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SPECIAL ISSUE EDITORIAL

An overview and introduction to the special issue on seed dispersal on islands

INTRODUCTION

Island ecosystems are famous as natural laboratories for studies in ecology and evolution because of their isolated and relatively simple ecosystems, and islands have had a central role in the development of biogeography, too. Animal-mediated seed dispersal is an ecosystem process with central implications for the demography of plants and the diversity of plant communities, which, in turn, structure the seed dispersal interactions of the future.

Compared to continental ecosystems, animal-mediated seed dispersal interactions on islands have been relatively little studied. Out of thousands of islands worldwide, only a few have been the focus of more than a handful of seed dispersal studies. On the Galápagos Islands – global biodiversity 'crown jewel' islands that were the stage for some of the early empirical studies of gut-passage effects and the Janzen–Connell model (Rick & Bowman, 1961; Clark & Clark, 1981) – seed dispersal biology remains woefully understudied (Heleno *et al.*, 2011). Also in the Indomalayan Region, one of the richest island regions of the world in terms of number and geology of islands and species diversity, we still know very little about seed dispersal (Corlett, 1998). Perhaps, among all the archipelagos of the world, only the Canary Islands and the Balearic Islands would count as relatively well studied in this regard.

Nevertheless, among the 'noise' of all the quirky, endemic biogeography and evolutionary ecology that makes island biology so fascinating, there are some general patterns in seed dispersal dynamics on islands. For example, while plant diversity on islands can be quite idiosyncratic, insular frugivore communities around the world are often assembled from a fairly small number of taxonomical groups, e.g. lizards, tortoises, pigeons and bats (see Frontispiece to the special issue). Indeed, one of the few 'island syndromes' of seed dispersal seems to be an over-representation of frugivorous lizards, compared to continental ecosystems (Olesen & Valido, 2003).

Sadly, islands are also among the most devastated ecosystems world-wide, and perhaps especially so with respect to seed dispersal interactions. First, on islands, the disproportionate loss of large-bodied frugivores translates into the largest relative amount of recently extinct seed dispersal interactions (Hansen & Galetti, 2009), which, in turn, threatens the recruitment of large-fruited plant species (Wotton & Kelly, 2011). Large-bodied frugivores are especially important seed dispersers and little is known about the impacts of these extinctions. Second, biotic invasions by vertebrates and plants have disproportionally taken place on islands, and invasive species are currently considered the main threat to native biodiversity on many islands (Sax & Gaines, 2008; Kueffer *et al.*, 2010). It is clear that the better we understand direct and indirect effects of seed dispersal interactions between native and invasive species, the better we will be able to manage endangered native biodiversity. Third, and worryingly understudied, is how the perceived fragility of island ecosystems in the context of global change (Fordham & Brook, 2010) will affect seed dispersal on islands.

On the positive side, the simplicity of island ecosystems also means that they offer some of the most promising scenarios for advancing conservation and restoration science (Hansen, 2010), with seed dispersal representing a tractable and readily quantifiable process, and thus an excellent target for improving ecosystem management (Kaiser-Bunbury *et al.*, 2010). Taking a broader outlook, studies focusing on real islands are also of global importance in the current human-dominated era, the Anthropocene. Mainland ecosystems are fragmented into ever smaller and more isolated habitats, and mountain ecosystems are contracting their ranges upward in the face of climate change. Both of these processes lead to increasing numbers of small, insular habitats, where lessons learnt from real islands can likely be fruitfully (pun intended) applied.

Addressing many of these points, this special issue contains studies from islands around the world, ranging from investigations of broad regional patterns of frugivore diversity and evolution, to specific studies from single islands. We hope it will stimulate an increased interest in using islands as model systems for seed dispersal studies.

OVERVIEW OF PAPERS IN THE SPECIAL ISSUE

Despite the long-standing paradigm that island ecosystems differ from continental ones in generally being simpler, there are surprisingly few comparative studies that specifically address this question. We start off with two papers with large biogeographical scopes that provide detailed comparisons between frugivores and seed dispersal on islands and continents. In the first paper, González-Castro *et al.* (2012) provide the first example of a comparative study of community-level seed dispersal networks in three very similar ecosystems that differ along a gradient from continental (southern Spain), to continental islands (Balearic Islands), to oceanic islands (Canary Islands). They indeed found the island networks to be smaller and less complex than continental networks, but were unable to disentangle effects of insularity and community size. A logical next step would be to study several linked continental sites and islands that pairwise span a greater range of community sizes. Next, Rojas *et al.* (2012) perform a phylogenetic analysis of New World phyllostomid bats, an important disperser group, focusing on the role of diet specialization for the diver-

sification rates of bats in Antillean and continental ecosystems. In both biogeographical scenarios they found that frugivorous clades of bats had higher rates of diversification than did predatory clades, suggesting that diet shifts to frugivory may be a key evolutionary innovation in these bats.

From regional scales we then take a leap onto specific islands, going into detail with spatio-temporal patterns of dispersal mediated by particular frugivores and the seeds they disperse. Only with an increasing number of such studies can we hope to identify general patterns in the uniquely evolved interactions on islands around the world. A first step is to understand which frugivores move what seeds, and how far. Blake *et al.* (2012) focus on the iconic giant tortoises of Galápagos, among the last surviving island megafauna, and the seeds they disperse. Tortoise gut-passage did not influence germination rates greatly, but tortoises moved great quantities of seeds over long distances, demonstrating how they can drive large-scale seed dispersal dynamics. In relation to conservation and restoration, however, a potentially worrying finding was that seeds from introduced and invasive plant species made up the bulk of dispersed propagules. In a two-pronged study, Wotton & Kelly (2012) first build a mechanistic model to investigate seed dispersal distances by the kereru, *Hemiphaga novaeseelandiae*, the largest extant native frugivore in New Zealand and the fifth-largest surviving pigeon world-wide, and then analyse how body mass affects seed dispersal distances in volant avian frugivores globally. Their results show that despite being sedentary for extended periods, the kereru's long gut retention time meant that a majority of ingested seeds were defecated far away from maternal trees. This result was mirrored in the results of their global analysis, where both the time spent being sedentary and gut retention time increased with increasing frugivore body mass, but where retention time increased faster. Additionally, large-bodied birds flew longer distances. Overall they thus find strong evidence that large birds are disproportionately important as long-distance seed dispersers. Obviously, working with frugivores that don't move very long distances is equally important to obtain a fuller picture of seed dispersal. Piazzon *et al.* (2012) studied the medium-sized eyed lizard, *Timon lepidus*, and several of the plants whose fruits they eat on the Cíes Islands, Spain. They elegantly evaluate the spatial outcome of these interactions at a very fine resolution, by using detailed behavioural observations on lizard movement and experiments on gut passage and seed predation, combined with mapping of plants and habitat, to derive probabilistic models of seed shadows and seed rain.

The final three studies focus on the impacts of frugivore extinction, and on how introduced and invasive species integrate themselves in community-level dispersal interactions on islands. Due to the simplicity of island ecosystems, one commonly voiced concern is that such impacts are of a greater magnitude here than in continental ecosystems. Calviño-Cancela *et al.* (2012) studied the genetic consequences of dispersal disruption in one of the best-studied island seed dispersal systems, the lizard *Podarcis lilfordi* and the plant *Daphne rodriguezii* in the Balearic Islands, Spain. They found evidence of negative impacts of the loss of the disperser on genetic diversity in the smaller and more isolated plant populations; further, they suggest that the extinction of lizards may ultimately hinder pollinator-mediated gene flow, as a result of reduced probabilities of effective pollination among increasingly distant and scarce individuals. Next, Spotswood *et al.* (2012) investigate how an invasive alien plant and two introduced avian frugivores integrate themselves into very small and simple native seed dispersal networks on two islands in French Polynesia, across study sites spanning a gradient from low to high abundance of *Miconia calvescens*. Most importantly, they found that the two abundant introduced frugivores increased consumption of *M. calvescens* at high densities of this plant, while a scarce endemic fruit dove continued to forage mostly on endemic plants, and they discuss how this can influence the structure and outcome of network dynamics. Finally, Zuël *et al.* (2012) provide a highly applicable study of Telfair's skink, *Leiolopisma telfairii*, an endemic large-bodied lizard on Round Island, Mauritius, where it disperses seeds of both endemic and invasive plant species. The results from gut passage and germination experiments suggest that dispersal dynamics mediated by this endemic frugivore may benefit endemic plant species more than introduced plant species, providing a potential competitive long-term benefit for endemic plant species in invaded ecosystems.

WHERE DO WE GO FROM HERE?

Theodosius Dobzhansky famously said that 'nothing in biology makes sense except in the light of evolution'. To this we'd like to poetically add that the light of evolution – and ecology – shines much clearer and brighter on islands. We hope that the breadth of studies in this special issue makes it equally clear that island ecosystems are valuable model systems for basic ecological research, as well as serving as under-appreciated canaries in the global coal mine of the Anthropocene.

To further illustrate this point, we conclude with a hopefully inspiring, non-prioritized list of currently under-researched research foci in island seed dispersal, going from basic (top) to more applied issues (bottom), with an obvious degree of synergistic overlap between the two approaches among many of them:

- Post-dispersal seed fate (e.g. seed predation, seed germination and seedling establishment).
- Validity of the Janzen–Connell model on islands.
- Intra-island seed dispersal (e.g. detailed seed rain and seed shadow studies, development of predictive mechanistic models).
- Inter-island seed dispersal (e.g. effect of isolation and island 'neighbourhood').
- Mainland–island comparisons.
- Multi-island but intra-archipelago studies of the same species/genus.
- Island ontogeny studies focusing on seed dispersal interactions (e.g. niche pre-emption, character displacement, identifying general patterns and key events in the assembly of interaction networks in island ecosystems).
- Interaction networks.
- Control or eradication of invasive/introduced species as models for questions in basic ecology on a landscape scale.
- Impacts of global change.
- Comparative studies of seed dispersal in restored and unrestored habitats.
- Seed dispersal interactions as a biodiversity monitoring tool.

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Dennis M. Hansen[1]* and Anna Traveset[2]

[1]*Institute of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057, Zurich, Switzerland,* [2]*Institut Mediterrani d'Estudis Avançats (CSIC-UIB), C/Miquel Marque's 21, 07190-Esporles, Mallorca, Illes Balears, Spain*

**E-mail: dennis.hansen@ieu.uzh.ch*

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