OIKOS

Editorial

Special issue: Fruits, animals and seed dispersal: timely advances on a key mutualism

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Oikos
2022: e09220
doi: 10.1111/oik.09220
Subject Editor and
Editor-in-Chief: Dries Bonte
Accepted 19 January 2022

'As the mistletoe is disseminated by birds, its existence depends on birds; and it may metaphorically be said to struggle with other fruit-bearing plants, in order to tempt birds to devour and thus disseminate its seeds rather than those of other plants.'

C. Darwin (*The Origin of species*, 1859)

Equipped with his trademark ideas about the drivers of species' evolution, Darwin found new ecological insights everywhere he looked, even on something as ordinary as flowers and fleshy fruits. In the *Origins* (1959), he anticipated not only the functional underpinnings of pollen and seed-transport mutualisms between plants and animals, but also the fact that such mutualisms bear mechanistic significance for the structure of plant communities. Despite such early insights, it took more than a hundred years for biologists to start paying formal attention to plant–frugivore mutualisms. More than fifty years have now passed since the pioneering work of David and Barbara Snow (Snow 1971, Snow and Snow 1971) sparked Frugivory and seed dispersal (FSD) as a subdiscipline of ecology.

At the individual level, frugivory events and seed dispersal processes integrate research on the foraging ecology of frugivores in relation to the reproductive ecology of plants. The outcomes of frugivory and seed dispersal affect a number of ecological patterns and processes at different levels of organization, including movements, range dynamics of animals and plants, gene flow within and among populations across landscapes, and, ultimately, the regeneration of entire plant communities and ecosystems. Plant regeneration processes, in turn, influence the persistence of a myriad of life forms beyond the mutualistic partners involved in frugivory and seed dispersal interactions. Through its influences on plant community structure and diversity, frugivory is thus a process that affects the foundational underpinning of terrestrial ecosystems dominated by plants worldwide.

Advances in this fertile field have been marked by seven international conferences held in Mexico (1985, 1991), Brazil (2000), Australia (2005), France (2010), South Africa (2015) and most recently in the Corbett landscape of India (2020). The previous

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conferences enabled the publication of five important edited volumes (Estrada and Fleming 1986, Fleming and Estrada 1993, Levey et al. 2002, Dennis et al. 2007, Forget et al. 2011) that constitute a solid base to the FSD field. Here, in this shared special issue between Oikos and Journal of Avian Biology, we present a selection of 25 papers (23 here in Oikos and 2 in Journal of Avian Biology), presented at the FSD 2020 conference in India. Two papers focusing on bird-specific topics are available at Journal of Avian Biology, whereas other topics on ecology are published in this issue of Oikos. This set of papers exemplify current research advances on frugivory and seed dispersal ecology in a diversity of fronts.

Here, we start with a set of papers that explore uncharted patterns in frugivory and seed dispersal. For example, the piece by Green et al. examines the ubiquity of animal gut-dispersal (endozoochory) of seeds from plants that bear no fleshy fruits, reminding us that the seed dispersal processes of a large fraction of plants remains to be described. In this case, the authors show that endozoochory of many species of aquatic and ruderal plants can be a common accidental non-mutualistic process. Accordingly, the also often overlooked seed dispersal processes by animals that play dual roles as seed predators and seed dispersers is explored at local spatial scales in mice by Boone et al., who explore these patterns with respect to personality and perceived predation risk, and at large spatial scales by granivorous, island-traversing pigeons *Columba janthina* in Ando et al.'s paper. The largely overlooked role of pigeons as effective seed dispersal agents is further explored by Marrero and Nogales (Journal of Avian Biology 2021), who use DNA and microhistological methods to investigate differences between two island-dwelling *Columba* species.

The implications of frugivory and seed dispersal phenomena are observed at different levels of organization. At a fundamental level, the matching between the morphological and physiological traits of fleshy fruits and frugivorous animals are hypothesized to pose a first selection 'filter' determining which frugivore species serve as effective dispersers of seeds from fleshy-fruited species. In their paper, Whitehead et al. explain how fruit are important incubators of phytochemical diversity, supporting their ideas with empirical research on seed dispersal in Neotropical *Piper* species (Piperaceae). The ecological implications of a morphological trait – fruit skin hardness – is explored in the piece by Valenta et al., who conclude that hardness is most likely explained by biotic, rather than mechanical factors. Yet, the complexity of ecological systems causes multiple factors to jointly influence FSD processes, posing challenges to the understanding of the role of fruit traits. Some of these challenges are tackled by González-Varo et al. who disentangle the relative contributions of resource abundance, fruit morphology and fruit nutritional traits on the body condition of an abundant and important avian frugivore, the Sardinian warbler *Curruca melanocephala*.

Network analyses have revolutionized the studies of FSD interactions (Guimarães 2020), but they have been limited to scales that could hide important organismal-level variation in frugivory processes. The pieces by Friedemann et al. and Tonos et al., are novel because they analyze network interactions and properties at the scale of individual plants. Both studies highlight that interactions between individual plant species and frugivorous partners are influenced by intrinsic and extrinsic characteristics. Surprisingly, Friedmann et al. show that individual palm traits did not influence interaction patterns, while Tonos et al. found that few individual plants dominate interactions and receive most of the visits. These studies bring new insights about the effects of relative spatial positioning and distinct habitats in the individual-level variance experienced by plants on FSD metrics.

At the community level, understanding the functional outcomes of pairwise seed dispersal in communities has been central to several sub-topics of FSD research for decades (Schupp 1993, Schupp et al. 2010). However, measuring interaction outcomes in the field remains challenging, and there are still few studies capable of tracing community-wide interactions between fruiting plants and their consumers. In their piece, González-Castro et al. use a comprehensive community-wide dataset in which the functional outcomes of interactions between plants with disparate taxa of animal frugivores are traced, evaluating how well interaction frequency – a commonly used surrogate metric for functional outcomes – predicts actual ecological outcomes.

Frugivory and seed dispersal is not only affecting biodiversity at different levels of organization, but at different temporal and spatial scales. The temporal scale at which interactions are studied have a strong bearing on our ability to understand FSD processes. In general, the majority of ecological studies are limited to short time frames (i.e. usually a few months per year, or a few years) and, thus, we still know little about the long-term dynamics of FSD processes. Three of the special issue papers address this limitation by analyzing multi-year datasets. Campagnoli and Cristianini examine the temporal consistency of FSD interactions between plants, birds and ants in a neotropical savanna during two fruiting periods that are 15 years apart. The contribution by Campo-Celada et al. evaluates short and long-term changes, across approximately 40 years, in migratory frugivorous birds and demonstrate the negative consequences of global changes on the diversity, phenology and physical conditions of frugivorous bird species. The piece by Gratzer et al. examines the seed rain of wind-dispersed trees in an old-growth European forest to investigate how spatial and temporal (across 15 years) of seed production and deposition affects plant population recruitment dynamics.

Some of the persisting challenges to study animal-mediated seed dispersal stem from difficulties in measuring how and why frugivores move on landscapes. Advances in modelling during the last two decades have made it possible to theoretically explore frugivore movements and seed dispersal patterns in novel ways. This special issue features four pieces that explore conceptual advances in the modeling approaches. The piece by Morales and Morán-López, and that by Thierry et al. present concepts and agent-based models based on simulation models to understand landscape-specific

outcomes, while Borah and Beckman adapt the Movement ecology paradigm (Nathan et al. 2008) to investigate drivers behind frugivore movement and their potential impacts on seed dispersal. The contribution by Quintero et al. reviews the advantages and limitations of methods used for monitoring primary seed dispersal, proposing methods to cope with challenges involved in the merging of different types of data for analyses.

FSD processes both affect, and are affected by, patterns and processes that occur at local and landscape scales. Cazetta and Fahrig present a global meta-analysis on the effects of human-altered habitat spatial patterns at local and landscape scales on FSD processes. The novel piece by Monteiro et al. examines how landscape connectivity of Atlantic Forest fragments in Brazil influences not only the phylogenetic diversity of FSD interactions but also their evolutionary distinctiveness, while Camargo et al. use a field experiment in forest fragments to examine how variation in the frugivores' diversity across forest fragments relates to variance in the equalizing and stabilizing properties of frugivory on the seed rain of deforested areas. Also featured is the piece by Naniwadekar et al. (Journal of Avian Biology 2021) that explores the effect of hornbills on the spatial distribution of seeds in forests in India.

Our special feature concludes with papers exploring ways in which FSD interactions are altered by additional anthropogenic factors. One of the most important of these factors – the introduction of non-native species – is explored in two special issue papers. The piece by Vergara-Tabares et al. shows that dominance of invasive *Pyracanths* spp. in Argentina – by default considered to be detrimental – can actually have positive effects on FSD processes of native species. The piece by Heleno et al. analyzes how introduced animal species with larger gapes result in the 'up-sizing' and structural modification of an island-wide seed dispersal network. Anthropogenic provisioning is an under-studied way in which humans can alter FSD interactions. Sengupta et al. explore the various ways in which this occurs and explain how provisioning can positively and negatively influence the seed dispersal process. The last piece of the special feature is by Deshpande et al., examining how FSD processes that covary with landscape processes affect risks of zoonotic disease for people when fruit and seed resources are shared with bats in India.

We hope that this collection of papers at the cutting edge of the field serves to inspire new generations of researchers to continue expanding our knowledge of frugivory and seed dispersal systems worldwide, as they are essential components of the resilience of ecosystems and their biodiversity.

Edited by
Tomás A. Carlo, Eliana Cazetta, Anna Traveset, Paulo R. Guimarães and Kim R. McConkey.

Acknowledgements – We will like to give special thanks to the chair of the organizing committee of FSD India 2020, Dr. Soumya Prasad, as well as to the members of the organizing committee: H. S. Sushma, D. Mudappa, R. M. Borges, A. Datta, S. Radhakrishna, G. Ramaswami, J. R. Mukherjee, A. Sengupta, G. Shahabuddin and S. Sridhara, for making the conference possible.

Author contributions

Tomas Carlo: Conceptualization (lead); Writing – original draft (lead). **Eliana Cazetta**: Writing – review and editing (equal). **Anna Traveset**: Writing – review and editing (equal). **Paulo Guimaraes Jr**: Writing – review and editing (equal). **Kim McConkey**: Writing – review and editing (equal).

Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.XXXX> (Carlo et al. 2022).

References

Ando, A. et al. 2022. Highly mobile seed predators contribute to interisland seed dispersal within an oceanic archipelago. – Oikos 2022: e08068.

Boone, S. R. et al. 2022. Seed predation and dispersal by small mammals in a landscape of fear: effects of personality, predation risk and land-use change. – Oikos 2022: e08232.

Borah, B. and Beckman, N. G. 2022. Studying seed dispersal through the lens of movement ecology. – Oikos 2022: e08310.

Camargo, P. H. S. A. et al. 2022. Frugivore diversity increases in the seed rain on deforested tropical landscapes. – Oikos 2022: e08028.

Campagnoli, M. L. and Christianini, A. V. 2022. Temporal consistency in interactions among birds, ants and plants in a neotropical savanna. – Oikos 2022: e08231.

Campo-Celada, M. et al. 2022. Assessing the short and long-term variations in diversity, timing and body condition of frugivorous birds. – Oikos 2022: e08387.

Carlo, T. A. et al. 2022. Data from: Special issue: Fruits, animals and seed dispersal: timely advances on a key mutualism. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.XXXX>.

Cazetta, E. and Fahrig, L. 2022. The effects of human-altered habitat spatial pattern on frugivory and seed dispersal: a global meta-analysis. – Oikos 2022: e08288.

Darwin, C. 1959. On the origin of species by means of natural selection, or preservation of favoured races in the struggle for life. – John Murray.

Dennis, A. J. et al. 2007. Seed dispersal: theory and its application in a changing world. – CAB International.

Deshpande, K. et al. 2022. Forbidden fruits? Ecosystem services from seed dispersal by fruit bats in the context of latent zoonotic risk. – Oikos 2022: e08359.

Estrada, A. and Fleming, T. H. 1986. Frugivores and seed dispersal. – Dr. W. Junk Publishers.

Fleming, T. and Estrada, A. 1993. Frugivory and seed dispersal: ecological and evolutionary aspects. – Kluwer Academic Publishers.

Forget, P.-M. et al. 2011. Frugivores and seed dispersal: mechanisms and consequences of a key interaction for biodiversity. – Acta Oecol. 37: 517–682.

Friedemann, P. et al. 2022. The individual-based structure of palm-seed dispersers is explained by a rainforest gradient. – Oikos 2022: e08384.
González-Castro, A. et al. 2022. Changes in the structure of seed dispersal networks when including outcomes from both plant and animal perspectives. – Oikos 2022: e08315.
González-Varo, J. P. et al. 2022. Fruit abundance and trait matching determine diet type and body condition across frugivorous bird populations. – Oikos 2022: e08106.
Gratzer, G. et al. 2022. Does fine scale spatiotemporal variation in seed rain translate into plant population structure? – Oikos 2022: e08826.
Green, A. J. et al. 2022. Plant dispersal syndromes are unreliable, especially for predicting zoochory and long-distance dispersal. – Oikos 2022: e08327.
Guimarães Jr., P. R. 2020. The structure of ecological networks across levels of organization. – Annu. Rev. Ecol. Evol. Syst. 51: 433–460.
Heleno, R. H. et al. 2022. The upsizing of the São Tomé seed dispersal network by introduced animals. – Oikos 2022: e08279.
Levey, D. et al. 2002. Frugivores and seed dispersal: ecological, evolutionary and conservation issues. – CAB International.
Marrero, P. and Nogales, M. 2021. Trophic strategies of two sympatric endemic pigeons in insular ecosystems: a framework for understanding spatiotemporal frugivory interactions. – J. Avian Biol. 52: e02803.
Monteiro, E. C. S. et al. 2022. Forest cover and connectivity have pervasive effects on the maintenance of evolutionary distinct interactions in seed dispersal networks. – Oikos 2022: e08240.
Morales, J. M. and Morán López, T. 2022. Mechanistic models of seed dispersal by animals. – Oikos 2022: e08328.
Naniwadekar, R. et al. 2021. Gardeners of the forest: hornbills govern the spatial distribution of large seeds. – J. Avian Biol. 52: e02748.
Nathan, R. et al. 2008. A movement ecology paradigm for unifying organismal movement research. – Proc. Natl Acad. Sci. USA 105: 19052–19059.
Quintero, E. et al. 2022. Methodological overview and data-merging approaches in the study of plant–frugivore interactions. – Oikos 2022: e08379.
Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. – Vegetatio 107/108: 15–29.
Schupp, E. W. et al. 2010. Seed dispersal effectiveness revisited: a conceptual review. – New Phytol. 188: 333–353.
Sengupta, A. et al. 2022. The influence of provisioning on animal-mediated seed dispersal. – Oikos 2022: e08276.
Snow, B. K. and Snow, D. W. 1971. The feeding ecology of tanagers and honeycreepers in Trinidad. – Auk 88: 291–322.
Snow, D. W. 1971. Evolutionary aspects of fruit-eating in birds. – Ibis 113: 194–202.
Thierry, H. et al. 2022. Landscape configuration and frugivore identity affect seed rain during restoration. – Oikos 2022: e08323.
Tonos, J. et al. 2022. Individual-based networks reveal the highly skewed interaction of a frugivore mutualist with individual plants in a diverse community. – Oikos 2022: e08539.
Valenta, K. et al. 2022. Variation in ripe fruit hardness: a mechanical constraint? – Oikos 2022: e08074.
Vergara-Tabares, D. L. et al. 2022. Fleshy-fruited invasive shrubs indirectly increase native tree seed dispersal. – Oikos 2022: e08311.
Whitehead, S. R. et al. 2022. Fruits, frugivores and the evolution of phytochemical diversity. – Oikos 2022: e08332.