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Caterpillar - parasitoid food webs in New Guinea rainforest

Ph.D. Thesis

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Annotation

The thesis establishes baseline ecological parameters (parasitism rate, host specificity, and food web structure) for tropical external folivore - parasitoid food webs and finds the parasitoids strongly host specific. Further, it presents a new method for molecular detection of herbivore - parasitoid relationships, and describes some of the studied species to ensure long-term value of the ecological data.

Declaration [in Czech]

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List of papers and author contributions

I.

Parasitism rate and host specificity in a caterpillar - parasitoid food web from a tropical rainforest

Jan Hrček, Scott E. Miller, James B. Whitfield, Hiroshi Shima and Vojtěch Novotný

manuscript in review in *Oecologia*, a revision requested

[JH, VN and SEM conceived the study. VN led fieldwork. SEM, JBW and HS identified vast majority of insect specimens. JH analyzed the data and wrote the manuscript with contributions by VN and other authors.]

II.

Interaction intimacy drives the structure of plant - herbivore - parasitoid foods webs

Jan Hrček, Vojtěch Novotný, Scott E. Miller, M. Alex Smith, George D. Weiblen and Rebecca J. Morris
manuscript

[JH and VN conceived the study. VN led fieldwork. GDW, SEM and MAS provided DNA sequences for plants, herbivores and parasitoids. RJM helped with the analyses. JH analyzed the data and wrote the manuscript with contributions by VN, RJM, and other authors.]

III.

Molecular detection of trophic links in a complex insect host - parasitoid food web

Jan Hrček, Scott E. Miller, Donald L. J. Quicke and M. Alex Smith

Molecular Ecology Resources (2011) 11, 786–794

[JH conceived the study, led the fieldwork, dissected the caterpillars, and prepared samples for sequencing. DLJQ provided know-how on caterpillar dissection. MAS obtained DNA sequences. SEM identified hosts and provided extensive barcoding library. JH analyzed the data and wrote the manuscript with contributions by other authors.]

IV.

A new genus and three new species of parasitoid wasp from Papua New Guinea and redescription of *Trigonophatnus* Cameron (Hymenoptera, Braconidae, Rogadinae)

Donald L.J. Quicke, M. Alex Smith, Cornelis van Achterberg, Scott E. Miller and Jan Hrček

Journal of Natural History (2012) 46, 1369–1385

[DLJQ and JH conceived the study. DLJQ and CvA did the descriptions. MAS and SEM provided DNA sequences. CvA drew the figures. JH provided host data and SEM provided further information on hosts. DLJQ wrote the manuscript with contributions by other authors.]

Co-authors agreement:

Jan Hrček declares that he is the first and corresponding author of papers I, II and III with major contributions as stated above.

Donald L. J. Quicke, the first and corresponding author of paper IV, hereby agrees with the publication of paper IV in the Ph.D. thesis of Jan Hrček and confirms the above author contributions for this paper.

Jan Hrček



Donald L. J. Quicke, PhD.

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Introduction

Terrestrial food webs of plants, herbivores and their natural enemies harbor majority of global terrestrial biodiversity (Price, 2002), while parasitoids alone comprise approximately 10% of all described insect species (Godfray, 1994; Quicke, 1997). Most of this diversity is undescribed and lies in the tropics (Godfray, Lewis & Memmott, 1999). The knowledge on how these species interact is even sparser, with e.g. only ~7,000 interactions from estimated ~50,000 having been recorded in one of the best known plant - herbivore food webs from the tropics (Novotny *et al.*, 2010). Mapping the structure of these webs is a first step to understand how this astonishing diversity arose, how it is maintained, and what factors form major constraints on food web structure. Specifically, previous studies of food web structure have shown that insect communities tend to be structured by apparent competition through their natural enemies instead of direct competition like plant communities (Morris, Lewis & Godfray, 2005). Also, the general knowledge on herbivore natural enemies can guide first steps of biological control programs, which however always need experimental evaluation (Kidd & Jervis, 2005).

Folivores are the most diverse insect herbivore group and together with sap-suckers they are responsible for majority of insect herbivory worldwide (Coley & Barone, 1996). From folivores, the study of endophytic leaf-miners and the tri-trophic webs around them proved manageable in small teams, even in the tropics (Lewis *et al.*, 2002; Memmott, Godfray & Gauld, 1994). Leaf-miner communities are composed of several independent phylogenetic groups within Lepidoptera, Diptera and Coleoptera orders. Leaf-miners are usually specialized on individual plant species (Hespenheide, 1991). Parasitoids of leaf-miners are mostly parasitic wasps from the superfamily Chalcidoidea, followed by some Ichneumonidae and Braconidae. Leaf-miner parasitoids are commonly generalists, often attacking even hosts from different orders. About two thirds of parasitoid species live on their leaf-mining hosts externally (ectoparasitoids) and only one third lives inside their hosts (endoparasitoids). Another division for parasitoid life-styles is often used, dividing parasitoids to koinobionts, which allow their hosts to develop after parasitisation and idionbionts, which kill or paralyze the host during oviposition. (Askew & Shaw, 1986). There is however very close correspondence between endoparasitism and koinobiontism on one side and ectoparasitism and idiobiontism on another, and the differences become apparent only in quite close perspective. Leaf-miners suffer from high parasitism rate, commonly in the range of 40 - 70% (Hespenheide, 1991), and their populations are commonly regulated by parasitoids (Cornell & Hawkins, 1995).

The study of externally feeding folivores and their host plants and parasitoids is more demanding, and requires large number of field assistants, parataxonomists or volunteers in addition to a team of scientists (Dyer *et al.*, 2007; Janzen *et al.*, 2005; Novotny *et al.*, 2002). Most attention

traditionally goes to holometabolous larvae, because they are more specialized than adult Holometabola or Hemimetabola and represent about half of all external folivores in number of species, individuals, and biomass (Novotny *et al.*, 2002). The tropical larval external folivores are composed almost exclusively of Lepidoptera larvae, while in the temperate zone they also include sawfly and beetle larvae (Novotny *et al.*, 2006). Larval Lepidoptera are usually specialized on plant genus (Novotny *et al.*, 2002) and therefore less host specific than leaf-miners (Novotny & Basset, 2005). Food webs around externally feeding Lepidoptera are rarely studied as a whole, as most studies concentrate on larger and more attractive Macrolepidoptera which feed exposed on the vegetation and neglect smaller Microlepidoptera which live in semi-concealed situations like rolled or tied leaves. However, in the cases when they were studied, Microlepidoptera seem to be equally speciose and common as Macrolepidoptera.

This bias is especially apparent in studies of caterpillar - parasitoid food webs, as their structure is expected to strongly depend on the sampled hosts (Barbosa & Caldas, 2004; Gentry & Dyer, 2002; Janzen, 1995; Le Corff, Marquis & Whitfield, 2000; Sheehan, 1994; Stireman *et al.*, 2005; Stireman & Singer, 2003). Hawkins (1994) identified the degree of host concealment as a key parameter for parasitoid communities. Parasitism rate and parasitoid species richness increase with the degree of concealment from exposed feeders through leaf-rollers, web-tiers and case-bearers, and reach maximum values in leaf-miners and galls. It is therefore generally expected that parasitoid communities of semi-concealed Microlepidoptera are intermediate between that of entirely concealed leaf-miners and entirely exposed Macrolepidoptera also in other parameters like community composition and specialization (Godfray and Quicke, personal communication). Parasitoid communities on exposed hosts are composed of Hymenoptera: Braconidae and Ichneumonidae, Diptera: Tachinidae, and small proportion of Hymenoptera: Chalcidoidea (Barbosa *et al.*, 2004; Gentry *et al.*, 2002; Hawkins, 1994; Le Corff *et al.*, 2000). Also, almost all parasitoids of exposed caterpillars are endoparasitic koinobionts which develop inside a living host. Tropical Ichneumonidae might be less speciose than temperate ones (Owen & Owen, 1974), but other parasitoid groups do not seem to follow this trend (Eggleton & Gaston, 1990; Morrison, Auerbach & McCoy, 1979; Noyes, 1989). Parasitism rate in exposed hosts is usually 10 - 40%, and populations of exposed hosts are probably more commonly regulated by predators than parasitoids (Cornell *et al.*, 1995). There seems to be no clear latitudinal trend in parasitism rate, but Stireman *et al.* (2005) found parasitism rate to increase with climatic unpredictability.

Host specificity of external herbivore parasitoids was rarely quantified, because it requires analysis of a broad range of hosts so that parasitoid host ranges are not underestimated. The only explicit analysis on a larger dataset was limited to one superfamily of mostly semi-concealed hosts (Tortricoidea; Mills, 1992). From parasitoids of caterpillars in that study, ichneumonid wasps were the most specialized (with 5.1 host species in average), followed by braconid wasps

(7.8 hosts) and the least specialized tachinid flies (16.3 hosts). Further evidence comes from small scale studies and any generalization is fraught with problems of low sample size, narrow range of species examined and unexpectedly common misidentification of hosts, parasitoids or both, rendering the literature records useless for rigorous analysis of parasitoid host specificity (Shaw, 1994). Parasitoid host specificity has therefore not been subjected to meta-analysis like parasitism rate or parasitoid species richness on hosts (Hawkins, 1994). Nevertheless, some rough consensus emerged from the literature. Koinobionts are generally more specialized than idiobionts, as they are more intimately associated with their hosts and have to cope with the host immunity system (Askew *et al.*, 1986). Semi-concealed hosts are expected to have larger share of idiobiont parasitoids than exposed hosts and therefore should have less specialized parasitoids than exposed hosts. Tachinidae are koinobionts, but their larvae use host immunity encapsulation reaction to form a respiratory funnel and separate themselves from the inner environment of the host, therefore partially escaping the need to avoid host immunity (Eggleton & Gaston, 1992). Indeed, they were for a long time regarded to be less specialized than Hymenoptera parasitoids (Belshaw, 1994; Sheehan, 1994; Stireman *et al.*, 2005), with extreme records of up to 100 host species from different Lepidoptera families (Eggleton *et al.*, 1992). However, recent studies of morphology, DNA barcodes and ecology have shown that caterpillar-attacking Tachinidae might be more specialized than previously thought, commonly attacking only a few closely related hosts (Smith *et al.*, 2007; 2006). When the same methods were used to study Microgastrinae, the largest subfamily of Braconidae, the parasitic wasps were found to be most commonly monophagous and therefore even more specialized than Tachinidae (Smith *et al.*, 2008). Therefore, there is a clear need for new host specificity analyses which would cover all parasitoid groups to evaluate absolute as well as relative host ranges in caterpillar parasitoids.

Meanwhile, on the pages of main ecological journals the emphasis has moved from community structure and host specificity to food web structure. The most commonly used indices characterizing food web structure are connectance, compartmentalization, nestedness and modularity. Connectance is the proportion of realized links in the web. Compartmentalization is defined as the number of discrete compartments in the food web, disconnected from each other. Nestedness is a measure of the extent to which interactions between consumers and resources can be ordered so that host ranges of generalist consumers encompass host ranges of more specialized consumers. Modularity is the extent to which the food web can be split into unconnected or weakly connected modules. However, all these indices seem to be very strongly positively or negatively correlated with each other as well as with consumer specialization, with the correlation coefficient commonly reaching 80% (Graham *et al.*, 2009; Guimera *et al.*, 2010; Thebault & Fontaine, 2010). Therefore, although each of the indices describes slightly different aspect of food web structure (Fortuna *et al.*, 2010), in reality it is difficult to distinguish between them. The food web analysis paradigm also deals differently with species abundances (Bluthgen,

2010). While studying host specificity we try to control for the effect of abundance as far as possible, food web approach includes abundance as part of the food web structure. I see the main advantage of food web approach in simple representation of food webs, which facilitates comparison and therefore allows uncovering patterns which would be difficult to spot with traditional community ecology approach. On the other hand, the focus on linking pattern between resource and consumer species can lead to downplaying the impact the consumers have on the resources and vice versa. This is also because the link strength is commonly quantified in easily recordable ways because e.g. impact on fitness is difficult to measure (Berlow *et al.*, 2004).

Molecular tools for food web research

A relatively recent possibility for improving quality of trophic interaction data is incorporation of molecular evidence. This can be done through refining species concept of studied organisms, or molecular detection of the interactions. Species concept has the potential to strongly influence the outcome of food web structure analysis, changing species numbers as well as specialization and food web indices. DNA sequence data provide a line of evidence for species concept independent from morphology. However, DNA sequencing is still too expensive to be regularly used on datasets of thousands or tens of thousands specimens which are common in tropical food web research. The currently only feasible way to obtain DNA sequence data for large food web projects with expensive fieldwork is collaboration with the International Barcode of Life project which provides sequencing of 658bp long section of mitochondrial cytochrome oxidase I gene (DNA barcode in strict sense) for free or for a subsidized cost. Ideally, the molecular evidence would include several, mainly nuclear gene fragments, because mitochondrial DNA differs in heredity patterns from nuclear DNA. But mitochondrial genes are easily amplified even from degraded material, and the DNA barcode shows very good correspondence with species limits in areas with well known fauna. For example, in Europe, DNA barcodes are expected to unambiguously identify 95% of Lepidoptera species (Hausmann *et al.*, 2011). Both morphology and DNA barcode based identification is prone to errors, but when put together should provide high quality species concept. In the few tests done so far, the change due to inclusion of molecular information in species concept did not change the outcome of food web analyses (Kaartinen *et al.*, 2010; Smith *et al.*, 2011), but it is reasonable to include the best available evidence when possible. A related issue to species concept is description of new species. Parasitoid species encountered in the tropics are almost always undescribed, which hinders accumulation of knowledge and cross-referencing of species between studies. However, parasitoid taxonomists are few, overloaded, and tend to prefer material with good quality collateral information like host records or DNA sequences, both of which are surprisingly scarce in taxonomic literature.

Until recently, the detection of host - parasitoid interactions depended solely on host rearing. Rearing supplies adult host and parasitoid specimens which are more amenable to identification than their larvae, but has also two major disadvantages. First, it has to be successful, which is not a trivial task. Rearing success is rarely reported, but is usually only 30 - 50% (Novotny, personal communication). This lowers sample sizes for analysis and opens a possibility for skewed results if host or parasitoid species differ in rearing success. Second, in order to establish a link between a parasitoid and its host species, the host has to be identified in larval stage, which can be difficult or impossible, especially in small caterpillars. Molecular methods based on species specific PCR primers have been used to link parasitoids with hosts (Traugott *et al.*, 2008), but are not scalable to complex communities of hundreds of species because they require testing for each species individually, or in small batches.

Aims

This thesis builds on large scale insect ecology project in Papua New Guinea which has been for several years rearing externally feeding caterpillars for host specificity analysis (Novotny *et al.*, 2002; Novotny *et al.*, 2004), but postponed analysis of parasitoids and only stored them together with the original rearing information needed to link them to their hosts.

I took this opportunity to work mostly with already collected material with the following aims:

- i) Sort available parasitoid material to family/subfamily and liaise with parasitoid taxonomists to get the parasitoids identified.
- ii) Get DNA barcodes in collaboration with International Barcode of Life project for large proportion of the specimens as an additional line of evidence for parasitoid species concept.
- iii) Analyze parasitoid community structure, parasitism rate, parasitoid host specificity, and the structure of the plant - herbivore - parasitoid food web.
- iv) Try to develop molecular methods for host - parasitoid link detection in complex food webs.
- v) Collaborate with parasitoid taxonomists on species descriptions to ensure long-term value of the caterpillar - parasitoid data.

Summary

Chapter I analyses parasitism rate and parasitoid host specificity in a complex caterpillar - parasitoid food web from lowland rainforest in New Guinea. Semi-concealed caterpillars (leaf-rollers, leaf-tiers) were more common and suffered higher parasitism rates than caterpillars which fed fully exposed. However, the taxonomic and life strategy composition of parasitoid communities was very similar between semi-concealed and exposed host. Semi-concealed hosts and their parasitoids are therefore the largest, yet understudied component of caterpillar - parasitoid food webs and are much closer to exposed host in parasitism patterns than to fully concealed leaf-miners. Parasitoid host specificity was highest in Braconidae, lower in Diptera: Tachinidae, and, unexpectedly, the lowest in Ichneumonidae. This result challenges the long standing view of low host specificity in caterpillar-attacking Tachinidae. For biological control it follows that semi-concealed hosts should be more amenable to control by parasitoids, and Braconidae should be the best biocontrol agents for caterpillar stage, because they are the most host specific.

Chapter II shows how interaction intimacy drives food web structure in a way that low intimacy of herbivore interactions with their host plants leads to high intimacy of interactions with their parasitoids and vice versa. It analyses a similar dataset as chapter I (rescaled to 1ha area) using network analysis tools and compares the results with published food web structure for leaf-miner webs. Further, it uses plant and insect DNA barcodes together with published phylogenetic information to construct community phylogenies for all three trophic levels and test the effect of phylogenies on food web structure. Phylogenies have weak effect of food web structure, probably because the usual split and separate analysis of folivorous Lepidoptera on external and internal feeders already accounts for most of co-variance between phylogeny and food web structure.

Chapter III describes the development of molecular methods for detection of herbivore - parasitoid interactions in complex communities. It uses DNA barcoding of hosts, parasitoids, host remnants and parasitoid larvae dissected from caterpillar hosts and matches the sequences to an extensive library of local species. It thus records 93 previously unknown trophic interactions between 37 host species from a wide range of Lepidoptera families and 46 Hymenoptera and Diptera parasitoid species. Molecular detection proved especially useful in cases where distinguishing host species in caterpillar stage was difficult morphologically, or when the caterpillar died during rearing. The chapter also shows that molecular methods can outperform rearing on an example of two moth species not distinguishable in caterpillar stage and their parasitoids.

Chapter IV is the first of a series of publications that describe parasitoid taxa new to science encountered during the Papua New Guinea insect ecology project and thus increases the long-term value of the data. It describes a new genus of parasitic wasp with three new species and re-describes a rare genus. It also provides host records for the treated species based on rearing and molecular identification of host remnants. One further taxonomic publication from parasitoid material gathered in course of the New Guinea project was already published (Quicke *et al.*, 2012), while several others are in review (Quicke *et al. Cystomastacooides*), or in preparation (Sharkey, Shima, personal communication). Further, the collaboration with Barcoding of Life initiative already resulted into two publications based partially on parasitoid specimens and data from this thesis (Quicke *et al.*, 2012; Smith *et al.*, 2012).

The thesis establishes baseline ecological parameters (parasitism rate, host specificity, and food web structure) for tropical external folivore - parasitoid food webs and compares them with previously published food webs for internally feeding leaf-miners. The parasitoids of external folivores are much more host specific than leaf-miner parasitoids. Therefore, there is little room for indirect interactions between external folivores through their parasitoids. Further, the thesis presents a new method for molecular detection of herbivore - parasitoid relationships, and describes some of the studied species to ensure long-term value of the ecological data.

Future directions

Future research can widen the scope of this thesis by considering spatial variation in caterpillar - parasitoid food web structure, both within the studied environment of lowland tropical forest and along altitudinal and latitudinal gradients. For example, Ichneumonidae parasitoids are reported to be more species rich in lower latitudes, but there are no data on their altitudinal distribution. Also, the high host specificity of caterpillar parasitoids combined with relatively low parasitism rate of ~10% suggests that the caterpillar parasitoids living in the tropics might be under strong pressure from intra-guild predation by caterpillar predators. However, quantification of predation on parasitized caterpillars requires further development of molecular detection techniques.

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Chapter I

Parasitism rate and host specificity in a caterpillar - parasitoid food web from a tropical rainforest

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(manuscript in review in *Oecologia*, a revision requested)

Parasitism rate and host specificity in a caterpillar - parasitoid food web from a tropical rainforest

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ABSTRACT

The processes maintaining the enormous diversity of herbivore - parasitoid food webs depend on parasitism rate and parasitoid host specificity, the two most important food web parameters which have not been adequately quantified in caterpillar - parasitoid community studies. The two parameters have to be evaluated in concert to make conclusions about importance of parasitoids as natural enemies and guide biological control. We document parasitism rate and host specificity in a highly diverse caterpillar-parasitoid food web encompassing 266 species of Lepidoptera hosts and 172 species of hymenopteran or dipteran parasitoids from a lowland tropical forest in Papua New Guinea. We found that semi-concealed hosts (leaf-rollers and leaf-tiers) represented 84% of all caterpillars, suffered a higher parasitism rate than exposed caterpillars (12% vs. 5%) and their parasitoids were also more host specific with equally low share of the more generalist idiobionts (2%) as in exposed caterpillars. Semi-concealed hosts should therefore be generally more amenable to biological control by parasitoids than exposed ones. Parasitoid host specificity was highest in Braconidae, lower in Diptera: Tachinidae, and, unexpectedly, the lowest in Ichneumonidae. This result challenges the long standing view of low host specificity in caterpillar attacking Tachinidae and suggests high suitability of Braconidae and low suitability of Ichneumonidae for biological control of caterpillars. Semi-concealed hosts and their parasitoids are the largest, yet understudied component of caterpillar - parasitoid food webs and they are much closer to exposed host in parasitism patterns than to fully concealed leaf-miners.

Chapter II

Interaction intimacy drives the structure of plant - herbivore - parasitoid foods webs

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(manuscript)

Interaction intimacy drives the structure of plant – herbivore – parasitoid foods webs

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ABSTRACT

Intimacy of inter-specific interactions has been suggested as a key factor determining the structure of food webs with implications for food web stability. Food web structure is well known for species-rich tri-trophic webs centred on leaf-miners, but data on webs centred on other folivorous guilds are scarce, which hinders testing the effect of intimacy on food web structure.

We analyze the structure of a complex plant - external folivore - parasitoid food web from 1ha of secondary forest in Papua New Guinea, evaluate the degree to which sampling and phylogeny influence the structure of the food web, and compare our results to previous results on tri-trophic leaf-miner webs.

The herbivory level of our web was more connected and nested, and showed higher potential for indirect interactions than the parasitism level. This pattern is exactly opposite to food web structure reported previously for leaf-miner webs, which are weakly connected at herbivory level and strongly connected at parasitism level. The food web structure correlates with intimacy at both herbivory and parasitism level in webs centred on both external folivores and leaf-miners. Further, the effect of intimacy also cascades over trophic levels, as endophagy at herbivory level promotes ectophagy in parasitoids and vice versa.

Contrary to intimacy, sampling and phylogeny of the interacting species had only a weak effect on food web structure. We further show that herbivore species degree at herbivory level correlates with its species degree at parasitism level, indicating stronger than random interdependence between the trophic levels. We also report inconsistent results of compartmentalization and modularity with their relative versions and show by rarefaction analysis that the null model commonly used for the relative versions might be inappropriate.

Our results open a way for more realistic food web models and suggest external folivore and leaf-miner tri-trophic webs as a good model system for experimental tests of the effect of food web structure on its stability, as they include both strongly and weakly connected sub-webs on each trophic level.

Chapter III

Molecular detection of trophic links in a complex insect host - parasitoid food web

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Molecular Ecology Resources (2011) 11, 786–794

Molecular detection of trophic links in a complex insect host–parasitoid food web

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Abstract

Previously, host–parasitoid links have been unveiled almost exclusively by time-intensive rearing, while molecular methods were used only in simple agricultural host–parasitoid systems in the form of species-specific primers. Here, we present a general method for the molecular detection of these links applied to a complex caterpillar–parasitoid food web from tropical rainforest of Papua New Guinea. We DNA barcoded hosts, parasitoids and their tissue remnants and matched the sequences to our extensive library of local species. We were thus able to match 87% of host sequences and 36% of parasitoid sequences to species and infer subfamily or family in almost all cases. Our analysis affirmed 93 hitherto unknown trophic links between 37 host species from a wide range of Lepidoptera families and 46 parasitoid species from Hymenoptera and Diptera by identifying DNA sequences for both the host and the parasitoid involved in the interaction. Molecular detection proved especially useful in cases where distinguishing host species in caterpillar stage was difficult morphologically, or when the caterpillar died during rearing. We have even detected a case of extreme parasitoid specialization in a pair of *Choreutis* species that do not differ in caterpillar morphology and ecology. Using the molecular approach outlined here leads to better understanding of parasitoid host specificity, opens new possibilities for rapid surveys of food web structure and allows inference of species associations not already anticipated.

Keywords: cytochrome oxidase I, Diptera, Hymenoptera, immature stages, Lepidoptera, Papua New Guinea

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Introduction

Molecular methods are becoming a critical tool necessary for the identification of small, morphologically uniform organisms and their biological remnants (Greenstone 2006). Until now, the molecular detection of host–parasitoid links was confined to food webs with a limited number of species, predominantly in agricultural systems (Garipey *et al.* 2007). The most extensive such study published so far included nine parasitoid and three hyperparasitoid species of a single host species (Traugott *et al.* 2008).

In this study, our intention is to bring these methods farther into the realm of community ecology, where interactions in the tens or hundreds of species are commonplace. It is already common to use molecular methods for refining species concepts in community ecology studies, e.g. Janzen *et al.* 2009; Kaartinen *et al.* 2010; Smith *et al.* in

press, 2008; so it is a logical next step to use them for mapping between-species interactions. Accurate description of host–parasitoid interactions is crucial for understanding host specificity, arguably the main parameter of host–parasitoid food webs. Knowing host specificity is important for estimates of arthropod diversity (Novotny *et al.* 2002) and explanations of its origin (Schemske *et al.* 2009). In an applied context, it is crucial for the selection of biological control agents (Miller 2007). The structure of the food web itself provides important information, as it can differ both qualitatively and quantitatively among habitats (Tylianakis *et al.* 2007), seasons (Lewis *et al.* 2002) and guilds (Novotny *et al.* 2010), and it is thus important to describe it as precisely as possible.

To date, host–parasitoid interactions have been mapped by rearing the host larvae, until either a host or a parasitoid adult emerged. Rearing provides adult specimens that are tractable for taxonomic identification and provides evidence that the parasitoid can successfully develop in the host. The main caveat of rearing is that

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Chapter IV

A new genus and three new species of parasitoid wasp from Papua New Guinea and redescription of *Trigonophatnus* Cameron (Hymenoptera, Braconidae, Rogadinae)

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Journal of Natural History (2012) 46, 1369–1385

A new genus and three new species of parasitoid wasp from Papua New Guinea and redescription of *Trigonophatnus* Cameron (Hymenoptera, Braconidae, Rogadinae)

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Vojtechirogas novotnyi gen. nov. & sp. nov., *V. heberti* sp. nov. and *V. wantok* sp. nov. reared from *Philiris helena* (Snellen) (Lepidoptera: Lycaenidae) feeding on *Macaranga* spp., in northern lowland Papua New Guinea, are described and illustrated. Based on molecular data, on the modified vein 2-SC+R of the hind wing and the inclivous vein r-m of the forewing, *Vojtechirogas* gen. nov. appears most closely related to the monotypic genus *Trigonophatnus* Cameron, 1907, also from Papua New Guinea. These two genera differ from one another markedly in many characters usually considered important in Rogadinae systematics such as the presence/absence of a subbasal lobe of the claws, of the mediolongitudinal carina of the metanotum and of the basal triangular area of the second metasomal tergite. *Trigonophatnus* is redescribed and illustrated and is reported as a parasitoid of *Hypochrysops chrysargyrus* (Lepidoptera: Lycaenidae) based upon molecular analysis of host remains. Additional specimens of *Vojtechirogas* gen. nov. are reported but not assigned to species because of lack of molecular data in this morphologically uniform genus.

Keywords: cytochrome oxidase I; DNA barcoding; Lepidoptera; hosts; Rogadini; Lycaenidae

Introduction

The South-East Asian and Australasian members of the subfamily Rogadinae are still poorly known, and with the exception of the distinctive Spinariini (van Achterberg 2007), no group has been revised. At the generic level, identifications have been assisted by the work of Chen & He (1997) on the Chinese fauna which includes several elements that are typical of more tropical faunas. No key specific to the Australasian region has been published and very little work has been carried out on it since the early 20th century. Recently, a large herbivore and parasitoid rearing programme in Papua

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Education

2002 - 2005 B.Sc. in Biology, University of South Bohemia
2005 - 2008 M.Sc. in Entomology, University of South Bohemia
2008 - present studies for PhD in Zoology, University of South Bohemia,
Thesis: Caterpillar - parasitoid food webs in New Guinea rainforest,
Supervisor: Prof. Vojtech Novotny

Professional Appointments and Travel

2006 - present Biology Center, Czech Academy of Sciences
2006 one year stay at [New Guinea Binatang Research Center](#), PNG
2009 four months stay at New Guinea Binatang Research Center, PNG
2012 one month stay at University of Edinburgh, UK, Graham Stone lab

Languages: Czech (native), English, Melanesian Pidgin, German

Publications

- Novotny, V., Miller, S.E., **Hrček, J.**, Baje, L., Basset, Y., Lewis, O.T., Stewart, A.J.A., & Weiblen, G.D. (2012) Insects on plants: explaining the paradox of low diversity within specialist herbivore guilds. *American Naturalist*, 179, 351-362.
- Quicke, D.L.J., Smith, M.A., Van Achterberg, C., Miller, S.E., & **Hrček, J.** (2012) A new genus and three new species of parasitoid wasp from Papua New Guinea and redescription of *Trigonophatnus* Cameron (Hymenoptera, Braconidae, Rogadinae). *Journal of Natural History*, 46 (21-22), 1369-1385.
- Quicke, D.L.J., Smith, M.A., Miller, S.E., **Hrček, J.** & Butcher, B.A. (2012) *Colastomion* Baker (Braconidae, Rogadinae): nine new species from Papua New Guinea reared from Crambidae. *Journal of Hymenoptera Research*, 28, 85-121.
- Quicke, D.L.J. and 21 co-authors (2012) Utility of the DNA barcoding gene fragment for parasitic wasp phylogeny (Hymenoptera: Ichneumonoidea): data release and new measure of taxonomic congruence. *Molecular Ecology Resources*, 12, 676-685.
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- Hrček, J.**, Miller, S.E., Quicke, D.L.J., & Smith, M.A. (2011) Molecular detection of trophic links in a complex insect host-parasitoid food web. *Molecular Ecology Resources*, 11, 786-794.
- Konvicka, M., Novak, J., Benes, J., Fric, Z., Bradley, J., Keil, P., **Hrček, J.**, Chobot, K., & Marhoul, P. (2008) The last population of the Woodland Brown butterfly (*Lopinga achine*) in the Czech Republic: habitat use, demography and site management. *Journal of Insect Conservation*, 12, 549-560.

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- Hrček, J.**, Miller, S.E., Whitfield, J.B., Shima, H. & Novotny, V. Parasitism rate and host specificity in a caterpillar - parasitoid food web from a tropical rainforest.
- Sladeczek, F.X.J., **Hrček, J.**, Klimes, P. & Konvicka, M. Interplay of succession and seasonality reflects resource utilization in an ephemeral habitat.
- Quicke, D.L.J., Smith, M.A., **Hrček, J.** & Butcher, B.A. *Cystomastacoides* van Achterberg (Braconidae, Rogadinae): first host record and descriptions of two new species from Thailand and Papua New Guinea.

Smith, M.A, Fernández-Triana, J. and 18 co-authors. DNA barcoding and the taxonomy of Microgastrinae wasps (Hymenoptera, Braconidae): impacts after eight years and nearly 20,000 sequences.

Reviewed manuscripts for Molecular Ecology, Molecular Ecology Resources, and Insect Conservation and Diversity.

Student supervision

Martin Volf (M.Sc., finished 2012): How does leaf chemistry and host phylogeny structure communities of external leaf chewing herbivores on willows?

Martin Libra (B.Sc., finished 2012): Intraguild predation of predators on parasitoids.

Martin Volf (B.Sc., finished 2010): Structure of leaf chewing herbivore community on willows.

František Sládeček (B.Sc., finished 2010): Succession in dung beetle communities.

Conferences

BES Annual Meeting, University of Sheffield, 2011 (oral): Molecular identification allows inclusion of predators into a plant-caterpillar-parasitoid food web.

23rd International Congress of Entomology, Durban, South Africa, 2008 (oral): Parasitoid communities attacking leaf chewing Lepidoptera in New Guinea rainforest.

Founding Meeting of the Czech Society for Ecology, Třeboň, Czech Republic, 2008 (oral): Parasitoid communities attacking leaf chewing Lepidoptera in New Guinea rainforest.

3rd European Congress on Social Insects, St. Petersburg, Russia, 2005 (two posters): Spatial and temporal distribution of nests of *Myrmica* ants hosting *Maculinea alcon* (J. Hrcek, M. Janda and Z. Krenova), Ants in New Guinea rainforest canopy (M. Janda and J. Hrcek).

Grants

three small undergraduate grants,
since 2007 involved in grant applications of the PNG group of Vojtech Novotny.

Outreach

Conveying the New Guinea research experience and leading entomology excursions (often both at the same occasion). Favourite groups to demonstrate: ants and other Hymenoptera, galls including gall ink making.

. secondary schools (talks at four different schools; one day field excursion; 2x ten days biological expedition to Corfu; 4x National Biology Olympiad training one day entomology excursion and talk; one day field excursion and talk for high school teachers)

. general public (half an hour radio interview, 2x talk about the New Guinea research on a music festival, talk in a local nature conservation club, talks at two primary schools)

References

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