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PLANT ANIMAL INTERACTIONS

Bryophyte dispersal by flying foxes: a novel discovery

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Abstract This research provides the first evidence of dispersal of bryophytes and associated microorganisms through ingestion by a highly mobile vertebrate vector, the spectacled flying fox (*Pteropus conspicillatus*). Bryophyte fragments were found in faeces collected at four *P. conspicillatus*' camps in the Wet Tropics bioregion, northeastern Australia. These fragments were viable when grown in culture; live invertebrates and other organisms were also present. Our study has significantly increased understanding of the role of flying foxes as dispersal vectors in tropical forests.

Keywords Bryophyte dispersal · Microorganism dispersal · Flying foxes

Bryophytes and their associated fauna represent a significant component of the diversity of many tropical forests (Ramsay and Cairns 2004), and dispersal syndromes involving them are important, but poorly understood, processes that help to maintain biodiversity (Laaka-Lindberg et al. 2003). Asexual reproduction via fragmentation is an important method of bryophyte reproduction, but has not previously been considered a significant method of dispersal (Heinken et al. 2001). There have been occasional recordings of adhesive bryophyte dispersal by animal vectors (epizoochory) (Davison 1976; Gerson 1982; Heinken et al. 2001; Kimmerer 1994) and also the dispersal of spores by flies in the case of the dung-mosses (entomophily) (Goffinet and Shaw 2004). Here we demonstrate that bryophytes and associated microorganisms may be dispersed over long distances via passage through the digestive tract of a highly mobile vertebrate, the spectacled flying fox *Pteropus conspicillatus*, representing the first reported case of bryophyte dispersal via the gut of an animal vector (endozoochory).

The spectacled flying fox is associated with the rainforest habitats of the Wet Tropics bioregion of northeastern Queensland, Australia, where it plays an important role in the pollination and dispersal of a variety of tropical plant species (Richards 1990). Flying fox faeces collected in traps located at four *P. conspicillatus*' camps in different vegetation types, in the Wet Tropics, contained a diversity of bryophyte fragments (ranging from fragments of whole shoots to separated leaves), belonging to 15 families of mosses, and thallose and leafy liverworts, with the relative abundance varying between camps (Fig. 1a). Bryophyte occurrence was greatest in samples from a camp located in wet complex notophyll vine forest (Tracey 1982) (22.8% of 685 faecal samples). We believe that bryophyte fragments in the faeces are evidence of ingestion rather than post-defecation contamination for a number of reasons: bryophytes were often highly fragmented and abraded and they were often tightly interwoven with the hair and fibre contents of both

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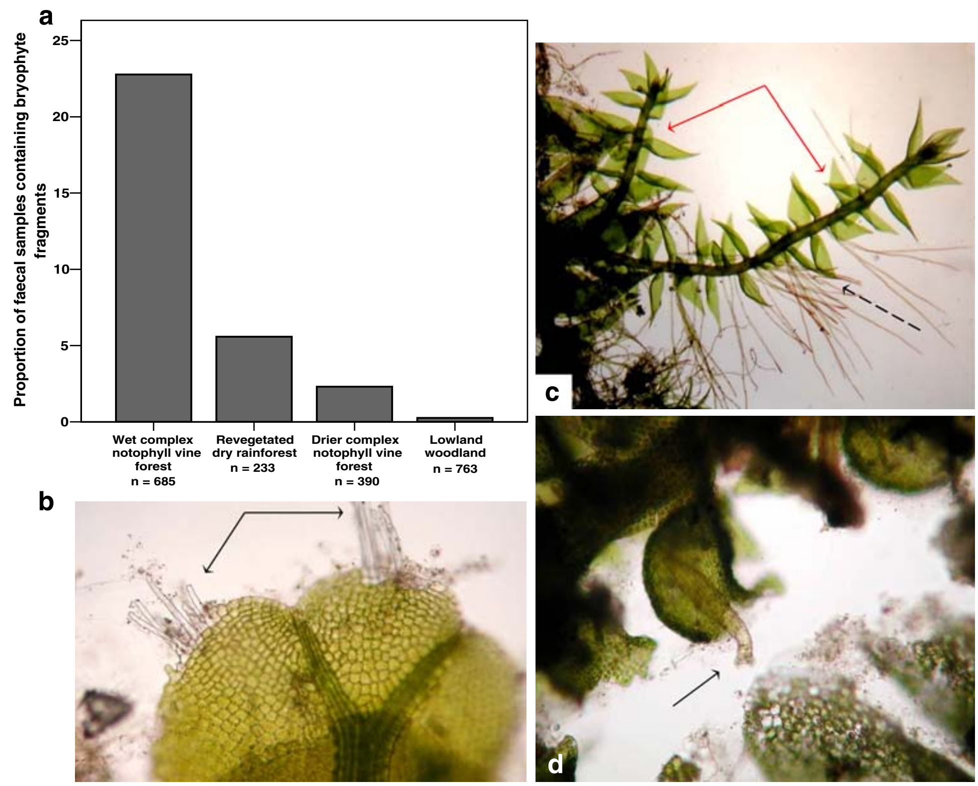

Fig. 1 **a** The proportion of faeces containing bryophyte fragments at four *Pteropus conspicillatus*' day camps (total $n = 2{,}071$). **b** New shoots (*arrow*) and rhizoidal development (*dashed arrow*) in a moss fragment (*Acroporium* sp.), after extraction from faeces and culture in distilled water. **c** Growth of rhizoids (*arrow*) from the margins of a thallose liverwort, *Metzgeria* sp., retrieved from *P. conspicillatus*' faeces and cultured in distilled water. **d** Rotifer (*arrow*) emerging from the lobule of *Frullania* sp., a leafy liverwort, retrieved from *P. conspicillatus*' faeces

hard and soft faeces; great care was taken to remove any foreign plant material that may have fallen on the surface of faeces, prior to analysis. The presence of bryophyte fragments intermingled with hair also suggests that bryophytes were consumed coincidentally with grooming, rather than directly targeted as a dietary item.

Bryophyte fragments isolated from the interior of flying fox faeces were found to be viable and capable of vegetative growth. When cultured in sterile distilled water (Goode et al. 1992), 52% of 48 fragments displayed rhizoidal development and/or shoot extension (Fig. 1b, c). A variety of microorganisms and invertebrates commonly found in association with bryophytes—cyanobacteria, algae, nematodes and bdelloid rotifers—were also found living in the cultured bryophyte fragments (Fig. 1d).

Our results also suggest that the ability of mosses in particular to regenerate through internal transmission via the gut of flying foxes may vary seasonally, perhaps in response to changes in the vector's diet. Faecal samples collected early in the fruiting season contained fleshier fruit and had a lower pH than faeces collected late in the season (Mann–Whitney *U*-test, $n = 16$, $Z = -2.31$, $P = 0.021$). A number of bryophyte species are well adapted for growth in more acidic environments [see Noguchi and Miyata (1957) in Chopra and Kumra (1988)], and success rates tended to be greater in bryophyte samples extracted from faeces during the earlier rather than later part of the season (17 out of 28 fragments in the early and seven out of 20 in the later part of the season; Monte Carlo RxW contingency table test, $n = 10{,}000$, $P = 0.089$, SE = +0.003).

The presence of numerous viable bryophyte fragments and associated microorganisms in the faeces of flying foxes suggests that spectacled flying foxes play an important role in the dispersal of much more than just the large plants of tropical forests.

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