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# Bird functional traits affect seed dispersal patterns of China's endangered trees across different disturbed habitats

Ning Li<sup>1\*</sup> , Zheng Wang<sup>2</sup>, Xinhai Li<sup>3</sup> and Zhaohui Li<sup>1</sup>

## Abstract

**Background:** The most dominant global threat to natural forests and their biodiversity is land-cover change, which has negative impacts on both species persistence and ecosystem functions. Land-cover change could alter animal behaviour and disrupt seed dispersal mutualisms. However, its effects on the role of bird functional traits in seed dispersal are not well studied.

**Methods:** In the present study, we assessed the contributions of bird functional traits (behavioural traits: food habit, foraging pattern, foraging frequency, and habitat specialisation; morphological traits: weight, body length, wing length, and tail length) to both seed removal patterns and seed dispersal distances of an endangered and native tree species, Chinese yew (*Taxus chinensis*), in farmland, patchy habitat, and natural habitat, of southeast China.

**Results:** We found that the ability of *T. chinensis* trees to form seed dispersal mutualisms with local birds varied across the different disturbed habitats. As a consequence of these mutualisms, more seeds were removed by birds from the patchy habitat than from the other two habitats. The number of seeds removed increased with bird foraging frequency. Moreover, the dispersal distance from the three habitats differed, and the longest dispersal distances were observed at both the patchy habitat and the farmland site. Seed dispersal distance increased with bird tail and wing length.

**Conclusions:** Our results highlight the importance of bird functional traits in the seed dispersal patterns of endangered trees across disturbed forest habitats, which should be considered for tree conservation and management.

**Keywords:** Functional traits, Seed dispersal, Frugivorous birds, Behavioural traits, Morphological traits

## Background

The most dominant global threat to natural forests and their biodiversity is land-cover change, which has negative impacts on both species persistence and ecosystem functions (Fahrig 2003; Tylianakis et al. 2008; Pogson 2015; Holyoak and Heath 2016). In Asia, many natural forests have been transformed to farmlands by local residents, resulting in several natural patches of forest within highly human-disturbed habitats (Foley et al. 2005; Haddad et al. 2015). Therefore, it is important to understand the effects of land-cover change on plant

regeneration in these disturbed habitats (Cordeiro and Howe 2003; Markl et al. 2012; Bai et al. 2017).

In general, seed-dispersal interactions between animals and fleshy-fruited plants form the basis of plant regeneration, which is one of the key factors influencing the persistence of plant communities (Janzen 1970). In various disturbed habitats, the seed dispersal pattern of frugivorous birds directly reflects their functional traits, especially their morphological traits (Larsen et al. 2005; Suding et al. 2008; Schupp et al. 2010; Bregman et al. 2016; Farwig et al. 2017). As many ecologists predicted, the body size of birds can be used to estimate the ecological role of birds in seed removal and can affect the degree of species-specific interactions in seed-dispersal distance (Perez-Méndez et al. 2015; Bregman et al. 2016;

\*Correspondence: lining196@126.com

<sup>1</sup> Institute of Applied Ecology, Nanjing Xiaozhuang University, Nanjing 211171, China

Full list of author information is available at the end of the article

Muñoz et al. 2017). Large-bodied birds can transport more seeds than small birds, and have the potential to facilitate seed dispersal among forest fragments (patches) owing to their longer dispersal distance (Spiegel and Nathan 2007; Wotton and Kelly 2012; Mueller et al. 2014; Li et al. 2017). However, increasing scientific evidence supports the concept that seed dispersal could be promoted by several bird functional traits (Schleuning et al. 2015; Muñoz et al. 2017). Thus, enhanced seed dispersal can be affected by not only bird morphological traits (e.g. body length, weight, wing length, tail length, etc.), but also by bird behavioural traits (e.g. foraging behaviour, flight behaviour, etc.) (Bregman et al. 2016; Farwig et al. 2017). Owing to the inherent difficulty of monitoring multiple bird functional traits in different disturbed habitats, empirical evidence supporting the extent of the role of bird functional traits in seed dispersal mutualism remains limited.

In the present study, we assessed the contributions of bird functional traits (behavioural traits: food habit, foraging pattern, foraging frequency, and habitat specialisation; morphological traits: weight, body length, wing length, and tail length) to both seed removal patterns and seed dispersal distance of an endangered and native tree species, Chinese yew (*Taxus chinensis* (Rehder and E.H. Wilson) Rehder), across farmland, patchy habitat, and natural habitat. We hypothesised that the seed removal patterns of these endangered trees vary across disturbed habitats and are strongly affected by bird foraging (behavioural) functional traits. In addition, we also tested how the bird flight (morphological) functional traits influence the seed dispersal distance across disturbed habitats.

## Methods

### Species and study site

*Taxus chinensis* is a dioecious, wind-pollinated species, distributed in evergreen broadleaf forests in China. Each year, female plants bear axillary cones, which develop into fleshy arils (commonly referred to as “fruits”), each containing a single seed, in autumn; an average Chinese yew tree bears more than 4000 fruits annually (Li et al. 2015, 2017).

We selected three populations of *T. chinensis* in the villages of Chongtuo and Guihe, which are located in the southern experimental area of the Meihua Mountain National Nature Reserve (MMNNR), in southwest Fujian Province, China (25°15′–25°35′N, 116°45′–116°57′E). The composition of the three populations are as follows: (1) a farmland population from Guihe that consists of two remnant mother trees in *Capsicum annuum* farmland (northeast slope; slope angle 15°; altitude 1180 m; tree coverage 5%); (2) a natural population from Guihe that consists of ten mother trees scattered in the evergreen

broadleaf forest (northwest slope; slope angle 32°; altitude 1178 m; tree coverage 80%); and (3) a patchy population, located in Chongtuo, that contains the largest wild *T. chinensis* population in China (approximately 490 adults). This patch of *T. chinensis* is interlaced with patches of farmland, bamboo, mixed bamboo, and broadleaf trees to form a fragmented landscape (northeast slope; slope angle 27°; altitude 1218 m; tree coverage 70%) (Li et al. 2015).

### Seed dispersal patterns generated by birds

To quantify how birds visited fruiting trees and how many seeds were removed from *T. chinensis* plants across the different sites, field observations were performed during the fruiting season (late October to early December) in all three habitats (farmland and natural habitat: 2012 and 2013; patchy habitat: 2011 and 2012). Observation points were located on opposing mountain slopes, and observations were made using a field scope (Leica 70, Leica Camera AG, Wetzlar, Germany) at distances ranging from 50 to 100 m. Each site was observed from 06:30 to 18:30 on observation days, for a total of 720 h of observation. During the observations, fruit-eating birds were identified and counted, and the foraging pattern (pecking, swallowing) and number of fruits they removed was recorded (i.e., fruits were either ingested on the tree or carried in the beak upon leaving the tree). From these records, we compared the number of seeds removed and frequency of foraging by frugivorous birds across the three habitats (number of fruits per visit × foraging frequencies) (Breitbach et al. 2010).

To quantify how far *T. chinensis* seeds were transported by birds, post-foraging movement behaviours of birds were studied in all three habitats (farmland, patchy, and natural). Each potential disperser leaving a given tree was tracked in a session that ended once visual contact was lost or if the focal bird could no longer be distinguished from its conspecifics. For each tracking session, the perching position of each bird was recorded every 30 s after it left the study tree, and observers noted nearby characteristic landmarks for subsequent verification of field distance estimates using a map. To estimate the real seed dispersal distance, we collected seeds that had been regurgitated by birds, and had fallen on the forest floor, the morning after an observation by finding the marked perching positions (regurgitated seeds refer to cleaned seeds without any aril that had been totally digested by birds) (Pan et al. 2016). We also assumed that the position in which the bird perched was a sufficient proxy for evaluating seed dispersal distance, as previously described (Breitbach et al. 2010). From these records, we compared seed dispersal distances across the three habitat types.

### Effects of functional traits on seed dispersal patterns

To quantify how bird functional traits affected seed dispersal patterns, we selected eight functional traits that are functionally related to the foraging and post-foraging flight behaviours of frugivorous birds (Moermond and Denslow 1985) as follows: foraging behaviours (food habit, foraging pattern, foraging frequency, weight, and length) and flight performance behaviours (wing length, tail length, weight, length, and habitat specialisation). All morphological traits were measured using two male and two female museum specimens of each bird species from local populations. In addition, data on food habits (frugivorous, omnivorous) and habitat specialisation (generalist, specialist) were compiled from *A Field Guide to the Birds of China* (MacKinnon et al. 2000). For the analyses, we used the mean measurement of each trait for each species. All morphological traits were log-transformed to approximate normality.

To quantify how bird functional traits affected seed removal, we first used a machine-learning algorithm (random forest model) to plot the partial effects of food habit, foraging pattern, foraging frequency, weight, body length, site, and year against the number of seeds removed (R package Random Forest) (Breiman 2001). Moreover, we also used the random forest model to plot the partial effects of bird flight traits (wing length, tail length, weight, body length, and habitat specialisation) on seed dispersal distance (R package Random Forest) (Breiman 2001).

## Results

### Seed dispersal pattern generated by birds

During the fruiting season, 5106 seeds (2012: 2341 seeds; 2013: 2765 seeds), 1091 seeds (2012: 719 seeds; 2013: 372 seeds), and 10,277 seeds (2011: 4704 seeds; 2012: 5573 seeds) were removed by 15, 13, and 22 bird species in the farmland, natural habitat, and patchy habitat, respectively. More seeds were removed from the patchy habitat than from the other two habitats. The most common forager at the farmland site was the Collared Finch-bill (*Spizixos semitorques*) (2012: 42 foraging events, 714 seeds; 2013: 40 foraging events, 690 seeds), whereas the Orange-bellied Leafbird (*Chloropsis hardwickii*) (2012: 23 foraging events, 184 seeds; 2013: 15 foraging events, 165 seeds) and Black Bulbul (*Hypsipetes leucocephalus*) (2011: 233 foraging events, 3728 seeds; 2012: 253 foraging events, 4048 seeds) were the most common foragers in the natural and patchy habitats, respectively. These birds were also the most common dispersers for *T. chinensis*, as determined by rates of seed removal from the three habitat types.

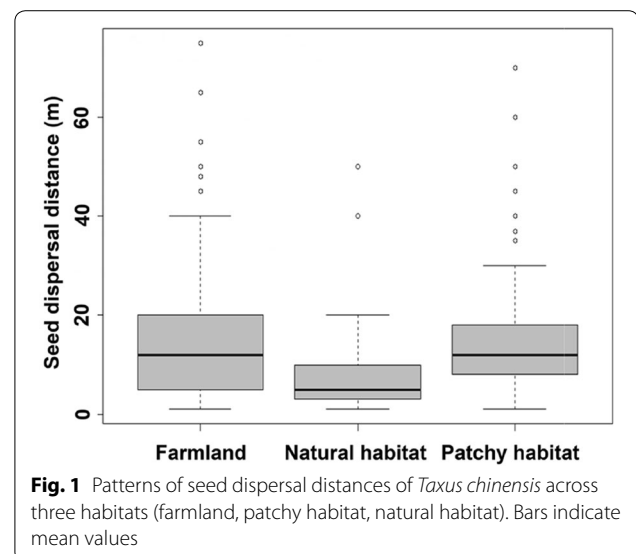
In addition, seeds were removed and taken to greater distances from the farmland than from the other two

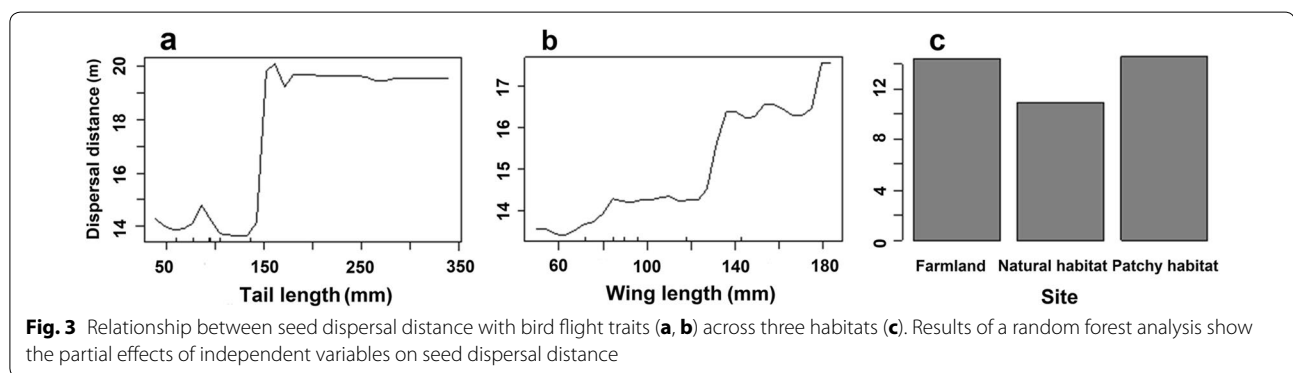
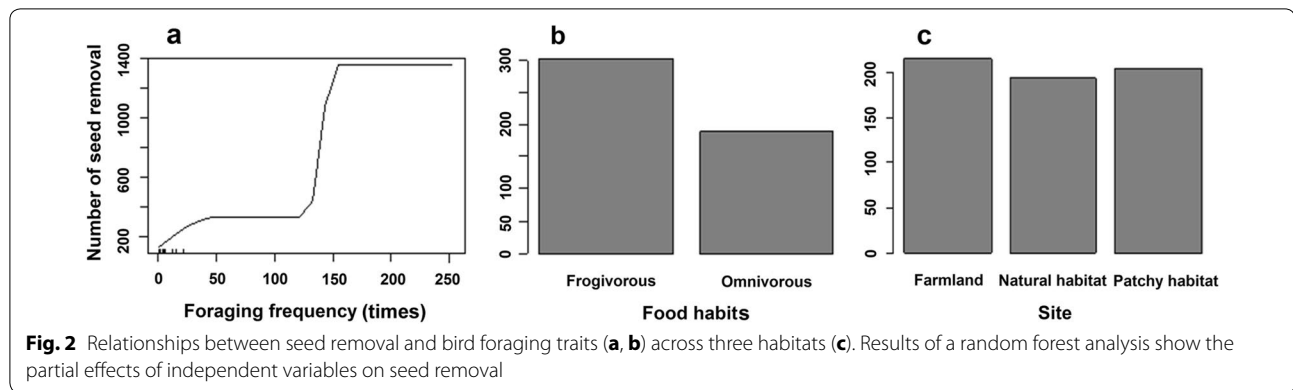
habitats. Dispersal distance (farmland: 65 m; natural habitat: 50 m; patchy habitat: 60 m) and mean dispersal distance (farmland: 15.2 m; natural habitat: 8.1 m; patchy habitat: 13.8 m) for seeds from the farmland site were greater than those of the other two habitats (Fig. 1).

### Role of bird functional traits in seed removal and seed dispersal distance

Considering the contributions of bird foraging traits to seed removal, the results of the random forest analysis showed 85.74% of seed removal data could be explained by eight variables: bird foraging frequency, weight, body length, food habit, site, year, habitat specialisation and foraging pattern. Only three variables (bird foraging frequency, food habit and site) significantly affected seed removal patterns. The results showed a clear positive association between bird foraging frequency and number of seeds removed (Fig. 2a). The contribution by frugivores to seed removal was higher than that by omnivorous birds (Fig. 2b), and more seeds were removed from the farmland site (Fig. 2c).

During field-based observations, a total of 687 seed dispersal distances were confirmed. Considering the contribution of bird flight traits to seed dispersal distance, 22.45% of seed dispersal distance could be explained by six variables (wing length, tail length, weight, body length, site and habitat specialisation). Three variables (bird tail length, wing length, and site) significantly affected seed removal patterns. The results of the random forest analysis demonstrated clear positive associations of bird tail (Fig. 3a) and wing length (Fig. 3b) with seed dispersal distance. The dispersal distance from the three habitat types differed, where the longest dispersal distances were observed at both the patchy habitat and the farmland site (Fig. 3c).





## Discussion

To the best of our knowledge, our study is the first to find that *T. chinensis* trees have the ability to form seed dispersal mutualisms with local birds across different disturbed habitats. As a consequence of these mutualisms, more seeds were removed by birds from the patchy habitat than from the other two habitats (Fig. 1). The number of seeds removed increased with bird foraging frequency (Fig. 2a). Moreover, the dispersal distances from the three habitats differed, where the longest dispersal distances were observed at both the patchy habitat and the farmland site (Fig. 3c). Seed dispersal distance increased with bird tail and wing length (Fig. 3a, b).

There are several possible reasons to explain why more *T. chinensis* seeds were removed by birds at the patchy habitat, mostly involving the habitat features of the patchy habitat. First, the community structure of the patchy habitat was simple, which could attract more birds to forage and remove the seeds (Breitbach et al. 2010). In addition, the co-fruiting plants found in the patchy habitat may have helped to attract birds to the vicinity of the focal trees (Schupp et al. 2010). Moreover, the longer dispersal distance observed at the farmland site (Fig. 1) could have been related to the lack of perching trees in

this disturbed habitat. As a consequence, birds had to fly farther to find trees to perch on (Cody 1985).

Foraging behavioural traits strongly affected bird seed removal patterns across the three habitats (Fig. 2), which could be explained by both bird and plant traits (Farwig et al. 2017). For the bird perspective, it has been shown that medium-sized birds are not as sensitive to disturbance as large-bodied birds (Moore and Swihart 2007; Breitbach et al. 2010), as the remaining forests still provide adequate shelter and food for the persistence of medium-sized birds in disturbed habitats. For the plant perspective, plant traits of *T. chinensis* also determined the persistence of birds in disturbed habitats, thus affecting the foraging behaviour of birds (Farwig et al. 2017; Muñoz et al. 2017). Crop size, fruit size, and height of *T. chinensis* could be good advertisements that attract birds (crop size: 4000 per mother tree; fruit weight: 7 g; height: 25–45 m) (Jordano and Schupp 2000; Martinez et al. 2008; Herrera and García 2009; Li et al. 2017). As a consequence, most of the bird species preferred to forage the “fruit” of this plant, and therefore chose the plant as their main food, which in turn determined the seed removal rate across the three habitats. Thus, the characteristics of the yew tree are a better predictor of seed removal rate in different habitats.

Furthermore, our results showed that seed dispersal distance increased with bird tail and wing length in all three different habitats (Fig. 3). Wing length played an important role in determining the dispersal distance of the birds in the present study, and was an indicator of the role of the birds' flight ability in dispersal distance, as the birds' flight ability has been shown to increase with increasing wing length (Muñoz et al. 2017). Thus, wing length exerts a positive effect on seed dispersal distance. Our results also highlighted the interaction between bird tail length and seed dispersal distance. Tail length affects the ability to steer, and thus the forest specialisation of the birds. Birds with long tail length have been shown to exhibit both high tolerance to forest adaptation and high potential for flight (Fahrig 2007; Li et al. 2017), thus resulting in their long dispersal distances in all habitats.

## Conclusions

Our results highlight the importance of the functional traits of birds in the seed dispersal patterns of endangered trees across disturbed habitats. Bird behavioural traits could determine the ecological role of the species in seed removal, while morphological traits of birds may affect the level of the species-specific contribution to seed dispersal distance across disturbed habitats.

## Authors' contributions

NL, ZW and ZL designed the study. NL performed data collection. NL, and XL conducted all statistical analyses. All authors contributed to the writing and editing of the manuscript. All the authors have read and approved the final manuscript.

## Author details

<sup>1</sup> Institute of Applied Ecology, Nanjing Xiaozhuang University, Nanjing 211171, China. <sup>2</sup> Co-Innovation Center for Sustainable Forestry in Southern China, College of Biology and Environmental Science, Nanjing Forestry University, Nanjing 210037, China. <sup>3</sup> Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China.

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## Competing interests

The authors declare that they have no competing interests.

## Availability of data and materials

The datasets used in the present study are available from the corresponding author on reasonable request.

## Consent for publication

Not applicable.

## Ethics approval and consent to participate

The experiments comply with the current laws of China in which they were performed.

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