## BioMove Project P01 (Univ. Potsdam/UFZ Leipzig), 3rd PhD student cohort

Supervising team: Volker Grimm, Melanie Dammhahn, Viktoriia Radchuk, Florian Jeltsch

## Intraspecific trait variation in movement behaviour as mechanisms for species coexistence

## 0. Brief expected profile of PhD student

The candidate should have an excellent Master in Ecology or related discipline but we will also consider candidates with a background in Mathematics or any Natural Science if they have experience in the design and analysis of computational models. A strong interest or background in behavioural ecology, movement ecology and/or community ecology is desirable. Experience in capturing and tagging small mammals, analysing spatial data (e.g. via GIS) and in applying complex statistical analyses (e.g. multivariate random regressions) would be appreciated.

## 1. Short Abstract

Intraspecific trait variation (ITV) has received much attention in behavioural ecology (i.e. animal personality) and ecology (e.g. individual niche specialisation) alike and is increasingly recognized as a key element of species persistence and coexistence. Here, we focus on individual differences in movement-related behaviour (boldness, exploration, activity) and assess its consequences for withinand between-species interactions. At this advanced stage, the project builds on (i) detailed knowledge on patterns of variation in ITV under natural conditions and their potential impacts on interactions between rodent species and (ii) on mechanistic models that allow exploring the longer-term consequences of ITV in movement-related traits on species coviability, i.e. the degree of temporary coexistence. In the next step, we will combine experimental manipulations of rodent movement options between habitat patches in the agricultural landscape and of ITV in a rodent meta-community with spatially explicit individual-based modelling to test how dynamic changes of landscape structure modulate the effect of consistent individual differences in movement-related behaviour on species coviability.

## 2. Background and previous work

Differential movement of individuals is a key mechanism generating spatial and temporal patterns of interacting individuals and populations. Individuals vary consistently in life-history, physiological and behavioural traits and such intraspecific trait variation (ITV) affects ecological communities<sup>1,2</sup>. ITVs are also omnipresent in movement and space use (e.g. dispersal, foraging movement, exploration)<sup>3</sup>. While patterns of variation are well demonstrated, the ecological consequences of ITV in movement-related traits are still not well understood. Consequently, most theoretical models in community ecology are based on mean trait values. Here, we combine empirical, experimental and modelling approaches (i) to test whether ITV in movement-related traits affects the local presence, density and spatial behaviour of individuals of co-occurring species, (ii) to determine the potential effects of differential movements for species coviability, and (iii) to illuminate whether and how dynamic landscape changes affect ITV and its consequences.

In the first part of the project (2015-2018), **PhD1** empirically revealed ITV in space use, movement and microhabitat use under natural conditions that were predicted by among-individual differences in boldness in two functionally equivalent and co-occurring rodent species, suggesting individual specialisation in spatial components of ecological niches<sup>4,5</sup>. Within-species variation in spatial niches affected between species spatial interactions in natural and experimental communities. Further, we

developed a method to decipher fine-scale behavioural responses of interacting individuals in ecological communities from movement data<sup>6</sup>.

In the second part of the project (2018-2021), **PhD2** developed a mechanistic model that mimicked the empirical patterns but is generic. This study showed that ITVs in foraging movement affect resource competition between functionally equivalent species and promote species coexistence<sup>7</sup>. In a further generic mechanistic model PhD2 included eco-evolutionary dynamics to test whether density-dependence strengthens the integration of key behavioural (movement-related responsiveness to resource variability) and life-history traits. Along a gradient of fluctuations in density-dependent selection, behavioural and life-history traits evolve to be aligned along a slow-fast continuum at the integr- and intra-populational level. Final steps of this PhD will focus on ITV in dispersal-related traits.

## 3. Objectives/Aims

The overall objective of this project is to understand how ITV in movement-related behaviour, in particular activity, exploration, and boldness, affects population persistence and species coviability. More specifically, we focus on the following objectives for the third part of the project, ideally combining empirical and modelling approaches:

(i) To test whether ITV in movement-related traits affects the local presence, density and spatial behaviour of individuals of co-occurring species in meta-community patches,

(ii) to determine the potential effects of differential movements for short-term local species coviability in meta-community patches, and

(iii) to illuminate whether and how dynamic landscape changes (e.g. in connectivity between habitat patches) affect ITV and its consequences on coviability.

## 4. Outline work program

The work program will have three major steps and combine experimental approaches with a rodent community as the study system and individual-based modelling. First, we will perform a large-scale experiment (as part of the *BioMove* joint experiment) under natural conditions and test how dynamic changes of landscape structures affect ITV in movement-related traits in a meta-community setting. By manipulating the matrix (i.e. agricultural fields) between habitat islands in the *AgroScapeLabs*, we will manipulate dispersal propensity through the matrix and, hence, meta-community connectivity. We will focus on a community of similarly sized rodent species including functionally equivalent pairs and perform intensive capture-mark-recapture at adjacent habitat islands, assess consistent individual differences in behaviour of different rodent species via standardized tests, and record movements of selected individuals. This will be done via VHF- or ATLAS-telemetry to quantify ITV in movement-related traits in populations of co-occurring rodents, dispersal across habitat patches and changes in ITV in populations.

Second, we will run an experiment under near natural conditions in large outdoor enclosures and create small populations of high or low ITV in movement-related traits of co-occurring rodents. By connecting populations differing in ITV using controlled dispersal corridors, we can record dispersal attempts and test for behavioural-type specific dispersal propensity, and allow only specific behavioural types to actually disperse. This experiment will allow to test whether ITV predicts coviability of two ecological similar rodent species and whether dispersal of specific behavioural types erodes or maintains ITV in populations.

Third, we will adopt the models developed by PhD2<sup>7,8</sup> and further develop them to mimic the new experiments. The model focussed on dispersal-related traits will be used to predict ITV-induced differences in connectivity between habitat patches. This model can be linked to a meta-community model, which integrates the *BioMove* joint experiment (*BioMove's* synthesis Postdoc). The models focussed on home-range-related traits will be compared and possibly combined with the dynamic homerange community model of project P11. We will use generic parameter settings, which broadly represent the species involved, to explore the scenarios of the experiments and make qualitative predictions. Based on results from the experiments the models will be refined and calibrated to explore further scenarios to identify and better understand the mechanisms by which ITV affects coviability in heterogeneous and dynamic landscapes.

#### 5. Linkage to 'BioMove' objectives

At the current stage, individual-based ecology is dominated by conceptual and opinion papers highlighting when and where individual differences might matter for ecological interactions among species. In strong contrast to the overt diversity of "ideas" is the paucity of theoretical models and experimental tests particularly for mobile organisms. Combining empirical, experimental and modelling approaches, this project will provide crucial insights into how ITV in movement-related traits affects local species assemblages and, thus, contribute to our mechanistic understanding of the processes generating biodiversity patterns. In particular, the project will help to identify the specific traits of organisms that potentially impact biodiversity, spatial and temporal scales at which movement impacts biodiversity, and whether differential movements of individuals affect species coexistence. In contrast to most theoretical models in community ecology, we will account for individual variation in the average phenotypic response and in plasticity to environmental variation in our individual-based models.

References

#### <sup>1</sup> Bolnick et al. 2011 *Trends Ecol Evol*, 26:183

- <sup>2</sup> Wolf & Weissing 2012 Trends Ecol Evol, 27:452
- <sup>3</sup> Spiegel et al. 2017 *Ecol Let*, 20:3
- <sup>4</sup> Schirmer et al. 2019 Oecologia, 189:647;
- <sup>5</sup> Schirmer et al. 2020 Proc Roy Soc B, 287:20192211
- <sup>6</sup> Schlägel et al. 2019 Methods Ecol Evol, 10:1234
- 7 Milles et al. 2020 Oikos, 129:1441; 8 Milles et al. in review Am Nat

## BioMove Project P02 (Leibniz IZW), 3<sup>rd</sup> PhD student cohort

Supervising team: Stephanie Kramer-Schadt & Viktoriia Radchuk, Niels Blaum, Volker Grimm

## Effects of host-pathogen dynamics on a community with moving hosts

## 0. Brief expected profile of PhD student

Candidates must have an excellent MSc in Ecology, Quantitative / Computational Biology or related fields. Candidates with a modelling background from other natural sciences will also be considered. Experience in process-based mathematical or simulation modelling is required. A solid background in disease and community ecology is desirable. Interest in conducting field work is an asset, a ringing permit for birds a dream.

## 1. Short Abstract

This project follows a novel approach to assess community dynamics under species interactions such as parasitism and competition in heterogeneous dynamic landscapes. By extending an existing singlespecies host-pathogen model to a multi-host model based on developed approaches in the BioMove research training group, the candidate will highlight how biodiversity patterns (coviability) are impacted by altered movement.

## 2. Background and previous work

Pathogens can alter the ways in which their hosts allocate energy to movement, leading to both increased and decreased host movement activity, either as an adaptive strategy for the host or due to manipulation by the parasite (Binning et al. 2017; Franz et al. 2018). These movement-mediated pathogen control strategies will ultimately lead to different biodiversity patterns at the host community level due to altered competition regimes at the individual level. Here, our aim is to understand the effect of host species as 'mobile pathogen links' on the co-viability of a whole host community.

Previous modelling work in BioMove used community models based on intraspecific trait variation (ITV) of two species competing for a common resource (P01, 2<sup>nd</sup> cohort), allometric scaling in the context of limited space for a community of species (P11), and a host-pathogen model (P02) in dynamic landscapes. The latter aggregated species interactions at the home range level and modelled the effect of host dispersal types on the coexistence of host and pathogen through 'assisted movement', i.e. the transport of pathogens via their hosts (P02, 1<sup>st</sup> cohort). The host-pathogen model has revealed stabilizing effects of movement on infection dynamics in heterogeneous landscapes (Scherer et al. 2020), and P02 PhD of the 2<sup>nd</sup> cohort currently explores the importance of the timing of life-history events for host-pathogen coexistence in temporally dynamic space (Kürschner et al. 2021). However, we are still far from understanding host movement as pathogen transport system and the functional role of pathogens in shaping a community of interacting species in transient landscapes.

## 3. Objectives/Aims

The proposed study extends the current bi-system of host and pathogen to a community model including several host species competing for a shared changing resource, while allowing host movement traits to evolve (or vary) under the impact of a common pathogen. In particular, this project addresses the following key questions:

- How does a pathogen impacting a community of hosts alter the host community structure by changing the strength of resource competition between hosts?

- What effects do different host movement traits that result in movement activities such as foraging, exploring, commuting or long-distance dispersal, thereby acting as pathogen transport systems, have on community structure?

- How is this interlinked with changing resource levels in dynamic agricultural landscapes and their feedback on host movement traits?

## 4. Outline work program

PhD 3 candidate will devote a first step to a synthesis by linking the above-mentioned modelling approaches from individual movement behaviour to community dynamics: Specifically, the candidate will include multiple host species competing for a resource, while being affected by a shared pathogen (in close collaboration with P11). We will combine two approaches: a modelling part using the concept of co-viability as overarching metric and, optionally if wished, an ATLAS field part conducting own field work with birds (see below) or using existing data of mammals to provide proof of concept.

1) The PhD candidate (in the following termed PhD 3) will model movement activities of different bird or mammal species competing for a resource in space, and define a trade-off between allocating resources gained (or lost) during movement either to reproduction or to immune defense (resourceallocation hypothesis). E.g., long-distance movements might be beneficial for resource gain and hence reproduction, while this positive effect can be levelled off for lower survival in the presence of pathogens. PhD 3 will investigate which movement strategy is best to survive under fixed and evolving pathogen virulence and different landscape configurations. Hence, PhD 3 will answer the questions of how diseases may affect coexistence of hosts.

2) We will model different movements traits (see before) of community members in a patchy landscape (heterogeneous in its distribution of food and fear; see P11), while accounting for single individuals transporting and exchanging pathogens such as ectoparasites. These ectoparasites will induce life-history changes (survival and reproduction) feeding back to the movement level; that is, ectoparasite manifestation comes at physiological costs reducing energy available for movement, ultimately reducing survival (McElroy & de Buron 2014). By letting movement traits adapt, PhD 3 will be able to assess community consequences of pathogen infections and competition for resources and to analyse co-viability of the community.

3) If wished, PhD 3 can conduct field work in the BioMove experimental area, where kettle holes embedded in a matrix of agricultural fields represent isolated habitat islands, while other kettle holes are closely connected to larger habitat patches. These habitats (islands or connected) represent important foraging arenas and shelter for different taxa, such as insects, amphibians and birds. We will use mist nets and traps (3 times per year for 2 years) to catch small to medium-sized birds (e.g., starlings; synergies with P03, PostDoc project on swallows by W. Ullmann and DFG Research Group by U. Schlägel) around the kettle holes. Check their infestation status with blood-sucking ectoparasites (e.g. louseflies *Crataerina pallida*, ticks *Argas reflexus*, mites *Dermanyssus gallinae* and bird lice *Mallophaga*) and equip them with transmitters of the recently established ATLAS system to derive information on their movements and interactions. We will then be able to compare parasite distributions in patchy habitats with those retrieved by the model. We expect that parasite infestation is higher in birds breeding and foraging in the densely populated island habitats than in connected ones with the latter diluting (movement and) parasites, and that the infestation level by ectoparasites will induce changes in movement patterns (e.g., Heeb et al. 1999).

#### 5. Linkage to 'BioMove' objectives

This project connects the telemetry-based field projects and the conceptual modelling clusters of BioMove, while including the new concept of co-viability at the core of the community analyses. PO2 will be a central part for the synthesis of the community modelling approaches, including the new conceptual link to co-viability. Moreover, it also includes evolutionary concepts (linked to pathogen virulence and movement traits) and makes the link to an innovative empirical part, thereby bridging movement ecology with community dynamics.

#### References

Binning SA, Shaw AK, Roche DG. 2018. Parasites and host performance: Incorporating infection into our understanding of animal movement. Integrative and Comparative Biology 57 (2): 267–280.

Franz M, Kramer-Schadt S, Greenwood A, Courtiol A. 2018. Sickness-induced lethargy can increase host contact rates and pathogen spread in water-limited landscapes. Functional Ecology 32(9): 1-11.

Heeb P, Werner I, Mateman AC, Kolliker M, Brinkhof MWG, Lessells CM, Richner H. 1999. Ectoparasite infestation and sex-biased local recruitment of hosts. Nature 400:63–5.

Kürschner T, Scherer C, Radchuk V, Blaum N, Kramer-Schadt S. (2021) Movement can mediate temporal mismatches between resource availability and biological events in host-pathogen interactions. Ecology and Evolution, accepted.

McElroy EJ, de Buron I. 2014. Host performance as a target of manipulation by parasites: a meta-analysis. J Parasitol. 100:399–410.

Scherer C, Radchuk V, Franz M, Thulke H, Lange M, Grimm V, Kramer–Schadt S (2020): Moving infections: individual movement decisions drive disease persistence in spatially structured landscapes. OIKOS 129, 651-667. doi:10.1111/oik.07002.

## BioMove Project P03 (Univ. Potsdam), 3<sup>rd</sup> PhD student cohort

Supervising team: Niels Blaum, Jana Eccard and Stephanie Kramer-Schadt

## Mobile link functions in unpredictable agricultural landscapes 2.0 – insights from manipulating transient matrix corridors and network analysis

## 0. Brief expected profile of PhD student

The candidate should have a background in Movement-, Landscape- and Behavioral Ecology, with an excellent MSc in Ecology or related discipline. Experiences in capturing and tagging animals with GPS collars, analysing big data sets (GPS tracking and acceleration data), and in applying advanced statistical methods (e.g., random forest, movement networks) are an asset.

## 1. Short abstract

Mobile links connect different kinds of habitat patches, thereby affecting biodiversity. This project analyses how specific animal-landscape-conditions (internal status, among-individual variation of hares and transient matrix corridors) affect the amount and frequency of mobile links. We will GPS-collar European brown hares (*Lepus europaeus*), a typical species in agricultural landscapes that provides genetic links (seed dispersal) and process links (foraging on potentially rare plant species). Transient matrix corridors and key sites of hares will be experimentally manipulated, and advanced network-based tools be applied for mobile link analysis (see below).

## 2. Background and previous work

The individual movements of mobile links across transient matrix corridors connect different kinds of habitat patches and can affect biodiversity dynamics therein (Lundberg & Moberg 2003, Schlägel et al 2020). **PhD 1** showed that the spatiotemporal variability of resources at landscape scale affected higher-level movement behavior of hares (e.g., increase in home range size with landscape structure) (Ullmann et al. 2018; Mayer et al. 2018). In contrast, home range adjustments to sudden resource changes caused by mowing or harvesting are less clear and a significant part of the variation in movement specific responses remain unexplained (Ullmann et al. 2020). Such high variation in movement responses is caused among-individual variation in behavior. Indeed, **PhD 2** found that home range size increased with the level of shyness (Stiegler et al. in prep 1).

A second feature in many agricultural landscapes are wind park constructions that provide resources that are more constant in space and time (i.e., small artificial grassland patches under wind turbines). **PhD 2** found that hares extensively use these metapopulation type grassland patches. Home range size and small-scale movements differed compared to hares in the dynamic landscape (Stiegler et al. in prep 2). One explanation for the difference may be the perceived risk affecting small-scale movements and resting site fidelity of hares. The risk seems lower in wind parks where hares rest and hide during the day under the constructions compared to open grasslands or crop fields, where they rest in natural shallow depressions. Interestingly, the new high resolution GPS data (1 location/ 4 min) also reveal frequent movements of hares from resting sites to and between habitat patches (e.g., grassland fragments) along transient matrix corridors (e.g., tracks created by land machines). This offers the unique opportunity to experimentally assess the impacts of transient habitat features for mobile link movements.

## 3. Objectives/aims

The key objective of the third PhD in P03 is to quantify changes in amount and frequency of mobile link movements (genetic and process links) that are critical for biodiversity in relation to specific hare-landscape-conditions. Conditions include the internal status of individuals, among-individual variation in behaviour, spatiotemporal variability of resources, accessibility of transient matrix corridors, and species richness of potentially linked habitat fragments.

## 4. Outline work program

The work plan consists of two main parts: (i) Field work: hares will be captured and tagged with GPScollars with internal acceleration sensors and monitored at high temporal resolution (1 location/ 4 mins; according to PhD 2). We will quantify among-individual variation along the shyness-boldness continuum via observations of vigilance behaviour during capture, collaring and release of the hares and relate them to behavioural information gained from accelerometer data. This method has been established by PhD 2 with hares in an enclosure at the IZW field station (Niederfinow, Germany) and successfully applied to hares in the field (Stiegler et al in prep. 1). To assess the relevance of transient habitat features for mobile link movements, we will experimentally manipulate existing transient matrix corridors (e.g., tracks created by land machines). In particular, movement data informed corridors that connect neighbouring grassland fragments or kettle-holes across the matrix will be artificially blocked and changes in movement behaviour recorded to advance our understanding of land use effects on mobile linkage. A second experiment will focus on the impact of disturbances at critical resting sites. We will disturb hares at these resting sites in crop fields, semi-natural grasslands and windparks and quantify changes in small scale movements relevant for mobile link functionality.

(ii) Movement data analysis: A total of 301.052 GPS locations and 3.724.529 acceleration measurements of 74 hares from PhD1+2 will be complemented with additional high-resolution GPS and acceleration data. Using this exceptionally big data set, PhD 3 will apply network-based tools (Jacoby & Freeman 2016) to link movement networks with behavioural networks. Movement networks allow the identification of the exact location of hare activity centres (nodes), movement paths (edges), and the frequency of movements between these nodes. Behavioural networks will specify the underlying behaviour of mobile link movements. They are based on the behaviour-specific ace-leration pattern analyses of PhD1+2 (e.g. resting, foraging) and new acceleration data of PhD 3.

**Optional field work1** (MSc-thesis): Comparison of plant diversity at nodes and random locations of the same habitat to estimate the relevance of plant diversity for node positions.

**Optional field work 2** (MSc-thesis): Identifying foraged plant species via feeding marks at artificial grassland patches in wind parks and collection of droppings therein with germination test.

**Optional modelling work**: High resolution movement and accelerometer data (proxy for activity/ energy expenditure) of hares enable to simulate mobile link networks considering individual variation in movement properties and personality types under alternative landscape and land use scenarios.

## 5. Linkage to 'BioMove' objectives

P03 integrates a strong temporal aspect of landscape dynamics aiming at a more mechanistic understanding of the linkage between land-use effects, individual movement responses, and its potential consequences for biodiversity-relevant genetic and process links. This will help to refine the mobile link pathway of the BioMove concept.

#### References

Jacoby MP & Freeman R (2016). Emerging Network-Based Tools in Movement Ecology. Trends in Ecology & Evolution 31: 301-314.

- Lundberg J & Moberg F (2003). Mobile link organisms and ecosystem functioning: implications for ecosystem resilience and management. Ecosystems 6:87-98.
- Mayer M, Ullmann W, Sunde P, Fischer C. & Blaum N (2018). Habitat selection by the European hare in arable landscapes: The importance of small-scale habitat structure for conservation. *Ecology and Evolution* 23:11619-11633.

Schlägel U et al. (2020). Movement-mediated community assembly and coexistence. Biological Reviews 96: 1073-1096.

- Stiegler J, Kramer-Schadt S & Blaum N (in prep 2). Disturbance or beneficial islands? Wind parks in agricultural landscapes affect space use and activity of a common mobile linker species
- Stiegler J, Lins A, Dammhahn M, Eccard JA, Kramer-Schadt S, Ortmann S, Blaum N (in prep 1). Exploration profiles drive herbivore activity patterns and space use.
- Ullmann W, Fischer C, Kramer-Schadt S, Pirhofer-Walzl K & Blaum N (2018). Spatiotemporal variability in resources affects herbivore home range formation in structurally contrasting and unpredictable agricultural landscapes. Landscape Ecology, 33(9), 1505-1517.
- Ullmann W, Fischer C, Kramer-Schadt S, Pirhofer-Walzl K, Glemnitz M & Blaum N (2020). How do agricultural practices affect the movement behaviour of European brown hares (*Lepus europaeus*)? *Agriculture, Ecosystems and Environment* 292: 106819

## BioMove Project P04 (U Potsdam), 3rd PhD student cohort

Supervising Team: Jana Eccard, Christian Voigt, Niels Blaum, Victoria Radchuk

## Movement in a Landscape of Fear (LoF) - Cascading effects on biodiversity and coexistence

## 0. Brief expected profile of PhD student

Candidates must have a MSc in Ecology or similar field, with profound experience in behavioral ecology and/or field-based experimental approaches. Additionally, candidates should have excellent statistic skills, should be fluent in English (both speaking and writing) and have a driver license for field work. Modelling skills are desirable.

## 1. Short Abstract

Foraging behaviour of consumers has direct effects on population abundance, diversity, and functional trait composition of their resource species community. Foraging may thus serve as a biotic filtering mechanism for this community and determinants of foraging may have cascading effects on resource communities. Using a novel concept and simple measure to quantify community effects of foraging as giving-up diversities (GUDiv), effects of foraging decisions can be quantified on  $\alpha$ -,  $\beta$ - and  $\gamma$ -diversity and functional trait composition of resource communities. GUDiv provides a framework linking theories of adaptive foraging and ecology of fear with community ecology, opening up prediction-based tests of cascading indirect predation effects across multiple trophic levels, of feedbacks between functional trait compositions of resource and consumer communities, and of effects of interindividual differences among foragers on resource communities.

# Effects of: functional traits ? combinations ? functional traits ? combinations ?

Foraging decisions of a consumer directly affect diversity and functional trait distribution of an assemblage of resource species in a food patch. This can be measured as Giving-Up diversity, i.e. the diversity at which the consumer quits foraging. The GUDiv approach is based on the Giving up density approach for single resource species described by (Brown 1988). The food items of each species left in each local patch, their species richness and abundance of each species after foraging comprise the  $\alpha$ -GUDiv.

Internal factors affecting foraging behaviour on the consumer's level include species, state, and selectivity of the forager. External factors, such as abiotic factors or interaction with other species may affect the foraging behaviour of the consumer. Even the risk perceived by a forager, i.e. the ghost of predation past or the landscape of fear (Brown et al. 1999) may affect foraging behaviour, and thus GUDiversity. The distribution of functional traits within the resource assemblage may directly feedback on foraging behaviour.

## 2. Background and previous work

We found that  $\alpha$ -GUDiv depended directly on the time animals spend in each patch. Further, the risk perceived by a forager affected GUDiv.  $\alpha$ -GUDiv was lower in safe patches (high vegetation) were animals could spend potentially longer time foraging, than in unsafe patches. The cumulative resource species left in an entire foraging landscape composed of patches harvested by a single forager comprises the  $\gamma$ -GUDiv. It was reduced with the cumulative time spent foraging in a landscape, and with the mean safety level of a landscape, however at a lower rate (more shallow slope) of  $\gamma$ - than the mean of local  $\alpha$  did. Consequently,  $\beta$ -GUDiv, the difference in biodiversity among patches of a landscape increased with increasing safety.

## 3. Objectives/Aims

The proposed study for the 3<sup>rd</sup> cohort will focus on bottom-up feedback loops. Functional traits of species (McGill et al. 2006) in the resource community, such as profitability of food items, handling time (size, shell), may affect foraging decisions and thus impact foraging effects of GUDiv on different trophic scales.

- a) How does the combination of distributions of different functional traits in the seed community (e.g. having many species with long handling time, vs having only one) affect foraging behavior?
- b) Is there a tri-trophic interaction of feedback loops with predation risk, i.e. do foraging decisions based on functional traits taken under high predation risk differ from those taken under low predation risk, and thus differently affect the Giving-up diversity of resources?
- c) How do individuals decide on which item / food species to consume next: are there invariant individual preferences, or do they function as Bayesian Foragers (adjusting the foraging behavior to the food community composition, which they themselves change with every removed food item?). This part of the project may be difficult to observe (but we could closely observe single food patches), we therefore may add modelling effects of different foraging strategies.

## 4. Outline work program

We will therefore conduct experiments in wild and artificial foraging landscapes, using wild rodents as foragers and providing them with food communities varying in functional trait combination. Food patches will consist of foraging trays filled with defined numbers of seeds representing different functional types of plants. Predation risk for the forager can be manipulated by providing differences in vegetation height, ground cover or illumination since rodents, as highly depredated species, readily respond to these cues (e.g. Eccard & Liesenjohann 2008). Wild foragers can potentially be tracked using the ATLAS system of a smaller scale, automated VHF tracking system to investigate the role of movement behavior of the consumer on resource species diversity.

For a) we will provide foragers with foraging landscapes of different functional trait combinations and investigate feedback loops on behavior and resulting GUDiv. For b) we will set the foraging landscapes in different risk landscapes to understand whether or how feedback loops are affected by risk. Using wild foragers in real landscapes, tracking will augment this investigation and provide information on movement behaviour. For c) we will model foraging processes with individual-based models, parameterized so as to closely reflect the empirical movement behavior, simulating changes of food diversity while foraging for different strategies (selectivity, random removal, encounter probabilities)

#### 5. Linkage to BioMove objectives

Results on the resource community level may reveal coviability patters of resource species, mediated directly by consumer behaviour, or indirectly by predators.

References

Brown JS (1988). Patch use as an indicator of habitat preference, predation risk, and competition. Behav Ecol Sociobiol, 22, 37–47.

Brown JS, Laundré JW, Gurung M. (1999). The Ecology of Fear: Optimal Foraging, Game Theory, and Trophic Interactions. *J Mammal*, 80, 385–399.

McGill BJ, Enquist BJ, Weiher E, Westoby M. (2006). Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution*, 21, 178–185.

Eccard JA, Liesenjohann T. Foraging Decisions in Risk-Uniform Landscapes. PLoS ONE. 2008;3(10):e3438.

## BioMove Project P05 (IZW Berlin), 3rd PhD student cohort

Supervising Team: Christian Voigt, Jana Eccard, Niels Blaum

## Bat-mediated trophic effects on farmland insect diversity

## 0. Brief expected profile of PhD student

Candidates must have a MSc in Ecology or similar field, with profound experience in behavioral ecology, analysis of acoustic parameters, spatial tracking of animals and/or field-based experimental approaches. Additionally, candidates should have a profound knowledge in multivariate statistics, specifically in the use of R, should be fluent in English (both speaking and writing) and have a driver license for field work. Knowledge of German is beneficial, but not mandatory, since field work takes place at remote place in Germany.

## 1. Short Abstract

By consuming other animals, predators may influence the distribution and diversity of their prey. These top-down trophic effects may depend on predator-specific movement patterns, which vary in space and time following, e.g., resource and competitor distribution. Insect predators, such as bats, may affect the abundance and distribution of insects, offering potentially ecosystem services. Using high resolution spatial tracking of bats and automated ultrasonic recording of bats, we plan to quantify the link between bat movements and their top-down trophic effect on farmland insect diversity. To this end, we will allow (control) or prevent (exclosure) bats the access to a set of plots with a pre-defined plant composition, and then measure the trophic effect of bats by comparing arthropod diversity and abundance between control plots and exclosures (Maas et al. 2019). By linking bat movements, and thus bat presence, to landscape features, we will model the spatial distribution of bat-mediated ecosystem services on farmland.

## 2. Background and previous work

Overall, we aim at understanding biodiversity patterns that are related to the spatial behavior of predators (Schlägel et al. 2020). In P05, we focus specifically on bat movements and their insect prey within the conceptual framework of the extended movement ecology paradigm (Nathan et al. 2008, Jeltsch et al. 2013). In collaboration with other members of the RTG Biomove, we have established a joint study site, the AgroScapeLabs, north of Berlin. There, we have tracked successfully bats with the cutting-edge technology of the Atlas-System (Weiser et al. 2015, Toledo et al. 2020). The Atlas system is a high-throughput VHF system that automatically triangulates the position of tagged animals based on signal delay at several receiving antenna stations. Encoded VHF signals allow the simultaneous tracking of several animals at high temporal and spatial resolution. Our earlier tracking studies have shown that common noctule bats prefer certain habitats when foraging above farmland (Roeleke et al. 2016, 2018, 2020). Based on acoustic surveys, we documented that local bat activity varied between species and depended largely on landscape features, such as edge structures, ponds and the intensity of farmland practice (Heim et al. 2017, 2018). Further, using metabarcoding of insect DNA in fecal pellets of bats, we have established a good understanding about which insect prey bats are consuming when foraging above farmland throughout the season.

## 3. Objectives/Aims

The proposed study will combine the study of animal movements with those of trophic interactions on a landscape scale level. Specifically, we will address the following questions:

a) What is the effect of foraging bats on insect abundance and diversity?

b) Does insect-feeding by bats alter the insect-mediated ecosystem services (pollination) and disservices (herbivory)?

c) Do landscape features within relatively homogenous farmland landscapes modify the top-down trophic effects of bats?

#### 4. Outline work program

We plan to measure the activity of syntopic bat species at experimental field exclosures based on automated ultrasonic detectors. This will allow us to quantify the species-specific effect of bats on local insect diversity. By quantifying the level of insect herbivory and seed production at experimental field exclosures, we will estimate how bat predation influences insect-mediated ecosystem services. Lastly, we will tag dozens of bats of syntopic species with miniaturized tags to estimate the spatial behavior of bats in our experimental area. By connecting information on how syntopic bats forage in response to landscape features, we envision to assess the spatial heterogeneity of bat-mediated trophic effects on the landscape level.

#### 5. Linkage to BioMove objectives

Our focus will be on the movement-mediated patterns of trophic effects on insect diversity using bats and their insect prey as a model.

#### References

- Heim, O., Lorenz, L., Kramer-Schadt, S., Jung, K., Voigt, C. C., & Eccard, J. A. (2017a). Landscape and scale-dependent spatial niches of bats foraging above intensively used arable fields. *Ecological Processes*, 6(1), 24.
- Heim, O., Lenski, J., Schulze, J., Jung, K., Kramer-Schadt, S., Eccard, J. A., & Voigt, C. C. (2018). The relevance of vegetation structures and small water bodies for bats foraging above farmland. *Basic and Applied Ecology*, 27, 9-19.
- Jeltsch, F., Bonte, D., Pe'er, G., Reineking, B., Leimgruber, P., Balkenhol, N., ... & Bauer, S. (2013). Integrating movement ecology with biodiversity research-exploring new avenues to address spatiotemporal biodiversity dynamics. *Movement Ecology*, 1(1), 1-13.
- Maas, B., Heath, S., Grass, I., Cassano, C., Classen, A., Faria, D., ... & Kross, S. (2019). Experimental field exclosure of birds and bats in agricultural systems—Methodological insights, potential improvements, and cost-benefit trade-offs. Basic and Applied Ecology, 35, 1-12.
- Nathan, R., Getz, W. M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D., & Smouse, P. E. (2008). A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, *105*(49), 19052-19059.
- Roeleke, M., Blohm, T., Kramer-Schadt, S., Yovel, Y., & Voigt, C. C. (2016). Habitat use of bats in relation to wind turbines revealed by GPS tracking. *Scientific reports*, *6*, 28961.
- Roeleke, M., Teige, T., Hoffmeister, U., Klingler, F., & Voigt, C. C. (2018). Aerial-hawking bats adjust their use of space to the lunar cycle. *Movement Ecology*, 6(1), 1-10.
- Roeleke, M., Blohm, T., Hoffmeister, U., Marggraf, L., Schlägel, U. E., Teige, T., & Voigt, C. C. (2020). Landscape structure influences the use of social information in an insectivorous bat. *Oikos*, 129(6), 912-923.
- Schlägel, U. E., Grimm, V., Blaum, N., Colangeli, P., Dammhahn, M., Eccard, J. A., ... & Jeltsch, F. (2020). Movement-mediated community assembly and coexistence. *Biological Reviews*, 95(4), 1073-1096.
- Toledo, S., Shohami, D., Schiffner, I., Lourie, E., Orchan, Y., Bartan, Y., & Nathan, R. (2020). Cognitive map–based navigation in wild bats revealed by a new high-throughput tracking system. *Science*, *369*(6500), 188-193.
- Weiser, A. W., Orchan, Y., Nathan, R., Charter, M., Weiss, A. J., & Toledo, S. (2016, April). Characterizing the accuracy of a self-synchronized reverse-GPS wildlife localization system. In *Proceedings of the 15th International Conference on Information Processing in Sensor Networks* (p. 1). IEEE Press.

## BioMove Project P06 (IZW), 3<sup>rd</sup> PhD student cohort

Supervising team: Viktoriia Radchuk, Stephanie Kramer-Schadt, Niels Blaum, Ulrike Schlägel

## Assessing performance and facilitating application of statistical methods to infer species interactions from telemetry data

## 0. Brief expected profile of PhD student

Candidates must have a completed MSc in any natural sciences, e.g. Ecology, Computational Biology, Ecological Modelling. Candidates with the degree in statistics and strong interest in movement ecology will also be considered. A sound experience in statistical analyses, programming in R, and development of process-based simulation models is required. Experience in statistical analyses of movement data or/and simulation of movement data is strongly preferred.

## 1. Short Abstract

Interactions of moving individuals, such as repulsion or attraction, may have implications for individual fitness, and thus biodiversity. Yet, this group of interactions remains understudied compared to classical interactions such as competition or predation, defined by population abundances. Recent methods provide an opportunity to infer interactions from movement data but differ in their assumptions, type of data they require, and specific research questions they can address. Moreover, they are based on advanced statistics. All together, this limits the use of these methods by field movement ecologists. The goal of this PhD project is to make these methods accessible to empiricists by clarifying their underlying assumptions. Making the methods available in the user-friendly software (if not yet done) and revealing the limits of methods application, i.e. by assessing the methods' performance under a general set of conditions such as amount of missing data, temporally and spatially heterogeneous environment, and varying sampling resolution. Both simulated and empirically collected movement data will be used to achieve these aims.

## 2. Background and previous work

New techniques available for tracking individual movement (e.g. the ATLAS tracking system http://move-ecol-minerva.huji.ac.il/page/3) result in increasingly larger amounts and higher resolution of collected movement data. Data collected on multiple simultaneously moving individuals offer the opportunity of analysing dynamic interactions among con- and heterospecifics. Interactions of moving individuals may have direct and indirect fitness consequences, and, in turn, affect population dynamics and ultimately modify biodiversity patterns. Therefore, understanding such interactions is important.

In response to increasing availability of high-resolution movement data, recently several methods were developed allowing to infer interactions from such data (e.g. <sup>1–4</sup>). These methods vary in the research questions they can address, the assumptions they make and the type of data they are applicable to. Whereas some methods focus on pair-wise interactions, others investigate collective movement behaviour in an attempt to disentangle the group-driven movement component from the individual, solitary behaviour. Similarly, some methods allow taking into account environmental covariable(s) (e.g. habitat quality), while others do not. Importantly, these methods are usually based on advanced statistical methods such as hidden Markov models, step-selection functions, and kriging, and may not be easily accessible to field practitioners collecting the movement data. Therefore, there is a need to facilitate the use of existing methods by empiricists by: 1. Cataloguing

the existing methods with regard to the research questions they can address; 2. Systematically clarifying the underlying assumptions and data requirements of each method; 3. Whenever not yet available, implementing the method in a user-friendly software (e.g. in R packages).

Additionally to making the existing methods generally accessible to empirical movement ecologists, assessing the limits of methods' application is needed. Indeed, although each method was tested to a certain degree, its performance was not scrutinized under a variety of conditions, such as presence of missing data and their amount, varying sampling resolution, dynamic and spatially heterogeneous environments. Yet, knowing how the method performs under such conditions is needed so as to establish the limits under which the method can be applied and to ensure its proper use with the empirical data.

One of the supervisors (Ulrike Schlägel) has vast experience in analysing movement data and has developed a method<sup>1</sup> allowing to infer type and strength of interactions for a particular individual towards each concurrently moving individual. This method thus quantifies asymmetric interactions, when one individual might be attracted to the other, while the other one showing avoidance or neutral behaviour. Telemetry datasets on simultaneously moving individuals were collected in the first and second cohort of BioMove PhDs (e.g. bats, voles) and are potentially available for (further) analyses. Currently, the ATLAS system is used by Post-Docs Ullmann and Roeleke to collect foraging movement data on multiple individuals of aerial insectivores (bats and swallows), at high temporal resolution. Own tracking data collection is also possible, if desired. The experience of BioMove colleagues will facilitate cataloguing the research questions about interactions based on movement data and help revealing obstacles the empiricists face when analysing their data.

## 3. Objectives/Aims

The overall goal of this PhD project is to make existing methods for inferring interactions from the telemetry data widely accessible to empiricists collecting those data. Specific objectives:

- i) Cataloguing the research questions regarding the interactions of moving individuals and the respective methods that can address them;
- ii) Making explicit the assumptions underlying the existing methods, and types of data they require / can handle;
- iii) Assessing the reliability of the existing methods with regard to missing data, varying sampling resolution, and temporally and spatially heterogeneous environments.

## 4. Outline work program

1) The student will assemble a list of research questions that are asked in different studies assessing the interactions from movement data. For this the student will conduct a literature review and work closely with other BioMove PhDs (e.g. projects P02, P05) and BioMove postdocs Ullmann and Roeleke.

2) The student will review the literature and compile methods for inferring interactions from the movement data. To get a deep understanding of these methods together with the limits of their application, we will simulate movement data with known properties, i.e. effects of biotic (presence and proximity of con- and heterospecifics) and abiotic (temperature, wind, landscape structures) variables on individual movement and interactions among individuals. Next, a virtual ecologist approach<sup>5</sup> will be used to sample the simulated data by mimicking the telemetry data collection process. These data will then be analysed to address the (selected) typical research questions (from

the list assembled in 1), by applying the appropriate existing statistical method(s). We will compare the obtained parameter estimates with the 'true' ones, used for data simulation, to assess the accuracy and precision of the methods. We will then assess the robustness of the statistical methods to several factors: i) amount and placement of missing data within the movement track, ii) temporal and iii) spatial environmental heterogeneity. For this, we will vary each factor and repeat the simulation of movement data and their statistical analyses.

3) By closely collaborating with BioMove PhDs and Post-Docs whose projects are focused on assessing interactions from ATLAS movement data (a particular type of telemetry data), the PhD will apply the statistical method that is most appropriate in each particular case. Such collaboration will potentially reveal further aspects that could facilitate the application of methods by empiricists. On the one hand, this collaborative work will benefit other BioMove projects via the expertise of the PhD student in particular statistical methods. On the other hand, it will result in a better overview of difficulties the empiricists encounter when analysing movement data, which will contribute to the review aiming to overcome such difficulties and facilitate the use of these methods by field ecologists.

#### 5. Linkage to 'BioMove' objectives

This project belongs to the cluster 3 'integration and synthesis' of BioMove and closely links to the two general questions Q1 (*How does land use alter movement processes and their impact on biodiversity in dynamic agricultural landscapes*) and Q2 (*Which spatial and temporal scales are key to understand the linkage of movement and biodiversity dynamics in agricultural landscapes*?). In order to understand how movement affects biodiversity it is paramount to be able to quantify interactions of moving individuals, therefore this project directly relates to the main BioMove objective.

#### References

Schlägel, U. E. *et al.* Estimating interactions between individuals from concurrent animal movements. *Methods in Ecology and Evolution* 10, 1234–1245 (2019).

Langrock, R. et al. Modelling group dynamic animal movement. Methods in Ecology and Evolution 5, 190–199 (2014).

Calabrese, J. M. *et al.* Disentangling social interactions and environmental drivers in multi-individual wildlife tracking data. *Philosophical Transactions of the Royal Society B: Biological Sciences* 373, 20170007 (2018).

Cozzi, G., Maag, N., Börger, L., Clutton-Brock, T. H. & Ozgul, A. Socially informed dispersal in a territorial cooperative breeder. *Journal of Animal Ecology* 87, 838–849 (2018).

Zurell, D. et al. The virtual ecologist approach: simulating data and observers. Oikos 119, 622–635 (2010).

## BioMove Project P07 (Univ. Potsdam), 3<sup>rd</sup> PhD student cohort

Supervisor team: Ralph Tiedemann, Guntram Weithoff, Florian Jeltsch, Niels Blaum

## Mobile linkers stabilize coviability in limnic metacommunities

## 0. Brief expected profile of PhD student

The candidate must have an MSc in Evolutionary Biology, Ecology or a related discipline. Strong preference will be given to applicants experienced in bird catching and marking. We further appreciate experience in tagging animals with GPS collars and/or in DNA metabarcoding as well as a good command on bioinformatics/large data set analyses. A driving license would be of additional value.

## 1. Short Abstract

Aquatic plants as well as limnic plankton have limited or absent active dispersal abilities, but produce propagules for passive dispersal. This project specifically focusses on the role of vertebrate species as mobile linkers connecting disjunct aquatic habitat patches (i.e., the Uckermark's ponds and kettle holes), thereby maintaining a metapopulation structure for aquatic plants and plankton species. In facilitating connectivity among ponds, mobile linkers may hence stabilize and/or equalize the diversity of the species they transport. The activity patterns and habitat preferences of these mobile linkers likely differ both among species and among individuals. Resulting dispersal trajectories can be complex and may constrain exchange among particular sites for the transported propagules. This constitutes a filter for the cohesion in the metacommunity, impacting both diversity and coviability. We will GPS- or ATLAS collar ducks (mostly mallard *Anas platyrhynchos*) to directly assess movement patterns and – by washing the captured birds – to verify transport of propagules. Further, we will intensely sample faeces from Wild boar *Sus scrofa*, Raccoon *Procyon lotor*, and Roe deer *Capreolus capreolus*. The faeces will be subjected to DNA metabarcoding to infer species transported. Further, microsatellite/SNP analysis of faeces will allow for individually genotyping the linker, thereby revealing activity/roaming patterns across the landscape through time.

## 2. Background and previous work (focus on PhD cohort 2 of Project P06/07/08)

Previous work demonstrated that (1) local populations are genetically different among kettle holes in both aquatic plants (Lozada-Gobilard *et al.* 2021) and zooplankton, (2) there is passive dispersal across the matrix, enabling recolonization of empty patches; there is some effect of wind and insect pollinators on passive dispersal, however this factors only partially explain the population genetic pattern observed, and (3) there is anecdotal evidence (camera traps, fur analysis) for the mobile linker function of our focus vertebrate taxa. The duck tracking system was validated for a few specimens. DNA faeces analysis and suitable DNA metabarcoding protocols, as well as protocols for individual genotyping have been established.

## 3. Objectives/Aims

The key objective of the third PhD in P07 is to proof the link between the activity of mobile linkers and the aquatic community diversity and coviability in ponds/kettle holes (cf. Schlägel *et al.* 2020). Ultimately, the species- and individual specific movement of the mobile linkers is to be related to geographic distance among habitat patches, the structure and composition of the surrounding matrix, and the specific habitat features of ponds and kettle holes to arrive at a functional understanding of which factors promote resp. hinder mobile linker-mediated dispersal in limnic metacommunities.

#### 4. Outline work program

The work plan of the PhD is divided into field work, lab work, and data analyses.

**Field work** (year 1-2): Ducks will be captured and tagged with GPS collars at defined ponds/kettle holes and their movement will be subsequently automatically recorded. Faeces samples from Wild boar, Raccoon, and Roe deer will be sampled in a standardized manner throughout different seasons. Pond DNA samples may be additionally taken, where necessary, to add to the data obtained in cohort 2.

**Lab work** (year 1-2): Limnic metacommunities will be characterized from faeces by DNA metabarcoding, genotyping established barcoding genes (rbcL, COI). Metabarcoding of specific ponds has been performed in cohort 2, but additional ponds will be analysed, if necessary. Mobile linker individuals will be identified by informative SNPs/microsatellites, following established protocols (e.g., Apio *et al.* 2010; Lah *et al.* 2016).

**Data analysis** (year 2-3): Both GPS data and DNA based individual genotyping will be utilized to reveal individual home ranges as well as movement networks among conspecific/heterospecific mobile linkers. The DNA data will additionally enable inference of population size and structure for the mobile linker species. DNA metabarcoding data will be processed in advanced bioinformatics pipelines and futher analysed using multivariate statistics.

#### 5. Linkage to 'BioMove' hypotheses, objectives and concepts

This project will analyse how the specific landscape context and human impact of agricultural landscapes affect (i) the spatial and temporal scale of movement in mobile linkers, (ii) the influence of structure and composition of the surrounding matrix, and (iii) the scale, at which potential links may influence local aquatic metacommunities. This will help to refine the mobile link pathway of the BioMove concept. In particular, it will reveal the role of mobile linkers in stabilizing/equalizing the diversity of limnic metacommunities and hence unravel their contribution to the coviability among their members.

#### References

- Lah L, Trense D, Benke H, Berggren P, Gunnlaugsson Þ, Lockyer C, Öztürk A, Öztürk B, Pawliczka I, Roos A, Siebert U, Skóra K, Víkingsson G, Tiedemann R (2016) Spatially explicit analysis of genome-wide SNPs detects subtle population structure in a mobile marine mammal, the Harbor porpoise. *PLoS ONE* **11**, e0162792.
- Lozada-Gobilard S, Schwarzer C, Dyer R, Tiedemann R, Joshi J (2021) Genetic diversity and connectivity in plant species differing in clonality and dispersal mechanisms in wetland island habitats. *Journal of Heredity,* in press.
- Schlägel UE, Grimm V, Blaum N, Colangeli P, Dammhahn M, Eccard JA, Hausmann SL, Herde A, Hofer H, Joshi J, Kramer-Schadt S, Litwin M, Lozada-Gobilard SD, Müller MEH, Müller T, Nathan R, Petermann JA, Pirhofer-Walzl K, Radchuk V, Rillig MC, Roeleke M, Schäfer M, Scherer C, Schiro G, Scholz C, Teckentrup L, Tiedemann R, Ullmann W, Voigt C, Weithoff G & Jeltsch F (2020). Movement-mediated community assembly and coexistence. Biological Reviews 96: 1073-1096.

Apio A, Kabasa JD, Ketmaier V, Schröder C, Plath M, Tiedemann R (2010) Female philopatry and male dispersal in a cryptic, bush–dwelling antelope (*Tragelaphus sylvaticus*): a combined molecular and behavioural approach. *Journal of Zoology* **280**, 213-220.

## BioMove Project P08 (Univ. Potsdam), 3<sup>rd</sup> PhD student cohort

Supervising team: Guntram Weithoff, Ralph Tiedemann, Viktoriia Radchuk

## The role of scale-dependent movement and dispersal on zooplankton meta-community structure in kettle-holes of varying hydroperiod.

## 0. Brief expected profile of PhD student

Candidates must have a MSc in Ecology or in a related field. A degree in freshwater or marine ecology is preferred. Further, a solid background in experimental population and community ecology is desirable.

## 1. Short Abstract

Within the agricultural landscape NE of Berlin, a large number of small water bodies (kettle holes) originating from the last glacial period exists. These kettle holes are regarded as hotspots of biodiversity harbouring plenty of species (animals and plants), ranging from purely aquatic ones over amphibians and semi-aquatic ones to wetland species. In this project, we focus on zooplankton as a diverse group with a high dispersal potential. We aim to disentangle the effects of movement/dispersal, colonization, and life-history on biodiversity and coviability of zooplankton in a kettle hole meta-community.

## 2. Background and previous work

The numerous kettle-holes in the study area vary in hydroperiod ranging from permanent water bodies to ephemeral ponds that dry out regularly or irregularly challenging the adaptive behaviour and life history of species that are typically restricted to the aquatic phase. Thus, this landscape represents a large matrix for an aquatic meta-community such as zooplankton. One relevant factor is temperature, because it is not only influencing population growth and survival of zooplankton in general, high temperatures are also indicative for upcoming dry outs and thus represent a warning signal for zooplankton to produce resting eggs; the typical dispersal stages. We found within the Brachionus-species complex strains that differ in their heat tolerance, as well as strains differing in their propensity to produce resting stages, underlining the role of temperature for zooplankton. The dispersal of zooplankton can be driven by wind (most likely during drought) or by animal vectors (most likely during the aquatic phase). Based on a seasonal field study, PhD 1 found a high species turn-over among ponds including a (weak) directional wind effect on species composition. Using field mesocosms, colonization of empty patches took only a few weeks and is higher close to permanent ponds compared to dried-out ponds, possibly due to animal vectors, since along with zooplankton, also aquatic plants (duck weed) were dispersed. Another important factor for the community composition in the ponds is the presence of an egg bank in the sediment. Most zooplankton species produce seasonally resting stages that can withstand harsh environmental conditions such as drought, heat or UV-light. We found that sediments from dry ponds harbour a high number of viable resting stages of many species allowing for rapid re-colonisation after re-wetting. Thus, we can assume that after rewetting local species compete with dispersing ones and we aimed to disentangle the process of hatching from the sediment and dispersing animals. First results from a field mesocosm experiment conducted by PhD 2 revealed that the species composition hatching from the sediment is different from the dispersed one. Since the dispersal of zooplankton and their individual, active movement act on different spatial scales, we also analysed the active movement behaviour. In particular, we studied the behavioural response to UV-light, using video filming. Studying three

common rotifer species, we found a species-specific avoidance behaviour to UV-light. In a recent study, we found that a rotiferan predator also induces an avoidance behaviour in its rotiferan prey, demonstrating the relevance for individual movement for species interactions.

## 3. Objectives/Aims

The proposed study will disentangle the different processes driving coexistence and coviability of zooplankton in a pond meta-community. The key objectives are:

- To quantify the role of key life history traits in shaping pond meta-communities. In particular, the interplay among temperature tolerance, resting egg production and dispersal capability will be analysed.
- To quantify local adaptation of zooplankton, as a pivotal factor for the competition between local (resident) populations and dispersing ones.
- To study the effect of individual, active movement of zooplankton on species interactions. We will focus on the avoidance behaviour of consumers in response to UV-light or predators and its consequences for the diversity of the prey community.

## 4. Outline work program

The project is based on the findings of the preceding work and the work plan consists of three main sub-projects a) a meta-community experiment in which multiple mesocosms of different environmental characteristics will be set-up in the laboratory. They are inoculated with natural samples from the field and/or with laboratory strains. The mesocosms will differ in the temperature regime to mimic variable drying conditions. We will manipulate the connectivity by manually transferring water or sediment (including resting stages) among mesocosms. b) Since dispersal is only successful when immigrants can compete with local populations, common garden experiments will be conducted to estimate potential local adaptation. Therefore, field samples will be taken, zooplankton populations will be separated and their performance under home and away conditions will be tested. This will allow for a quantification of the competitive abilities of local and immigrating populations. The results will complement the study on the interplay of life history and the environment. c) in the third part, experiments will be employed to study the effect of the individual movement/avoidance behaviour of selected zooplankton species on the diversity of their phytoplankton prey: Vertical glass tubes will be inoculated with defined plankton communities with zooplankton species that differ in their behavioural response to environmental stressors such as UV or predation. In replicated experimental runs with and without these stressors, the effect of vertically moving herbivorous zooplankton on the phytoplankton diversity will be quantified.

## 5. Linkage to BioMove objectives

This project is embedded into the overarching question on how movement and dispersal drive species diversity and coviability. In particular, it contributes to the BioMove hypothesis that variation in movement traits increase the coviability of interacting species. In addition, it will be investigated how consumer movement behaviour affects prey community diversity.

## BioMove Project P09 (Freie Universität Berlin), 3<sup>rd</sup> PhD student cohort

Supervising team: Matthias C. Rillig, Marina Müller, Florian Jeltsch

## Quantifying movement of filamentous fungi on an individual hypha basis using micro-structured environments

## 0. Brief expected profile of PhD student

Candidates must have a MSc in Ecology, Microbiology, Mycology or in a related field. Further, a solid background in experimental ecology and statistics is desirable.

## 1. Short Abstract

Filamentous fungi, organisms that occupy key positions in terrestrial ecosystems, have only recently been aligned with the movement ecology paradigm. In this project, we focus on quantifying movement-related traits of fungi at the individual hypha level. We aim to describe, for a set of co-occurring fungi, the range of navigation ability using Soil Chips, microstructured environments that serve as arenas for observing movement traits. These data will fuel individual-based modelling endeavors that commenced in the second cohort of BioMove.

## 2. Background and previous work

We have previously offered a framework for the inclusion of filamentous fungi in the framework of movement ecology (Bielcik et al. 2019). Building on this work, and on work constructing an individual-based model of fungal growth in a structured environment, we now wish to quantify movement related traits in fungi, and to include the parameters estimated in experimental work in the model. To this end, we will take advantage of recent progress in the use of Soil Chips (Aleklett et al. 2021), microstructured environments that have been adapted for use with filamentous fungi. We are currently exploring potential conditions for coviability of fungal mycelia in simulated structured environments, using individual-based models. An additional goal is therefore to experimentally verify such coviability outcomes.

## 3. Objectives/Aims

The proposed study will disentangle the different processes driving coviability of filamentous fungi in a soil community. The key objectives are:

- To experimentally quantify the individual hyphal movement traits of a set of fungi
- To relate these movement traits to colony-level behavior data already available for these fungi
- To model interactions of filamentous fungi using individual based models to discover conditions of coviability in structured environments

## 4. Outline work program

The project is based on the findings of the preceding work, in particular on individual-based models in structured environments, and will capture quantitative data of movement related traits of fungi. The set of fungi to be used has already been characterized in a large trait-based ecology effort of the host lab, and offers a wealth of data to explore in terms of the relationship of movement traits with all other traits collected (architectural, physiological, ecological, trophic, biochemical). The **work plan**  consists of a) establishing a soil chip system, adopting it for the approximately 30 fungi that form the culture collection; relate these movement traits (e.g. ability to navigate around obstacles or acute angles) with all other mycelium-level traits already collected to uncover potential tradeoffs (for example, fungi with high maximum growth rates may not be the best at navigating challenging obstacles); b) performing experiments with this set of fungi (focusing on individual hyphae of single species) to capture movement related traits c) exploring the data obtained in the context of an individual based model of hyphal behaviour with the goal to ascertain if and under what conditions divergent expression of movement-related traits could lead to coviability among fungal species in the same environment.

#### 5. Linkage to BioMove objectives

This project is embedded into the overarching question on how movement and dispersal drive species diversity and coviability. In particular, it contributes to the analysis of the BioMove hypothesis that variation in movement traits increases the coviability of interacting species.

#### References

Bielcik M, Aguilar-Trigueros CA, Lakovic M, Jeltsch F, Rillig MC. 2019. The role of active movement in fungal ecology and community assembly. Movement Ecology 7: 36; doi: 10.1186/s40462-019-0180-6

Aleklett K et al. 2021. Fungal foraging behaviour and hyphal space exploration in microstructured Soil Chips. The ISME Journal; doi: 10.1038/s41396-020-00886-7

## BioMove Project P10 (ZALF Müncheberg), 3<sup>nd</sup> PhD student cohort

Supervising team: Marina Müller, Guntram Weithoff, Volker Grimm, Matthias Rillig

## Community composition, dispersal ability and niche competition of phytopathogenic fungi influenced by small water bodies in heterogeneous agricultural landscapes

## 0. Brief expected profile of PhD student

Candidates must have a very good MSc in phytopathology, ecology, microbiology, phytomedicine or related fields. A broad expertise in techniques related to microbiology and molecular biology for taxonomic identification and microbial ecological behavior is required. A solid background in community ecology is desirable.

## 1. Short Abstract

This project will investigate small water bodies (kettle holes) in agricultural landscapes as hot spots for the development, the diversity and the distribution of phytopathogenic, mycotoxin producing fungi into the surrounding cereal fields. Specifically, we will focus on the following questions: Is the microbial diversity at the edges of kettle holes higher than the adjacent fields and do kettle holes thus serve as a permanent source of infection of wheat plants? Is the dispersal ability or the aggressiveness of the immigrating fungi of greater importance for a successful infection of wheat plants? What is the relative role of the properties of kettle holes (i.e. size and water regime of kettle holes, distance among them and the plant diversity at their edges) in structuring the metacommunity of phytopathogenic fungi in agricultural landscapes?

## 2. Background and previous work

Microclimatic conditions influence the temporal and spatial distribution patterns and the wind-driven spread of phytopathogenic Fusarium and Alternaria fungi (Schiro et al. 2018, 2019a, 2019b). At local scale (within a wheat field of approx. 50 ha), we observed a strong correlation between climatic conditions and the abundance of the fungi, but this varied across fungal genera. Fusarium fungi only grew in places with elevated ambient humidity with marked seasonal variation. The spore spread of Fusarium also varied in space and time and followed a canopy moisture gradient. In contrast, fungi of the genus Alternaria were more homogeneously distributed within the wheat fields. Their hot spots were mostly in warm and dry areas. The environmental niche of these two fungal genera appears to be separated due to their varying sensitivity to bacterial antagonists and their different aggressiveness to the host plants (Müller et al. 2018, 2020). In her ongoing work, PhD student 2 currently investigates the dispersal capacity of different Fusarium and Alternaria fungi at defined wind speeds in a wind tunnel. This will contribute to explain the different fungal abundance patterns in the field. At the same time, the student is studying the interactions between co-occurring fungal and bacterial competitors: we will elucidate how temporally staggered colonization affects the growth and the mycotoxin production of the immigrant and co-occurring microorganisms on the wheat plants (Hoffmann et al. 2021). Overall, we aim to understand the interactions of pathogens and antagonists, the fungal immigration processes, priority effects, and the role of the toxins as virulence factors involved.

## 3. Objectives/Aims

We are comparing the *Fusarium* and *Alternaria* community in different agricultural wheat fields surrounded by heterogeneous or homogeneous landscape elements to assess spatially effective barriers in landscapes. The structure and (dis-)similarity of these fungal communities may be related

to the dispersal ability of the individual members of these communities. PhD 3 will include the kettle holes as important driving factors for the distribution of microorganisms because:

a) The water area and water flow as well as the temporal flooding of kettle holes increase the soil moisture and the canopy air humidity in the adjacent fields. This enhances not only the fungal development but also the spore production and the spore release of phytopathogenic fungi. However, the different spore types of these fungi (ascospores, conidiospores) react in different ways to changed moisture conditions and therefore, their distribution could be influenced differently.

b) We hypothesize that kettle holes are keystone structures for the dispersal of phytopathogenic fungi. The different plants and especially grasses at the edges of kettle holes could be considered as a permanent source of inoculation for a persistent infection of the neighbouring fields.

The aim of this project is to understand the trade-offs between spore dispersal and niche competition during the colonization of new habitats after spread processes of the phytopathogenic *Fusarium* and *Alternaria* fungi along a humidity gradient from kettle holes to the adjacent field areas.

## 4. Outline work program

The **work plan** will consist of three steps:

(i) The candidate will analyse the fungal community structure at the edges of several kettle holes as well as in the adjacent wheat fields along a humidity gradient from kettle hole to field and assess how community (dis-)similarity is affected by kettle hole type and distance.

(ii) The candidate will investigate whether the fungal community composition along these gradients from kettle holes to agricultural wheat fields are determined by different spore dispersal ability and/or by different niche competition during the infection and invasion processes.

(iii) Mesocosm experiments with potted plants placed along this gradient will help to assess the importance of kettle holes (with enhanced humidity conditions) as well as of weeds (without enhanced humidity conditions) as key structures for the distribution of phytopathogenic fungi within wheat fields.

## 5. Linkage to 'BioMove' objectives

This project addresses the similarity of microbial metacommunities colonizing weed plants and crop plants and will clarify the relationships between dispersal ability, dispersal distances and niche competition within the plant microbiota under enhanced humidity conditions and long-lasting infection pressure around the kettle holes. Competition for spatial and temporal niches, priority effects as well as competitive exclusion via chemical aggression can act as mechanisms contributing to the coviability of organisms. The trade-offs between dispersal processes and competition could better explain the infection processes by phytopathogenic fungi and the similarity and structure of field-scale and landscape-scale fungal metacommunities.

References

Hoffmann, A., Lischeid, G., Koch, M., Lentzsch, P., Sommerfeld, T., Müller, M.E.H. (2021) Cocultivation of *Fusarium, Alternaria* and *Pseudomonas* on wheat-ears affects microbial growth and mycotoxin production. Microorganisms MDPI (accepted)

Müller, T., Ruppel, S., Behrendt, U., Lentzsch, P., Müller, M.E.H. (2018) Antagonistic potential of fluorescent pseudomonads colonizing wheat heads against mycotoxin producing *Alternaria* and *Fusaria*. Frontiers in Microbiology 9, Article 2124.

Müller, T., Lentzsch, P., Behrendt, U., Barkusky, D., Müller, M.E.H. (2020) *Pseudomonas simiae* effects on the mycotoxin formation by fusaria and alternaria in vitro and in a wheat field. Mycotoxin Research 36, 2, 147-158.

Schiro, G., Verch, G., Grimm, V., Müller, M.E.H. (2018) *Alternaria* and *Fusarium* fungi: differences in distribution and spore deposition in a topographically heterogeneous wheat field. Journal of Fungi 4, 2, Article: 63.

- Schiro, G., Müller, T., Verch, G., Sommerfeld, T., Mauch, T., Koch, M., Grimm, V., Müller, M.E.H. (2019) The distribution of mycotoxins in a heterogeneous wheat field in relation to microclimate, fungal and bacterial abundance. Journal of Applied Microbiology 126, 1, 177-190.
- Schiro, G., Colangeli, P., Müller, M.E.H. (2019) A metabarcoding analysis of the mycobiome of wheat ears across a topographically heterogeneous field. Frontiers in Microbiology 10, Article 2095.

## BioMove Project P11 (Univ. Potsdam), 3<sup>nd</sup> PhD student cohort

Supervising team: Florian Jeltsch, Volker Grimm, Stephanie Kramer-Schadt

From movement energetics to individual home-range formation and tri-trophic community dynamics: a novel, allometric modelling approach to explore biodiversity loss caused by landscape changes.

## 0. Brief expected profile of PhD student

Candidates must have a MSc in Ecology or related fields. Candidates with a modelling background from other natural sciences will also be considered. Experience in process-based mathematical or simulation modelling is required. A solid background in community ecology is desirable.

## 1. Short Abstract

This project will extend a novel approach to dynamically model vertebrate community changes in heterogeneous dynamic landscapes. Based on an allometric approach, home range dynamics of a large number of competing individuals will be simulated using mechanistic considerations of the energetic consequences of movement. In a second step, an additional dynamic trophic level will be included to consider dynamic responses of the vertebrate community to a common predator under different scenarios of habitat loss, fragmentation, and resource dynamics. The refined model will reveal novel insights into the complex linkage between individual movement and behavior and overall biodiversity dynamics.

## 2. Background and previous work

Movement rules of individuals define the space use of species since they determine how individuals use their heterogeneous environment. At the biodiversity level, it is therefore essential to identify the key factors influencing individual movements in response to habitat characteristics and land-use changes, which ultimately alter resource availability such as food and shelter. However, inferring from individual space use to community composition and biodiversity is challenging given the high number and variability of individual organisms and the complexity of their spatio-temporal interactions. In particular movement costs are very rarely considered even though they are known to incur significant costs for animals and drive their behavior. An individual-based, spatially-explicit but static modelling approach to tackling this problem, originally introduced by Buchmann et al. (2011, 2012, 2013), was further refined and developed into a dynamic individual-based community model in project 11 of BioMove. In the first PhD-cohort of BioMove project P11 the static, allometric modeling approach was adapted to investigate the consequences of landscapes of fear on home range dynamics and other prey community metrics (Teckentrup et al. 2018, 2019). PhD 2 extended this static approach towards the **dynamics** of home range formation, and the resulting population and community changes in dynamic landscapes. In her ongoing work PhD 2 focuses on the question of how intraspecific behavioral differences ('animal personalities') influence the negative effects of landscape fragmentation. The novel dynamic approach includes new processes such as reproduction, mortality, and juvenile dispersal. The inclusion of juvenile dispersal adds an important explicit movement process, which is known to impact biodiversity dynamics. The trait-based, dynamic modeling approach provides a new way of scaling up from individuals to vertebrate biodiversity patterns under dynamic environmental conditions, while enabling novel coviability analyses at the community-level (Jeltsch et al. 2019).

3. Objectives/Aims

The proposed new studies will extend the previous individual-based modelling approach to include and explore two new aspects that impact biodiversity dynamics: (i) instead of allometric relationships, a mechanistic consideration of the energetic consequences of movement, and (ii) a third dynamic trophic level of predators.

In particular, this project addresses the following key questions:

- What are the individual energetic consequences of changing resource availabilities, resource use, competition and behavioral variability in dynamic fragmented landscapes and how do they impact longer term species coviability?
- How does a third dynamic trophic level of predators impact the effects of fragmentation and habitat loss on species coviability?

## 4. Outline work program

In the **first part** of the PhD study the PhD candidate will review existing approaches to model energetic consequences of movement (compare Malishev et al. 2021). This review will be conducted together with the BioMove PostDoc Cara Gallagher. In a next step the PhD candidate will identify the most suitable approach to mechanistic consideration of the energetic consequences of movement for the individual-based community model. The following implementation of this approach into the existing community model can be based on an existing C++ or NetLogo version of model. The new model will be systematically evaluated in a thorough sensitivity analysis. It will then be used to systematically explore effects of dynamic landscape changes (e.g. habitat loss, fragmentation, land use changes, resource decline induced by climatic changes) at the level of individuals, populations and communities.

In a **second part** the PhD candidate will implement a third trophic level in the model consisting of one or more predator species that use the modelled vertebrate community as a dynamic resource. This extension of the model will provide a novel individual-based, spatially-explicit community model with three dynamic trophic levels. Dynamic landscape scenarios will vary available resource patches, degree of fragmentation and temporal resource dynamics. Based on these landscape scenarios, the PhD candidate will systematically explore the potentially stabilizing effects of a dynamic common predator on the vertebrate species' community.

Depending on data availability, the modeling approach will be compared and adapted to real systems (e.g. through allometric relationships). Comparable outputs include explicit patterns of home range distributions (e.g. size distributions or spatial distribution in the study landscape), predator-prey scaling patterns, or community composition and structure (e.g. including relative abundance of species with given body mass at habitats with defined level of fragmentation).

## 5. Linkage to 'BioMove' objectives

By linking individual movement (energetics) and behavior with community dynamics at two or three trophic levels this project is at the core of BioMove objectives. It enables crucial investigations on how variation in individual movement impacts biodiversity dynamics and, vice versa, how biodiversity patterns impact individual movement. This project will further shed light on the role of land use and specific landscape features (e.g. amount and fragmentation of resources and shelter habitat) in the coviability of species in dynamic agricultural landscapes.

#### References

Buchmann CM, Schurr FM, Nathan R, Jeltsch F (2011) An allometric model of home range formation explains the structuring of animal communities exploiting heterogeneous resources. Oikos 120: 106-118.

Buchmann CM, Schurr FM, Nathan R, Jeltsch F (2012) Movement upscaled – the importance of individual foraging movement for community response to habitat loss. Ecography 35: 436-445.

Buchmann CM, Schurr F, Nathan R, Jeltsch F (2013) Habitat loss and fragmentation affecting mammal and bird communities - the role of interspecific competition and individual space use. Ecological Informatics 14: 90–98.

Jeltsch F, Grimm V, Reeg J, Schlaegel UE (2019). Give chance a chance: from coexistence to coviability in biodiversity theory. Ecosphere 10(5):e02700. 10.1002/ecs2.2700

Malishev, M., & Kramer-Schadt, S. (2021) Movement, models, and metabolism: Individual-based energy budget models as next-generation extensions for predicting animal movement outcomes across scales. Ecological Modelling, 441, 109413.

Teckentrup L, Grimm V, Kramer-Schadt S, Jeltsch F (2018) Community consequences of foraging under fear. Ecol. Model. 383: 80-90.
Teckentrup L, Kramer-Schadt S, Jeltsch F (2019) The risk of ignoring fear: Underestimating the effects of habitat loss and fragmentation on biodiversity. Landscape Ecology 34(12): 2851-2868. 10.1007/s10980-019-00922-8