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RESEARCH

Bat dispersal of fern spores in New Zealand

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Abstract: Fern dispersal is generally considered to be anemochorous. In New Zealand, short-tailed bats *Mystacina tuberculata* consume fern spores. We conducted a germination experiment of bat faecal pellets collected from three roost locations in Pureora Forest Park (North Island) to estimate the viability of fern spores that had survived bat gut passage. Spores of *Cyathea*, *Dicksonia*, *Hymenophyllum*, and *Microsorum* were recorded in the faecal pellets. Of 31 spores in 120 faecal pellets (c. 1 in 4 faecal pellets contained spores), 13 germinated, with a mean abundance of viable spores per faecal pellet of 0.2 ± 0.3. Short-tailed bats should therefore be considered as potential dispersal vectors of ferns in New Zealand forests.

Keywords: bat, chiropterochory dispersal, endozoochory, germination experiment, pteridophyte

Introduction

Dispersal limitation is a determinant of the presence of a species in a local community (Harper 1977; Ozinga et al. 2005). Ferns produce abundant spores (asexual propagules by which ferns disperse); for example, tree ferns (*Cyathea* spp.) can produce up to half a million spores per annum (Conant 1978). Most spores are dispersed by wind (Tryon 1970, 1986). The distance that spores travel varies by release height and wind velocity: for short-statured terrestrial ferns, the vast majority of spores disperse < 2 m; for taller ferns it is up to 100 m in closed forest conditions, and in open environments up to a couple of kilometres (Raynor et al. 1976; Moar et al. 2011; Rose & Dassler 2017), and a small percentage are dispersed much greater distances (Wolf et al. 2001).

A potential additional dispersal vector of fern spore is zoochory (Boch et al. 2016). Evidence of potential zoochory of ferns dates from as early as the Triassic with spores extracted from herbivore coprolites (Fiorelli et al. 2013). Birds, rodents, bats, and invertebrates consume fern sporangia as a primary nutrition source, or through secondary consumption (Parry-Jones & Augee 2001; Arosa et al. 2010; Sugita et al. 2013; Boch et al. 2016; Hervías-Parejo et al. 2019). Germination percentages of spores after gut passage through wood mice (*Apodemus sylvaticus*) were much lower (< 1%; Arosa et al. 2010) than through invertebrates (50–78%; Boch et al. 2016). Although fern spores do germinate after gut passage in bats (Sugita et al. 2013), we know of no studies that have determined the percentage of spores that germinate following bat consumption. Examination of faecal material and stomach contents of New Zealand endemic short-tailed bats *Mystacina tuberculata* has identified presence of *Cyathea* spp. and *Dicksonia squarrosa* spores (Daniel 1976), but the viability of spore material that has passed through the gut of a short-tailed bat is unknown. In this study we examined spore viability of material located within short-tailed bat faecal pellets to establish whether short-tailed bats are a potential dispersal vector for ferns in New Zealand native forest.

Methods

We collected samples of bat faecal material from three short-tailed bat roost sites in the 450 ha Pikiariki Ecological Area (38°26′ S, 175°39′ E) of Pureora Forest Park, Waikato, central North Island. The bat roosts were located within three separate tree trunks: (1) standing dead trunk (species unknown), (2) mataī *Prumnopitys taxifolia*, and (3) māhoe *Melicytus ramiflorus*. Samples comprised up to 50 g of faecal pellets from the base or floor of each roost cavity. The faecal samples were returned to the laboratory in ziplock bags and refrigerated (c. 4 °C).

Forty faecal pellets were taken at random from each roost (120 in total) and dried at 21°C for five hours in a drying oven. After inspection for any potentially wind-dispersed spores on faecal pellet exteriors (only two spores were found at × 100 magnification), we ground the pellets, four at a time, using a pestle and mortar, and placed the ground remains in petri dishes (four ground pellets per dish) containing filter paper moistened with 1 cm^3 of water. The petri dishes were sealed (to control for moisture loss in the growth chamber) using silicone food wrap and placed in a growth chamber lit for 14 h per 24 h cycle, with a maximum temperature of 21°C (14 h) and a minimum of 14°C (10 h). The conditions in the growth chamber were set five degrees higher than the mean local high temperature of Pureora (15.7°C; https://cliflo.niwa.co.nz/; accessed May 2020) to encourage fast germination of viable spores (Juárez-Orozco et al. 2013). The petri dishes

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were inoculated for a 14-day period and were re-moistened after 7 days (Goller & Rybczyński 2007; Brock et al. 2019).

Samples in petri dishes were mounted on a dissecting microscope and observed under × 40 magnification. Fern spores were identified, under × 100 magnification, to genus or spore type (trilete or monolete) where distinguishing features were not clearly visible (Large and Braggins 1991). Germination status (binary: whether or not there was evidence of the first rhizoid penetrating the spore coat) of all fern spores was recorded. All analyses were conducted using R-3.2.3. (R Core Team, 2015).

Results

Fern spores recorded from within bat faecal pellets included *Cyathea* (n = 5), *Dicksonia* (2), *Hymenophyllum* (3) and *Microsorum*[1] (3) as well as monolete (6) and trilete (12) spores that could not be further identified (Table 1). The 31 spores were not evenly distributed between roost samples (40 faecal pellets per roost): 20 spores were identified from the dead tree roost sample, 11 from the māhoe roost, and none from the mataī roost (Table 1). The abundance of fern spores per roost sample was 10.3 ± 10.0 ($\bar{x}$ ± SD) and the abundance of fern spores per faecal pellet 0.3 ± 0.6.

Of 31 spores in 120 faecal pellets, 13 germinated (41.9%). All *Microsorum* spores germinated, 3 of 5 *Cyathea*, one of two of *Dicksonia*, four of 12 of unidentified trilete, one of three of *Hymenophyllum*, and one of six unidentified monolete spores. The mean abundance of germinating fern spores per faecal pellet was 0.2 ± 0.3, or approximately one germinating fern spore per 5 faecal pellets.

Table 1. The results of the spore viability experiment in two short-tailed bat roosts; numbers of spores recorded are followed by numbers and genera of viable spores in parentheses.

Dish	Roost sampling locations	
	Dead trunk	**Māhoe**
1	5 (1 *Hymenophyllum*, 2 *Cyathea*)	6 (1 monolete, 1 trilete)
2	5 (1 *Cyathea*, 1 *Dicksonia*)	0
3	6 (2 *Microsorum*)	0
4	0	0
5	0	0
6	0	0
7	0	5 (1 trilete, 1 *Microsorum*)
8	4 (2 trilete)	0
9	0	0
10	0	0
Total	**20 (9)**	**11 (4)**

Discussion

Our study is the first in New Zealand to show that fern spores dispersed by bats can germinate. The fern spores that germinated from short-tailed bat faecal samples (in the orders Cyatheales, Hymenophyllales and Polypodiales) were either part of the bat's diet, or ingested through secondary consumption of prey (e.g., wētā, *Hemideina* sp.), or the prey's habitat (Daniel 1976, 1979). This study highlights the potential of fern spores to survive gut passage of bats, and supports the findings of Sugita et al. (2013) who germinated spores of *Asplenium setoi*, a birds-nest fern, from fruit bat faecal material, and those of Boch et al. (2016) who suggested that fern dispersal via endozoochory is likely to be frequent. Although the experimental process we used to germinate the spores did not use conditions comparable to those recorded at Pureora from where the spores were sampled, the study was designed to answer the question of whether spores remain viable after gut passage.

The low abundance of viable spores present in the faecal pellets (0.2 ± 0.3) does not necessarily limit the significance of bats as dispersers of ferns. A single bat can readily produce up to six faecal pellets as a stress response when being handled (K Collier, unpubl. data); and although data on *Mystacina* gut retention time etc. and faecal/gut productivity are not available, it is not improbable that a bat passes at least two viable spores per day at a distance from the parent sporophyte. However, estimates of the likely number of viable fern spores moved by a population of bats require greater sampling effort. Gut retention time is one determinant of the likely distances that the spore material is transported in the bat gut (Wotton & Kelly 2012). However, defecating habit away from the roost, e.g. during flight or foraging etc., is not known, so it is not possible to establish substantively the dispersal kernel or frequency of viable fern spore dispersal without further work on the ecology of the short-tailed bat.

Further research replicating the study with large sample sizes, under environmental conditions mimicking the habitats the faecal pellets were collected in, and extraction of spores from the samples to permit a sterile environment in which to establish spore viability would establish the range of fern taxa dispersed by bats. Work into gut passage retention time and faecal productivity in bats would usefully inform the volume and likely distance travelled by a spore. Lastly, other taxa such as birds, lizards, and introduced mammals should be considered as potential dispersal vectors (both horizontally and vertically) of ferns in forests.

[1] Microsorum has recently been revised into *Dendroconche* and *Zealandia* (Testo et al. 2019). Which of these two genera the spores are from is uncertain; hence the retention of the old genus.

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