Global ecology: insect-plant interactions in tropical rainforests

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INTRODUCTION

About 1.8 million species are known on Earth. This includes > 1 million insect species, 250,000 species of higher plants and 69,000 species of fungi (Hammond, 1992). Roughly, nearly half of insect species are herbivores, feeding on live plants (Strong *et al*., 1984), which implies that, potentially, 456,000 species of herbivores might interact with 250,000 host plants (1.1×10^{11} interactions possible). Evidently, the distribution of many insects and host plants do not coincide and many herbivore species only feed on a handful of different hosts, so that the total of species interactions between insects and plants must be much lower.

On the other hand, we also need to appreciate that many insect species feed on fungi and mosses and, more crucially, that global estimates of insect species may scale between 6-10 million species (Novotny *et al*., 2002). Ecology may be considered as the science to study interactions between species on Earth. Given that nearly half of global biodiversity on Earth is supported by tropical rainforests, it is not an exaggeration to state that most species interactions on Earth involve insect herbivores and plants in tropical rainforests. Hence the title of this short essay, referring to 'global ecology', in which I will briefly discuss the diversity of insect-plant interactions in tropical rainforests, and the main factors influencing them. Most of examples in the text refer to studies performed by my colleagues and myself over recent years in Australia, Papua New Guinea, Cameroon, Gabon, Brazil, Guyana and Panama.

HOW TO EXPLAIN THE DIVERSITY OF INSECT-PLANT INTERACTIONS IN TROPICAL RAINFORESTS?

First, rainforests are more diverse than temperate forests. Several explanations, not mutually exclusive, account for this situation:

- greater stability of tropics in past history (as opposed to recent glaciations in temperate areas);
- predation and competition in the tropics may result in higher speciation rates;
- solar energy may control organic diversity in non-limiting water conditions;
- tropical ecosystems may provide more ecological niches (species packing).

This essay mostly relates to the last concept. In particular, as developed below, the diversity of microhabitats for herbivores appears higher in tropical than in temperate forests. For example, the array of tree crowns in a tropical forest is often heterogeneous, including trees of different species, sizes, phenologies (flowering, leaf flushing) and ages. Thus, tropical forests include spatially complex and temporally dynamic three-dimensional structures. Such systems are particularly conducive to the stratification, niche differentiation and habitat segregation of forest organisms, especially insect herbivores.

Second, each host plant species provide a variety of feeding niches for herbivores, such as trunk & wood, flowers, seeds & fruits, sap, leaves, roots. Herbivores may also modify plant tissues, creating new structure such as mines and galls. Third, interactions between insects and plants involve both herbivores (herbivory, pollination, seed predation and dispersal) and non-herbivores. A widely known case for the later includes ant mutualism with plants. In these interactions, plants obtain nutrients from animal remains brought by ants and the defense of their foliage by ants, whereas advantages to ants include nesting sites, extra-floral nectaries and food-rich structures.

Last, indirect insect-plant interactions are also common. For example, leaf-cutting ants represent the most important 'herbivores' in terms of leaf damage in Neotropical forests. They cut leaves to grow a specific fungus underground and feed on it. This allows these specialized ants to exploit many plant species in the forest. In the same vein, the 'superabundance' of ants in tropical forest canopies (often > 50% of arthropod individual collected) can be explained by ant predation but laso by ants obtaining indirectly energy from plants, via extrafloral nectaries or mutualism with homopterans sucking sap and rejecting honweydew on which the ants feed (Davidson *et al*., 2003).

FACTORS INFLUENCING INSECT-PLANT INTERACTIONS

Alpha, beta & gamma-diversity

As exemplified by a survey of homopteran species for two years with different methods in nine 20x20m sites within a 2km radius in Panama, local diversity (alpha diversity) of both plant and herbivore species is rather high, with noticeable differences even at this small scale. This results from the high local heterogeneity of the rainforest (Fig. 1).

Why is species turnover of insect herbivores between sites (beta diversity) high in tropical forests? A first explanation pertains to rainfall patterns and the occurrence of different plant species at different locations. For example, only 24% of leaf beetle species are common to two sites situated at the extremes of a 70km rainfall gradient in Panama (Charles & Basset, 2005). A second and similar explanation pertains to altitudinal gradients and different hosts plants. For example, out of all caterpillars feeding on three species of *Ficus* occurring both in lowland and montane forests of New Guinea, only 17% of species feed on these hosts in both forest types (Novotny *et al*., 2005).

Hence, a combination of rainfall, altitude and historical factors result in a variety of forest types, plants, and, particularly, of herbivore species. What is the magnitude of herbivore species turnover when altitude, rainfall and host plants are controlled for? It is rather low (proportion of shared species > 50% up to 500km: Novotny *et al*., 2007), emphasizing the role of the above factors.

With regard to the regional distribution of plant and herbivore species, the later is more difficult to assess and often poorly known. Frequently, herbivore distribution may be smaller than that of host, being limited by microclimatic conditions. However, certain herbivores may also feed on different host-plants, with the potential to be widely distributed. This issue clearly requires further investigations.

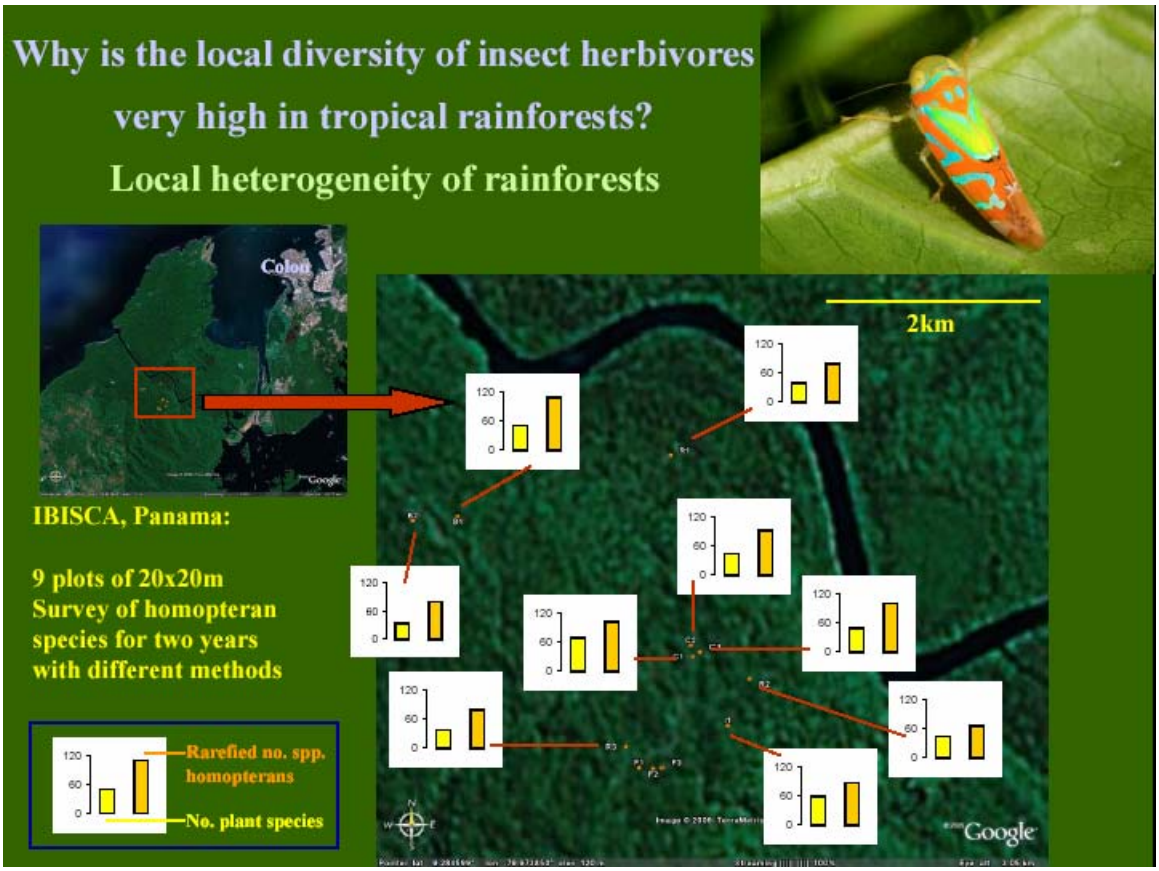

Fig.1. Project IBISCA in Panama: local species richness of plants (yellow bars) and sap-sucking homopterans (orange bars).

Vertical distribution of herbivores from the understorey to the upper canopy

Abiotic and biotic conditions from the understorey to the upper canopy of closed tropical rainforests may drastically vary for insect herbivores (i.e., solar energy, air temperature, relative humidity, wind, leaf area density, abundance of young leaves and flowers, level of secondary metabolites, etc.). Several lines of evidence indicate that herbivore abundance and species richness in the upper canopy may often be higher than in the understorey (Basset *et al*., 2003). In particular, comparison of conspecific saplings and trees of one tree species in Panama indicated that leaf chewers were 2.9 and 3.5 times more abundant and species-rich on mature trees, and that host stage and young foliage area explained 52% of the variation in herbivore spatial distribution (Basset, 2001).

A larger project in Panama (www.ibisca.net), including 30 entomologists using 14 sampling programmes, compared the vertical distribution of various arthropod groups in Panama. Preliminary results indicated that the upper canopy and forest litter represent the most productive and species-rich habitats in closed tropical rainforests. However, patterns of stratification may differ between taxonomical and ecological groups (Fig. 2).

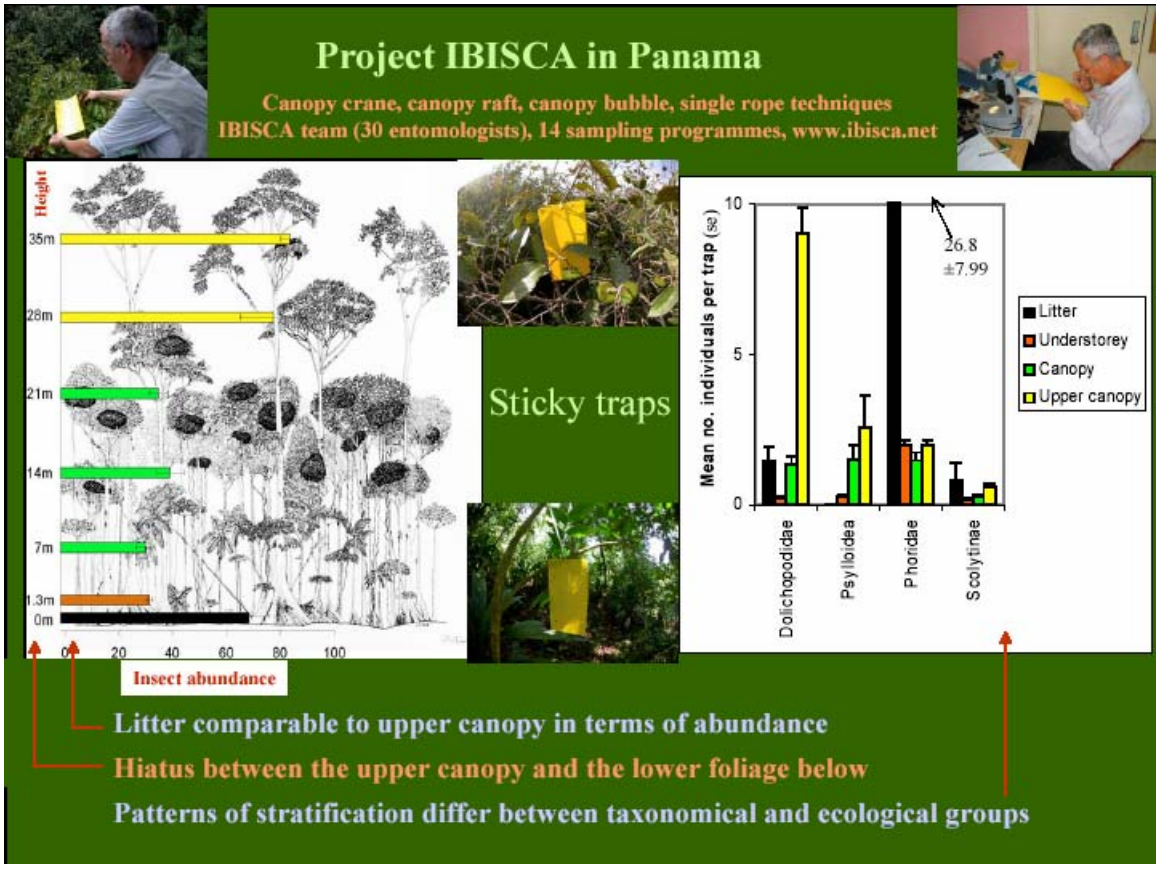

Fig.2. Project IBISCA in Panama: vertical distribution of arthropod groups, as inferred with sticky traps.

Succession and disturbance

Many tropical successions start with pioneer trees, rather than with annual herbs, and represent a permanent and predictable habitat for herbivores (Leps *et al.,* 2001). Further, sap-sucking and leaf-chewing insects do not respond similarly to natural disturbance, as observed in small, medium-sized and large forest gaps in Guyana. Even modest logging rates can impact 29% of herbivore species in the understorey, without accounting for the greater impact on canopy herbivores (Basset *et al*., 2001). There is an urgent need to understand well the impacts of forest logging on insect herbivores in tropical rainforests, and how different they may be from the effects of natural disturbance.

Temporal distribution: seasonality and effects of plant phenology

In the tropics, insect herbivores may have several generations per year and adults often occur during extended periods of time, unlike in temperate areas (Novotny & Basset, 1998). This all-year round higher pest pressure in the tropics may explain why tropical plants have higher levels of secondary metabolites, as compared to temperate plants (Coley & Barone, 1996). Most rainforest herbivores are finely tuned to the phenology of the host-plant, which may be more unpredictable in the tropics than in temperate forests (Basset, 1991).

Host-plant effects

These include principally plant identity per se, as well as plant stage and the age of plant tissues (ontogenic development). These and related factors influence herbivore host specificity (i.e., the kind and number of plant species that herbivores feed upon). Host specificity typically depends on evolutionary interactions between plant and insects. A strict coevolution scheme (where herbivore phylogeny closely matches plant phylogeny) is rather rare in tropical rainforests (example of *Ficus* and pollinating Agaonidae). Rather, many herbivores are either generalists (i.e., they feed on unrelated plant species) or specialists (i.e., they feed on one plant species or related plant species, being congeneric or confamilial). A plant species may thus easily interact with hundreds of insect species (Fox, 1988).

In Papua New Guinea, caterpillars appear more specific than adult beetles or katydids feeding on foliage (*Novotny et al.,* 2002). Massive rearing of 60,000 leaf-feeding caterpillars, 2,500 wood-boring longhorn beetles and 8,000 fruit flies confirmed different levels of host specificity among these groups and that many herbivore species are able to feed on several and related host plant species, especially when belonging to large (speciose) plant genera (Novotny *et al*., 2002; unpublished data).

Most herbivores prefer young foliage, which is softer and has higher levels of water and nitrogen than mature leaves. Further, many sap-sucking species are particularly sensitive to leaf turnover and nitrogen translocation. This is illustrated by results of feeding tests with numerous weevil species in Panama (Fig. 3). However, preferences for young leaves are influenced by body size. Small leaf-chewing insects tend to be more specialized on young leaves (Cizek, 2005).

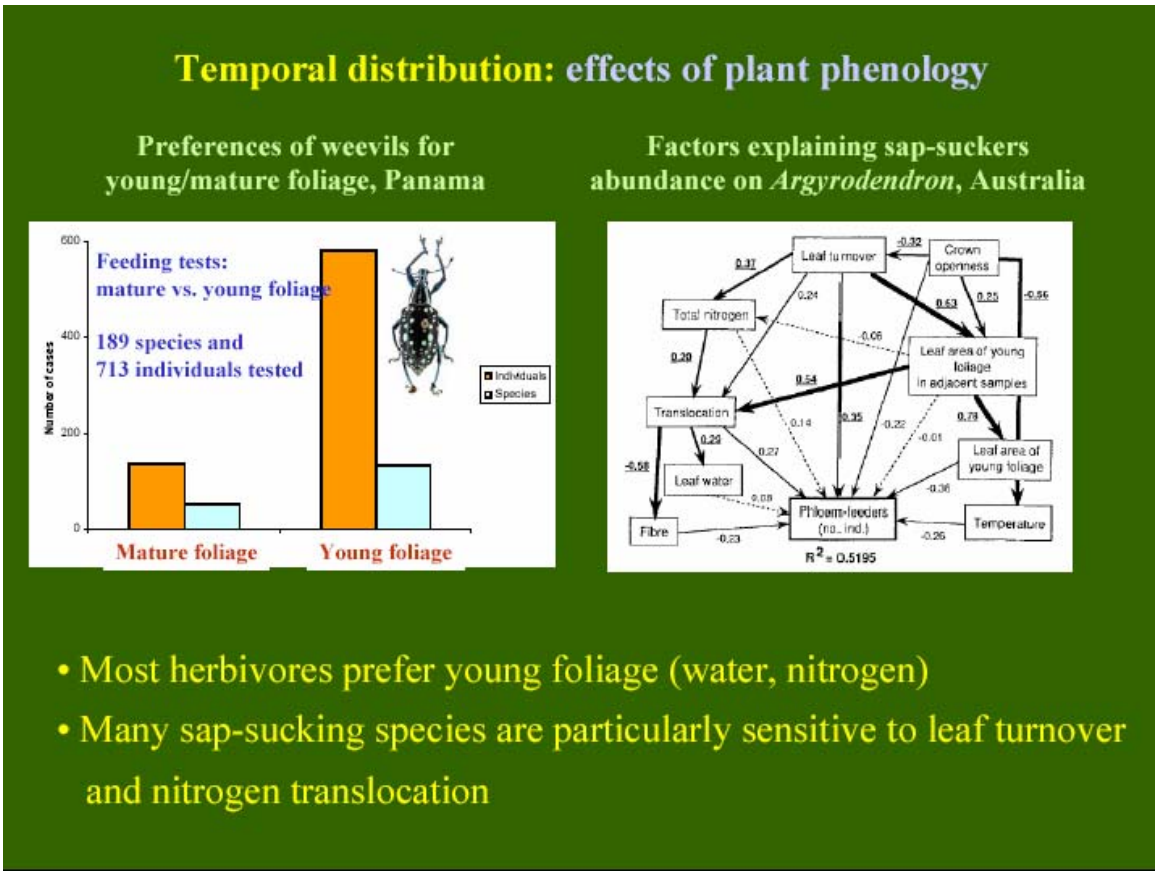

Fig.3. Effects of plant phenology: feeding tests of weevils in Panama and effects of leaf turnover on sap-sucking insects in Australia.

CONCLUSIONS

Tropical rain forests represent very different environments than temperate forests for insect herbivores. Tropical rainforests appear spatially more heterogeneous than temperate forest (more habitats, plants, vertical gradients). High local species richness in tropical rainforests is maintained, in part, by the high heterogeneity of the rainforest and the variety of feeding niches and microhabitats available. Faunal turnover depends mainly on rainfall, altitude and host plants; it is high between very different forest types. However, faunal turnover of herbivores feeding on a particular host in contiguous lowland forests is rather low. This results from the dominance of large plant genera and low insect specificity on congeneric hosts.

A specialized, rich and poorly-known herbivore fauna may occur in the upper canopy. This fauna need to be collected/observed in situ. Numerous specialized herbivores of the upper canopy may be doomed to extinction when tall tropical forests growing on flat terrain are logged, since they cannot feed on plants in the understorey or in forest gaps. This may represent a massive extinction of genetic diversity. Proper access to the upper part of the canopy appears crucial for a sound understanding of many forest processes (pollination, seed predation, herbivory).

The composition of herbivore communities is determined by plant phylogeny most strongly on the levels of genera and families. Very few herbivores feed on a single plant species, particularly when closely related plant species are available. Many congeneric and confamilial hosts-plants in tropical forests facilitate host-switching. Resource use, in terms of host-specificity, may be broader for tropical than for temperate herbivores (Novotny *et al.,* 2006). Tropical herbivores may be less specialized than previously thought in terms of resource use. However, they may be more specialized in terms of habitat use (i.e., specific habitats located in different forest strata).

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