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The seed dispersal kernel

Organizers : **Patrick A. Jansen** (Smithsonian Tropical Research Institute, Panama & Wageningen University, The Netherlands) and **Kimberly M. Holbrook,** Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Sevilla, Spain

The seed dispersal kernel – the probability density function of the dispersal distance for an individual or population – is the ultimate quantitative descriptor of seed dispersal in plants. Dispersal kernels have strong potential for hypothesis testing because they allow dispersal modeling as well as direct comparisons of dispersal among individuals and populations. Dispersal kernels should be a standard anticipated outcome of dispersal studies. This symposium features a general introduction to dispersal kernels followed by six studies that address the most important methods for estimating seed dispersal kernels.

#	**Speaker**	**Title**
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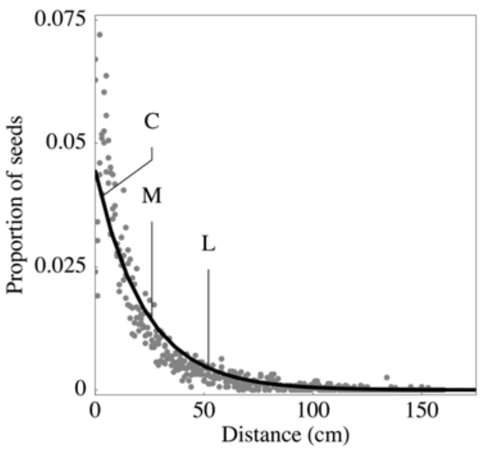
2	Kuprewicz, E.	Estimating seed dispersal kernels by tracking seeds: The effects of large terrestrial mammals on the fates of seeds with various defense strategies in a Costa Rican rain forest
3	Robledo-Arnuncio, J J.	Genetic Estimation of the Seed Dispersal Kernel
4	Visser, M.	Measuring dispersal kernels through inverse modeling: density dependence of seed dispersal in a Neotropical palm.
5	Kays, R.	Estimating seed dispersal kernels from fine-resolution animal movement data: better to be breakfast or dinner?
6	Soons, M.	Estimating dispersal kernels through mechanistic modelling
7	Terborgh, J.	Saplings arise from dispersed seeds

Figure from Molofsky et Ferdy (2005). Online article



Plenary 30’

What on earth is a dispersal kernel?

Roger Cousens[1]

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Modellers coined the term "kernel". It sounds scientific, is embedded in theoretical work, so now everyone is using it. But the one word is being used to mean two very different things. Many papers confuse the frequency of seeds dispersing a given distance with the density of seeds arriving at a particular point. These are quite different, and have very different shapes, but both are being called kernels. Modellers usually model "in one dimension" but parameterise their models with data from two dimensions. The result is that mistakes are being made, interpretations of results are inappropriate, and in many papers it is unclear what the authors have done. In this paper, I will yet again plead for a consistent use of nomenclature. I will explain the difference between the two types of dispersal "curve", review the use of the term "kernel" by modellers, give examples of where nomenclature is ambiguous and examples of where errors have been made in predicting dispersal patterns.

Oral 15’

Estimating dispersal kernels by tracking seeds

Erin Kuprewicz[1]

[1] Department of Biology, University of Miami

In neotropical forests, mammals are major seed dispersers and predators. The positive and negative effects that mammals have on seeds influence tree propagation yet little is known about how the interplay between frugivore handling strategies and seed defenses affect seed fates. Central American agoutis (*Dasyprocta punctata*) scatter-hoard seeds and collared peccaries (*Pecari tajacu*) consume and kill most of the seeds they find. The goals of this study were to assess how agoutis and peccaries affect the survival of fruits and seeds at Estación Biológica La Selva, Costa Rica, how hoarding by agoutis affects diaspore survival, and how terrestrial mammals influence young seedling survival. I tracked seed fates of 5 large-seeded plant species, monitored seed predation of artificially-hoarded diaspores, and assessed the survival of young seedlings protected from or exposed to mammals. Non-defended and chemically-defended seeds suffered high levels of predation by peccaries. Artificially-hoarded diaspores escaped invertebrate and vertebrate predation while exposed seeds suffered high beetle infestation or removal by mammals. All seedlings within mammal exclosures survived after four months whereas seedlings exposed to mammals had variable, often low, levels of survival. In peccary-rich forests, physically-defended seeds are more likely to survive to germinate than unprotected or toxic seeds. If seeds can survive to germinate, young seedling survival is likely not limited by mammals.

Estimating dispersal kernels through paternity analysis

Juan J. Robledo-Arnuncio[1]

[1] CIFOR-INIA

Unlike seed-tagging and non-genetic inverse modelling approaches, genetic parentage analysis allows making inferences on the individual origin of dispersed seeds for large seed samples originating from many potential maternal plants; it thus provides a powerful mean for dispersal kernel fitting based on mother-seed dispersal distances. This is especially true since the genetic analysis of maternally inherited diploid seed tissue has solved the longstanding two-parent dilemma inherent in parentage analysis of cosexual species, which burdened kernel estimation models with usually arbitrary assumptions on the relative location of parent pairs. Several methodological and sampling issues must still be considered, however, in order to estimate accurately the dispersal kernel using exact maternity assignment based on maternal-origin seed tissue. Using simulated and empirical data, I describe here the logic behind available methods, highlighting the importance of (i) properly accounting for the spatial arrangement of seed collection sites relative to source plants, (ii) sampling scale and intensity, and (iii) kernel function selection. I further provide some practical sampling recommendations and discuss ways of using immigrant seeds from outside the study area in order to incorporate long-distance dispersal.

Measuring dispersal kernels through inverse modeling: density dependence of seed dispersal in a Neotropical palm

Marco D. Visser[1], Patrick A. Jansen[1], S. Joseph Wright[2], Helene Muller-Landau[2]

[1] Wageningen University, The Netherlands, [2] Smithsonian Tropical Research Institute, Panama

Understanding the mechanisms that allow species coexistence in complex systems like tropical forest is a fundamental challenge facing scientists today. One leading hypothesis, dispersal limitation, states that the distribution of species depends on their ability to disperse to suitable habitats. Here we tested the previously unexplored hypothesis that seed dispersal by animals can be negatively density-dependent. Specifically, we expected that clumping of conspecific adults would increase intra-specfic cometition for seed dispersers, resulting in reduced seed dispersal compare to isolated trees. We measured effects of adult density on seed dispersal distances in the palm *Attalea butyracea* on Barro Colorado Island, Panama. We sampled dispersed seeds from the soil at varying distances from adult trees at sites that ranged widely in *Attalea* density. Then we used inverse modeling (IM) to estimate dispersal kernels and compared those across sites. We found that IM-estimated dispersal distances, obtained from fitted dispersal kernels, were indeed negatively related to the density of adults. This provides evidence that animal-mediated seed dispersal can decline with increasing fruiting tree density likely due to satiation. This reduction in seed dispersal effectiveness should increase dispersal limitation, causing less seeds to reach sites suitable for germination and growth. Density-dependent dispersal may therefore facilitate tree species coexistence.

Estimating seed dispersal kernels from fine-resolution animal movement data: better to be breakfast or dinner?

Roland Kays[1], Elise M.H. Knecht[2], Patrick A. Jansen[3], Martin Wikelski[4]

[1] New York State Museum, [2] Alterra, Center for Ecosystem Studies, Wageningen [3] Wageningen University and Center for Tropical Forestry Science, [4] Max Plank Institute for Ornithology

Our understanding of seed movement is restricted by the difficulty of tracking individual seeds. New GPS tags allow high resolution movement data for animals. This opens the possibility of combining animal movement data with seed retention times to estimate a dispersal kernel. However, animals do not move evenly throughout the day but follow daily rhythms. For example, typical birds are most active in the morning, less active in the afternoon, and have no nocturnal movement. We used GPS tags with accelerometer activity sensors to track toucan (4 *Ramphastos sulfuratus* and 2 *R. swainsonii*) movement at 15min intervals in Gamboa, Panama. We used their pattern of movement and activity to distinguish bouts of feeding and generated trajectories of seeds eaten in each of these implied feeding bouts. We use these to estimate the probability that toucan would move a particular distance over a particular time interval. We also estimated regurgitation times for toucans by feeding ripe fruits (*Virola nobilis*) to captive toucans. Finally, we calculated the dispersal kernel by combining these probabilities of regurgitation and movement over time to estimate the proportion of seeds that would move various distances away from the mother tree. We will present this seed dispersal kernel for *Virola* and toucans and show the effect of time of day on seed movement. We will also illustrate a variety of real bird and mammal movement kernels using tracking data from www.movebank.org.

Estimating dispersal kernels through mechanistic modelling

Merel Soons[1]

[1] Ecology & Biodiversity group, Institute of Environmental Biology, Utrecht University

Seed dispersal kernels describe the distribution of dispersed seeds in space. They are very useful to ecologists because they inform us where the majority of dispersing seeds will end up, how far seeds can disperse, and with what probabilities. However, seed dispersal kernels are very difficult to quantify. This is mostly because the seeds that travel over the longest distances are extremely difficult to track, resulting in a lack of data on the long-distance end of the dispersal kernel. One way to address this problem and quantify complete dispersal kernels is mechanistic modeling. In this approach, models are built that describe the mechanisms underlying the dispersal process. These models are then tested against trapping and tracking data at short to medium distances, and (when found accurate) used to extrapolate to cover the full dispersal kernel. A great benefit of this approach is that it allows us to assess which processes determine the dispersal kernels. Also, through model sensitivity analysis, it allows us to assess which seed, plant and environmental variables are most important in determining dispersal distances. In this way mechanistic modeling does not only help us quantify dispersal kernels, but also helps us understand which variables and processes contribute to shaping the kernels – and to what degree.

Saplings arise from dispersed seeds

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[1] Nicholas School of the Environment and Earth Sciences, Duke University

For nearly 8 years we have monitored a grid of 289 - 0.5 m^2 seed traps in hyperdiverse floodplain forest at the Cocha Cashu Biological Station in Perú. Approximately 900 trees ≥10 cm dbh have crowns that overhang the 1.44-ha grid. With traps every 7.5 m, few fruiting events escape detection. By knowing the locations and crown dimensions of fruiting individuals, the seed rain can be partitioned into dispersed vs. undispersed fractions. Species differ greatly in the fraction of seed crops that are dispersed, with values ranging from <10% to nearly 100%. The rain of dispersed seeds is extremely sparse. For example, the rain of “intact” (presumptively dispersed) seeds of the two most abundant non-palm tree species at Cocha Cashu is 0.11 and 0.10 seed per m^2-y. Concurrent monitoring of sapling recruitment in the same area has shown, a) that sapling recruitment is very low in the vicinity of fruiting adults, and b) that dispersed seeds carry probabilities of producing saplings that are many times greater than those of undispersed seeds. Calculated seed dispersal kernels that treat undispersed and dispersed seeds as equal are therefore biologically invalid. Studies of disperser ranging behavior indicate that the rain of dispersed seeds is widely mixed on scales much larger than the nearest-neighbor distances between adult trees. These findings imply that a loss of disperser function will lead to a sharp reduction in the diversity of species that can persist over time.