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Natural and Cultural History of the Golfo Dulce Region, Costa Rica

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Due to the orographic formation of its interior and its humid climate, the Golfo Dulce Region is rich with biodiversity, containing very dense flora and fauna. After HOLDRIDGE (1971), the region was subdivided into different zones, including the tropical rainforest, the tropical wetland forest, and tropical premontane rainforest. The biogeographical situation in this area shows many similarities to the flora and fauna in the Amazon and the Colombian Chocó Region and serves as a land bridge with a valuable genetic base between North and South America. After unregulated seizure of land by agricultural settlers, lumberjacks, and large landowners in the 1940s and 1950s, regulated, state-subsidised settlement reform intended to support agricultural exports in the 1960s, and intensification of the livestock industry in the 1970s, primary and secondary forest reserves have shrunk to a minimum. The constant expansion of monocultures on new land has far-reaching consequences for the local ecosystem.

The conservation and sustainable use of tropical forests is established in the Forest Declaration, Convention on Climate Protection, and Convention on the Protection of Species, which demonstrate worldwide concern for these issues. As a regional example, in the 4,304.80 km^2 drainage basin, the ACOSA (Área de Conservación OSA), which covers an area spanning the Cantons Osa, Golfito und Corredores, aims to protect species diversity within the 17 game preserves, which are 44.7% covered by forest, through integration and an alliance with the Parques Nacionales, Vida Silvestres y Forestales (Fig. 2). The main sector of the Corcovado National Park on the Osa Peninsula covers 424 km^2 and the Piedras Blancas National Park covers 148 km^2. The altitude ranges from sea level to 745 m on the Osa Peninsula (Cerro Rincón and Cerro Mueller in the Fila Matajambre) and to 579 m in the Esquinas forest (Cerro Nicuesa). The Golfo Dulce Forest Reserve (592 km^2) was established between the two parks, thereby forming a natural forest corridor.

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Diversity, biogeography and ecology of insects in the Pacific lowlands of Costa Rica with emphasis on La Gamba

Diversidad, biogeografía y ecología de los insectos en las tierras bajas del Pacífico de Costa Rica con énfasis en La Gamba

Christian H. SCHULZE

Abstract: The paper provides some general information on the diversity, biogeography and ecology of insects in the Pacific lowlands of Costa Rica with emphasis on the area of the "Tropenstation La Gamba". It is stressed that intensive collecting and standardised sampling of insects is urgently needed to improve our knowledge of the fauna of La Gamba. So far, preliminary checklists for the area are only available for butterflies and dragonflies. The poor knowledge of the local fauna also limits biogeographical interpretations. Available information on the seasonality of insect communities, important feeding modes of insects (such as dung and carrion feeders, herbivores, pollinators and leaf-cutter ants), the predominant importance of ants (particularly army ants) as predators and ant-plant mutualisms are briefly summarised. Finally, some insect conservation issues are stressed.

Key words: insects, diversity, biogeography, vertical stratification, tropic guilds, feeding modes, coprophagous insects, carrion feeders, herbivores, leaf-cutter ants, army ants, ant-plant mutualism, conservation, Costa Rica, Pacific lowland rainforest.

Resumen: El artículo proporciona información general sobre la diversidad, biogeografía y ecología de los insectos en las tierras bajas del Pacífico de Costa Rica con énfasis en el área de la "Estación Tropical La Gamba". Se hace hincapié en la urgente necesidad de una recolección intensiva y de un muestreo estandarizado de insectos, para mejorar nuestro conocimiento sobre la fauna de La Gamba. Hasta el momento, listas de cotejo preliminares para la zona sólo están disponibles para las mariposas y libélulas. El escaso conocimiento de la fauna local también limita las interpretaciones biogeográficas. Se resume la información disponible sobre la estacionalidad de las comunidades de insectos, los modos más importantes de alimentación de los insectos (comedores de estiercol y carroña, herbívoros, polinizadores y hormigas cortadoras de hojas), la significativa importancia de las hormigas (en particular las hormigas soldado) como depredadores y el mutualismo hormiga-planta. Por último, se destacan algunos temas relacionados con la conservación de insectos.

Palabras clave: insectos, diversidad, biogeografía, estratificación vertical, gremios tropicales, modos de alimentación, insectos coprófagos, comedores de carroña, herbívoros, hormigas cortadoras de hojas, hormigas soldado, mutualismo hormiga-planta, conservación, Costa Rica, bosque lluvioso de las tierras bajas del Pacífico.

Insect diversity and biogeography

Insects represent the most diverse invertebrate taxon with c. 950.000 described species so far (GROOMBRIDGE 1992) and an estimated global number of more than 5 million species (ØDEGAARD 2000). As in the majority of other taxonomic groups, the highest insect species richness can be found in tropical regions (GROOMBRIDGE 1992), particularly regions covered by tropical rainforest. Unfortunately, for all highly diverse insect groups no species inventories are available for the area around La Gamba and the adjacent Esquinas forest. Very preliminary checklists are now available at least for butterflies (WIEMERS & FIEDLER, this volume) and dragonflies (HOFHANSL & SCHNEEWEIHS, this volume) for the vicinity of the Tropical Research Station La Gamba.

That the region is largely unexplored by entomologists is also demonstrated by a literature search carried out by the author, which showed that almost no insect material from this part of Costa Rica was included in recent revisions of Central American insect taxa or descriptions of new species discovered in Costa Rica. The "Tropenstation La Gamba" offers an ideal base for collecting activities aiming to achieve a better coverage of the regional insect species inventory. However, this

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Fig. 1: *Historis odius*, a common nymphalid butterfly frequently seen at the Tropical Research Station La Gamba feeding on rotting fruits at the Tropical Research Station La Gamba (Photo: C.H. Schulze).

goal can be only achieved through intensive national and international collaborations.

In Corcovado National Park with a size of 36.000 ha at least 220 butterfly species excluding skippers (Hesperiidae), hairstreaks (Lycaenidae) and metal marks (Riodinidae) were recorded by DeVries (1983) (see also DeVries 1978). A similar number of 150-200 species can be expected for the area in the vicinity of the "Tropenstation La Gamba", representing about one quarter of the total number of butterfly species recorded from Costa Rica (Wiemers & Fiedler, this volume). The total of 32 dragonfly species was recorded at La Gamba by Hofhansl & Schneeweihs (this volume). Estimates based on their data predict a maximum of slightly more than 50 dragonfly species for the area, which would represent less than 20% of Costa Rica's ca. 300 Odonata species (Esquivel 2006). However, the dragonfly survey by Hofhansl & Schneeweihs only covered the dry period, thereby most likely underestimating the total species richness of the region. Furthermore, they might have missed some species which might spend a substantial amount of their time hunting for prey in the canopy.

Many insects show a prominent vertical stratification inside the forest. Lowland forests such as at La Gamba are particularly characterised by a distinct vertical stratification. Light regime, microclimate and vegetation structure differ significantly between the forest canopy and the dark understorey, which is reflected in changes of insect species richness and composition between vegetation layers as reported from Costa Rican rainforests (e.g. DeVries 1988, Brehm 2007) and other tropical regions (e.g. Schulze et al. 2001). The availability of adult and larval resources can be an important factor shaping the vertical stratification of insects (Brehm 2007, Schulze et al. 2001).

Our poor knowledge on the insect fauna of La Gamba limits any biogeographical interpretations. The insect fauna of Costa Rica represents a bridge between faunas of Central and South America as emphasised by DeVries (1987) for butterflies. The fauna of the Pacific slope is increasingly characterised by South American taxa towards the south. However, until more complete species inventories of selected insect groups are available for La Gamba, its biogeographical linkage with neighbouring regions to the north and south cannot be explored further.

Seasonality of insects

According to Janzen (1983a) diurnal insect activity in Costa Rican rainforests, quantified by adults present on the vegetation, reaches its annual low in the rainy season during September-November, while the annual high seems to be February-March. In sweep samples of rainforest edges and understorey on the Osa Peninsula, foliage inhabiting insects seemed to have their highest density and species richness during the dry season (Janzen 1973).

In Corcovado, new foliage acquires most of its annual damage in late March and April, which is perhaps related to a peak in moth caterpillar density (Janzen 1983a). The phenology of many species may depend on seasonal changes of food availability, e. g plant characteristic periods of flowering, fruiting and the production of leaf flushes. In Corcovado National Park the rainy season winds generate numerous large tree falls between May and August. Janzen (1983a) suspect that this could be a peak oviposition time for wood boring insects (e.g. beetles of the families Scolytidae, Cerambycidae and Buprestidae). Not only terrestrial insects but also aquatic species assemblages may show a strong seasonality. During the rainy season, small puddles on the forest floor, in leaf bracts and in tree cavities contain many aquatic insects (Janzen 1983a). Many of these small and only temporarily available water bodies dry up in the dry season. Some species may highly adapted to these ephemeral habitats such as a dragonfly species observed by Janzen (1983a), whose larvae can move on the forest floor to search for remaining pondlets after the initially colonised body of water has dried out.

Although studies on seasonal changes of insect species richness and abundance are not available from La Gamba, I except similar patterns to those found in Corcovado National Park by JANZEN (1983a). Many insect species occurring in La Gamba are be present during the whole course of the year. However, seasonally induced abundance fluctuations may be of enormous ecological importance shaping reproduction cycles of animals such as insectivorous birds, which depends on insects as food source.

Ecology and feeding modes of insects

All major trophic guilds and feeding modes can be found in tropical insects and a variety of taxa are involved in important ecosystem processes such as the decomposition of dung, carrion and dead wood, contributing to nutrient cycling. Many tropical insects were have able to evolved a sometimes highly specialised feeding behaviour or frequently exploit resources only rarely used at higher latitudes, probably due to the high diversity of permanently available food resources. For example, the vast majority of temperate zone butterflies exclusively feed on flower nectar, while in tropical butterfly communities, a large proportion of species feed on rotting fruit (many Nymphalidae species; compare also WIEMERS & FIEDLER, this volume; Fig. 1) or visit other decaying organic matter such as animal carrions. Furthermore, large numbers of male butterflies sometimes gather at moist places where they take up minerals such as sodium, or nitrogenous compounds derived from decaying organic matter (e.g. BECK et al. 1999). Substances acquired through this "puddling" are transmitted to the female mate with the spermatophore (e.g. KARLSSON 1998).

The tropics are characterised by otherwise extremely unusual feeding associations such as the one between sloth moths (Lepidoptera: Pyralidae, Chrysauginae) and sloths. Sloth moths are placed in several genera (*Cryptoses*, *Bradypodicola*, *Bradypophila*), which are not monophyletic (SOLIS 2007). The adult moths spend their lives in the fur of sloths. It has been suggested (WOLDA 1985) that there the sloth moths may receive some protection from avian predators and possibly find nutrients in secretions of the sloths' skin and/or the algae present on the fur. Some sloths may carry up to 120 moths (WAAGE & BEST 1985). Larval stages of the moths live in and feed on the sloths' dung. The female moths presumably leave the sloths during defecation to deposit their eggs on the dung. Newly emerged moths migrate to the forest canopy to locate a sloth.

The following paragraphs stress some selected feeding modes of tropical insects but do not aim to provide a comprehensive summary. Indeed, several functional groups such as parasitic insects are only briefly mentioned although they may play ecologically important roles, e.g. by controlling populations of insect pests of tropical cash crops.

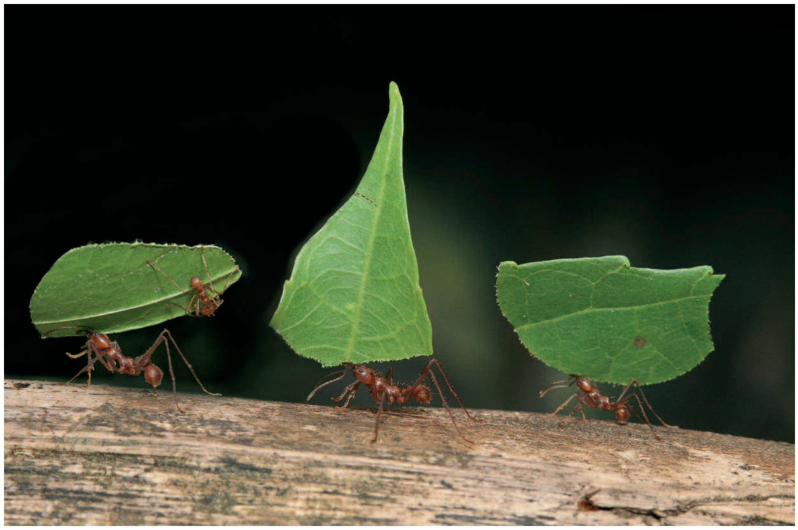

Fig. 2: Leaf-cutting ants of the genus *Atta* are commonly encountered in a large variety of habitats around La Gamba. Note the small "hitchhiker" ant riding on leaf (Photo: A. Schneider).

Carrion and dung feeders

Based on his experiences in Costa Rica, JANZEN (1983a) assumed that carrion feeding insects may be less important than in temperate habitats of the New World. He observed that any dead vertebrate of small size is found in daytime by a vulture or at night by an opossum or other scavenger and reduced to bones and a quantity of skin within 24 hours. When scavenging vertebrates were excluded from the carcass by cages, only a few flies appear, and the carcass was quickly covered by ants and ant tumulus (CORNABY 1974). Besides the fast exploitation of carcasses by vertebrate scavengers the subsequent monopolisation of the remaining parts by ants may be responsible for the low number of other insects which are able to exploit this food source.

Except for some observations published on dung beetles from Corcovado National Park by JANZEN (1983a), I am not aware of any study on coprophagous insects from the southern Pacific lowlands of Costa Rica. The standardised sampling of scarab dung beetles using baited pitfall traps (e.g. HARVEY et al. 2006, SHAHABUDDIN et al. 2005) at La Gamba would, in particular, be most welcome to complete our picture on resource use and habitat specificity of Central American dung beetles.

Fig. 3: The hawkmoth *Eumorpha megaeacus* (Hübner, [1819]) resting on a leaf; wing coloration and shape imitate a dead leaf (Photo: P. Weish).

Herbivorous insects

The largest proportion of insect species feed on different parts of plants either externally or internally. The predominant majority of insects with an ectophagous feeding mode are represented by folivorous larvae of the order Lepidoptera and by leaf chewing beetles (e.g. family Chrysomelidae). Endophagous herbivores include leaf miners (e.g. many Microlepidoptera), seed predators (e.g. beetles of the family Bruchidae, pyralid moths), as well as fruit, root, stem and branch borers (e.g. larvae of various moth species and beetles of the families Cerambycidae, Buprestidae and Scolytidae). Many examples on host plant specificity of Costa Rican insects are provided in Janzen (1983b).

Leaf cutter ants

One of the most prominent insects encountered at La Gamba are leaf cutting ants of the genus *Atta* carrying pieces of fresh leaves from their feeding sites to their nests (Fig. 2). The underground nests of the leaf cutter ant *Atta cephalotes* (Linnaeus, 1758) can contain up to five million workers, ranging from very small (2 mm in length) to media workers (ca. 10 mm) and large soldiers (up to 20 mm). Most of the leaf collecting is done by the media workers (Stevens 1983). Leaf cutting ants grow a fungus on the leaf material, from which they collect the swollen tips of the hyphae (gongylidia) as food (e.g. Hölldobler & Wilson 1990). Mature colonies may have several hundred of these fungus gardens which are interconnected by a complex network of tunnels (Stevens 1983).

A curious behaviour in leaf cutting ants of the genus *Atta*, which can be also frequently observed at La Gamba, is the "hitchhiking" of small minim workers on leaf fragments carried by larger workers (Fig. 2). One important function of this behaviour may be the defence of leaf carriers against parasitic flies of the family Phoridae. The females of phorid flies attack leaf carriers and deposit eggs on their head capsules. It appears that the parasitic flies require leaf fragments to stand on during oviposition. Therefore, only leaf carriers are attacked by flies. The presence of hitchhikers reduces both the time parasites spend on leaf fragments and the probability that they will land in the first place (Feener & Moos 1990). Other functions of hitchhikers may be the preparation of the leaf fragment before it enters the nest (Linksvayer et al. 2002).

Adult *Atta* colonies contribute to the nutrient cycling in terrestrial habitats in the neotropics (Logu et al. 1973) and may have significant effects on the structure and/or composition of tropical forests (Farji-Brener & Medina 2000). While the activity of leaf cutting ants around their nests create gaps in the plant understorey, the nests and their surroundings serve as centres of recruitment for small plants after they are abandoned. Thus, like canopy gaps, ant nests could play an important role in the recruitment of new individuals and the maintenance of plant species diversity in tropical forests (Garrettson et al. 1998).

Insects as pollinators

The vast majority of Costa Rican higher plants (excluding most grasses and sedges) are pollinated by insects, although reproductive individuals are often hundreds of metres apart. Beside thousands of small, mostly short distance pollinators such as flies, small moths, small beetles, and solitary and social wasps and butterflies, large bees and hawkmoths (Sphingidae) may represent the most important long distance pollinators potentially carrying pollen over kilometres (Janzen 1983a).

Many flowers have a long tongue and are very visible at night due to their white color (Janzen 1983a). Such flowers are often pollinated by hawkmoths (Fig. 3) capable of reaching the offered nectar with their long proboscis. Large bees are another conspicuous element of the pollinators in Costa Rica which forage for nectar and pollen in all vegetation layers of the forest, including large carpenter bees of the genus *Xylocopa* (Janzen 1983a), which can also frequently be observed at La Gamba. Many insect pollinators appear to be rather opportunistic visiting a large variety of different flowers such as stingless bees (tribe Meliponini within the family Apidae; Michener 2000). Although stingless bees certainly play an important ecological role as pollinators, Costa Rican species are true generalists with regard to selection of both nest sites and flowers (e.g. ROUBIK 1989, SLAA 2003). A stingless bee species can visit flowers of up to 100 plant species within the course of one year (HEITHAUS 1979).

One of the most specific tropical insect-plant pollination systems is the interaction between fig wasps (Agaonidae) and figs (*Ficus*). Most species of figs have their own species of pollinating fig wasps. Once the small green figs are developed thousands of fig wasps are attracted to the tree. Females enter the young fig through a hole (ostiole) and pollinates receptive stigmata located in the inner lacuna of the fig. The females oviposit down the styles and die after oviposition. Wingless male wasps emerge from their ovarian containers, when the fig seeds reach their full size. The males locate females in floret bases, cut into the cavity, insert their abdomen to copulate, and then aid the females in leaving the florets (JANZEN 1983a). Females then fill their pollen pockets at the newly opened anthers and leave the fig through exit holes cut in the wall of the still unripe fig by the males. Females then search for another fig which is in a receptive state (JANZEN 1983a).

The importance of ants in tropical ecosystems

In Costa Rican lowland rainforests, as in other tropical areas, ants probably represent the most important insect group with respect to biomass. It has been suggested to one third of the entire biomass in lowland rainforests is composed of ants and termites (HÖLLDOBLER & WILSON 1990). In the neotropics, these two groups, along with bees and wasps can make up more than 75% of the total insect biomass (BECK 1971, FITTKAU & KLINGE 1973).

As emphasised by HÖLLDOBLER & WILSON (1990), "ants and termites are the superpowers of the insect world". Ants, being predominantly predators, are correspondingly the greatest enemies of termites and both occasionally compete for nesting sites in rotting wood and leaf litter (HÖLLDOBLER & WILSON 1990). Ants represent the most important arthropod predators in tropical lowland habitats and army ants in particular have long been a prime target for study by naturalists (HÖLLDOBLER & WILSON 1990). The species *Eciton burchelli* (WESTWOOD, 1842) (Fig. 4) is one of the best studied army ants. During the night, colonies of *E. burchelli* are in "bivouac", meaning temporarily camped in a more or less exposed position, usually between buttresses of forest trees, beneath fallen tree trunks or at any sheltered spot along the trunks and main branches of trees. The bivouac is created by the bodies of the workers and consists of between 150.000 and 700.000 workers (HÖLLDOBLER & WILSON 1990). Thousands of immature forms and a single mother queen are located in the centre of this ant conglomerate. After dawn the bivouac begins to dissolve and a raiding column emerges and grows away from the bivouac with a speed of 20 metres per hour (HÖLLDOBLER & WILSON 1990). While the workers race along chemical trails, the larger soldiers follow on either side of the column. The soldiers, with their large heads and long, sickle shaped mandibles (Fig. 4) serve almost exclusively as a defence force (HÖLLDOBLER & WILSON 1990). *E. burchelli* is a "swarm raider", meaning that for-

Fig. 4: Foraging army ants (*Eciton burchellii*) with large soldiers characterized by their sickle-shaped mandibles and smaller workers (Photo: W. Huber).

Fig. 5: Workers of an *Azteca* ant species at the entrance hole leading to a nest cavity inside the hollow internode of a *Cecropia* plant (Photo: W. Huber).

aging workers spread out into a fan shaped swarm. These swarms kill any animal life on their path, which fails to escape, including large spiders, scorpions, and insects, and even snakes, lizards and nestling birds (HÖLLDOBLER & WILSON 1990).

Ant plant mutualism

Ant plant mutualisms are a common phenomenon in tropical regions and are also frequently observed at La Gamba (BURGER 2003). The strongest evidence for ant plant mutualism comes from the existence of domatia or other plant structures that serve no evident purpose other than to shelter ant colonies (HÖLLDOBLER & WILSON 1990). The association between *Azteca* ants (subfamily Dolichoderinae) and *Cecropia* trees represents the most conspicuous ant plant mutualism in the neotropics (HÖLLDOBLER & WILSON 1990, LONGINO 1989, SCHUPP 1986).

Azteca colonies nest inside hollow nodes developed by the *Cecropia* trees (Fig. 5). *Cecropia* trees produce glycogen-containing food bodies, which may contain carbohydrates, lipids, and proteins (e.g. AGRAWAL & DUBIN-THALER 1999, O'DOWD 1982, RICKSON 1973). *Azteca* ants consume the food bodies, patrol the plant and, in many cases, successfully reduce herbivory and increase the fitness of plants relative to conspecifics without ant protectors (ROCHA & BERGALLO 1992, SCHUPP 1986, VASCONCELOS & CASIMIRO 1997). SCHUPP (1986) demonstrated that *Cecropia* trees grow more vigorously when occupied by *Azteca* ants than when the ants have been removed. Thus, the interaction is directly beneficial to *Cecropia* trees. In addition to reducing herbivory, *Azteca* efficiently remove vines from occupied juvenile trees (SCHUPP 1986).

Several studies on ant plant mutalism have been conducted at La Gamba, particularly on the interaction between plants of the genus *Piper* (Piperaceae) and ants of the genus *Pheidole*. These studies emphasised the importance of food bodies provided by *Piper* plants as a high-energy food source, with a chemical composition that matches the nutritional needs of the plant-inhabiting *Pheidole* ants (FISCHER et al. 2002). Furthermore, a study on this ant-plant mutualism from La Gamba was the first to prove unequivocally that ants provide nutrients to ground rooted understorey myrmecophytes. FISCHER et al. (2003) showed that the studied *Piper* species was able to take up ant derived nitrogen.

Insect conservation

A substantial number of insect species depending on forest habitats frequently visit adjacent countryside habitats. For example, as mentioned by JANZEN (1983a) for some forest butterflies at Corcovado National Park several species of butterflies at La Gamba also frequently visit *Lantana* and *Stachytharpeta* flowers, which grow at pastures, roadsides and other succession sites adjacent to the forest margin, for nectar feeding. However, several of these butterfly species depend on larval foodplants predominantly restricted to the forest. Therefore, surveys assessing the conservation value of human dominated habitats (in the vicinity of remaining forest remnants) for forest insects might be extremely misleading when conclusions are only drawn from records of adult butterflies.

Butterflies with smaller distribution ranges appear to be less able to make use of human-modified environments in Costa Rica (HORNER-DEVINE et al. 2003, THOMAS 1991). In contrast, species with a wide distribution are often able to colonise a wide range of different human-dominated habitats, such as the fruit feeding nymphalid *Historis odius* (FABRICIUS, 1775) (Fig. 1). Its distribution ranges from the southern United States to South America. In Costa Rica it occurs in the forest canopy as well as near human habitations, where the adults feed on rubbish (DEVRIES 1987 and own observations).

The restriction of the vast majority of endemic butterflies to the wet lowlands of Costa Rica to pristine forest habitats clearly indicates that deforestation represents a major threat for insect diversity (THOMAS 1991). The countryside at La Gamba characterised by natural forest, different types of secondary forests, agroforestry systems, and annual cultures offers many possibilities for studying the effects of forest conversion and modification on insect diversity. Initial data on butterflies (WIEMERS & FIELDER, this volume) and dragonflies (HOFHANSL & SCHNEEWEIHS, this volume) are published in subsequent sections of this book.

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