant one, actually. To begin with, habitats are shaped by major *physical* and *climate factors*, such as susceptibility to recurrent storms and flooding, local patterns of seasonal rainfall and temperature fluctuations (including the length of the flight season), susceptibility to fire, proximity to coastal salt spray or tidal inundation, specialized soil composition, and so forth.

A long and bewildering list of *ecological factors* also play a role, including habitat density and patchiness; availability of patrol corridors or hilltopping sites; availability of hostplants; availability of adult food sources; proximity of adult food to hostplants—and of both to shelter; availability of damp soil for puddling; habitat color (relative to camouflage strategy); density and variety of local predators and parasitoids; incidence of lepidopteran diseases (viral, bacterial, and fungal); availability of protected overwintering spots; availability of protected surfaces for pupation; presence of attending ant species for those species requiring it, etc.

Just how specialized habitat requirements can be is apparent from the findings of Dave Norris's prodigious work on Northern Metalmarks. A Connecticut field biologist,



Norris began to locate metalmark colonies in 1989. Initially, he would overlay geological survey maps (which show surface topography) with USDA soil maps, in order to locate calcareous outcrops. After screening more than 500 potential sites with off-season visits, and later with in-season fieldwork, he determined that the presence of open cedar woods was a key indicator of potential metalmark habitat. But even sites with suitable hostplants and topography were not used if the nearest suitable nectar source (normally Butterflyweed or Black-eyed Susan) was more than 50 meters away. Indeed, adults rarely stray more than 40 to 50 meters from either hostplant or nectar locations. Over more than a decade of work, Norris has found and monitored 30 previously unknown metalmark colonies in the Connecticut-New York-New Jersey area.

SPECIFIC EAST COAST BUTTERFLY HABITATS

Low-Growth Habitats: Transition and Disturbed

Although definitive statistics are not available, it is reasonable to suggest that people most frequently see butterflies in *disturbed* or *transitional habitats*. This is where most people occur, for one thing, but in addition more than 90% of East Coast butterfly species use a “disrupted” habitat during some portion of their life cycle.

(continued)