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Bulbuls and crows provide complementary seed dispersal for China's endangered trees

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Abstract

Background: Different functional frugivores generally exhibit unequal contributions, both in terms of quantity (seed removal) and quality (seedling recruitment), to effective seed dispersal of plant species. However, variations in this dispersal pattern generated by frugivores across different regions are still unknown.

Methods: In our study, we evaluated the contributions of two functional frugivore bird groups, the bulbuls (Pycnonotidae) and crows (Corvidae), in both the seed removal and seedling recruitment of the endangered Chinese yew tree (*Taxus chinensis*) across three different geographical regions in eastern China.

Results: The dominant crow species, *Urocissa erythrorhyncha*, was the most common disperser crow species at all sites, while the dominant bulbul species varied across the three sites. Furthermore, the two functional groups of dispersers diverged in the aspects of seed removal (quantity) and seedling recruitment pattern (quality). While bulbuls outperformed crows in seed removal (quantity), crows took more seeds to a safer site for seedlings (quality).

Conclusions: Our results highlight the importance of variations in the effective seed dispersal patterns of different functional disperser groups across different regions in the conservation and management of endangered tree species.

Keywords: Complementary seed dispersal, Effective seed dispersal, Seed removal, Seedling recruitment, *Taxus chinensis*

Background

In tropical and temperate forests, more than 75% of woody species depend on frugivores for primary or secondary seed dispersal (Howe and Smallwood 1982). Seed dispersal is important for determining the composition, diversity, and structure of plant communities (Nathan and Muller-Landau 2000; Levine and Murrell 2003), which has important implications for the conservation and management of endangered plants (Trakhtenbrot et al. 2005).

For the conservation of endangered fleshy-fruited plants, it is important to explore how the plants form an effective dispersal pattern across different regions, which is the key strategy for preventing endangered populations from collapsing (Bascompte and Jordano 2007; Li et al. 2015a; Razafindratsima and Dunham 2015). The effective dispersal pattern is often estimated as the number of seed removal by frugivores (quantity) and the relative contribution of frugivores to seedling recruitment (quality) (Schupp 1993; Schupp et al. 2010). Operating under this view, most empirical studies have traditionally evaluated the role of dispersers in determining the effective dispersal patterns of plant species based on the above two aspects (Carlo et al. 2013; Rey and Alcántara 2014). However, the range of plant species always varies across different regions, causing variations in the effective disperser species and thus affecting the regeneration patterns of plant species at different sites. Therefore, information on effective dispersal may be important for implementing effective conservation strategies for plant species (Burns 2002, 2003). Given the inherent difficulty

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in studying effective dispersal patterns across plant distributional ranges, empirical evidence supporting the contribution of disperser species in endangered plant conservation remains limited.

In this study, we assessed the contributions of two functional groups of bird species (bulbuls and crows) in determining the effective dispersal patterns of Chinese yew (*Taxus chinensis* (Rehder and E.H. Wilson) Rehder) across three regions in eastern China. Specifically, we investigated: (1) the variation in the foraging behavior of bulbuls and crows on *T. chinensis* across regions, and how this variation impacts their seed removal, and (2) the variation in the perching behavior of bulbuls and crows across regions, and how this affects the birds' contribution to seedling recruitment.

Methods

Species and study sites

T. chinensis is a relic species that is endemic to China. This species is designated as "endangered" in the International Union for Conservation of Nature (IUCN) Red List (2013 version), and is ranked as a first priority protected species by the Chinese government (Tomas et al. 2013). The regeneration of the wild population of *T. chinensis* is not only limited by low pollination rates, seed-predator pressure, and low seedling survival rates, but also limited by different bird species (Li et al. 2015b).

For our study, we selected three field sites in eastern China (Shuangkeng village in Anhui, Chongtou village in Fujian, and Tongkeng village in Zhejiang) that had dense populations of *T. chinensis*. The Shuangkeng village [30°00′N, 117°18′E; 540 m above sea level (a.s.l.)] is located in the southern part of Anhui Province, and contains 35 individual trees, which are distributed in a human-modified bamboo (*Phyllostachys heterocycla*) patch (Li et al. 2015a). The Chongtou village (25°15′–25°35′N, 116°45′–116°57′E; 960 m a.s.l.) is situated in the Meihua Mountain National Nature Reserve in Fujian Province, and contains the largest wild population of *T. chinensis* (approximately 490 adults) in eastern China, including 200 trees that are over 500 years old (Li et al. 2015b). The Tongkeng village (30°00′N, 119°22′E; 553–638 m a.s.l.) contains the largest natural population of *T. chinensis* in Zhejiang Province (approximately 109 adults), including 34 trees that are more than 500 years old (Li et al. 2015a).

Seed removal by bulbuls and crows across different regions

For studying seed removal by bulbuls and crows across different regions, 10 aggregated mother trees were observed during two fruiting seasons (from late October to early December; Shuangkeng: 2010 and 2011; Chongtou, Tongkeng: 2011 and 2012) at each site. Observations were made with binoculars from a hideout located at least 25 m away from the trees. Each mother tree was observed for an 8-h period once a day during the seasons, with observations being terminated when no more fruits remained on the mother trees.

For each bird that visited the mother tree, we recorded the species and the number of fruits swallowed during visits. If a group of conspecific birds visited the tree, we only focused on the most visible individual (Altmann 1974; Breitbach et al. 2010). After field study, we compared the visiting frequency and foraging amount per visit by each disperser species as a quantity pattern across different regions. Moreover, we used a machine-learning algorithm, random forest model, to plot how bird visiting frequency, foraging amount per visit, bird species, sites, and years influence the numbers of seeds that were removed (R package *RandomForest*) (Breiman 2001).

Perching by dominated bulbuls and crows across different regions and its contribution to the seedling recruitment pattern

We first used 10 m × 10 m habitat cells to digitize the three study sites. Overall, we set 100 sampling cells in Shuangkeng, Chongtou, and Tongkeng, respectively. We then investigated the 1-year-old seedlings ($H \leq 10$ cm) in each cell of each site to determine the suitable recruitment habitat for *T. chinensis.*

For modeling the contributions of birds to seedling recruitment, we monitored the perching frequencies of two dominant species of bulbuls and crows during the fruiting period, from late October to early December (Breitbach et al. 2010; Li et al. 2015a, 2016). Bird perching was observed from high vantage points on the hills using binoculars. Birds were selected randomly and tracked in sessions that ended once visual contact was lost or if the focal bird could no longer be distinguished from the other conspecifics. During the sessions, the habitat used by birds and their position were recorded every 30 s (Breitbach et al. 2010; Spiegel and Nathan 2012).

We used the function to perform univariate Kriging models to interpolate seedling number and bird perching frequency in the sampled habitat plot. The method used for spatial interpolation is the *krige* function in the R package *gstat*. We tested the number of seedlings in the habitat cells by a generalized mixed-effect model, in which the perching frequencies of the bird species and sites were the covariates, while the survey year and their interaction term were the random effects. Because the numbers of seedlings were count data, the function *glmer* in the R package *lme4* was used to run the generalized mixed-effect model with a Poisson link function.

Results

Seed removal by bulbuls and crows across different regions

We performed 400 h of tree observations at each site. Five bulbul species and four crow species were recorded that dispersed the seeds of *T. chinensis*. The composition of disperser species and visiting frequency were similar at Shuangkeng and Tongkeng. However, these parameters at Chongtou differed, compared to the other two regions. More bulbul and crow species with high visiting frequencies were recorded at Chongtou. The Red-billed Blue Magpie (*Urocissa erythrorhyncha*) was the most common disperser species of crow at all sites. However, the dominant bulbul species varied across the three sites. The Mountain Bulbul (*Hypsipetes mcclellandii*), Black Bulbul (*H. leucocephalus*), and Chestnut Bulbul (*H. castanonotus*) were the most common bulbuls at Shuangkeng, Chongtou, and Tongkeng, respectively (Table 1).

Table 1 Common bird dispersers visiting *Taxus chinensis* across different geographical regions

Bird species	Number of visits per year			Foraging amounts of fruits per visit (mean ± SE)		
	Shuangkeng	Chongtou	Tongkeng	Shuangkeng	Chongtou	Tongkeng
Crows						
Urocissa erythrorhyncha	23	15	28	5.4 ± 1.8	16.3 ± 9.1	6.4 ± 1.9
Copsychus saularis		21			8.0 ± 3.5	
Dendrocitta formosae		12			19.9 ± 11.5	2.0
Corvus macrorhynchos		1			10.0	
Bulbuls						
Hypsipetes castanonotus	22	13	49	4.6 ± 1.4	9.6 ± 9.9	3.0 ± 0.9
Hypsipetes mcclellandii	75	2	12	4.2 ± 1.2	12.0 ± 4.0	3.3 ± 0.8
Hypsipetes leucocephalus		243			16.0 ± 14.6	
Pycnonotus jocosus		1			16.2 ± 14.2	
Spizixos semitorques		4			11.3 ± 7.9	

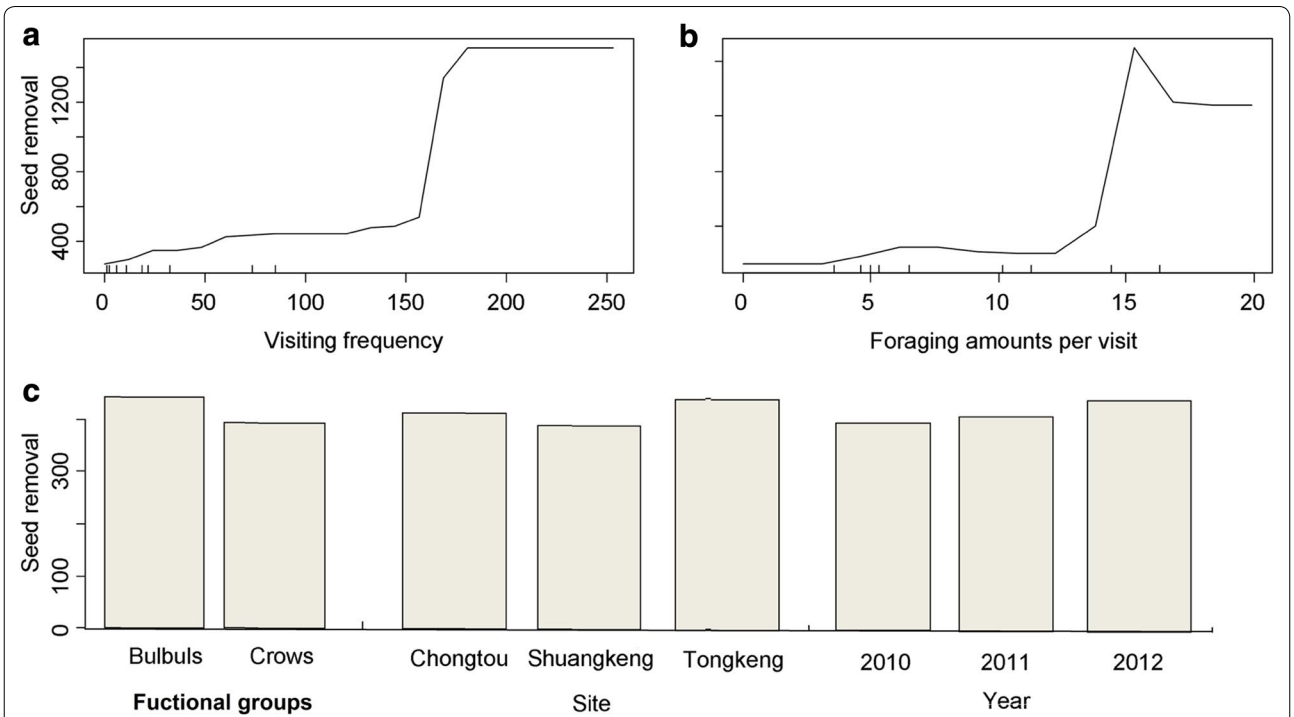

Fig. 1 A machine learning algorithm, random forest, for testing the association between seed removal and bird visiting frequency (**a**), foraging amounts per visit (**b**), bird functional type, site and years (**c**) across different geographical regions in eastern China

The random forest results showed a positive association between the visiting frequencies of birds and seed removal across the three sites (Table 1). The birds contributed more to seed removal at Tongkeng in 2012 than at the other sites and years. Moreover, bulbuls contributed more to seed removal than crows across all the sites (Fig. 1).

Effective seed dispersal patterns across different regions

In the seedling census, we recorded 94, 693, and 245 seedlings at Shuangkeng, Chongtou, and Tongkeng, respectively. Although the distribution patterns of seedlings differed among the three sites, it was consistently affected by the post-foraging perching behaviors of bird dispersers (Fig. 2).

The generalized linear mixed-effects model (GLMM) showed that both bulbuls and crows significantly contributed to the number of seedlings (GLMM, bulbuls: $p < 2e{-}16$; crows: $p < 2e{-}16$) (Table 2) and the contribution of crows to seedling recruitment pattern was higher than that of bulbuls, which was consistent among the three sites (Fig. 3; Table 2).

Discussion

We have shown that different functional dispersers diverged in the aspects of seed removal and seedling recruitment pattern. While bulbuls removed more seeds than crows, crows improved seed dispersion probably by transporting the seeds to a safer site, an aspect of seedling recruitment pattern.

Bulbuls removed more seeds (Table 1; Fig. 1) thanks to certain characteristics of this group (food habits, flocked foraging, and population size). These characteristics place them in the birds-*T. chinensis* interactive system, as described by Li et al. (2015a, b), who found that the

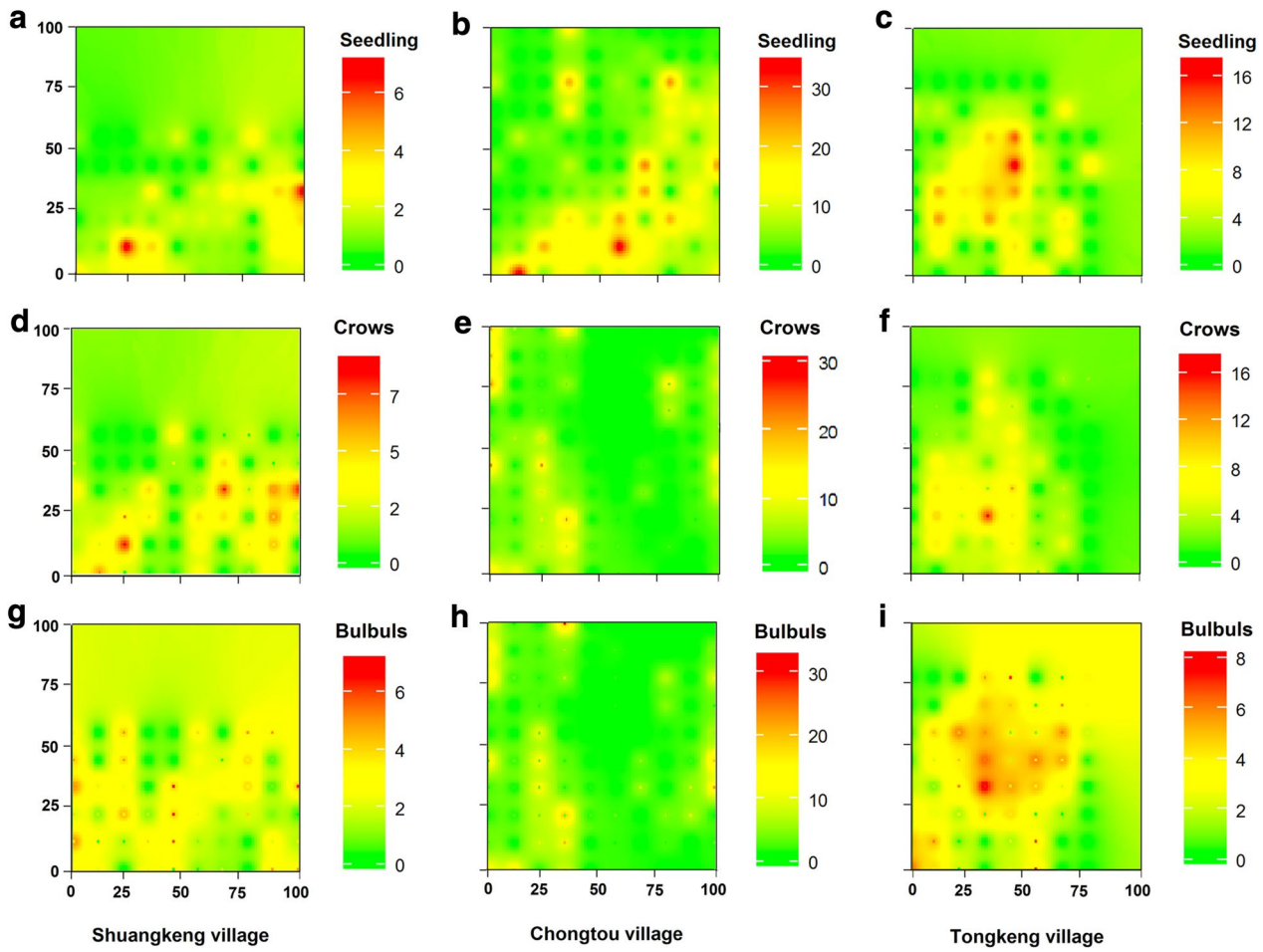

Fig. 2 Distribution of 1-year-old seedlings of Chinese yew (*Taxus chinensis*) (**a**–**c**) and perching frequency of bird dispersers (**d**–**i**) across different geographical regions in eastern China. **a**–**c** show the number of *Taxus chinensis* seedlings at Shuangkeng, Chongtou and Tongkeng respectively; **d**–**f** show 276, 512, 412 perching behaviors of the dominant crow (*Urocissa erythrorhyncha*) at Shuangkeng, Chongtou and Tongkeng respectively; **g**–**i** show 258, 878, 412 perching behaviors of the dominant bulbul (*Hypsipetes mcclellandi*) at Shuangkeng, Chongtou (*H. leucocephalus*) and Tongkeng (*H. castanonotus*) respectively; Coloured contours are interpolated from the values of the corresponding variables in the centroid of each habitat cell

Table 2 A generalized linear mixed-effects model showing the association between number of seedlings and perching frequencies of the most common crows and bulbuls across different geographical regions

Fixed effects	Estimate	SE	*Z* value	*p* value
Factors				
Intercept	1.605	0.036	43.59	< 2e−16***
Crows	0.042	0.004	10.95	< 2e−16***
Bulbuls	0.051	0.004	11.37	< 2e−16***
Shuangkeng	− 1.774	0.150	− 11.86	< 2e−16***
Tongkeng	− 1.299	0.103	− 12.65	< 2e−16***
Crows: Bulbuls	− 0.003	0.001	− 4.80	1.62e−06***
Crows: Shuangkeng	0.158	0.026	6.12	9.10e−10***
Crows: Tongkeng	0.132	0.011	12.34	< 2e−16***
Bulbuls: Shuangkeng	− 0.033	0.037	− 0.90	0.3707
Bulbuls: Tongkeng	0.040	0.016	2.53	0.0113
Random effects	Variance	SD		
Groups				
Year	0	0		

Significance level: *** $p \approx 0$; Dominant crow: Red-billed Blue Magpie (*Urocissa erythrorhyncha*); Dominant bulbuls: Mountain Bulbul (*Hypsipetes mcclellandii*) at Shuangkeng, Black Bulbul (*Hypsipetes leucocephalus*) at Chongtou and Chestnut Bulbul (*H. castanonotus*) at Tongkeng

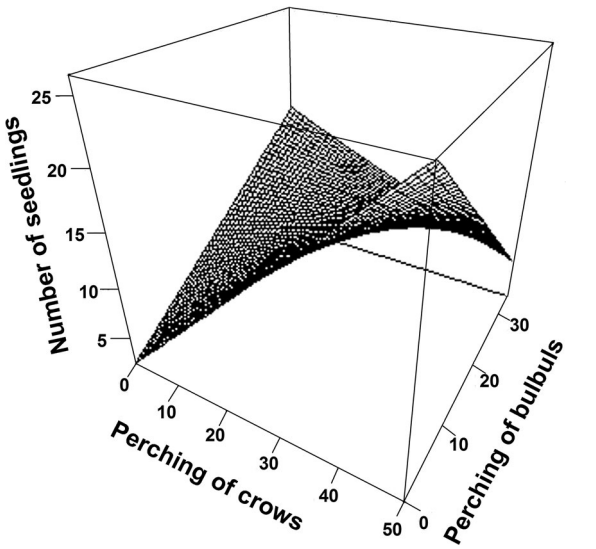

Fig. 3 A generalized linear mixed-effects model showing the interaction effects of bulbuls and crows to the number of seedlings across different geographical regions

obligate frugivores (bulbuls) consumed more seeds than the omnivores (crows). Moreover, the population size of bulbuls was larger than that of crows (Li et al. 2015a, b), leading to flocked foraging. This foraging strategy may result in the higher seed removal rates by bulbuls (McConkey and Brockelman 2011). This phenomenon has been detected in other studies on bird-dispersed *Juniperus ashei* and *Prunus avium* trees (Chavez-Ramirez and Slack 1994; Breitbach et al. 2010).

Our results also showed the importance of two functional groups of disperser species in relation to the seedling recruitment pattern of *T. chinensis* (Figs. 2, 3; Table 2). We found that bulbuls contribute less to the seedling recruitment pattern than crows. This difference may be explained by the differences in the habitat adaptation and body size of the birds, which, in turn, influence where the seeds are ultimately deposited (Jordano and Schupp 2000). For instance, the generalist crows have high tolerance to disturbance than the specialist bulbuls. Consequently, crows use a greater variety of sites than bulbuls (Babweteera and Brown 2009; Li et al. 2015b). This is important for the germination of yew seeds, especially in disturbed areas. Because the patches (e.g. bamboo patches) where the yew seeds could germinate were scattered over a large area, and were surrounded by the patches that were not suitable for the germination of the yew seeds (Li et al. 2015a) (e.g. carya or tea plantations), the post-foraging movement of the specialist bulbuls was limited; however, the post-foraging movement of the generalist crows was negligibly affected by the artificial landscape (Li et al. 2015b). Moreover, the larger crows may deposit *T. chinensis* further than the smaller bulbuls (MacKinnon et al. 2000), because body size is usually correlated with home range, bird movement, and gut passage time (e.g. Spiegel and Nathan 2007; Calviño-Cancela and Martín-Herrero 2009).

Conclusions

Our study highlighted the importance of studying the interaction between different functional disperser groups and endangered trees across different regions. Two functional groups of bird dispersers, bulbuls and crows, having complementary roles in seed removal and seedling recruitment, suggest the importance of considering these aspects in future plant conservation and management plans.

Authors' contributions

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

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Competing interests
The authors declare that they have no competing interests.

Ethics approval and consent to participate
Not applicable.

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