

Meeting report

Frugivores and seed dispersal: mechanisms and consequences for biodiversity of a key ecological interaction

Pedro Jordano^{1,*}, Pierre-Michel Forget²,
 Joanna E. Lambert³, Katrin Böhning-Gaese^{4,5},
 Anna Traveset⁶ and S. Joseph Wright⁷

¹*Integrative Ecology Group, Estación Biológica de Doñana, CSIC, Avda. Americo Vespucio s/n, Isla de La Cartuja, E-41092 Sevilla, Spain*

²*Muséum National d'Histoire Naturelle, UMR 7179, 1 Avenue du Petit Château, 91800 Brunoy, France*

³*Department of Ecological Anthropology, University of Texas at San Antonio, One UTSA Circle, San Antonio, TX 78249, USA*

⁴*Goethe Universität, Department of Biological Sciences, Siesmayerstr. 70, 60323, Frankfurt (Main), Germany*

⁵*Biodiversity and Climate Research Centre (BiK-F), Senckenberganlage 25, 60325 Frankfurt (Main), Germany*

⁶*Institut Mediterrani d'Estudis Avançats (CSIC-UIB), c/Miquel Marqués 21, 07190-Esporles Mallorca, Illes Balears, Spain*

⁷*Smithsonian Tropical Research Institute, Box 0843-03092, Balboa, Ancon, Republic of Panama*

*Author for correspondence (jordano@ebd.csic.es).

The 5th Symposium on Frugivores and Seed Dispersal, held in Montpellier (France), 13–18 June 2010, brought together more than 220 researchers exemplifying a wide diversity of approaches to the study of frugivory and dispersal of seeds. Following Ted Fleming and Alejandro Estrada's initiative in 1985, this event was a celebration of the 25th anniversary of the first meeting in Veracruz, Mexico. Frugivory and seed dispersal are active research areas that have diversified in multiple directions since 1985 to include evolution (e.g. phylogenetic diversity and dispersal adaptations), physiology (e.g. sensory cues and digestion), landscape ecology (movement patterns), molecular ecology (e.g. gene flow, genetic diversity and structure), community ecology (e.g. mutualistic interaction networks) and conservation biology (effects of hunting, fragmentation, invasion and extinction), among others. This meeting provided an opportunity to assess conceptual and methodological progress, to present ever more sophisticated insights into frugivory in animals and dispersal patterns in plants, and to report the advances made in examining the mechanisms and consequences of seed dispersal for plants and frugivores.

Keywords: conservation biology; dispersal; fragmentation; frugivory; hunting; movement ecology

1. INTRODUCTION

Plant 'movement' is largely limited to the dispersal of pollen and seeds, with seed dispersal providing the

only means for most plants to colonize new habitats or escape competition, pathogens and herbivores associated with their mothers. These events are, in turn, closely tied to the evolution of plant life-history traits [1] and vegetation dynamics [2]. Wind, water, gravity and a host of animal species disperse seeds. Frugivores and granivores that consume fruits and seeds, and inadvertently disperse some seeds, underpin the natural regeneration cycles of roughly 60–80% of all plant species [3]. Few natural vegetation types could persist in their present state without animal-mediated seed dispersal. These mutualisms involve reciprocal benefits, and many animal species critically depend on the use of fleshy fruits or seeds as food resources. This pivotal interdependence is central to multiple ecological processes, including coevolutionary interactions among suites of partner species, colonization and large-scale range dynamics of plants, the evolution of highly specialized life-history traits and the sequence of seasonal changes and processes in natural habitats. As just one example, the evolution of frugivory has contributed to large-scale biodiversity patterns through the evolutionary diversification of several clades of primates, bats, fishes, reptiles and birds [4,5].

The 2010 Frugivory and Seed Dispersal Symposium provided an opportunity to exchange new information on how, where and why animal and plant species engage in mutually beneficial interactions and to explore the consequences at both ecological and evolutionary time scales. A quick overview of the main themes of the four previous Frugivory and Seed Dispersal Symposia [6–9] reveals how research themes and topics have expanded since 1985. Organism-oriented research predominated in the first meetings, with many studies documenting patterns of fruit use and consumption by animals and the immediate consequences for plants in terms of seed removal away from the seed-bearing plant and escape from density- and distance-dependent mortality of seeds and seedlings. The predictable patterns in fruit use and seed removal that were documented served to frame the fundamental theory that continues to motivate research into seed dispersal and frugivore–plant interactions [10,11]. Since the third Frugivory and Seed Dispersal Symposium [8], there has been an important shift towards understanding the mechanistic processes behind those interactions. Here, we highlight several themes that emerged in the 2010 Frugivory and Seed Dispersal Symposium.

2. ANIMAL MOVEMENT AND PLANT TRAITS: IMPLICATIONS FOR THE PARTNERS

Two plenary sessions addressed the tremendous diversity of plant–animal interactions that contribute to seed dispersal. There were in-depth reviews of seed dispersal by a wide range of frugivores, including primates, hornbills, megafauna (e.g. elephant), fishes and remarkably, earthworms. Plant–granivore interactions in which the dispersal agent also consumes and kills a large portion of seeds characterize conifers, oaks, palms, rodents and finches and received particular attention. This diversity of organisms and interaction patterns illustrates how animal-mediated seed dispersal underpins the evolution of natural

communities around the world via networks of reciprocal interactions between plants and animals.

Several sessions addressed physiological, chemical and morphological mechanisms at the fruit–frugivore interface. These included odour and volatile emissions, fruit pulp nutrients, plant secondary metabolites and traits that mediate seed dispersal by invertebrates. Some of these fruit characteristics (e.g. odour) are rarely considered in frugivory studies and provide new insights into the complexity of the evolution of fruit displays. Others such as visual cues and colour in fruit displays illustrate distinct evolutionary trends for colour–nutrient associations and the ways in which these associations provide reliable signals in plant–animal communication. The animal side was also considered. The digestive physiology and fruit use of frugivorous ‘carnivores’ like the binturong and kinkajou differ markedly from other similar-sized frugivores. Likewise, fruit preferences of South African frugivores depend on digestive efficiencies and the types of sugars fruits contain. The interaction between frugivores and the chemical composition of fruits and seeds has direct effects on seed escape from pathogens and establishment success, as well as on seed dissemination. As an example, the consumption of chilies by frugivores removes essential lipids from the seed surfaces and thereby ‘camouflages’ dispersed seeds from their predators. Sessions on Organismal and Natural History Research included many new insights into the subtle interactions taking place at the fruit–frugivore interface, with the outcomes of plant–frugivore interactions embedded in multiple and diversified interactions among effective seed dispersal agents, seed predators and seed pathogens.

3. DISPERSED SEEDS: WHO MOVED THEM, AND FROM WHERE?

The movements of dispersal agents determine the spatial template for seed dispersal, which, in turn, determines the spatial template for germination, seedling establishment and the subsequent growth and mortality of plants. Thus, the outcomes of the interactions between seeds and their dispersal agents have far-reaching influences for plant population and community dynamics and genetic diversity and structure. The 2010 conference included two sessions focusing on movement ecology that encompassed theory (see §4 below), empirical analysis of seed dispersal distributions, ecological studies at the landscape level and field applications of new technologies for tracking the movement behaviour of frugivores, and the consequences for gene flow and the genetic structure of plant populations. This is certainly one of the most fascinating and quickly developing fields in seed dispersal research and often depends on a highly multi-disciplinary approach. Researchers are actively combining genetic data (DNA polymorphisms), high-resolution tracking of frugivore movements and imaginative mechanistic models of fruit processing and seed dissemination to robustly estimate the probability of seeds reaching a specific distance from the maternal plant source. High-resolution tracking of frugivore movements facilitates finer assessment of

the complexity of bi-dimensional seed shadows at stand or landscape scales. These techniques and modelling efforts have not only allowed for robust characterization of seed dispersal shadows, but have also provided insight into the contributions of particular frugivores to seed dispersal to different distances. For example, long-distance dispersal by frugivorous megafauna (including mammals and birds) is often characterized by a directional component that enables the colonization of new forest patches and the maintenance of connectivity in fragmented landscapes. A dedicated symposium addressed the patterns and processes of scatter-hoarding dispersal in oaks. These foundation species dominate many temperate forests, and interdisciplinary studies of oak seed dispersal are revealing critical bottlenecks limiting their regeneration.

4. THE ECO-EVO OF FRUGIVORY AND SEED DISPERSAL

The consequences of plant–frugivore interactions have multiple evolutionary implications that we are just beginning to understand. Two sessions addressed these evolutionary implications, both from theoretical and empirical perspectives. These talks illustrated the value of combining modelling with ecological experiments, in order to assess the evolutionary potential of dispersal-related traits. The strong selective pressures imposed by the high costs of dispersal-related traits and high mortality at the seed and seedling stages can favour rapid evolution through selection over ecological time. These basic ingredients can promote the evolution of disparate fruit/seed traits in species-rich communities like tropical forests and eventually favour diversification in plant and frugivore clades. Islands provide natural laboratories for the evolution of dispersal adaptations and several speakers used insular model systems to illustrate key elements of seed dispersal mutualisms that can be particularly sensitive to the loss of any of their elements. The isolation and restricted species pool of animal frugivores (lizards, tortoises, bats and pigeons) that comprise most insular assemblages make them sensitive to extinctions and introductions of exotic partners. The first empirical data showing that exotic species can replace extinct disperser taxa and restore lost ecosystem functions were provided by a nice example of the Aldabran giant tortoise replacing two extinct tortoises in Mauritius.

5. DISRUPTING MUTUALISMS: ANTHROPOGENIC IMPACTS ON FRUGIVORES AND FRUITS

What would the natural world look like if we lost the frugivorous and granivorous animals that disperse seeds? Depending on the habitat type, the natural regeneration cycle and recruitment of a large fraction of plant species would be changed. Local extinctions might or might not follow, as many species achieve some seed dispersal with the haphazard intervention of surviving dispersal agents. Yet, a drastic decline in seed removal success, increased clumping and increased genetic differentiation among populations owing to a loss of long-distance dispersal events, and

a disproportionately high mortality of seeds to pathogens and predators can be expected. Examples and case studies were presented in sessions dedicated to human impacts, habitat loss and defaunation. For example, hunters often focus on frugivores with consequences that extend well beyond the reductions in the abundances of game species. Even low levels of hunting can drastically impoverish frugivore communities and disrupt dispersal systems. The documented consequences of hunting and also of habitat fragmentation include truncated dispersal kernels, with a loss of long-distance dispersal events and changes in density-dependent mortality, clumping and recruitment success of many plants. These consequences integrate direct anthropogenic impacts on selected frugivores and granivores, and the indirect effects for the remaining frugivores and granivores and the plant community. These effects can ultimately translate into rapid evolutionary shifts in seed and fruit traits, as shown for palms in fragmented landscapes and for herbaceous species in field experiments. Important themes in several talks and a number of poster presentations included the consequences of human-driven biological invasions. Seed dispersal studies can inform decision makers and managers as they design plans to control invasive species. Finally, the loss of animal frugivores is expected to accelerate the negative effects of climate change, as plants have to move in space to 'track' their preferred climatic conditions and are only able to do so if animals transport seeds through increasingly fragmented landscapes.

6. PERSPECTIVES

This meeting brought together researchers studying plant–frugivore mutualisms from a wide range of perspectives, presenting work on a broad array of topics including eco-physiology, conservation biology, climate change biology, landscape ecology, population genetics, biogeography, evolutionary ecology and phylogenetics. The common ground was to understand the pervasive influences that seed dispersal has on plant populations, and how this feeds back on animals shaping multiple aspects of their life histories and evolutionary diversification. These mutualistic interactions include key process for the functioning of many different ecosystems, from deserts to rainforests, yet they are affected by rapidly changing ecological conditions and seriously threatened by human activities. New conceptual frameworks such as movement ecology, complex networks of interactions among species and their associated ecological functions and services, and landscape-level analyses combined with models of range shifts should provide much needed steps towards future advances. Plant–frugivore research illustrates the increased collaboration and integration across

fields that characterizes modern science, with a combination of in-depth knowledge of the natural history of organisms, sophisticated use of technology to quantify movement patterns and their effects on seed dispersal, and integration through mechanistic models. These are very important ingredients for a predictive science that will enable us to frame robust predictions of the consequences of the loss of plant–frugivore interactions for natural and human-modified habitats. With these tools we will be able to better diagnose critical situations, develop early warning signals of failed seed dispersal, and design actions for efficient restoration of ecological functions.

We are grateful to the sponsors la Région Languedoc-Roussillon, Montpellier Agglomération, CNRS-INEE, the University of Montpellier 2 and INRA-ComEvol who provided generous support for this meeting. The publishers CABI, CSIRO Publishing, Oxford University Press and Wiley-Blackwell granted the prizes for the 2010 David W. Snow Award.

- 1 Ronce, O. 2007 How does it feel to be like a rolling stone? Ten questions about dispersal evolution. *Ann. Rev. Ecol. Evol. Syst.* **38**, 231–253. (doi:10.1146/annurev.ecolsys.38.091206.095611)
- 2 Howe, H. F. & Miriti, M. N. 2000 No question: seed dispersal matters. *Trends Ecol. Evol.* **15**, 434–436. (doi:10.1016/S0169-5347(00)01965-0)
- 3 Wang, B. & Smith, T. 2002 Closing the seed dispersal loop. *Trends Ecol. Evol.* **17**, 379–385. (doi:10.1016/S0169-5347(02)02541-7)
- 4 Fleming, T. 2005 The relationship between species richness of vertebrate mutualists and their food plants in tropical and subtropical communities differs among hemispheres. *Oikos* **111**, 556–562.
- 5 Fleming, T., Breitwisch, R. & Whitesides, G. 1987 Patterns of tropical vertebrate frugivore diversity. *Ann. Rev. Ecol. Syst.* **18**, 91–109. (doi:10.1146/annurev.es.18.110187.000515)
- 6 Dennis, A., Schupp, E., Green, R. & Westcott, D. 2007 *Seed dispersal: theory and its application in a changing world*. Wallingford, UK: CAB International Publishing.
- 7 Fleming, T. & Estrada, A. 1993 *Frugivory and seed dispersal: ecological and evolutionary aspects* Dordrecht, The Netherlands: Kluwer Academic Publishers.
- 8 Levey, D., Silva, W. & Galetti, M. 2002 *Frugivores and seed dispersal: ecological, evolutionary, and conservation issues*. Wallingford, UK: CAB International.
- 9 Estrada, A. & Fleming, T. 1986 *Frugivores seed dispersal*. Dordrecht, The Netherlands: Dr. W. Junk Publishers.
- 10 Janzen, D. H. 1970 Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**, 501–528. (doi:10.1086/282687)
- 11 Howe, H. F. 1993 Specialized and generalized dispersal systems: where does the paradigm stand? *Végétatio* **108**, 3–13.