**ORIGINAL RESEARCH**

# Sympatric primate seed dispersers and predators jointly contribute to plant diversity in a subtropical forest

Yuan Chen[1,2] · Kim R. McConkey[3] · Pengfei Fan[1]

## Abstract

Mutualistic and antagonistic plant–animal interactions differentially contribute to the maintenance of species diversity in ecological communities. Although both seed dispersal and predation by fruit-eating animals are recognized as important drivers of plant population dynamics, the mechanisms underlying how seed dispersers and predators jointly affect plant diversity remain largely unexplored. Based on mediating roles of seed size and species abundance, we investigated the effects of seed dispersal and predation by two sympatric primates (*Nomascus concolor* and *Trachypithecus crepusculus*) on local plant recruitment in a subtropical forest of China. Over a 26 month period, we confirmed that these primates were functionally distinct: gibbons were legitimate seed dispersers who dispersed seeds of 44 plant species, while langurs were primarily seed predators who destroyed seeds of 48 plant species. Gibbons dispersed medium-seeded species more effectively than small- and large-seeded species, and dispersed more seeds of rare species than common and dominant species. Langurs showed a similar predation rate across different sizes of seeds, but destroyed a large number of seeds from common species. Due to gut passage effects, gibbons significantly shortened the duration of seed germination for 58% of the dispersed species; however, for 54% of species, seed germination rates were reduced significantly. Our study underlined the contrasting contributions of two primate species to local plant recruitment processes. By dispersing rare species and destroying the seeds of common species, both primates might jointly maintain plant species diversity. To maintain healthy ecosystems, the conservation of mammals that play critical functional roles needs to receive further attention.

**Keywords** Mammals · Seed dispersal · Seed predation · Seed size · Rare species · Plant richness

## Introduction

Mutualistic and antagonistic plant–animal interactions are key processes that promote the coexistence of plant species and thus maintain plant diversity (Montesinos-Navarro et al. 2017; Villar et al. 2020). Fruit-eating animals exist along a seed dispersal and predation continuum, with some animals being mainly predators and others mainly dispersers (van Leeuwen et al. 2022). The numerous studies of seed dispersers at the community level highlight their substantial impacts on local plant recruitment (i.e., a critical stage for plant communities), by regulating long-term plant population dynamics (Traveset et al. 2012) and diversity patterns (Wandrag et al. 2017; Chanthorn et al. 2018). Sympatric seed predators can also regulate these diversity processes (Paine et al. 2016). The combination of seed dispersers and predators that co-exist within a habitat can, therefore, jointly contribute to plant species diversity (Villar et al. 2020). Although seed dispersal and predation may affect plant coexistence and diversity in contrasting ways, the ecological processes of how these two paths jointly affect plant recruitment are relatively poorly known, hindering predictions of the roles animals have in mediating community processes (Larios et al. 2017).

Linking plant traits to animal-mediated seed dispersal and predation is a key approach to understand how animals

✉ Pengfei Fan
  fanpf@mail.sysu.edu.cn

1  School of Life Sciences, Sun Yat-Sen University, Guangzhou 510275, China

2  School of Tropical Agriculture and Forestry, Hainan University, Haikou 570228, China

3  School of Environmental and Geographical Sciences, University of Nottingham Malaysia, 43500 Semenyih, Selangor, Malaysia

maintain plant diversity. When foraging on fruits or seeds, animals routinely select species with specific traits (e.g., fruit density, seed size, nutrient content, chemical deterrents) (Muñoz et al. 2017). Seed size has been shown to be an especially important trait in mediating plant recruitment (Adler et al. 2013). On one hand, size is regarded as a threshold that determines whether consumers swallow a seed or not. It directly affects the number of dispersed seeds and seed survival rate for each species (Muñoz et al. 2017; Soltani et al. 2018). Seed selection by predators may also be size-dependent, which could result in different fates for seeds of varying sizes (Muñoz and Bonal 2008; Maron et al. 2012). On the other hand, seed size itself is an important life history trait for plants. Larger seeds have advantages in responding to the challenges of stressful environments (Gallagher 2013). In this scenario, seed dispersal and predation by animals can affect the reproductive investment of each plant species, which would indirectly alter the outcomes of seedling establishment (Dylewski et al. 2020; Maron et al. 2021).

Current size-based approaches in seed dispersal and predation focus on analyses of large-seeded species to detect the relationship between animal seed selection and plant recruitment. There is a limited range of dispersers that have the physical ability to swallow large-sized seeds, and these animals are more frequently large- and medium-sized mammals (Chen and Moles 2015). Recent studies have confirmed the crucial, often irreplaceable, role of these animals (e.g., elephants and gibbons) in dispersing large seeds (McConkey et al. 2015; Ong et al. 2022). A capability to disperse large seeds also confers an important role in dispersing seeds of different size, so that large animals play important community-level seed dispersal roles (Ong et al. 2022). In contrast, as an antagonistic interaction, mammalian seed predators consume seeds as a primary food resource, and they may prefer selectively larger seeds to optimize energy intake (Muñoz and Bonal 2008; Maron et al. 2012). If so, seed predators could conversely reduce the advantages of large-seeded species, which could regulate local plant diversity (Larios et al. 2017).

Seed dispersers and predators can also alter the negative density dependence (NDD) in plant species with different abundances, which is a newly identified mechanism by which animals might influence plant diversity (Chanthorn et al. 2018; Luskin et al. 2021; Song et al. 2021). Based on a density-dependent foraging strategy, seed predators select abundant plant species with higher fruit production (Paine and Beck 2007; Gallagher 2013), causing massive reductions in the seedling establishment of abundant species (Hargreaves et al. 2019). Therefore, seed predators are natural enemies that contribute to NDD of dominant and common species. Interestingly, some seed dispersers forage selectively on rare species compared to common species (Carlo and Morales 2016; Morán-López et al. 2018). These

rare-biased seed dispersal processes may weaken the NDD effects on rare species to a large extent, thereby increasing entire species richness in local communities (Camargo et al. 2022).

In this study, we explored how seed size and abundance of plant species mediate the effects of two primate species on plant recruitment. In a subtropical forest of southwestern China, sympatric western black crested gibbons (*Nomascus concolor*) and Indochinese gray langurs (*Trachypithecus crepusculus*) were selected as the study subjects. Gibbons are among the most important frugivores in southeast Asia, and they disperse seeds of various sizes (McConkey 2000; Fan et al. 2008; Ong et al. 2022). By contrast, langurs regularly consume fruits and seeds, and are frequently pre-dispersal seed predators (Sun et al. 2007), though they can disperse a few small-seeded plants (Tsuji et al. 2017). We conducted seed germination experiments to evaluate seed dispersal effectiveness (SDE, Schupp et al. 2010) of gibbons and langurs; and we integrated feeding observations and fecal analyses to quantify seed predation rate (SPR) of langurs. We also measured seed size, and species abundance of interacting plants and included these traits when analyzing SDEs/SPRs of gibbons and langurs for different plant species.

Here, we predict that gibbons will (1a) disperse species with a wide range of seed sizes, especially rare species, (1b) provide high SDEs for medium- and large-seeded species, and (1c) have positive impacts on the germination. We expect that langurs will (2a) destroy the seeds of most of the plant species they consume, especially the common or dominant species, (2b) have high SPRs on large-seeded species, and (2c) have negative impacts on the germination of the few plant species they may disperse.

# Materials and methods

## Study site

This study was conducted at the Dazhaizi Gibbon Research Station (24°21′ N, 100°42′ E) in Wuliangshan National Nature Reserve, Central Yunnan, China (Fig. 1). The total area of the nature reserve is 31,313 ha, and the area of our study site is about 1000 ha. The primary forest types in this region are semi-humid evergreen broad-leaf forests at an altitude of 1900–2200 m, mid-mountain humid evergreen broad-leaf forests at an altitude of 2200–2750 m, and rhododendron dwarf forests at an altitude of 2750–3000 m (Peng and Wu 1998). The entire area has probably been influenced by generations of selective cutting and other anthropogenic disturbances (Ma et al. 2015). Owing to past disturbance, our study area lacks large-sized avian frugivores (e.g., hornbills), while some mammalian seed dispersers such as masked civets are close to extinction (Gan 2018). Apart from langurs,
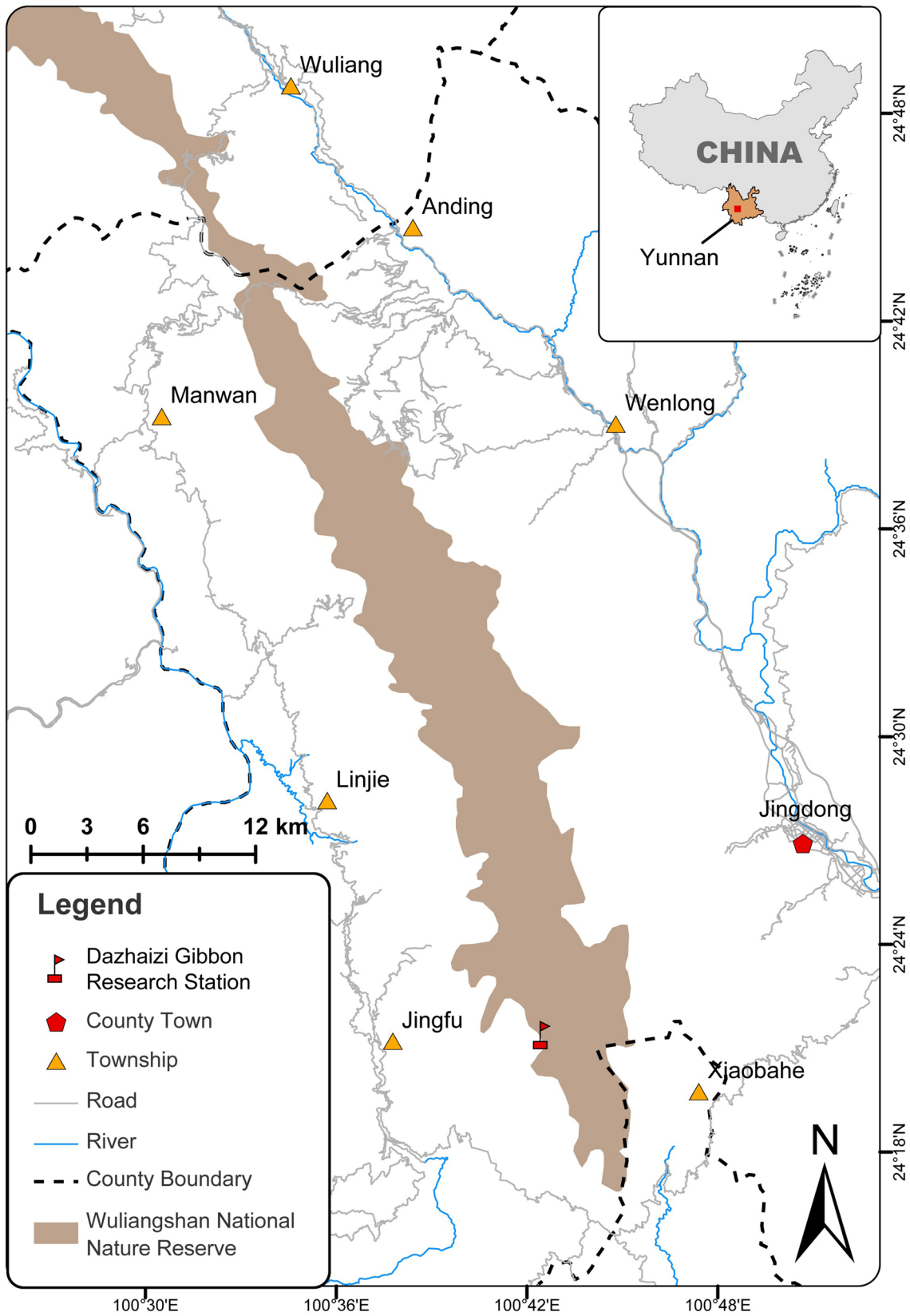
**Fig. 1** The location of Dazhaizi Gibbon Research Station in Mt. Wuliang, China

rodents and wild boars are the remaining guilds that may cause large seed losses, mainly through post-dispersal seed predation (Chen unpublished data).

The annual average temperature around the research station from January to December 2011 was 15.7 °C, with the lowest and highest monthly average temperatures occurring in January (10.1 °C) and June (19.2 °C), respectively. In this period, the total precipitation was 1793 mm, during which May–October was the rainy season (84% of the rainfall occurred) (Guan et al. 2013).

## Study subjects

Western black crested gibbons and Indochinese gray langurs are the most common primates in the forested region of Mt. Wuliang. Sympatric stump-tailed macaques (*Macaca arctoides*) and Assamese macaques (*M. assamensis*) are rare at the study site (Chen et al. 2020). The current gibbon population is around 600 individuals (Fan et al. 2021), while langurs have a larger abundance with ~2000 individuals (Ma et al. 2015). Since 2003, we have performed long-term monitoring and investigation of gibbons at the Dazhaizi Research Station. At present, three groups of gibbons (code-named G2, G3, G4) with home ranges around the station have been well-habituated. Researchers can track and observe them closely. In addition, we began studying a sympatric group of langurs of around 80 individuals in 2009, and successfully habituated them in 2010 (Ma et al. 2020). Due to the continuous growth of the group size, this group gradually split into three groups (a total of ~180 individuals) over the past ten years (code-named A1, A2, B1). Our previous studies found that the gibbons' annual diet consists of more than 50% fruit (Fan et al. 2009; Chen et al. 2020). By contrast, langurs were more folivorous (56.8% leaves in the annual diet), but the proportion of fruits and seeds they consumed also exceeds 50% in fruit-rich seasons (Fan et al. 2015; Chen et al. 2020). The home ranges of gibbons and langurs were approximately 200 ha and 420 ha, respectively (Chen et al. 2020). In the present study, we selected the three gibbon groups and two langur groups (A1 and A2) as the subjects. During the study period, groups G2, G3, and G4 had 11, 6, and 8 individuals, while there were around 90, and 20–30 individuals in groups A1, and A2, respectively.

## Data collection

### Behavioral observations

We conducted regular feeding observations of the two langur groups for a total of 5 days per month, from September 2019 to January 2021. During the observations, we used 10-min scan sampling to record fruit and seed consumption of all the visible group members. If an individual was observed manually processing, chewing, or swallowing fruits and seeds during a scan, we recorded the specific plant species (Chen et al. 2020). Over the study period, we obtained a total of 3116 records of fruit or seed consumption in the langur groups. These behavioral data were integrated with subsequent fecal analysis to determine whether each plant species had the seeds destroyed, or whether some seeds survived gut passage and were deposited in feces. If seeds of a species consumed by langurs were not found in feces, they were assumed to be destroyed by langurs.

Within the same months for tracking langur groups, we conducted behavioral observations of three gibbon groups for a total of 5–10 days per mouth. Tracking gibbons while collecting enough feces in the wild was challenging because of their small group size and fast locomotion mode compared to langurs. In order to maximize the quantity of fecal samples collected, we have only opportunistically obtained a small number of feeding data of gibbons during this study. However, since diet of the same gibbon groups has been intensively studied by previous researchers, and seed destruction is rare by gibbons (below 13%, Fan et al. 2008; Ning et al. 2019), we assumed that the role of seed predation was insignificant in our study.

### Seed collection and analysis

During the tracking of gibbon and langur groups, we collect feces from visible individuals in a few minutes after they defecated. Because both gibbons and langurs are canopy dwellers, their feces often break into pieces while falling to the ground, we used tweezers and zip lock bags as assistant tools to collect feces. After marking the time and location information on collection bags, they were returned to the station for analysis. In total, 315 langur feces and 271 gibbon feces were collected during the study period. The fecal samples were rinsed through a sieve (mesh diameter: 1 mm) to separate out intact seeds (Chancellor et al. 2017). After air drying on absorbent papers (2–3 days), we counted and classified the collected seeds, which were identified by comparing them with fresh fruits or seeds collected in the field and by referring to local floral books and botanists. Langurs frequently consumed fruits of *Choerospondias axillaris*, but the seeds were dropped from the langur's hand after the pulp was partly consumed. We also considered that this process may sometimes result in potential seed dispersal, and thus collected 50 seeds under maternal trees when langurs consumed the fruits. In addition, we used a vernier caliper to measure the diameters of seeds dispersed or destroyed by the primates (15 seeds for each plant species). The measurements were completed from defecated and dropped seeds for dispersed seeds and from fresh fruits for destroyed seeds. We defined 1 mm ≤ diameter < 5 mm as small-sized seeds, 5 mm ≤ diameter < 10 mm as medium-sized seeds, and

diameter ≥ 10 mm as large-sized seeds (Trolliet et al. 2016). Two plant species (*Ficus neriifolia* and *Actinidia indochinensis*) were not retained in the fecal analysis because the seeds are smaller than the mesh (< 1 mm). Finally, we stored all the seeds in a cardboard box.

## Seed germination trials

To evaluate the fate of the seeds dispersed by gibbons and langurs, we sowed all seeds separated from primate feces and 50 seeds dropped from langurs. These seeds were sown as a treatment group. Sowing was carried out at the end of every month or early the following month after the feces were collected (Fedriani and Delibes 2009), and the duration between seed collection and the beginning of the seed germination trials is 3–32 days. Seeds collected from mature fruits of the defecated species were considered as a control group. We manually cleaned the seeds extracted from the fruits to remove the pulp. A total of 24 plant species were selected (24 for gibbons and three for langurs), and 50 seeds per plant species were sown as control for gibbons and langurs, except for two species (*Choerospondias axillaris* and *Toddalia asiatica*), which were sown with only 30 seeds. We also sowed all seeds from the control group within one month.

Seeds in the treatment and control groups were randomly sown in nursery trays under a lightly shaded platform in the station (Fig. S1). The number of seeds in each tray (40–200 seeds) varied according to seed size. Since the space of each nursery tray is fixed, small seeds were sown more than large seeds. We obtained soil from accessible areas in the primates' habitat, and it was visually examined to ensure that no other seeds were present. After sowing the seeds, we checked each tray every 3 days to count the emergence of the radicles above the soil surface, and to water them (Fig. S1). To provide suitable conditions for seed germination, we kept the soil moist. If a seed germinated, we removed it from the tray so that we could easily count the radicles and prevent it from affecting the germination of other seeds. We continuously recorded the species, number, and date of seed germination (Trolliet et al. 2016). Seed germination was monitored from January 2020 to October 2021 (when no radicles emerged within 3 months).

## Investigation of plant abundance

We set up plots and transects within the primates' home ranges to conduct a general survey of plant species abundance. From October to December 2004, we set up 250 20 m × 20 m plots (in total 10 ha) along six contours with a 100 m altitudinal interval from 2100 to 2600 m (Table S1). Due to rugged terrain in the habitat, we set up 15–70 plots at different altitudes, and each plot was separated by a distance of 100 m (Tian et al. 2007). In addition, we set up three

2 m-wide transects (Length: 815 m, 1200 m, and 1710 m) with a total area of 0.75 ha (1750 m, 2150 m, and 2550 m above sea level) to increase the size of the sampled area in February 2021. In transect and plot establishment, we used a handheld GPS to determine altitude. In each plot and transect, all trees and shrubs with a diameter at breast height ≥ 10 cm were identified and recorded. We combined the results from both plot and transect surveys to determine plant species abundance. We defined plant species with < 1 individual/ha (total abundance) or not found in the plant plots but whose seeds were recovered in the feces as rare species, those with 1–10 individuals/ha as common species, and those with ≥ 10 individuals/ha as dominant species in this region (McConkey et al. 2018). We did not survey abundances of liana species.

## Data analysis

The SDEs (Seed Dispersal Effectiveness) of gibbons and langurs for each consumed species were calculated as Quantity (number of defecated seeds) × Quality (seed germination rate) in our study (Schupp et al. 2010). We used the R package "effect.lndscp" to establish SDE landscapes for both primate species (Jordano and Rodriguez-Sanchez 2017). The SPRs (Seed Predation Rate) were the proportions of consumption records for each plant species in the diet of langurs for which the seeds were destroyed (i.e., the total number of consumption observations for a given species divided by the total observations for all species) (Ganesh and Davidar 2005). Only plant species whose seeds were never found in the feces were included. Species for which consumed seeds were subsequently found in the feces were excluded because these species were dispersed at least some of the time; however, we recognize that some seeds of these species may also have been destroyed by langurs. A Pearson's Chi-squared test was used to identify whether gibbons dispersed more seeds of rare species than common and dominant species and whether langurs destroyed more seeds of common and dominant species compared to rare species. Polynomial regression models were used to analyze the relationship between seed size and SDEs of gibbons, species abundance and SDEs, seed size and SPRs of langurs, and species abundance and SPRs. Seed size and species abundance were set as independent variables, while SDEs and SPRs were set as dependent variables, in which SDEs and SPRs were log-transformed to reduce skew in the residuals. Additionally, we used the Pearson's Chi-squared test, and Wilcoxon rank sum test to compare the difference of seed germination efficiency (rate and mean time) between treatment groups and control groups in gibbon- and langur-dispersed species, respectively. All data were analyzed in R 4.2.2 (R Core Team 2023).

# Results

## Gibbons are legitimate seed dispersers

We recovered 4907 intact seeds belonged to 44 plant species from 81.9% of gibbon feces (n = 271); on average, each fecal drop contained 18.1 seeds (range 0–139). Each gibbon defecated on average two times per day (range 1–4). When considering the population size of gibbons (i.e., 600 individuals) in Mt. Wuliang, they could disperse approximately 21,720 seeds per day. Seeds of *Nyssa javanica*, *Tetrastigma delavayi*, and *Pygeum topengii* were most frequently dispersed (Table S2, Fig. 2). Seeds of 84.1% of species (n = 44) germinated under experimental conditions (Table S2). *Kadsura coccinea*, *P. topengii*, and *Celastrus hindsii* showed higher germination rates than other species

(Table S2, Fig. 2). Gibbons had high SDE for *P. topengii* (value = 297.5), *T. delavayi* (210.1), and *N. javanica* (126) (Fig. 2).

## Langurs are primarily seed predators

The results of feeding observations show that langurs consumed fruits of 55 species over 17 months, among which fruits of *C. axillaris*, *Actinodaphne* sp., and *Mucuna sempervirens* were mainly consumed (Table S3). Langurs dropped seeds around the maternal trees when they consumed fruits of *C. axillaris* and *Elaeocarpus lanceifolius*, and they consumed seeds and/or fruits of the other 53 species. However, we only recovered 563 intact seeds of five species from 29.2% of langur feces (n = 315) (Table S4), and each fecal drop contained an average of 1.8
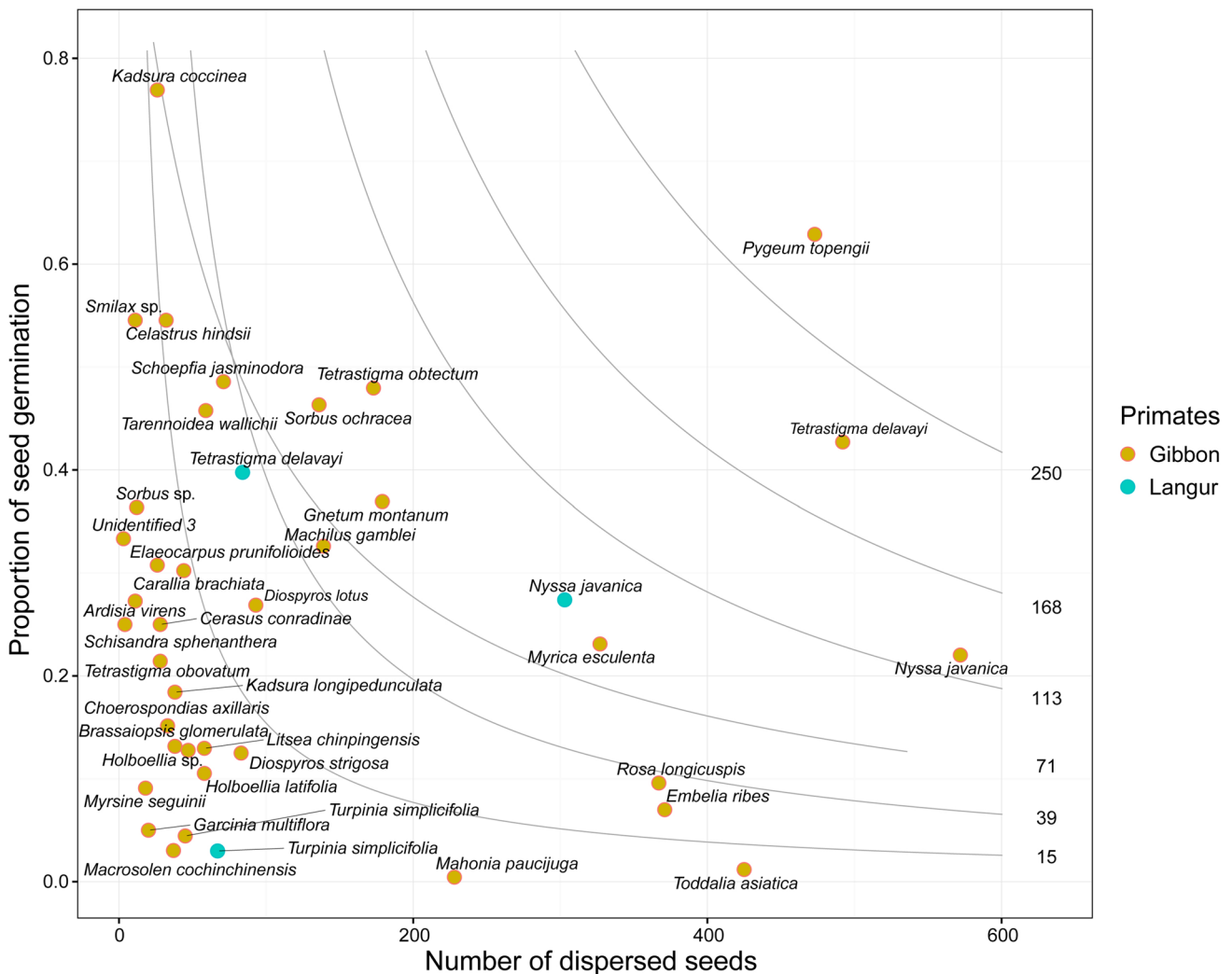


**Fig. 2** Effectiveness landscapes of seed species dispersed by western black crested gibbons (37 species of germinated seeds) and Indochinese gray langurs (three species of germinated seeds) in Mt. Wuliang, China. The isoclines indicate all combinations of quantity and quality that result in the same effectiveness

seeds (range 0–24). Each langur defecated on average 1.7 times per day (range 1–3). When weighting the population size of langurs (i.e., 2000 individuals) in the study area, they could disperse about 6120 seeds per day. Moreover, langurs destroyed 48 species of seeds they consumed, with relatively high SPRs for seeds of *Actinodaphne* sp. (value = 0.09), *M. sempervirens* (0.09), and *Castanopsis hystrix* (0.09) (Table S3).

## Dispersal outcomes by gibbons vs. langurs

In general, gibbons and langurs interacted with a total of 81 woody plant species, with an overlap of 13 species (e.g., *P. topengii*, *Litsea chinpingensis*, and *Carallia brachiata*) which were dispersed by gibbons and destroyed by langurs (Table S2, S3). Of the five langur-dispersed species, only seeds of three species (*N. javanica*, *T. delavayi*, and *Turpinia simplicifolia*) germinated after dispersal (Table S4); gibbons also dispersed all five species. For *T. delavayi*, gibbons had a higher SDE than langurs. For *N. javanica*, gibbons dispersed more seeds than langurs, but less seeds germinated. For *T. simplicifolia*, the SDEs were almost the same for gibbons and langurs (Fig. 2).

## Effects of seed size on seed dispersal and predation

Of the 44 species dispersed by gibbons, 29.5% were small-seeded, 54.5% medium-seeded, and 15.9% large-seeded (Fig. 3a, Table S2). By contrast, of the 48 seed species destroyed by langurs, 27.1% had small seeds, 33.3% had medium seeds, and 31.3% had large seeds; we could not obtain seed sizes for 4 species (Fig. 3a, Table S3).
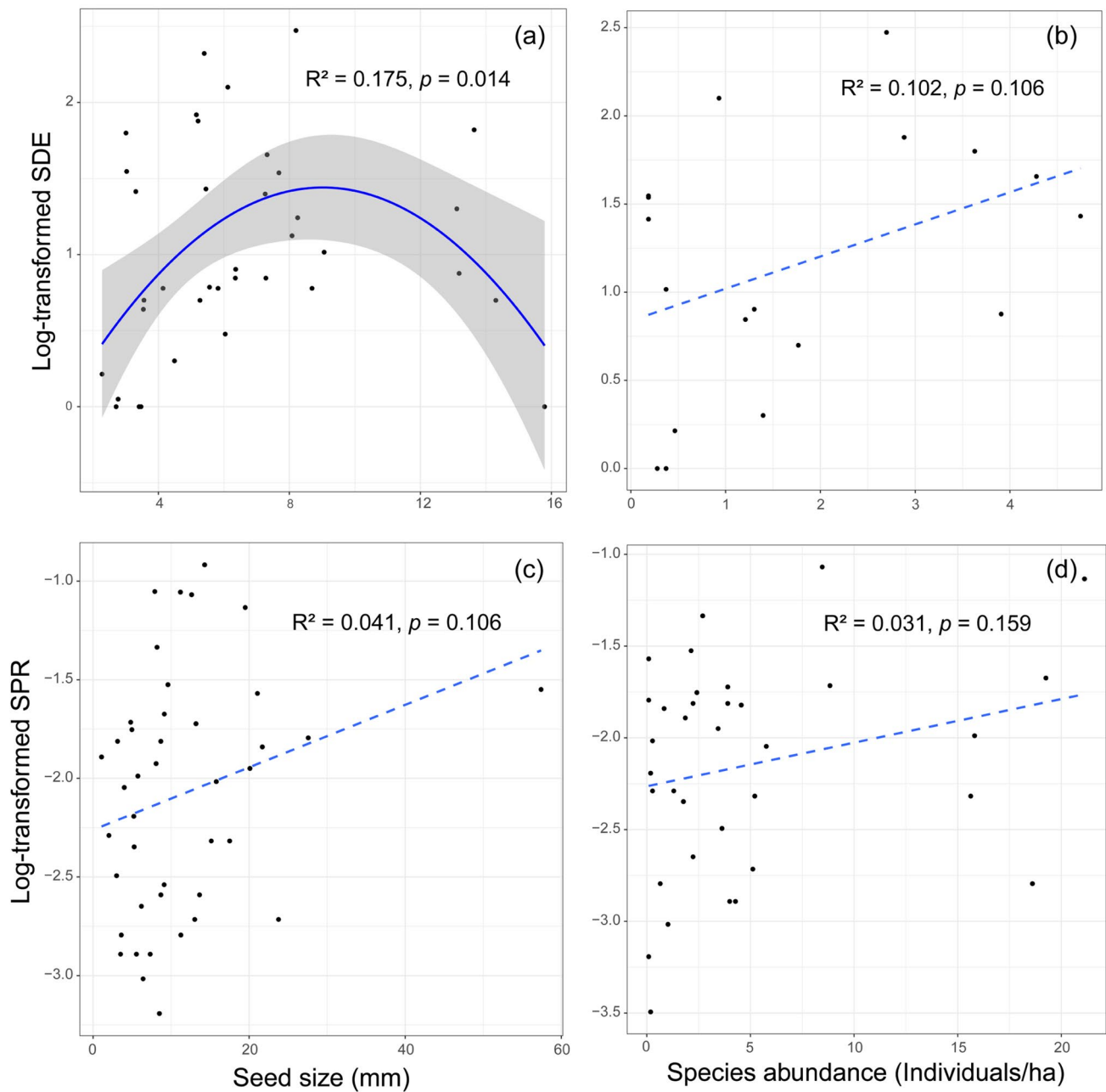
The relationship between seed size and SDE by gibbons showed a unimodal trend ($R^2 = 0.175$, $p = 0.014$), with 9 mm seeds having the highest SDE (Fig. 4a). However, there was no significant relationship between seed size and SPR by langurs ($R^2 = 0.041$, $p = 0.106$, Fig. 4c). Thus, gibbons had a higher SDE for medium-sized seeds; whereas, SPR by langurs was not size-dependent, and they exploited seeds of a diverse size range within this community.

## Effects of species abundance on seed dispersal and predation

We identified 44 rare, 66 common, and 16 dominant species through plant surveys (Table S5). Of the 44 seed species dispersed by gibbons, 40.9% were rare, and 25% were common (Fig. 3b). We did not survey abundances of 15 liana species that were dispersed by gibbons. In contrast, of the 48 seed
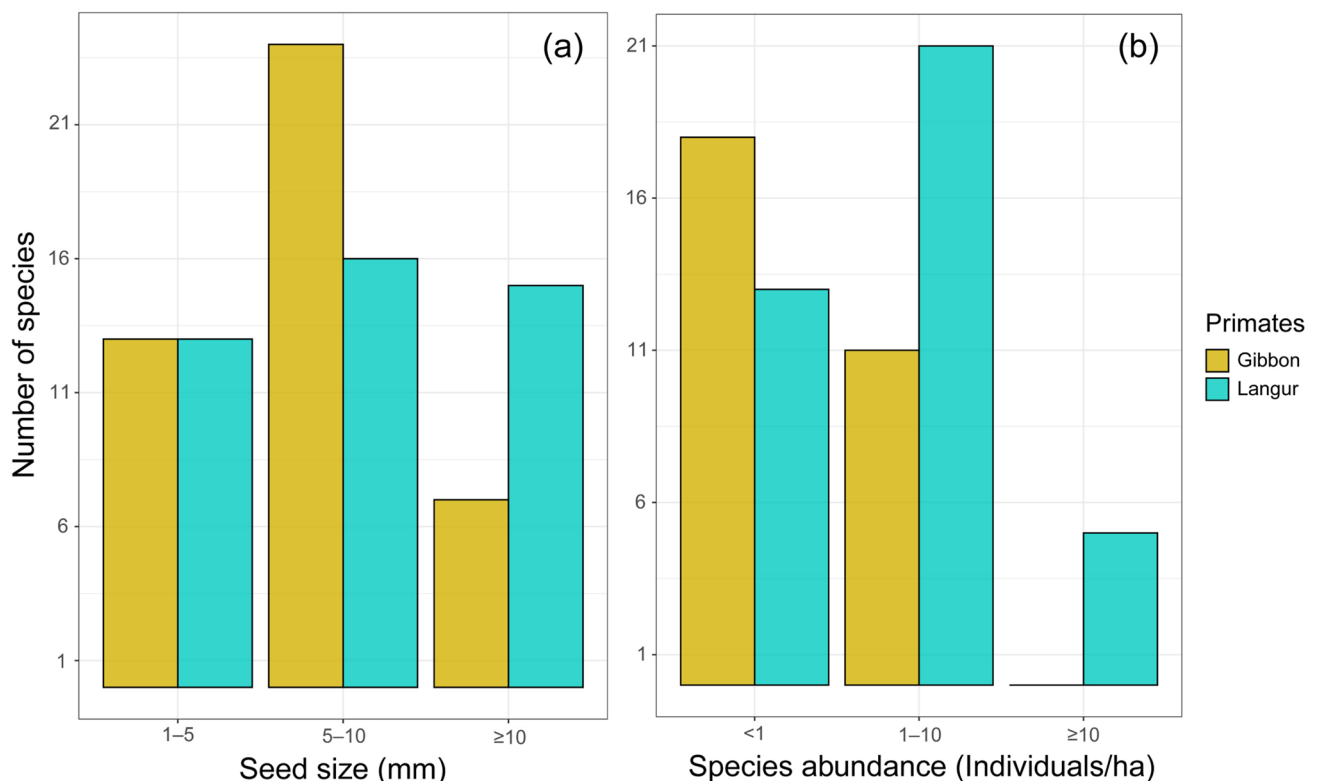


**Fig. 3** Distribution pattern of seed size (**a**), and species abundance (**b**) of plant species dispersed by western black crested gibbons and destroyed by Indochinese gray langurs in Mt. Wuliang, China

**Fig. 4** The relationship between seed size (**a**), species abundance (**b**) and seed dispersal effectiveness (SDE) of plant species that interact with western black crested gibbons [The model (**a**): $\log(SDE) = 1.037 + 0.485 \times$ seed size$-1.856 \times$ seed size$^2$], and the relationship between seed size (**c**), species abundance (**d**) and seed predation rate (SPR) of plant species interacted with Indochinese gray langurs in Mt. Wuliang, China. The full line indicates the model was statistically significant, while the dashed lines indicate the model was not significant

species destroyed by langurs, 27.1% were rare, 43.7% were common, and 10.4% were dominant (Fig. 3b). We did not survey abundances of nine liana species that were destroyed by langurs.

Based on the total species abundance, gibbons dispersed more seeds of rare species (40.9%, n = 44) than common species (16.6%, n = 66) ($\chi^2 = 6.792$, $p = 0.009$), and did

not disperse any dominant species (Table S5). By contrast, langurs destroyed seeds of 29.5% of rare species (n = 44), 31.8% of common species (n = 66), and 31.3% of dominant species (n = 16) (Table S5). There was no significant difference among different species abundances (Rare vs. common: $\chi^2 = 0.002$, $p = 0.966$; rare vs. dominant: $\chi^2 < 0.001$, $p = 1$; common vs. dominant: $\chi^2 < 0.001$, $p = 1$). We did not find
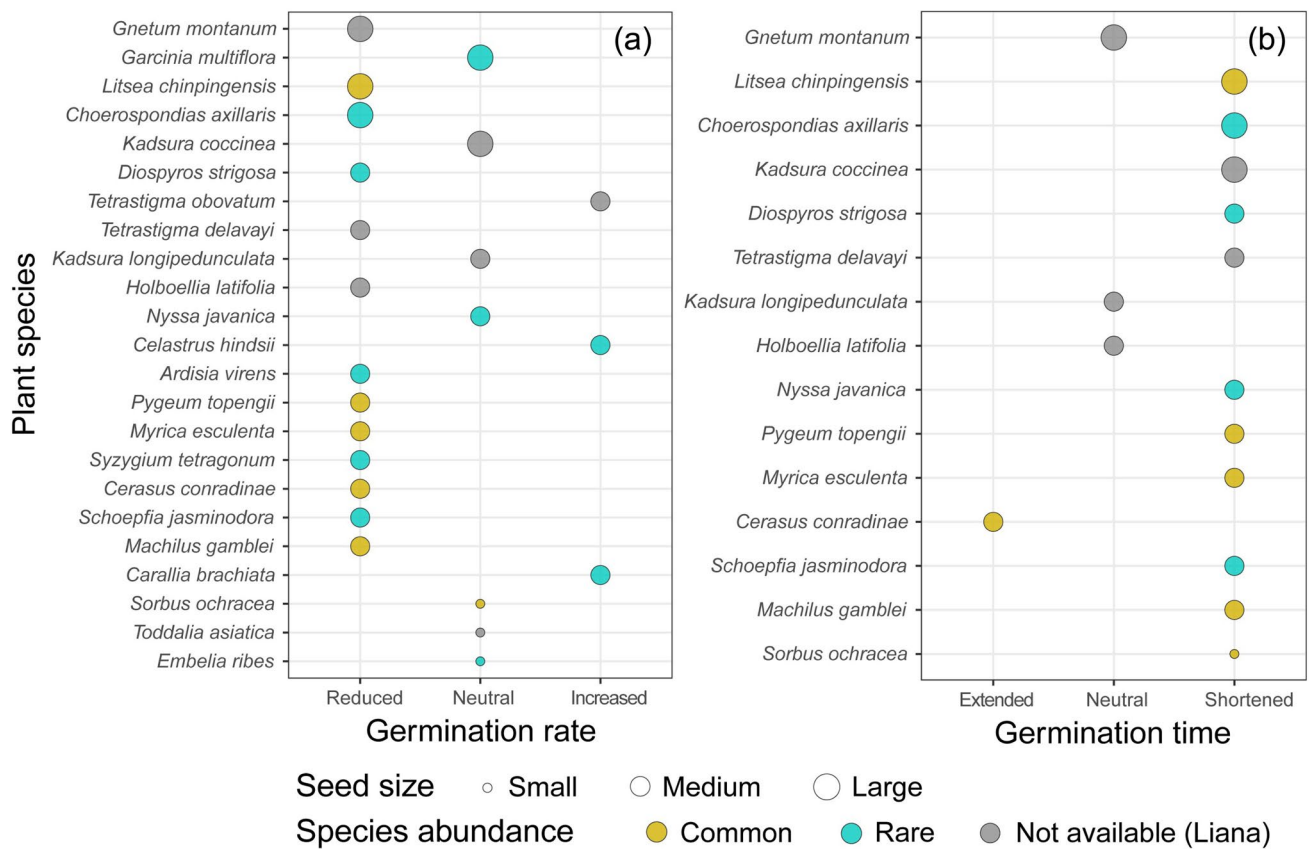
**Fig. 5** Germination rate (**a**) and mean germination time (**b**) of treatment seeds (recovered from the feces of western black crested gibbons) versus control seeds (removed from fresh fruits) with different size and species abundance in Mt. Wuliang, China. Plant species are ordered according to seed size

a significant relationship between the abundance of plant species and SDE ($R^2 = 0.102$, $p = 0.106$, Fig. 4b) or SPR ($R^2 = 0.031$, $p = 0.159$, Fig. 4d).

### Effects of primate gut passage on seed germination

By comparing seed germination rate (SGR) between treatment and control seeds from 24 gibbon-dispersed species, we found that gibbons significantly increased SGRs of 12.5% of species and significantly reduced SGRs of 54.2% of species, while germination of the remaining species were unaffected by gut passage (Fig. 5a). Gibbons had a positive effect on SGRs of 20% of medium-seeded species ($n = 15$) and 20% of rare species ($n = 10$). However, they had a negative effect on SGRs of 60% of large-seeded species ($n = 5$), 66.7% of medium-seeded species ($n = 15$), 83.3% of common species ($n = 6$), and 50% of rare species ($n = 10$) (Fig. 5a, Table S6). Comparing seed germination time (SGT) between treatment and control seeds for 19 gibbon-dispersed species, gibbons significantly

shortened SGTs of 57.9% of species (Fig. 5b). SGTs were substantially shortened for 75% of large- ($n = 4$), 58.3% of medium- ($n = 12$), and 100% of small-sized seeds ($n = 1$), and for 83.3% of common ($n = 6$), and 80% of rare species ($n = 5$). Only one medium-seeded and common species (i.e., *Cerasus conradinae*) had a significantly extended SGT after gibbon gut passage (Fig. 5b, Table S7).

The comparison between treatment and control seeds from two langur-dispersed species showed that the SGR of *T. delavayi* (a medium-seeded species) was reduced significantly, while *N. javanica* (a rare and medium-seeded species) showed no differences in SGR (Table S8). These effects were the same as gibbon-mediated seed dispersal for the same species (Fig. 5a, Table S6). Similar to gibbons, langurs also shortened significantly the SGT of the two plant species (Table S7, S9). Additionally, all the seeds of *C. axillaris* which langurs dropped did not germinate (Table S8), probably because they consumed immature fruits. Therefore, langurs caused seed destruction of *C. axillaris* in this scenario.

## Discussion

Our study provides insights into how sympatric seed dispersers and predators jointly affect local plant recruitment. In the forest region of Mt. Wuliang, western black crested gibbons were legitimate dispersers for most consumed species, showed a higher effectiveness for medium-sized seeds and dispersed more seeds of rare species than common and dominant species. In contrast, Indochinese gray langurs were primarily seed predators, with a tendency to destroy common species more often than rare and dominant species, but with no effect of seed size on predation. Although langurs dispersed the seeds of three species, gibbons dispersed these same species effectively (Fig. 2). The importance of langurs as seed dispersers may be limited in our study area, while gibbons have been noted to rarely destroy seeds (McConkey 2000; Fan et al. 2008). Gibbons also have quite narrow habitat requirements, which means they usually disperse seeds into suitable microsites for germination under the forest canopy (McConkey 2000; McConkey et al. 2015). Therefore, these two primate species play functionally distinct roles in the forest. Through dispersal and predation of plant species with varying seed size and abundance, gibbons and langurs have contrasting influences on seed fate and plant recruitment, which might jointly maintain local species diversity.

Our findings regarding the effect of seed size on dispersal and predation contrast with previous studies (Maron et al. 2012; Ong et al. 2022). While gibbons are recognized as important dispersers of large seeds at the community level (Ong et al. 2022), they were more effective dispersers of medium-sized seeds at our study site. These results imply that many plant species with medium-sized seeds may rely mainly on gibbons for recruitment within this community, particularly due to the rarity of other potential dispersers in the study site (Gan 2018). Even though large-seeded plants have few dispersers, they have high performance of sapling establishment owing to more sufficient nutrients in the seeds (Gallagher 2013; Lebrija-Trejos et al. 2016). Gibbons dispersed a relatively small number of large-seeded species, but other mammals occurring in the study site also disperse these species. *Choerospondias axillaris* is dispersed by deer (Brodie et al. 2009) and *Gnetum montanum* is frequently dispersed by bears at other study sites (Albert-Daviaud et al. 2022). By contrast, small-seeded plants may mainly rely on the dispersal of small frugivores (such as fruit-eating birds with high species richness, Luo 2004; Jordano et al. 2007). Interestingly, langurs showed no size-based patterns in the seeds they destroyed, which means they could be limiting the recruitment of plants across a diverse range of seed sizes. Rather than seed size, chemical and mechanical defenses within

the seeds might regulate seed predation by langurs (Larios et al. 2017). To understand how the plant species targeted by langur seed predation are able to recruit and contribute to local diversity, future studies should measure chemical defenses and identify their effective dispersers.

Although gibbons dispersed seeds of several common species, they dispersed significantly more rare plants in the community. By increasing the dispersal of rare species, gibbons can reduce NDD, as has been shown for avian frugivores (Camargo et al. 2022). This stabilizing process could be an important and general mechanism maintaining local species richness (Carlo and Morales 2016; Camargo et al. 2022). Additionally, langurs as mainly seed predators destroyed a large number of seeds from common species, and this predation pressure could limit the recruitment of these plant species in the ecosystem. The role of langurs may thus be similar to other natural enemies (such as pathogens) that contribute to the NDD of common species (Fricke et al. 2014; Luskin et al. 2021). In general, the joint, contrasting, contributions of these two primates could be critically beneficial to maintain plant diversity in the forest region of Mt. Wuliang.

Our results show that gibbons significantly shortened the SGT of 58% of dispersed species, yet the SGR of 54% of species were reduced significantly. However, many experiments conducted in the tropical regions show that primates (including gibbons on Borneo) had neutral or positive impacts on both rate and duration of seed germination (McConkey 2000; Fuzessy et al. 2016). The inconsistent SGR results may be explained by high species competition in the tropical forests (Brown 2014), where plant species produce a large number of seedlings that compete for recruitment. In the present study, the effects of gibbon gut passage on seed germination might have displayed varied advantages for the dispersed plant species. Gibbons could play a key role in seed dispersal for a limited number of species, such as a medium-seeded and rare species *Nyssa javanica*, which had relatively high SGR, while they may fulfil a subordinate role for other species with reduced SGR. On the contrary, if gibbon gut passage could increase SGR of all dispersed species, a large number of radicles would be present around the feces, which may be detrimental for the development of seedlings owing to NDD (Song et al. 2021). Therefore, the combination of reduced SGR and shortened SGT may increase the overall seedling establishment for gibbon-dispersed species in subtropical forests.

To our knowledge, this is the first study in which animal-mediated seed dispersal and predation in a subtropical forest are quantified together. Although we focused on a relatively early stage of plant recruitment, our results highlight that sympatric mammalian seed dispersers and predators may jointly contribute to local plant species coexistence and diversity maintenance. We concluded that both are integral

parts of the ecosystem they inhabit. Unfortunately, some animal guilds have experienced drastic population changes in the Anthropocene, and this is the case for primates in Mt. Wuliang. Due to long-term human disturbance, interspecific competition, and climate change, the population and distribution of gibbons have experienced a rapid decline during the last century (Fan 2017; Chen et al. 2020; Yang et al. 2021), which may lead to the gradual loss of their ecological functions—even before the species itself is lost (Valiente-Banuet et al. 2015; McConkey and O'Farrill 2016). The conservation and recovery of such seed dispersers would be of great importance in the future (Rogers et al. 2021; Ong et al. 2022). At the same time, we need to pay more attention to multiple ecological interactions between fruit-eating animals and their food plants (i.e., the relationship between food supply and seed dispersal or predation). After all, the maintenance of healthy ecosystems is dependent on the stability of ecological interactions.

**Data availability** The datasets used and analysed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Conflict of interest** None of the authors have a conflict of interest to report.

**Ethical approval** Ethics approval was not required according to local legislation.

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