Metacommunity dynamics of Ostracoda (Crustacea) in Central American bromeliads (Bromeliacea)

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Abstract

Ecological and applied conservation practices are currently more and more placed in a metacommunity context. A good theoretical framework for this concept exists. Empirical data however is scarce and in particular the dispersal process, the central concept in connecting communities, remains a black box. The present project aimed at increasing our insight in the role of dispersal as community structuring process in metacommunities. We here fore studied aquatic invertebrates in bromeliads with particular attention for seed shrimp (Ostracoda). The dynamic nature of bromeliads and the small well defined communities make this system particularly valuable for metacommunity research. We made strives to develop this habitat as a model system for metacommunity dynamics.

Fieldwork was in Cusuco National Park (CNP) and Pico Bonito National park (PBNP), Honduras and the project consisted of three parts. In Part 1 the study system was described and placed in a global context, setting the base for further studies. This included the identification of aquatic invertebrates in the bromeliads with the description of several new taxa (e.g. Ostracoda and Chironomidae). Subsequently the abiotic environment, such as the daily water temperature and pH fluctuations in the bromeliad leaves, was recorded and described. We reviewed crustacean observations in phytotelmata worldwide.

In part 2 the applicability of classic ecological and biogeographic patterns to bromeliad aquatic invertebrate diversity was tested. From classic patterns (richness–altitude, richness–environment, richness–habitat size, richness–habitat complexity and richness–isolation relationships), only the relationship between habitat size (bromeliad size) and richness was significantly present. The ephemeral bromeliad habitat requires high colonization dynamics to sustain populations of aquatic invertebrates and this feature results in a large background noise. We therefore tested the relative importance of random dispersal versus habitat selection during community assembly with experimental set-ups (artificial bromeliads) and found that habitat selection plays a crucial role.

In the third and last part we looked in the relationship between forest stability and crustacean diversity. For this we developed a wind pressure model generating hurricane exposure values on a high resolution (50x50m) scale for CNP (Honduras). The generated values, indicating the vulnerability to high intensity weather events, were correlated with bromeliad aquatic crustacean diversity. This relationship suggests that the passively dispersing crustaceans in these systems are dispersed by high intensity weather events.

In conclusion, we completed the envisaged goals for the project. Large strives are set towards the use of aquatic invertebrates in bromeliads as model systems for ecological research and metacommunity dynamics through descriptive studies, successful experiments and models.

Keywords: community structure, diversity, conservation, hurricane, Honduras

1. Introduction

The notion that communities should be studied in spatial and temporal scales, linking other communities in the region, led to the development of the metacommunity concept (Hanski 1998, Leibold et al. 2004). The development of metacommunity models was a big step towards the understanding of natural communities and biodiversity patterns with promising perspectives in many fields in ecology and evolution and with many applications in conservation and nature management. An understanding of the factors structuring a metacommunity is the base for understanding biodiversity patterns at a global scale (Jocque et al. 2010). The core element of metacommunities is the **dispersal process** linking different communities in a region. Based on the exchange intensity of organisms between communities, different models are recognized. At one end of the gradient with high exchange of individuals (in one direction) is the **mass effect model**, the model changes to **species sorting** with decreasing dispersal and to **patch dynamics** at the other end of the gradient. Despite the importance of dispersal in the metacommunity concept, this is the process that is the least understood, and for which only few empirical data are available. Especially the quantification of the process and how dispersal links different temporal and spatial scales largely remain a black boxes (Clobert et al. 2000).

One of the reasons why little empirical evidence is present on metacommunity dynamics is the lack of a generally accepted model system for metacommunity studies. Surprisingly, until now no single habitat used to study community ecology and evolution is generally accepted as model system. Community ecological studies quickly become very complex with increasing numbers of species. The wide variety of factors affecting the interspecific relations further adds to the difficulty of understanding the processes driving community dynamics. In order to achieve a suitable balance between tractability and realism, a balance is needed between a diverse enough community to be realistic, but not too diverse to overcomplicate the overall picture. In this perspective, community ecologists are becoming increasingly interested in small natural habitats as study systems (Srivastava et al. 2004).
Small aquatic water bodies are potentially valuable for studying ecological and evolutionary topics, and are therefore receiving a surge of interest (Blaustein and Schwartz, 2001; Srivastava et al. 2004; De Meester et al. 2005). These habitats, including phytotelmata (plant-held water bodies), contain well-delineated communities, allowing for a clear definition of local and regional species pools. Despite being small and simple, these habitats house a surprisingly high diversity of aquatic invertebrates (Kitching, 2000), well suited to the study of ecological interactions in realistic settings. Most organisms are active dispersers, meaning they can disperse in the adult stage to colonize new habitats (e.g. Culicidae, Chironomidae, Syrphidae and different families of Coleoptera). However, more permanent populations of phytotelmata are characterized by the presence of passive dispersers. These are aquatic invertebrates that need a dispersal vector to colonize new habitat patches. This is remarkable considering that most habitat patches, being plants, have only a short lifespan. The passive dispersers in bromeliads are mostly Ostracoda, Cladocera and Copepoda. The limited lifetime of the plant structures makes that the inhabitants require a high and flexible dispersal ability of the inhabitants that comes with an active dispersal compared to vector dependent passive dispersal. Aquatic invertebrate communities in bromeliads therefore typically have only a small number of passive dispersers (e.g. Ostracoda) and a dominance of active dispersers (e.g. Culicidae). This required dynamic aspect in metacommunity dynamics clearly sets these habitats apart from other, more permanent, small water bodies, where the

representation of both dispersal strategies is much better balanced. Despite the scientific value of bromeliad habitats, the information available comes mostly from scattered studies. In these studies little information is presented on for instance basic water characteristics (pH and water temperature), environmental variation and extreme values, occurring species (most species are new to science) and community structuring factors to mention just a few (but see Frank and Lounibos 1987, Kitching et al. 2000).

The present project aims at increasing our understanding of the dispersal process through the quantification of dispersal dynamics in metacommunities and evaluates the effect on community structure, diversity patterns and ecosystem aspects. As part of the project we will develop aquatic invertebrates in bromeliads as a model system to study metacommunities. Data will be gathered with additional sampling and experimental set ups.

2. Methodology and results

Overall the project went as planned. The only issue worth mentioning is the inclusion of all aquatic invertebrates in some ecological analyses. The data generated on aquatic Crustacea alone sometimes was not sufficient to tackle the aimed research questions, in which cases, analyses were extended to include the complete aquatic invertebrate communities in the bromeliads. The schedule also included some minor changes triggered by obstacles encountered during fieldwork. These included issues obtaining export permits for the samples, but nothing that set back the project too much. The destruction of a long running (1 year) experimental setup due to deforestation of the forest plot in CNP was the most difficult setback.
In the following section we will go over the original objectives (in bold) and directly under that comment on their realisation.

Part 1. Strategic objective : Description of organisms and habitat.

> **1. Development of a model system for ecology and evolutionary biology, through the three dimensional characterization of bromeliad populations in a cloud forest and high resolution abiotic characterization (*with data loggers for pH, water temperature, conductivity and oxygen*) and biotic characterization (identification of occurring species in the habitat).**

Abiotic habitat characterization is completed and published (Jocque and Kolby 2012). Based on an intensive survey with data loggers we surveyed pH and water temperature in bromeliads in different levels of the forest, up to 34 m high in the canopy.
The biotic characterization is largely finished. Most of the occurring invertebrate species in the bromeliads are identified to species level, or at least separated in morphospecies confirmed by taxonomic specialists in the relevant groups. Selected new species were described (Mendes et al. 2011) or descriptions are still in progress (Schmelz and Jocque, Bravo and Jocque) but these manuscripts should be submitted in the near future.

Bravo F. and **Jocqué M.** Reworking based on comments reviewers. A new species of *Telmatoscopus* Eaton (Diptera, Psychodidae) from Honduras; a Holarctic representative in Central America. Zootaxa.

Jocqué M. and Kolby J. 2012. Acidity of tank bromeliad water in a cloud forest, Cusuco National Park, Honduras. International Journal of Plant Physiology and Biochemistry. 4: 59-70.

Mendes H., Andersen T. and **Jocqué M.** 2011. A new species of *Polypedilum* Kieffer from bromeliads in Parque Nacional Cusuco, Honduras (Chironomidae: Chironominae). Zootaxa: 3062: 46-54.

Schmelz R. and **Jocqué M.** In preparation. Two new species of Enchytraeidae (Oligochaeta) from epiphytic bromeliad pools in an Honduran cloud forest, the first enchytraeid species known and described from phytotelmata.

2. Taxonomy of Ostracoda: (re-) description of (new) species

Two undescribed species of Ostracoda were collected from the bromeliads in Honduras. The first is a typical bromeliad specialist, and is described as *Elpidium meredonensis* (Pinto and Jocque 2013). This is the first species of Ostracoda described for Honduras. The second ostracod species commonly occurring in the studied bromeliads turned out to be a completely new genus and the description is still in process. The drawings are completed, and the manuscripts is in its final phase and should be submitted soon (Jocque et al. In preparation).

Pinto R. L. and **Jocqué M.** 2013. A new species of *Elpidium* (Crustacea, Ostracoda) from bromeliads in Cusuco National Park, Honduras. Zookeys: 313: 45-59.

Jocqué M., Pinto R. L. and Martens K. In preparation. A new genus of bromeliad inhabiting and salamander dispersed ostracods in Honduras. Zookeys.

3. A (worldwide) review of Crustacea inhabiting Phytotelmata, based on literature and focusing on the dispersal.

Besides two species of Ostracoda, we also recorded two Anomopoda (*Ceriodaphnia laticaudata* and *Alona bromelicola*) on a regular basis in the bromeliads in Honduras. To better place the occurrence of passively dispersing zooplankton in such highly ephemeral habitats, we composed a literature review to evaluate how commonly Crustacea occur in phytotelmata (plant held water bodies). The review is published in the Journal of Crustacean Biology (Jocque et al. 2013).

Jocqué M., Fiers F., Romero M., and Martens K. 2013. Crustacea in phytotelmata: a global overview. Journal of Crustacean Biology. 33, 451-460.

Part 2. Strategic objective: The disentangling of community structuring factors, quantification of the dispersal process and ecosystem dynamics.

4. Dispersal process of Bromeliad inhabiting Ostracoda: 1) To identify the main dispersal vectors of Ostracoda *(direct observations and experimental set ups)*, 2) To quantify the dispersal dynamics of Ostracoda *(experimental setups)*

We made the first observation of Ostracoda (*Candonopsis s.l.* sp.) dispersal through salamanders worldwide. Results will be included with the description of the ostracod genus (Jocque et al.).
Besides direct observations, experimental set-ups (Jocque and Preziosi, see point 5 below) further confirmed the importance of amphibians for the local dispersal of Ostracoda. On a larger scale we found strong indications that Ostracoda are dispersed by high intensity weather events (Jocque et al., see point 7 below).

Jocqué M., Batke S., Stok W. and Field R. In preparation. Riders on the storm; passively dispersing zooplankton communities in bromeliads are sustained by hurricanes.
Jocqué M., Pinto R. L. and Martens K. In preparation. A new genus of bromeliad inhabiting and salamander dispersed ostracods in Honduras. Zookeys.
Jocqué M. and Preziosi R. In preparation. Habitat selection on habitat structure drives early community assembly in dynamic aquatic ecosystems. Functional Ecology.

5. To identify the community structuring factors and ecosystem dynamics.

A manuscript on the **community structuring factors** in bromeliads was submitted to Hydrobiologia and we are currently reworking the manuscript based on constructive suggestions form the reviewers (Jocque and Field submitted). In this manuscript we use the standardised data collected from 2006-2007 on aquatic invertebrates in bromeliads to test to what extent classic community structuring factors apply. This dataset includes 157 communities from a single location and is one of the largest standardized datasets on aquatic invertebrates in bromeliads currently available. More specifically we tested for the presence of species richness–altitude, richness–environment, richness–size, richness–habitat complexity and richness–isolation relationships for aquatic invertebrates communities in Cusuco National Park, Honduras. We found that invertebrate species richness and abundance correlated most strongly, and positively, with habitat size. Less than 20% of the variation in community composition was explained by the tested variables. Apart from bromeliad size (equivalent of the species–area relationship) and the number of bromeliads in the (cluster) metacommunity, we found remarkably little evidence of classic biogeographic and ecological relationships in this system.
Community composition correlated with altitude, bromeliad size and position. The turnover component of dissimilarity between the communities correlated with altitude, while the nestedness-resultant component was related to bromeliad size. The unexplained variance could reflect a large stochastic component in the system, associated with the ephemerality of the habitat patches (both the plants themselves and the fluctuations in their water content) and stochasticity due to the dispersal dynamics in the system.

Aquatic invertebrates in bromeliads are a highly dynamic habitat system characterised by a small patch size and a high dynamic, in particular with high emigration rates. These characteristics result in a small contribution of most classic biogeographic factors to the community composition in these systems and are mostly driven by factors affecting the colonisation success.

To look in the **ecosystem dynamics** of this system, we tested for the presence of habitat selection in community assembly of newly created artificial bromeliad containers. Besides random dispersal followed by differential establishment success, active habitat selection (AHS) provides an alternative driver for the assembly of ecological communities. Although the importance of habitat selection is generally acknowledged, little is known about the relative importance of both random and targeted dispersal in natural metacommunities, and about the cues used for targeted dispersal by component species. Given that reliable cues of habitat quality are available, we hypothesized that AHS could potentially increase alpha diversity and reduce beta diversity in the bromeliad metacommunities.
We tested this with a colonization experiment using aquatic invertebrates inhabiting natural water bodies in bromeliads (phytotelmata). Results from an experiment run in 2011 were submitted to the Journal Functional Ecology, but rejected because it was not possible to differentiate the observed effect of habitat selection from habitat complexity. We therefore repeated the experiment in 2013 with added treatments for habitat complexity, and its in preparation for resubmission to Functional Ecology (Jocque and Preziosi). In the final experiment we investigated the effect of physical structure (with and without bromeliad leaves) and habitat complexity (with and without submerged bromeliad leaf bases) on the community assembly of aquatic invertebrates in artificial phytotelmata in Honduran cloud forest.
We found a strong effect of habitat selection increasing alfa and reducing beta diversity in the containers with leaves. Over 1/4th of the variation in community structure during assembly could be explained by the difference in habitat structure. Our results show how physical habitat characteristics in highly dynamic systems play a key role in the colonisation process and how habitat selection and in particular multispecies habitat selection has strong consequences for diversity patterns in a metacommunity.

Jocqué M. and Field R. Aquatic invertebrate communities in tank bromeliads: how well do classic ecological patterns apply? Hydrobiologia.
Jocqué M. and Preziosi R. In preparation. Habitat selection on habitat structure drives early community assembly in dynamic aquatic ecosystems. Functional Ecology.

6. Ecosystem interactions – quantification of interaction strengths - evaluate how the extinction of key species (amphibians) can result in cascading effects.

This experiment was not completed as the experimental set-up was destroyed due to illegal deforestation. Based on results from research component 3 in this project, looking into the relationship between forest stability and diversity, it seems unlikely that the current hypothesis would hold. Considering the difficult logistics and the long term requirements for the set-up, we decided not to repeat this experiment and instead focus more on the model to test the correlation of forest stability with large weather events (part 3).

Part 3. Application

7. Development of a preliminary index of ecosystem age/health based on the crustacean (aquatic invertebrate) diversity in bromeliads. This conservation index would be comparable to the biotic index for rivers and aims to reflect the nature value of an ecosystem in terms of time it would take to assemble a particular community in a specific setting.

This is the most challenging part of this project. A straightforward option to evaluate forest quality would be to perform an in depth biodiversity survey of several forest plots and see with what components bromeliad aquatic invertebrate diversity correlates. This approach is both time consuming and requires a high level of expertise to reliably name the other taxa in the forest. As an alternative approach we evaluated forest quality by looking into (natural) disturbance. For our study site, we modeled hurricane exposure values as a proxy for forest stability (Batke et al. submitted) and looked how well these values explained observed diversities of Crustacea in bromeliad clusters (metacommunities).

Model developement

High energy weather events are often expected to play a substantial role in biotic community dynamics and large scale diversity patterns but their contribution is hard to prove. We provide a detailed overview on how to generate hurricane exposure data at a mesoclimate level for a specific region. As a case study we modelled landscape hurricane exposure in Cusuco National Park (CNP), Honduras with a resolution of 50 m x 50 m patches. Data from the National Oceanic and Atmospheric Administration (NOAA) were used to calculate the size of historical hurricanes, their wind speed intensities and directions. The model calculations for hurricane wind fields were based on a pressure-wind model. The hurricane model results were combined with a digital elevation map (DEM) to produce an exposure vulnerability site score (EVSS) for different locations within CNP. The model results were validated on the ground using visual tree assessments and rope climbing methods. Eleven hurricanes were found to have affected CNP between 1995 and 2010. The highest EVSS's were predicted to be on South and South-East facing sites. Ground validation demonstrated that the South-solution explained most of the observed tree damage. The model using EVSS also performs significantly better than simple exposure models, explaining up to 90 % of the observations in the field. We believe that our suggested method can be used to make and test predictions regarding species distribution, composition and diversity changes along a gradient of hurricane exposure. This model (Batke et al.) was resubmitted after review to Plos one and is expected to be published soon.

Relationship forest stability versus crustacean diversity in bromeliads

Making use of the hurricane exposure as a proxy for forest disturbance we tested the relationship between habitat stability and crustacean diversity in bromeliads. Based on the dominant predictive Hurricane model with hurricanes coming from the South, the survey was aimed to cover and provide enough replication in the predicted hurricane exposure categories. We sampled clusters of 10 bromeliads for Crustacea in CNP all over the park. In each bromeliad cluster the ten largest bromeliads were selected. We sampled 85 clusters (850 bromeliads).

The richness, both maximum and average, differed between the hurricane exposure categories of the South model, and peaked at mid exposure (value 3) (Fig. 1). For average richness (SS = 20.949, 4 degrees of freedom, MS = 0.624, F = 3.190, p = 0.017), post hoc (Fisher) test showed significant differences of richness between category 3 and both category 2 (p = 0.001948) and 4 (p = 0.033695). Maximum richness (SS = 9.682, 4 degrees of freedom, MS = 2.421, F = 2.975, p = 0.024),), post hoc (Fisher) test showed significant differences of richness between category 3 with richness in category 1 (p = 0.016171) and 2 (p = 0.010119).

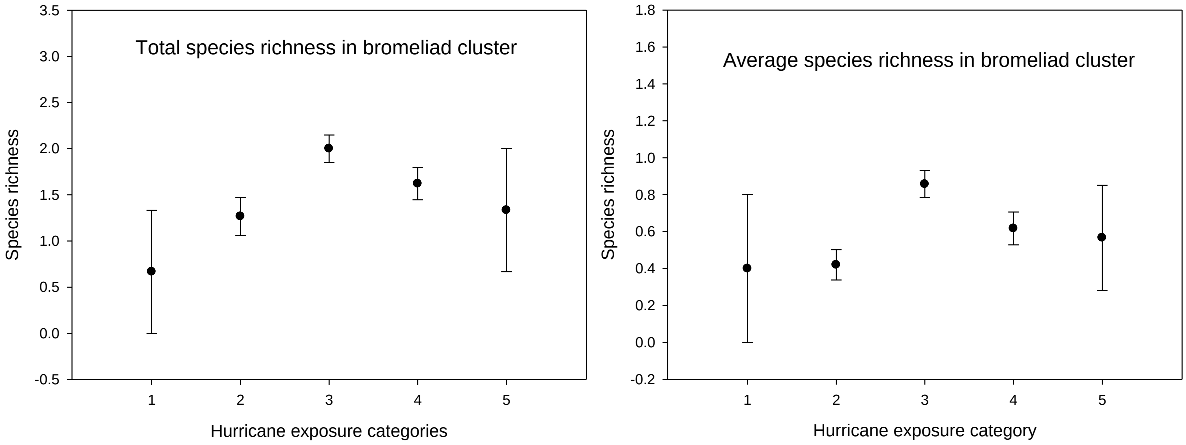

Figure 1. Relationship crustacean diversity with hurricane exposure categories in the total (left) and average (right) species richness in bromeliad clusters in CNP, Honduras.

Jocqué M., Batke S., Stok W. and Field R. In Preparation. Riders on the storm; passively dispersing zooplankton communities in bromeliads are sustained by hurricanes.

Batke S., **Jocqué M.**, Kelly D. Submitted. Modelling hurricane exposure and wind speed on a microclimate scale: a case study from Cusuco NP, Honduras. Plos One.

3. Distribution and valorisation

A copy of the published papers is added with the report. If required, a copy of the manuscripts in preparation can be forwarded to illustrate the level of completion.

Journal articles submitted or in preparation

Batke S., **Jocqué M.**, Kelly D. Submitted. Modelling hurricane exposure and wind speed on a microclimate scale: a case study from Cusuco NP, Honduras. Plos One.

Bravo F. and **Jocqué M.** Reworking based on comments reviewers. A new species of *Telmatoscopus* Eaton (Diptera, Psychodidae) from Honduras; a Holarctic representative in Central America. Zootaxa.

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Journal articles published or in press

Jocqué M. and Kolby J. 2012. Acidity of tank bromeliad water in a cloud forest, Cusuco National Park, Honduras. International Journal of Plant Physiology and Biochemistry. 4: 59-70.

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Pinto R. L. and **Jocqué M.** 2013. A new species of *Elpidium* (Crustacea, Ostracoda) from bromeliads in Cusuco National Park, Honduras. Zookeys: 313: 45-59.

Only publications prepared as part of the project are presented.

List of scientific engagements abroad.

- Ireland 2011 - (11-12 May), Mary Kelly Quinn, University College Dublin.
Preparation of fieldwork in Honduras
- Honduras 2011 - June-August (6 weeks), Cusuco National Park
Fieldwork, collecting samples and experimental set-ups
- USA 2012 - May (3 weeks) - Jessica Ware (Rutgers University) and Rosser Garrison (institute for pest control). Practical guidance how to extract DNA from self collected samples up to the sequence.
- Italy, Modena 2012 - (14-18 May), Italian workshop on phylogenetics and applications.
Course analysis molecular data.
- Honduras 2012 - May-July (6 weeks), Cusuco National Park and Pico Bonito National Park
Fieldwork, collecting samples and experimental set-ups
- Madagascar 2012 - July-August (4 weeks), Mariarano
Sampling temporary aquatic habitats, collecting Ostracoda.
- Honduras 2013 - May-July + August (7 weeks), Cusuco National Park and Pico Bonito National Park. Fieldwork, collecting samples and experimental set-ups.
- USA 2013 - July (2 weeks), International Conference of Conservation Biology (ICCB) 2013.

***Prospects on a long term integration in the Belgian research landscape after termination of this fellowship*.**

This postdoctoral research fellowship and position at the Royal Belgian Institute for Natural Sciences (RBINS) in Brussels provided me with the necessary time to reinforce my specialization as wetland ecologist both nationally and internationally. My priority during this two year fellowship was to obtain a more permanent research position in Belgium. Long term research possibilities in Belgium are limited and during this period only few positions opened. These two years however provided me with a valuable opportunity to disseminate my research results and forge strong collaborations with scientists both nationally and internationally. My national collaborations seriously increased my visibility in Belgian research, increasing chances for a research position in Belgium on the long run. The international collaborations resulted in the seclusion of a postdoctoral position at the lab of Prof. Dr. Jessica Ware (Rutgers University, New Jersey, USA), a prestigious researcher in ecology and evolutionary research. This position allows me to continue my research. This postdoctoral position in the USA, which is valuable research experience for my career, together with my renewed Belgian contacts will hopefully lead to a more permanent research position in Belgium in the future.

Contribution of this project to the research Institute and « Belgian » research in general.

This project crossed many disciplines and therefore required collaboration with a large number of experts both nationally and internationally. The international collaboration with many researchers and prominent research groups for this research project made available expertise and facilities from different research groups to the RBINS and the partners in the Belgian research landscape. The challenging fieldwork in Honduras together with international collaboration helped place Belgium on the map for Central American biodiversity research and also contributed to the international emission of Belgian research.
Also in the RBINS the current research project stimulated collaboration involving several researchers at the RBINS, with some joined publications.