



Movement ecology, dispersal kernels, and genetic effects (part II)

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Spatial patterns of seed dispersal by Neotropical tamarin monkeys, *Saguinus mystax* and *Saguinus fuscicollis*

Eckhard W. Heymann¹, Kathrin Lüttmann¹, Birgit Ziegenhagen², Christoph Knogge³, Dietmar Zinner⁴, Ronald Bialozyt²

¹ Verhaltensoekologie & Soziobiologie, Deutsches Primatenzentrum, ² Philipps-University of Marburg, Conservation Biology, ³ UFZ Leipzig, ⁴ Kognitive Ethologie, Deutsches Primatenzentrum

Spatial patterns of primary seed dispersal provide the template for further processes like secondary dispersal and regeneration and are important for understanding gene flow and plant genetic population structure. Following the fate of individual seeds, which is necessary for spatial analyses, is an inherently difficult task. In a field study in Peruvian Amazonia we determined dispersal distances and kernels produced by two small Neotropical monkeys (*Saguinus mystax*, *S. fuscicollis*). We employed a rigid criterion for data collection (seed dispersal distances were only determined if between seed swallowing in a given tree and defecation of seeds no other tree of the same species was visited by the monkeys). In a second field study, we focussed on a specific plant genus (*Parkia*) and – additionally to the observational approach – used microsatellites to identify maternal trees of dispersed seeds. Observational and genetic dispersal distances match closely, giving reliability to previous



purely observational data. Our spatial data indicate that tamarins produce strongly leptokurtic seed dispersal curves and may vary between plant species, but very few (<3%) seeds actually land close to source trees. Furthermore, dispersal kernels show that sleeping sites may represent foci of tamarin seed dispersal. We conclude that once the reliability of observational data has been confirmed through genetic analyses, they can provide insights into the on spatial patterns of seed dispersal.

Seed dispersal of the Brazil nut tree (*Bertholletia excelsa*) by scatter-hoarding rodents in a central Amazonian forest

Torbjørn Haugaasen¹, Joanne M. Tuck Haugaasen², Carlos A. Peres³, Rogerio Gribel², Per Wegge¹

¹ Department of Ecology and Natural Resource Management, Norwegian University of Life Sciences, ² Laboratório de Genética e Biologia Reprodutiva de Plantas, Coordenação de Pesquisas em Botânica, Instituto Nacional de Pesquisas da Amazonia, ³ Centre for Ecology, Evolution and Conservation, School of Environmental Sciences, University of East Anglia

This paper summarises recent work on dispersal of the Brazil nut tree (*Bertholletia excelsa*) by scatter-hoarding rodents in central Amazonia, Brazil. We provide results from three different experiments, including the first ever study to track the fate of cached Brazil nuts across seasons. We also describe an entirely new method to study natural Brazil nut dispersal; tracking manipulated and tagged fruits containing individually marked seeds. Results show that agoutis usually moved intact fruits away from their original location below the parent tree before either hiding them or gnawing through the pericarp to reach the seeds inside. Caching behaviour was strongly affected by seasonal resource abundance; caching rates, dispersal distances and cache longevity differed significantly between seasons. Agoutis also appear to be highly skilled at retrieving their buried Brazil nuts, although cache pilferage may account for large numbers of retrieved seeds, as shown by our third experiment. We conclude that our new method does not inhibit fruit handling by agoutis and provides a realistic approach to investigate natural seed dispersal of Brazil nuts. Agouti behaviour is, to a large extent, driven by resource seasonality and cache pilferage appears to be a prominent feature of Amazonian scatter-hoarding systems.



Ecological significance of seed secondary metabolites in a rodent-dispersed tree: adaptation to seed-eating dispersers?

Kazuhiko Hoshizaki¹, Yasue Yamamoto¹, Yu Masuya¹, Mitsue Shibata², Hiromu Moriya¹, Yuko Yoshizawa³

¹ Dept of Biological Environment, Akita Prefectural University, ² Tohoku Research Center, Forestry and Forest Products Research Institute, ³ Dept of Biotechnology, Akita Prefectural University

Large, rodent-dispersed seeds often contain secondary metabolites that exhibit deterrence to antagonists. While such compounds can discourage seed eaters, their significance for seed-eating dispersers is complex; seeds should both attract dispersers and escape predation. To elucidate the role of seed secondary metabolites, as well as seed size, in tree-rodent mutualism, we focused on escin, which is a major secondary metabolite in *Aesculus turbinata* seeds. We determined escin concentrations in 150 mature seeds and found substantial variation (1.4-6.8%) among individual seeds. As escin concentration was independent of seed size, we followed the fate of seeds of known escin concentration and weight to explore how they affected rodent behavior. Results showed that seed removal was unaffected by both factors, whereas consumption was mainly influenced by escin concentration. Thus, escin is an important determinant in the dispersal success of this species. We also examined seasonal patterns of escin content in immature seeds to test if the observed variations in mature seed escin concentrations coevolved with the seed-rodent interactions. Escin concentrations varied similarly in immature seeds and did not correlate with the extent of predation by insects. We therefore conclude that the variation in escin concentrations may be a compromise between minimizing predation and facilitating dispersal, and that this polymorphism may stabilize rodent responses by providing low-escin seeds.

Effectiveness of seed dispersal by five frugivorous carnivores: implication for their differential role in forest recruitment and regeneration

Youbing Zhou¹

¹ Research Center for Plant Ecology, Institute of Botany, the Chinese Academy of Sciences

Fleshy-fruited plants are usually dispersed by an array of frugivores, differing in the effectiveness of the dispersal service they provide to the plant. The digestive characteristics, body size, feeding behaviour and movement patterns of animal dispersers are hypothesized to affect seed dispersal distances and consequently their effectiveness as dispersers. We tested this hypothesis by comparing the seed dispersal effectiveness of five frugivorous carnivores, masked palm civets (*Paguma larvata*), Chinese ferret-badgers (*Melogale moschata*), yellow-throated martens (*Martes flavigula*), black bears (*Ursus thibetanus*) and hog-badgers (*Arctonyx collaris*) in a fragmented subtropical forest of central China. Our results indicate five frugivorous carnivores as seed dispersers, using the terminology of Schupp (1993), have differential effectiveness. An empirically parameterized mechanistic model showed that the five dispersers switch roles as a function of spatial-scale. Civets took many fruits and acted across heterogeneous habitat, thus they had the significant accelerating role in forest recruitment and regeneration. Martens dispersed most seeds within the local habitat and had



the significant accelerating role in forest recruitment within homogeneous habitat while tiny role in forest regeneration across heterogeneous habitat. Our findings indicate that common species, which are usually neglected by conservationists, have multi-function in forest ecosystem.

Dispersal and recruitment patterns of palms inferred through parentage analysis

*Juanita Choo*¹

¹ University of Texas at Austin

Palms are keystone species in many tropical lowland rainforests. In many regions overhunting and illegal poaching are depleting the population of key seed dispersers including agouti, pacas, monkeys, and tapirs. In this study we consider the dispersal and recruitment patterns of a fully censused population of the palm *Attalea phalerata* in a protected forest of the Peruvian Amazon, and seek to understand the contribution of frugivores to palm population dynamics. Using microsatellite markers, we genotype all seedlings and juveniles to putative seed-producing parents in the study plot. Our preliminary results indicate nearly half of palm seedlings and juveniles originate from palms outside of our study area suggesting high levels of seed dispersal activity and gene flow at this scale. The majority of the oldest juveniles also originated from outside of the study plot. We also found the spatial patterns of offspring recruitment are consistent with Janzen-Connell's predictions of distance- and density-dependent mortality. Our preliminary findings highlight the importance of frugivore-mediated seed dispersal and gene flow to *Attalea phalerata* population and their importance in facilitating the escape of seedlings and survival to reproductive age. We predict severe impacts on the long-term persistence of *Attalea phalerata* populations if hunting activities are not mediated.

Gastropodochory in myrmecochores: when slugs do the job of ants

*Manfred Türke*¹, Eric Heinze¹, Kerstin Andreas¹, Kerstin Reifenrath², Sarah Svendsen¹, Martin Gossner¹, Wolfgang Weisser¹

¹ Institute of Ecology, University of Jena, ² Animal Ecology and Tropical Biology (Zoology III), University of Wuerzburg

In beech-dominated forests in Central Europe, many spring geophytes show adaptations to seed dispersal by ants. Ants, however, can be rare. Motivated by observations of slug feeding on seeds we investigated seed consumption of myrmecochores by slugs. In a seed predation experiment in beech forests we found that seed removal was strongly reduced when gastropods were excluded. The contribution of insects including ants and rodents to seed removal was less. In the laboratory, slugs either consumed elaiosomes or swallowed seeds intact. Swallowed seeds were defecated undamaged and germinated as well as control seeds, indicating the potential for seed dispersal by slugs. We also recovered seeds of myrmecochores in the faeces of slugs caught in forests. We calculated seed dispersal distances by slugs combining data from slug tracking in forest plots and of gut passage times assessed in the laboratory. Mean dispersal distance was 4.3 m for a dry and 5.7 m for a wet



tracking event. This is several times higher than mean dispersal distances assessed for ants in other studies. We also found that slug defecated seeds were less attractive to rodents than control seeds, suggesting that slug gut passage reduces seed predation risk. Seed removal in the forest was reduced for defecated seeds, too. Our results demonstrate that slugs are significant consumers of elaiosomes or entire seeds of ant-dispersed plants. They also indicate that slugs act as seed dispersers of these plants.

How does pollen and seed movement influence local spatial genetic structure of a tropical understory plant?

Marina Côrtes¹, Emilio Bruna², W. John Kress³, Maristerra R. Lemes⁴, Rogério Gribel⁵, Maria Uriarte¹

¹ Ecology, Evolution and Environmental Biology, Columbia University, New York, NY.

² Dept. of Wildlife Ecology & Conservation & Center for Latin American Studies, University of Florida, Gainesville, FL, ³ Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA, ⁴ Laboratório de Genética e Biologia Reprodutiva de Plantas (LabGen), Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, AM, Brazil, ⁵ Laboratório de Genética e Biologia Reprodutiva de Plantas (LabGen), Instituto Nacional de Pesquisas da Amazônia (INPA), Manaus, AM, Brazil

Studies evaluating the contribution of pollen and seed movement to local gene flow are rare. We conducted such study on the herbaceous plant *Heliconia acuminata*, a hermaphroditic, self-incompatible, hummingbird pollinated and bird-seed dispersed species in Central Amazonia. Using 9 microsatellite loci we analyzed parentage and characterized fine-scale spatial genetic structure of reproductive plants and seedlings in one site of continuous forest in the Biological Dynamics of Forest Fragments Project, Brazil. By assigning seedlings to the most likely parent pair, medians of effective pollen and seed dispersal were 56.6m (3.2-119.7m) and 35.4m (4.5-105.8m) respectively, which exceeded median distances between neighboring reproductive plants (2.52m) and between seedling and the nearest reproductive plant (2.98m). This indicates that pollination and, especially, seed dispersal might not be as spatially limited as previously thought. Accordingly, *Heliconia* population presented a weak genetic structure as evidenced by S_p , a metric of decrease of pair-wise kinship coefficients between individuals with distance ($S_p = 0.004$ for seedlings and 0.002 for reproductive plants). *Heliconia* frugivores (*Turdus albicollis* and manakins) might disperse seeds farther than recently estimated. In addition, post seedling establishment processes, such as density dependent mortality and biparental inbreeding depression are likely to act on early recruitment resulting in longer effective gene movement.