Novotny’s lab food web projects

The Department of Ecology team studies fundamental ecological and phylogenetic mechanisms generating and maintaining biodiversity on ecosystem, landscape, regional and continental scales, surveys insect biodiversity patterns from communities to continents, and devises practical measures for the conservation of this biodiversity. This research spans from populations through communities to insect macroecology and phylogeny, using molecular methods, laboratory ecophysiological experiments, field surveys and ecological experiments, as well as modeling. Our studies include a wide range of insect taxa from all trophic levels, as well as host vegetation and vertebrate predators. Geographically, we are focused both on temperate and tropical ecosystems, with centers of our research activity in Europe, Asia (Japan, Malaysia, Thailand), America (Panama), Africa (Cameroon), and the Pacific (New Guinea). Here are some examples of current research, mostly focused on food webs that are led or participated in by the Novotny’s lab:

Conservation research and conservation action in tropical rainforests

Our research contributes to rainforest conservation by (i) addressing biological questions of conservation relevance, (ii) developing practical conservation approaches for rainforests owned by indigenous people, and (iii) monitoring the biodiversity status of rainforests (Fig. 1). In particular, we have studied the effect of rainforest fragmentation on bird diversity to assess biodiversity value of small, village-operated rainforest reserves in New Guinea (Sam et al. 2014, *J. Field Ornit.* 85, 152–167). Further, we have explored and implemented direct-payment schemes to indigenous communities, using conservation royalties to promote rainforest reserves (Novotny 2010, *Biotropica* 42, 546-549), and are one of the internationally recognized leaders in tropical conservation capacity building, using paraecologists recruited from indigenous communities (Novotny et al. 2012, pp. 154-7 in Lowland et al., Methods in Forest Canopy Research, Univ. California Press). We have also participated, for Papua New Guinea, in a highly collaborative survey of the status and key threads faced by tropical reserves world-wide (Laurance et al. 2012, *Nature* 489, 290-294).

Figure 1. Tropical conservation: Border between village rainforest reserve and agricultural landscape in Papua New Guinea (A), bird diversity retained in village reserves of different sizes compared to continuous forest (B), Palm Cockatoo (*Probosciger aterrimus*), one of the species susceptible to forest fragmentation (C), social experiment with conservation royalties paid to village reserve owners (D) and global analysis of quality trends in tropical reserves, including our report on Papua New Guinea (E).

Dimensions of tropical insect diversity

Our work has provided some of the most accurate estimates of both local and global diversity for tropical arthropods. A recent collaborative study in lowland forest in Panama (Basset et al. 2012, *Science* 338, 1481-1484) used spatially and temporally replicated design for ~20 different sampling methods to assess total diversity of arthropods in 6,000 ha of lowland forest,
estimated at 25,000 species (Fig. 2). This was the first such estimate provided for a tropical forest.

Our long-term study of plant-insect interactions in New Guinea provided have factual basis to challenge the widely held assumption that herbivore species coexistence in the tropics is a consequence of finely divided plant resources and consequently reduce global estimates of arthropod diversity from 30 to ~6 million species (Hamilton et al. 2010, Amer. Nat. 176, 90-95, Hamilton et al. 2013, Oecologia 171, 357-365), now widely accepted by the research community.

Global patterns in insect host specificity: key to explain the phenomenon of hyper-diverse tropics?

Extreme diversity of insects in the tropics requires explanation. One of the hypothesis suggests that insect herbivores not only have more host plant species available on tropical vegetation, but also divide these resources more finely between species, and are more specialized than temperate zone insects. This suggestion has been controversial, but our recent comprehensive analysis, where our team, represented by seven authors, played an important role, showed globally increasing host specificity from temperate to tropical ecosystems for insect herbivores, explaining thus partly the increased tropical diversity in insects (Forister et al. 2015, PNAS 112, 442-447). The study also introduced new quantitative description of host specificity, based on the discrete truncated Pareto distribution.

Herbivores and their plants: niche theory does not fit plant-herbivore food webs in rainforests

We have assembled host records for >250,000 herbivorous insects including ~2,500 species and 11 feeding guilds in PNG (Novotny et al. 2010, J. Anim. Ecol. 79, 1193-1203). This matrix, comprising >8,000 plant-insect and insect-insect trophic interactions, is among the largest data sets for tropical ecosystems and, although incomplete, “likely to be as good as it
gets”, as commented in the Editor’s choice feature on our paper (Lewinsohn 2010, *J. Anim. Ecol.* 79, 1143-5). We used this data set for to the first estimate of the dimensions of a rainforest plant-herbivore food web at ~200 plant species hosting ~9,500 herbivore species involved in ~50,000 distinct trophic interactions.

We tested the predictions of niche theory, postulating that more specialized herbivore guilds should be able to reach higher diversity per plant species as they could divide the available resources more finely. However, we found exactly the opposite pattern of negative correlation between host specificity and species diversity among six folivorous guilds (Fig. 4), suggesting other mechanisms important in community assembly, including the effects of both host and herbivore phylogeny (Novotny et al. 2012, *Am. Nat.* 171, 351-362).

![Fig. 4. Plant-herbivore food webs in tropical forests show a wide range of structural features (A); in particular, host specificity of herbivores is negatively correlated with their diversity per plant species (B), at variance with the predictions of niche theory. The food web structure can be partially explained by phylogenetic signal, illustrated here between plant species (green) and geometrid (left) and pyralid (right) moths (C).](image)

**Testing the Ehrlich & Raven’s coevolutionary theory: Complicated relationship between the phylogeny, chemistry and ecology of plants and their herbivorous communities**

In the course of evolution, plants have acquired a wide range of defenses against herbivores. Ehrlich & Raven’s coevolutionary theory suggests that diversification of defensive traits is driven by strong impact of novel traits on insect herbivores. We tested the theory using willows in Central Europe, studying their phylogeny, secondary chemistry and folivorous insects. We found that predictably, the content of salicylates, a novel group of defensive metabolites in willows, was correlated with low diversity and high host specificity of herbivores. Despite these effects, salicylates were lost in some *Salix* lineages. This was probably because salicylates were costly, as they reached up to 22% of dry leaf mass, but did not decrease the overall abundance of herbivores (Fig. 5). The lineages lacking salicylates may thus benefit from their loss and redirect energy into other defenses or growth. We showed that the balance between costs and benefits of defensive traits is not necessarily in favor of novel compounds as predicted by the Ehrlich’s & Raven’s theory (Volf et al. 2015 *J. Anim. Ecol.* in press, *Ent. Exp. Appl.* in press). We are presently replicating this study using *Ficus*, another species-rich genus of trees, and their insects in New Guinea.

![Fig. 5. Phylogeny of 10 *Salix* species (A, loss of salicylates in red). The relationships between salicylate content and the diversity (B) and density (C) of their folivorous insect communities (each](image)
point representing one *Salix* species) shows that the loss of salicylates does not increase herbivore pressure; *S. caprea* (D), one of the species that lost salicylates.

**Mechanisms structuring population genetics in tropical insect herbivores: host plants or geography?**

Our surveys within a 500x150 km of lowland rainforest documented low beta diversity of herbivorous insects, but detected genetic differentiation of their populations, based on mtDNA analysis. Approximately half of Lepidoptera species exhibited geographic differentiation of populations independent from host plant species, such as in *P. disjuncta* (Fig. 6) specialized on a single host while one third of species were structured in response to their host plant species. The remaining species, e.g., *A. pusilla*, showed a uniform genetic structure within the entire study area (Craft et al. 2010, 107, 5041-5046).

![Image](image_url)

**Fig. 6.** Genetic diversification of Lepidoptera in a 500 x 150 km rainforest area in New Guinea (A) was explained by geography and by host plant species. The mtDNA haplotype networks (colours represent the geographic origin of specimens, as shown in A, diameter is relative to the number of specimens, and lines represent genetic distances between haplotypes; each mark represents a single nucleotide substitution) are shown for *P. disjuncta* (B) exhibiting geographic differentiation, and *A. pusilla* (C) unresponsive to geography. The specimens were reared in field camps as in (D).

**Ants: bottom-up effects of vegetation on the communities in tropical rainforests**

Our team is running on-line database Ants of New Guinea (http://www.newguineants.org/) that is the best resource on ant taxonomy for that region. Building on this foundation, we have analysed ecological determinants of increasing ant diversity in the course of rainforest succession, from secondary to primary rainforest vegetation (Klimes et al. 2012, *J. Anim. Ecol.* 81, 1103–1112). This study was the Editor’s choice, and C. Parr (*J. Anim. Ecol.* 81, 937–9) commented that “...Klimes et al. raise the bar by addressing the deceptively simple, yet inherently complex, question of why species richness is lower in secondary forests. Using the first plot-scale inventory of arboreal ant nests, combined with an innovative rarefaction technique, they ... highlight the contribution of beta diversity to the higher richness in primary forest.” This study also described 5 new species (Klimes & McArthur 2014, *Myrmec. News*, 20, 141-158) and showed that the species diversity of foraging ants is mostly generated by tourist ants coming from the surrounding trees rather than locally nesting ants, highlighting thus the importance of ant nest sampling (Klimeš et al. 2015, *PLoS ONE* in press).

![Image](image_url)

**Fig. 7.** Complete census of ant nests in primary (A) and secondary rainforests documented differences in species diversity (B) that were explained by beta diversity in ant communities between trees, as well as the structural differences of vegetation (tree size and density), rather than differences in tree density.
diversity between the forests (C); *Camponotus wanangus* is a newly described species from the study (D).

**Ants: key predators of herbivorous insects?**

The role of ants as predators in rainforest communities was studies experimentally, as we reduced the density of all arboreal ants within 0.05 ha primary and secondary forest plots by 80% for 10 months (Klimes et al. 2011, *Ecol. Entomol.* 36, 94–103), showing surprisingly low impact on insect herbivores. We are following up on this discovery using experimental exclosures of ants, birds, and bats to quantify relative effects of different predators, while also assessing the effects of parasitoids.

We used artificial caterpillars as baits (Low et al. 2014, *Ent. Exp. Appl.* 152, 120-126) to monitor predation rate along a complete altitudinal rainforest gradient in New Guinea (Sam et al. 2014, *Ecography* 37, doi: 10.1111/ecog.00979) and found that predation pressure decreases towards higher elevations. This seemingly simple pattern is a combination of rapidly decreasing predation by ants with elevation, and bird predation that is constant from lowlands to mid-elevations, then decreases. The dominant predators are thus ants in lowland forests, and birds at higher elevations (Fig. xx). Further, we have documented higher predation on artificially damaged leaves, both by ants and birds. This suggests both chemical and visual clues used by predators to focus on damaged plants.

**Tri-trophic food webs in tropical forests: plants, herbivores and parasitoids**

Fig. 9. Tri-trophic food web between 38 tree species, 11,621 caterpillars from 267 species, and 1,523 parasitoids from 166 species (A), taxonomic composition of parasitoids feeding on exposed and semi-concealed host guilds (B), and their differential host specificity (C), molecular identification of parasitoids dissected from two host species (D), and a newly described Colastomion maclayi (E).

**Trophic interactions as drivers of secondary succession in tropical rainforests**

Specialized herbivores and other natural enemies of plants could facilitate the coexistence of plant species through density dependent plant mortality. This mechanism, known as the Janzen-Connell hypothesis, was proposed 46 years ago but it has taken >40 years before this ecological hypothesis has been tested experimentally. There is a long tradition of community experiments in temperate grasslands, starting from the Rothamsted experiments in 1843 and continued later elsewhere (e.g., Cedar Creek LTER site, the Jena Experiment). We are adapting these experiments to study ecological succession in forests. We test the importance of biotic interactions as drivers of secondary succession in tropical rainforests by a series of replicated experiments manipulating successional food webs in order to uncover the effect of (i) fungal pathogens and mutualists, (ii) invertebrate herbivores, and (iii) invertebrate and vertebrate predators on the trajectory of plant succession. These experiments are taking place along an elevation gradient providing natural variation in the intensity of biotic interactions.

Fig. 10. Schematic representation of one block of 5 x 5 m plots in a garden experiment. The manipulation (red: reduction, blue: addition) on three target groups (insect herbivores, insect & vertebrate predators, and fungal pathogens & mutualists) are shown for the control and four treatments.

Fig. 11. Pilot experiment testing our methods on 5 x 5 m gardens in Wanang. A: start of the experiment, B: another block two months into the experiment; C: the effect of insecticide treatment (upper half of the image) can be clearly seen, D: example of pioneer vegetation after 2.5 years of succession; E: Palatability (the proportion of feeding in 50 no-choice experiments) of 62 common plant species to Oribius sp. 1, an extreme generalist that will be used to increase herbivore density in the lowland garden experiment.

**Lowland rainforest dynamics**

We are managing 50-ha Wanang forest dynamics plot, a member if the Center for Tropical Science network (with U. of Minnesota; plot’s PI: G. Weiblen and V. Novotny). The plot is in the Wanang Conservation Area (www.entu.cas.cz/png/wanang), in large lowland rainforest with largely intact vegetation and vertebrate populations. We have tagged and mapped >280,000 individual plants (with DBH>1cm) from >550 species. Presently we are in the middle of the first re-survey after five years, the period of time that included the strongest El Nino event in the past 20 years. We are also monitoring 200 fruit traps and 800 seedling plots in the CTFS plot. The plot serves as a basis for food web research, including ongoing studies of long-term insect dynamics (ants, termites, fruit flies,
butterflies), food webs comprising seed predators and herbivorous insects, bird communities etc. It is supported by a Swire field station nearby that provides accommodation and lab space, accessible also to visiting research teams from other institutions.

Fig. 12. Forest dynamics plot in Wanang, tagging plants in the plot, distribution of Pometia pinnata, and the Swire Field Station next to the plot.