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From hunting for new species to studying ecosystem processes – advances in entomological canopy research

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Introduction

"*The last biotic frontier*" (ERWIN 1983)

The forest canopy is still one of the least understood ecosystems of the world. Although science has made great progress in biodiversity research during the last century, almost nothing has been known about invertebrate communities in the forest canopy up to the 1980s. At that time Erwin described the forest canopy as the last biotic frontier (ERWIN 1983).

Erwin's description was mainly based on the fact that suitable canopy access techniques were missing at that time. The first who reached the canopy of mature trees were adventurer who searched for a new thrill. Other scientists trained monkeys to take samples in the canopy (MITCHELL et al. 2002). The first safe canopy access techniques were developed at the beginning of the 1970s in old growth forests of the Pacific North West (DENISON 1973).

The initial spark for forest canopy research was the estimation of global biodiversity based on a study of canopy beetles in the tropical rainforest of Panama using canopy fogging[1] (ERWIN 1982). Making several assumptions on the proportion of specialists, the proportion of beetles among insects, the proportion of insects living in the canopy etc., ERWIN estimated the number of insect species living in the tropics to be between 30-100 million (ERWIN 1988). This estimate was two orders of magnitude higher than previous ones. This caused an exclamation of surprise around the world and increased public and scientific interest in the biodiversity of our planet (WILSON 1999). As a result, many canopy research projects have been initiated, leading to an exponential increase in publications within international journals on canopy insect communities (Fig. 1). Initial studies focused mainly on the tropics where many new species were expected to be discovered, which indeed was confirmed. In temperate regions, canopy studies increased

[1] Canopy fogging, also known as insecticide knockdown, is an effective method for quantitatively sampling arthropods in tree crowns. By use of a fogging machine (Swing-fog) an insecticide (mostly natural pyrethrum) is blown in the canopy using white oil as carrier substance. Natural pyrethrum is highly arthropod-specific and breaks down within a few hours in direct sunlight, leaving no toxic residues. It is harmless to vertebrates.

with a considerable time lag, mainly because researcher did not expect spectacular new findings. While in North America especially SCHOWALTER and colleagues promoted research on canopy arthropods as early as the 1980s (SCHOWALTER et al. 1981, SCHOWALTER & CROSSLEY 1983, SCHOWALTER 1989) and continued in the 1990s and 2000s, in Central Europe only a few studies were published before the turn of the millennium (SCHUBERT 1998, SCHUBERT & AMMER 1998) and most were not published in international journals (ENGEL 1941, STEPANOVICOVÁ 1972, FLOREN & SCHMIDL 1999).

During recent decades, studying forest canopies has become a burgeoning and exciting field of research and has therefore attracted an increasing number of scientists. This has resulted in numerous projects and publications, including several books (LOWMAN & NADKARNI 1996, STORK et al. 1997a, LINSENMAIR et al. 2001, MITCHELL et al. 2002, BASSET et al. 2003b, BASSET et al. 2003c, LOWMAN & RINKER 2004, FLOREN & SCHMIDL 2008). Moreover, non-profit organizations such as the International Canopy Network (ICAN, http://academic.evergreen.edu/projects/ican/ican/) and alliances such as the Global Canopy Program (GCP, http://www.globalcanopy.org/) have been established. Since 1994, five International Canopy Conferences have been held, giving an international scientific platform for canopy scientists.

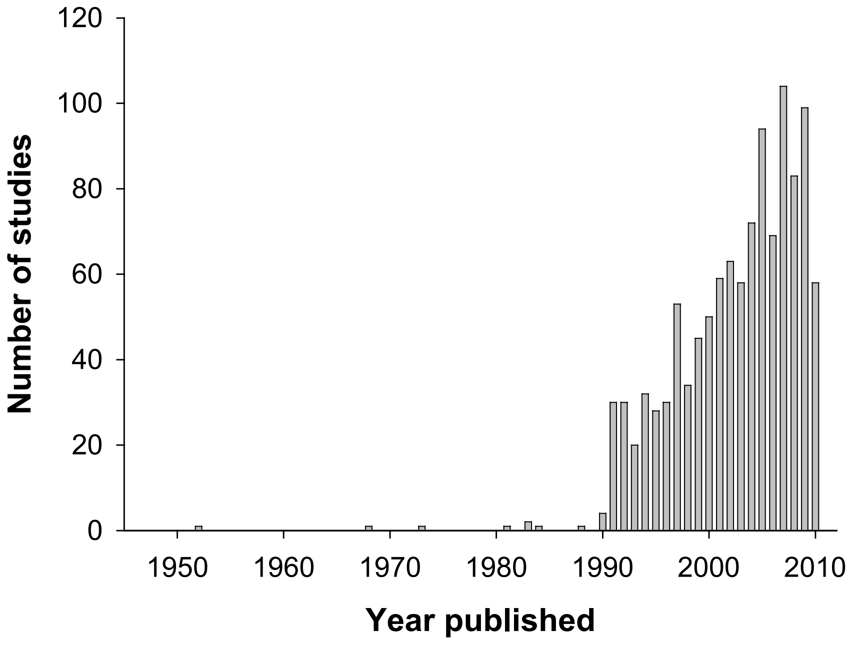

Fig. 1: The number of insect canopy studies published in international journals. Data from a Web of Science literature on the 6th of August 2010 (Topic=(forest canopy OR tree crown*) AND Topic=(insect* OR arthropod*)).

Advances in canopy access techniques

Since the first safe canopy access technique (DENISON 1973) a plethora of different methods for access and study of canopy arthropods have been developed (for reviews see e.g. MOFFETT & LOWMAN 1995, MITCHELL et al. 2002, BASSET et al. 2003d). Generally, ground based methods, such as canopy fogging, shooting down twigs or branches, shooting traps into the canopy or working with a telescopic rod, can be distinguished from canopy-based techniques where the canopy has to be accessed first. Before the late 1970s, the few researcher that accessed the canopy used ladders or installations of towers or canopy walkways. Later, climbing techniques were developed of which the single rope tree climbing (PERRY 1978) has become the one most commonly used (Fig. 2). More sophisticated technical methods have been developed during the last two decades. The first canopy crane was erected in a dry tropical forest in Panama in 1990 under the auspices of the Smithsonian Tropical Research Institute (STRI). Since that date, up to 12 crane sites have been established across the world, including six cranes in temperate forests and six in tropical forests that form the International Canopy Crane Network (STORK et al. 1997b, BASSET et al. 2003b, ROSLIN 2003; see Fig. 3). This network will be expanded by the Canopy Operation Permanent Access System (COPAS) in French Guiana, a fixed device consisting of an extendable number of towers that are arranged in a triangular system (CHARLES-DOMINIQUE et al. 2003). By the use of three guiding cables, and a helium balloon with gondola connected to a junction knot, the researcher will be able to reach almost all points within the system. Moreover, this system enables access to a much greater area and with less impact to the forest than is possible by cranes. Within the framework of the "Whole Forest Observatories", an international network for monitoring canopy biodiversity and global climate change, which was proposed by the Global Canopy Programme, additional canopy cranes are planned for installation in Ghana, Brazil, Malaysia, India and Madagascar (see http://www.globalcanopy.org).

Beside this permanent canopy access systems, scientists have used several more mobile systems such as the "Canopy Raft", the "Canopy Bubble", the "Canopy-Glider" and "IKOS house", which have been received high-public impact, promoting public interest in canopy ecology (see Fig. 2). For example, these systems were used in the large scale biodiversity initiative "Investigating the BIodiversity of Soil and Canopy Arthropods" (IBISCA), which started in Panama in 2003 and will be expanded to other parts of the world (BASSET et al. 2007).

New insights from canopy research

Forest ecosystems are three-dimensional and therefore the canopy cannot be neglected when focusing on either biodiversity or ecosystem functions. Many studies in the tropics (BASSET et al. 2003a, CHARLES & BASSET 2005, STORK & GRIMBACHER 2006) as well as in temperate forests (LINDO & WINCHESTER 2006, GRUPPE et al. 2008, GOSSNER 2009) have shown vertical stratification of forest insects. Although it is likely that not all species are necessary to maintain the functioning of forest ecosystems (TSCHARNTKE et al. 2005), many canopy species are involved in ecological processes such as herbivory, decomposition and nutrient cycling (LOWMAN & RINKER 2004). Thus, aboveground and belowground processes strongly interact, but the knowledge of the functional roles of arthropods in these bottom-up and top-down processes is still in its infancy (see HUNTER et al. 2003, REYNOLDS et al. 2003). While early canopy research focused mainly on biodiversity and description of new species to understand the value of the forest canopy habitats for insect species richness, it has increasingly turned to advanced functional approaches (e.g. WINCHESTER 1997, LOWMAN & MOFFETT 2003). This was primarily an outcome of advanced canopy access and study techniques. As soon as the importance of the forest canopy for ecological processes was recognized, newly established, large-scale functional biodiversity research projects have integrated the canopy as an important component for understanding ecological processes (see e.g. FISCHER et al. 2010).

How many species are there on earth?

Biodiversity is important for the maintenance of ecosystem function and provision of services (NAEEM et al. 2009). However, we still do not know how many species there are on earth. This crucial question was first posed by RAVEN (1985) and MAY (1988). Estimating the global biodiversity based on the studies of ERWIN in the tropical forest of Panama was the initial spark for canopy research as explained above. The publications of ERWIN began a large and controversial discussion about the number of species living on our planet. ERWIN (1982, 1988) estimated the total number of tropical arthropod species to be between 30 and 100 million based on samples of beetles from a single tree species (*Luehea seemanii*). He made a number of broad assumptions, some of them being highly criticized by other scientists, others being confirmed recently. 1) The assumption that at least twice as much species are living in the canopy compared to the forest floor has been challenged in recent decades based on new insights into soil processes (ANDRE et al. 1994, ANDRE et al. 2002). In response to ERWIN (1983), ANDRE et al. (1994) described the soil fauna as "the other last biotic frontier". 2) A second assumption is linked to the degree of effective specialization of herbivorous insects across all tree species. More recent studies suggest that host plant specificity in tropical herbivorous insects is much lower than assumed by ERWIN (1982) (see ODEGAARD et al. 2000, NOVOTNY et al. 2002), but the knowledge about host plant specificity is still unsatisfactory (NOVOTNY & BASSET 2005). 3) Further, ERWIN (1982, 1988) assumed the fraction of beetle species that are herbivorous to be high. This is also confirmed by more recent studies which have shown that more than 40% of global biodiversity is represented by plant-phytophage food webs (PRICE 2002). 4) The high estimated proportion of beetles in canopy communities has also been confirmed by many other studies. Beetles are provide important ecological functions and are the most species rich order, estimated to represent 25% of all species living on earth (ODEGAARD 2000, HUNT et al. 2007). HAMILTON et al. (2010) estimated that the percentage of beetles among canopy arthropods is between 25 and 66% and thus ERWIN's estimate of 40% is within this range. 5) Additionally, ERWIN (1982, 1988) assumed that most plant and arthropod species occur in the tropics. This is still unchallenged (MAY 2000) and therefore focusing on tropical systems for global species estimation is logical.

Fig. 2 a-h: Examples of canopy access and sampling techniques. The most common techniques of installing climbing ropes or trap fixations are: arrows (**a**) or crossbows (**c**). The single-rope climbing technique (**b**) is frequently used by canopy scientists. (**e**) Canopy fogging, a snap shot method, is mostly performed from the ground. In high trees such as this >50 meter high *Abies alba* in the Bavarian Forest National Park, climbing the tree is recommended for reaching the top parts of the tree crown. Trap systems such as branch traps (**d**) and composite flight-interception traps (**f**) enable continuous sampling over the whole period of leafing. More technical methods of canopy access include (**g**) Canopy Glider, (**i**) Canopy Bubble and (**j**) Canopy Raft. IKOS-house (**h**) is a mobile laboratory for canopy research. Photos: a, b, d, f: Klaus Deiters; c: Gerhard Heidorn; e: Heiner M.-Elsner; g: Maurice Leponce; i, j: Noui Baiben; h: Jérôme Orivel.


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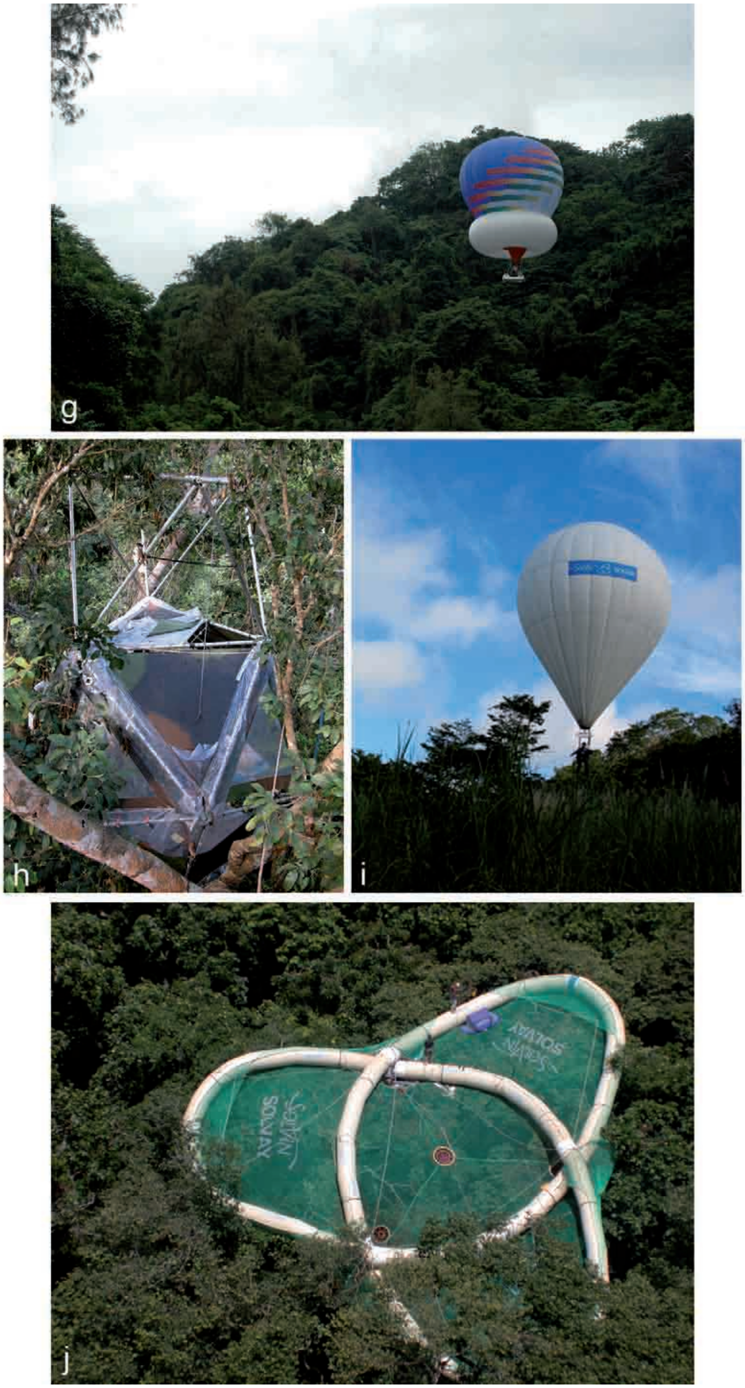
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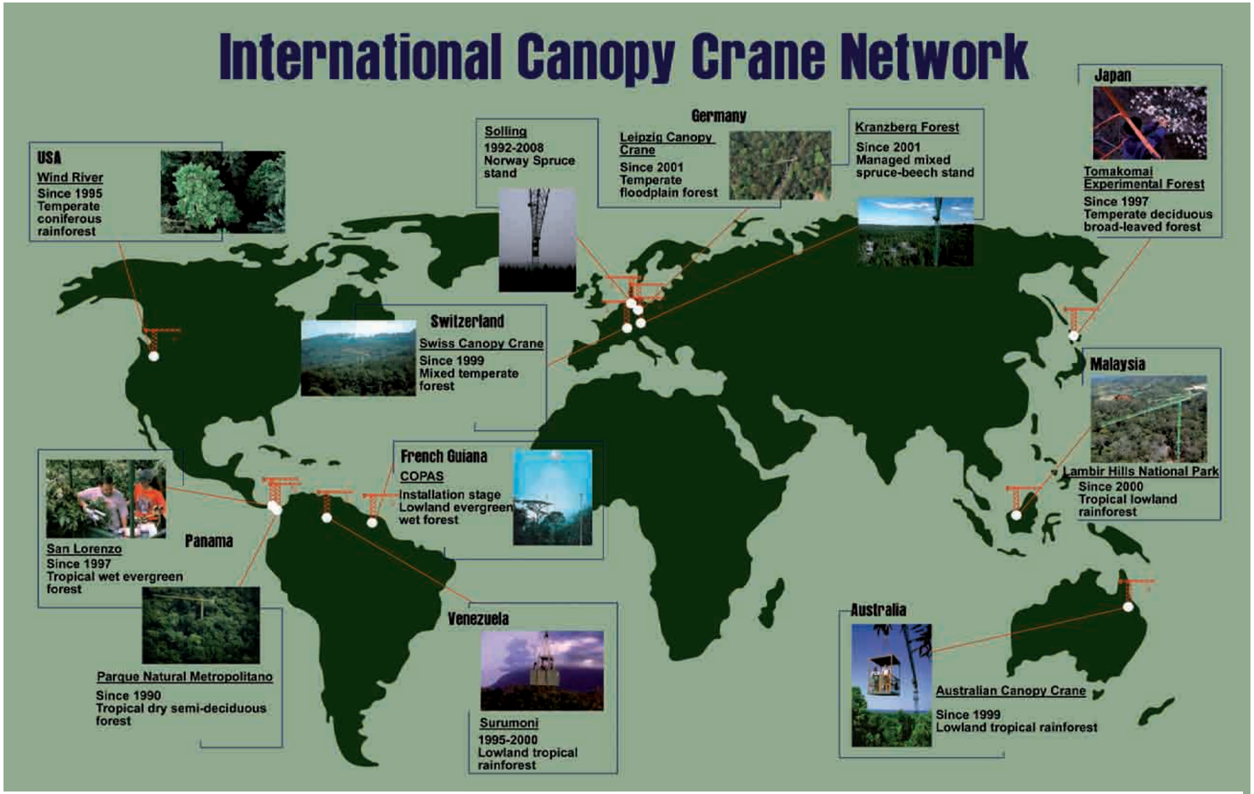

Fig. 3: Locations of the 12 crane sites scattered across the world, including six cranes in temperate forests and six in tropical forests. They form the International Canopy Crane Network. Within the framework of the "Whole Forest Observatories", an International Network for Monitoring Canopy Biodiversity and Global Climate Change, which was proposed by the Global Canopy Program, additional canopy cranes are planned for installation in Ghana, Brazil, Malaysia, India and Madagascar. © STRI, modified after the freely available map at: http://www.stri.org/english/ research/ facilities/terrestrial/cranes/canopy_crane_network.php

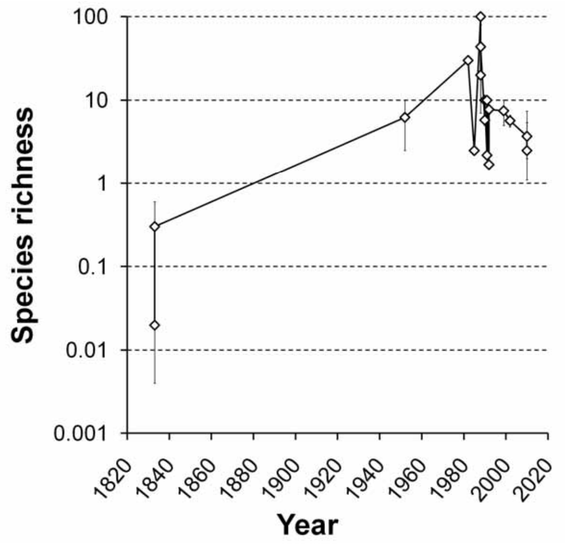

Fig. 4: History of global species richness estimation (log million), based on data given in ERWIN (2004) and supplemented by the results of the estimates of tropical biodiversity published by HAMILTON et al. (2010). Range or confidence intervals are given when available.

A few estimates of global biodiversity had already been performed prior to the publication of ERWIN (1982), but most of these were rather unscientific. These approaches were not testable (e.g. estimations of RAY and KIRBY, cited in WESTWOOD 1833) and prompted ERWIN (2004) to determine them as "divine insights", "guess-timates" and "anecdotes". Following ERWIN's (1982) estimation approach based on canopy samples, new estimates came out in quick succession, based on a variety of methods and models (see STORK 1993, ERWIN 2004; Fig. 4). Some approaches include estimations from known faunas and regions (e.g. SABROSKY 1952) and taxonomic expert opinion (GASTON 1991a, b), other models are based on body-size ratios (MAY 1988, 1990), taxon ratios (RAVEN 1985, STORK & GASTON 1990, HODKINSON & CASSON 1991) or herbivore-plant interactions (ODEGAARD 2000, NOVOTNY et al. 2002). The development of novel, sophisticated statistical estimation models and simulations can be seen as a major step forward towards narrowing the estimates of global biodiversity (MAY 2010). Most previous promising estimates such as those performed by ODEGAARD (2000) lacked an associated measure of variance. HAMILTON et al. (2010) incorporated uncertainty into Erwin's model parameter based on the most comprehensive tropical arthropod dataset available. Although this study revealed some drawbacks (e.g. models were based on plant-phytophage relationship only and did not account for probable host-plant change across the geographic range of the host), HAMILTON et al.'s (2010) estimates are the most reliable that exists today. These models predict medians of 3.7 million and 2.5 million tropical arthropods. Although 90% confidence intervals reach values up to 7.4 million species, these are far below the estimates of ERWIN (1982, 1988). Nevertheless, this suggests that approximately two-third of all arthropod species still await discovery and description. This implies that there remains a long way to reach the description of all species, given an estimated 1.6 to 1.7 million described species and 15,000 species described each year (MAY 2010).

Behavioural and faunistical highlights

Recent advances in canopy research have also revealed some amazing behavioral adaptations for living in the canopy. It is known that many species are restricted to the forest canopy, especially in the tropics. One might ask what happens if a species that has lost its flight ability, such as ants, fall down from a branch. Although they probably would survive the fall, they will land in a hazardous territory and climbing all the way up would be costly. Have these species evolved particular strategies to solve this problem? YANOVIAK et al. (2005, 2008, 2010) could impressively demonstrate that several neotropical as well as afrotropical arboreal ant species show directed aerial descent to return to their home tree trunk when falling down from a branch. These were the first studies to document such behaviour in insects. Previously, controlled descent was only known in non-flying arboreal vertebrates, to avoid predation or to locate resources.

Although most newly discovered species live in the tropics, some species are also discovered in temperate regions. Particularly in temperate rainforests, most new species are found by canopy studies. For example, approximately 60 new species were described on Vancouver Island within a few years (e.g. MARSHAL & WINCHESTER 1999, KLIMASZEWSKI et al. 2000). New species have also recently been described from the canopy of temperate forests of Central Europe. For example, DOCZKAL & DZIOCK (2004) discovered a new hoverfly species, *Brachyopa silviae* in Germany. This arboreal species is restricted to forest habitats which have a long tradition of old trees. Its larvae feed on bacteria and fungi growing in sap runs of old deciduous trees. Another Diptera from the genus *Oedalea* was discovered by STARK (2008) in samples obtained from canopy fogging in Germany, Slovenia and Romania. KÖHLER et al. (2009) found a hitherto undescribed cockroach species, from the genus *Ectobius* in tree crowns of larch. A few other specimens were found in crowns of spruce and oak in Germany and by light-trapping and branch-beating in Austria and Switzerland (unpubl. data). Although the number of newly discovered species based on canopy research is rather low compared to the tropics, canopy studies in Central Europe have revealed high abundance of several species that were assumed to be rare. One reason is the fact that canopies provide several habitats such as sun-exposed dead wood branches, mistletoes, epiphytes, rotholes and phytotelmata that provide habitats for specialized species.

Ecological theory

Canopy studies can also contribute to an advanced understanding of basic ecological theory such as metacommunity theory, and processes such as food-web dynamics and the role of phylogenetic relatedness of trees for colonization by arthropods.

Natural microcosms, which are small contained ecological systems, are a suitable tool for testing metacommunity[2] theory (LEIBOLD et al. 2004, SRIVASTAVA et al. 2004) and food-web dynamics (KITCHING 2001), because they are often embedded in a hierarchical spatial structure and are easy to manipulate. In tree crowns phytotelmata[3], water filled tree holes or bromeliads, are such microcosms. They are small aquatic habitats within terres-

[2] a set of local communities that are linked by dispersal of multiple interacting species
[3] a contained aquatic habitat formed naturally by a plant and populated by aquatic organisms.

trial ecosystems containing species-poor but individual-rich communities of arthropod larvae with simple food web structures. Microcosms, due to their small habitat size, are highly replicable and allow sufficient statistical power. Most models of metacommunity dymamics are based on three hierarchical levels (LEIBOLD et al. 2004), which might be highly applicable to phytotelmata because of its discrete boundaries: microsites within a phytotelm hold one individual, microsites are nested within localities that hold local communities (i.e. one phytotelm), and local communities are connected to each other as part of a metacommunity. Species composition in phytotelmata might be highly regulated by spatial dynamics such as dispersal (HARRISON & TAYLOR 1997), and evidence for this is provided by PARADISE et al. (2008) in a study of tree hole communities in North America.

SOUTHWOOD & KENNEDY (1983) have shown that single tree crowns can also be seen as habitat islands within a matrix that is more or less suitable for particular arthropod species. Besides species interactions, communities might also be influenced by spatial dynamics such as dispersal. In a study of Heteroptera and Coleoptera communities on oaks MÜLLER & GOSSNER (2007) showed that the proportion of herbivorous oak specialists increased significantly with increasing numbers of adjacent oak trees. This indicates that larger habitat patches within a closed forest canopy matrix support larger populations of herbivorous oak specialists. Not only the size of host tree patches but also the relatedness of the surrounding trees seems to affect insect communities. VIALATTE et al. (2010) demonstrated that the assembly of communities on hosts separated from their neighbours by long periods of evolutionary history is qualitatively and quantitatively different from that on hosts surrounded by closely related trees. Moreover, phylogeny plays an important role in the colonization of exotic species introduced from other parts of the world. A study by GOSSNER et al. (2009) on arthropod assemblages in tree crowns of exotic and native trees in Southern Germany revealed phylogenetic conservatism to be important in explaining colonization of exotic tree species by native insects.

Canopy insects and ecosystem processes

Forest canopy plays a key role in ecosystem processes. The major ecological functions and processes in the canopy are phyotosynthesis, nutrient and biogeochemical cycling, control of regional and global climate, herbivory, decomposition, pollination and seed dispersal. Arthropods affect most of these functions either directly or indirectly and are therefore very important in maintaining forest ecosystems (WEISSER & SIEMANN 2004). As pollinators and seed dispersers they ensure the regeneration of the forests. As herbivores, they hasten the return of nutrients that were fixed in the leaves to ground level and their recycling. As decomposers they influence the above- and belowground nutrient dynamics. Moreover, insect faeces and cadavers make nutrients available for mineralization.

Arthropods are the most abundant group of herbivores in most terrestrial ecosystems (LOWMAN & MORROW 1998) and are known to dramatically influence forest dynamics. They are therefore strongly connected to overall ecosystem processes like nutrient cycling (SCHOWALTER 2000). These links, however, are still poorly understood, especially those between forest canopies and forest soils (RINKER et al. 2001). Recent canopy studies, primarily those using canopy cranes, have revealed a high temporal and spatial variability in the herbivory within forests around the world (for a review see RINKER & LOWMAN 2004). Results ranged from 1 to 5% of total leaf area production in temperate forests to more than 300% (re-foliation after leaf loss) in Australian eucalypt forests. Moreover, high spatial variation occurs between forest types, stands, tree species and also within individual tree crowns. On a temporal scale, seasonal and annual dynamics occur in temperate as well as tropical forests. Seasonal dynamics are mainly caused by differences in leaf age, as young leaves are richer in nitrogen and water and therefore of higher quality to herbivores (MATTSON 1980). Consequently, defoliation events are usually associated with young leaves (SCHOWALTER 2000). Frass and greenfall (leave fragments dropped during herbivory) as well as throughfall (modified rainwater while passing the canopy) increase nutrients (C, N, P) in the forest soil and thus affect activity of arthropods (e.g. mites and collembolans) and therefore decomposition (REYNOLDS et al. 2000, REYNOLDS et al. 2003). HUNTER et al. (2003) found that nitrogen inputs in frass ranged between 0.3 and 1.1 kg per ha per year in the southern Appalachians, which is approximately 2-4 percent of that in annual litterfall under non outbreak situations. RINKER & LOWMAN (2004) cited another study that describes nitrogen inputs of 30 kg per ha per year during a short outbreak of a sawfly.

Decomposition is another important ecological process in which arthropods are deeply involved. Previous studies on decomposition have mainly focused on the forest floor, although the decay of organic material already begins in the canopy. Decomposition processes range from fungi that colonize senescent leaves (OSONO 2002) to decomposition of crown dead wood (SWIFT et al. 1976) to elevated soil processes (NADKARNI & LONGINO 1990, PAOLETTI et al. 1991, WINCHESTER 1997, WINCHESTER & BEHAN 2003, LINDO & WINCHESTER 2007). As these early decomposition processes affect later ones their influence on nutrient cycling of the forest ecosystem as a whole should not be neglected (FONTE & SCHOWALTER 2004). REYNOLDS & HUNTER (2004) emphasize that decomposer food webs in forest canopies are virtually unexplored and they cite this as critical priority for future work.

Conclusion

It can be concluded that canopy research is much more than just hunting for new species. Indeed the canopy fauna is rich in species, especially in the tropics and is therefore a good starting point for estimating global biodiversity. Furthermore, canopy species are involved in many ecosystem functions and processes and therefore the canopy is a habitat that should not be neglected in functional biodiversity studies. Although increased studies in forest canopies have revealed comprehensive, new insights into the importance of the canopy in ecosystem processes, there are still many open questions which should be addressed in future studies. Ecosystem processes in forests are quite complex and including interaction between all compartments - from the atmosphere over the canopy to the soil layers of the forest floor – is crucial for our overall understanding of forest ecosystems and their ecological functions. Based on advances in canopy access and study techniques including experimental manipulations, novel insights into functional and mechanistic relationships can be expected in the future.

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Zusammenfassung

Die Baumkronenforschung ist eine relative junge Disziplin der Entomologie. Als Initialfunke gelten die Arbeiten von Erwin Anfang der 1980er, die die bis dahin angenommene Anzahl der auf unserem Planeten lebenden Arten weit nach oben korrigierten. Die Entwicklung neuer Zugangs- und Beprobungstechniken führten in der Folge zu einem exponentiellen Anstieg an Forschungsprojekten im Kronendach der Wälder. Diese blieben zunächst hauptsächlich auf die Tropen beschränkt wo man sich die Entdeckung vieler neuer Arten versprach. Erst innerhalb der letzten Dekade gewann die Baumkronenforschung auch in Mitteleuropa zusehends an Bedeutung. Im Gegensatz zu den Tropen konnten hier zwar nicht so viele neue Arten entdeckt werden, die Annahmen zur Seltenheit bestimmter Arten mussten jedoch deutlich relativiert werden. Auch neue spannende Erkenntnisse zu Aspekten der Verhaltens- und Populationsökologie sowie der Evolutionsbiologie konnten auf Grundlage der Baumkronenforschung gewonnen werden. Darüber hinaus hat man vor allem erkannt, dass von Arthropoden getriebene Prozesse in den Baumkronen einen überaus wichtigen Beitrag zum Funktionieren von Waldökosystemen leisten in dem sie zum Beispiel Nährstoffkreisläufe beeinflussen. Die Betrachtung des Kronenraums als Bindeglied zwischen Atmosphäre und Boden ist zu einem zentralen Bestandteil waldökologischer Forschung geworden. Es sind in Zukunft noch viele spannende Erkenntnisse zu erwarten.

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