

RESEARCH ARTICLE

Individual behaviour shapes patterns of bird-mediated seed dispersal

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Abstract

1. Seed dispersal is a key component in a plant's life cycle, allowing the colonization of new habitat and eventually enabling range shifts. For animal-dispersed plants, the behaviour of seed-dispersing animals has direct consequences for the fate of a seed. However, there is little empirical evidence on how individual behaviour of animals affects seed dispersal.
2. Here we investigated the effects of individual behaviour on seed dispersal distance and location by analysing movement data of spotted nutcrackers (*Nucifraga caryocatactes*) during harvest and scatter-hoarding of Swiss stone pine (*Pinus cembra*) seeds. To assess individual variation in seed dispersal patterns, we compared daytime hourly displacement patterns across individuals. We further identified seed caching locations of individual birds and analysed their potential for pine regeneration.
3. We found that nutcrackers showed one of two distinct behaviours: short-distance seed dispersal and long-distance seed dispersal. The caching locations resulting from the two behaviours differed markedly in the regeneration potential of Swiss stone pine: seeds transported over short distances were cached at high elevations with high regeneration potential within the pine's current habitat, while seeds transported over long distances were cached at low elevations with low regeneration potential outside of the pine's habitat. The behaviours were not associated with bird body mass, relative wing length or sex.
4. Our results emphasize that intraspecific individual behaviours of seed-dispersing animals can have far-reaching consequences for ecosystem functions. As a major determinant of seed dispersal dynamics, individual behaviour should be taken into account for a better understanding of ecosystem functions under current and future environmental conditions.

KEYWORDS

ecosystem functions, GPS tracking, intraspecific variation, movement behaviour, *Nucifraga caryocatactes*, *Pinus cembra*, plant regeneration, scatter-hoarding

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1 | INTRODUCTION

Seed dispersal is a crucial ecological process that influences plant population dynamics, community structure and ecosystem functioning (Howe & Smallwood, 1982). More than 70% of the world's woody plant species rely on animals to move their propagules (Jordano, 2014). Among animal seed dispersers, birds are considered one of the most effective vectors of dispersal for plants, as their high degree of mobility allows them to move seeds over relatively long distances (Fandos et al., 2023). Hence, the behaviour of seed-dispersing birds is crucial in determining seed dispersal patterns and shaping vegetation dynamics on a global scale (Russo et al., 2006). So far, studies on seed disperser behaviour have typically focused on variation among species (e.g. González-Castro et al., 2022; Nowak et al., 2022; Schupp, 1993). For instance, studies on avian seed dispersal have shown that the movement behaviour of different bird species is strongly associated with their morphological traits (e.g. Böhning-Gaese et al., 2006; Hartfelder et al., 2020). Large-bodied birds and birds with long wings can transport seeds over longer distances than small-bodied birds and birds with short wings, making bird body mass and wing length good predictors of seed dispersal distance (Li et al., 2017; Mueller et al., 2014; Saavedra et al., 2014; Wotton & Kelly, 2012). Such trait-based approaches have been used to estimate seed dispersal patterns of specific plant species (Jordano et al., 2007; Pérez-Méndez et al., 2016), small communities (Li et al., 2018; Morales et al., 2013) and, more recently, on a whole-community scale (Donoso et al., 2020; Schleuning et al., 2015; Sorensen et al., 2020).

In recent years, researchers have increasingly stated the need to incorporate intraspecific variation, particularly behavioural differences, in the study of seed dispersal patterns (Feldman et al., 2019; Réale et al., 2007; Zwolak & Sih, 2020). Studies of intraspecific variation have shown that the behaviour of individuals within populations often deviates consistently (i.e. over repeated observations) from the population mean (Dall et al., 2004; Réale et al., 2007; Wolf & Weissing, 2012). For instance, recent empirical work has shown that individual variation in the behaviour of deer mice strongly mattered for seed dispersal, where the boldness of an individual explained whether it acted as seed predator or as seed disperser (Brehm & Mortelliti, 2022). However, assessing individual behaviour and its relation to seed dispersal is challenging, and is mostly studied in animals that can be kept in captivity for behavioural experiments, such as rodents (Zwolak & Sih, 2020). An alternative approach to infer individual behaviour is using spatially explicit movement data derived from GPS tracking to measure behavioural differences among individuals (Hertel et al., 2017, 2020). The use of spatially explicit movement data has been highlighted to improve our understanding of seed dispersal patterns, as successful seed dispersal depends first, on the exact movement of an individual and second, on the characteristics of the habitat patch where seeds are deposited (Auffret et al., 2017;

Schupp et al., 2010). However, studies that use spatially explicit movement data to investigate seed dispersal patterns remain sparse (but see Kays et al., 2011; Oleksy et al., 2015; Piazzon et al., 2012; Rodríguez-Pérez et al., 2012; Santamaría et al., 2007; Todd et al., 2022).

Here we analysed movement data of spotted nutcrackers (*Nucifraga caryocatactes*) in the Swiss Alps to quantify individual variation in seed dispersal behaviour and its potential effects on plant regeneration. Spotted nutcrackers are scatter-hoarding corvids known for their mutualistic relationship with the Swiss stone pine (*Pinus cembra*), a keystone tree species growing at the tree line in the European Alps and the Carpathian Mountains. Nutcrackers harvest pine seeds in late summer and cache them underneath the soil surface, thereby acting as the pine's primary seed disperser (Neuschulz et al., 2015). They rely on the cached seeds as their main food source throughout the year (Mattes, 1982). We used GPS tracking to record seed dispersal movements of nutcrackers during the time when the Swiss stone pine bears ripe seeds. First, we investigated whether seed dispersal varies among individual nutcrackers over repeated caching flights and whether nutcracker movements can be grouped into distinct behaviours, in the following referred to as behavioural types. Second, we tested whether the behavioural types are associated with specific traits of the birds, such as body mass, wing length and sex. Finally, we investigated whether the seed deposition sites frequented by the different behavioural types differ in environmental conditions crucial for pine regeneration.

2 | METHODS

2.1 | Study system and study site

The spotted nutcracker is an excellent study organism to investigate individual seed dispersal patterns, as in the Swiss Alps, the bird forms an exclusive mutualistic bond with one plant species, the Swiss stone pine (Mattes, 1982). Each bird maintains a distinct harvesting site where seeds are collected, as well as a distinct caching site where seeds are transported to and then stored in numerous small caches in the soil (Sorensen et al., 2022). Harvesting and caching sites can be located more than eight kilometres apart (Sorensen et al., 2022). Spotted nutcrackers are important seed predators, as they consume about 80% of the seeds they cache (Mattes, 1982). At the same time, nutcrackers are the principal seed dispersers for Swiss stone pine. The bird species is the only animal that is able to open the cones and extract the intact seeds so that seed caches forgotten by the bird can germinate and establish into pine trees (Mattes, 1982). Our study was located near Davos, in Grisons, Switzerland. In this region, Swiss stone pine occurs sparsely but can be regionally dominant, typically forming the tree line, while lower elevations are dominated by spruce (*Picea abies*) and larch (*Larix decidua*). Nutcrackers are naturally common in the area, with abundances highest in proximity to stands of Swiss stone pine.

2.2 | Data collection

We collected data of 39 GPS-tagged adult spotted nutcrackers during the years 2017, 2018, 2021 and 2022. Data collected in 2017 and 2018 have already been published in a study by Sorensen et al. (2020). Each year, we captured nutcrackers in August using mist nets without the use of playback or decoys. We erected three to four nets, each measuring 13 by 3 m, in the two valleys Flüela (46°48'00"N 9°54'17"E) and Sertig (46°44'08"N 9°51'03"E) in the centre of large pine forests where nutcracker activity was high. Captured nutcrackers were aged based on wing moult patterns, allowing us to distinguish between birds hatched in the year of capture (juveniles), and birds in their second year or older (adults) (Jenni, 1983). We used only adult birds for the analysis since we aimed to investigate matured seed dispersal behaviour. Of the 39 captured adults, we excluded eight individuals with less than 6 days of data, as we considered their data insufficient for a behavioural analysis. The remaining 31 birds consisted of 19 males and 12 females. Birds were tracked during August and September when Swiss stone pine is in fruit. We measured the birds' body mass, wing length and tarsus length. Sex was later determined based on DNA from collected feather samples, using primers commonly applied for the molecular sexing of birds (Fridolfsson & Ellegren, 1999). We fitted 6.6 g GPS trackers (Lotek PinPoint VHF-120) to the birds using a backpack harness (Rappole & Tipton, 1991). All tagged nutcrackers were >175 g, ensuring that the backpacks had a maximum of 3.8% body mass. The tags were pre-programmed to collect at least one GPS location ('fix') every hour from 10 AM to 4 PM local time, as nutcracker activity is highest during these hours (Sorensen et al., 2022). The collected data was stored on the tag and later downloaded remotely using very high frequency (VHF) receivers and antennas. Of the 31 individuals included in the analysis, 28 were tracked during a single season (18 males and 10 females), while three individuals were tracked during two consecutive seasons (one male and two females), due to the use of advanced solar-powered GPS tracking technology. Movement data of 13 nutcracker individuals collected in 2017 and 2018 have already contributed to a different analysis published by Sorensen et al. (2022). Ringing permits were issued by the Swiss Federal Office for the Environment (FOEN) and the Swiss Ornithological Institute. The 'Amt für Lebensmittelsicherheit und Tiergesundheit Graubünden' granted the ethical approval for animal experimentation and issued the licences GR/11E/2022, GR11/2021, 2018_16F, 2015_17.

2.3 | Replication statement

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
Species	Individual	31 tracked individuals

2.4 | Movement analyses: Hourly displacements and locations of caching sites

For every bird, we extracted two main measures from the GPS data: (i) hourly displacement and (ii) area and location of caching- and harvesting sites. We obtained the birds' hourly displacement by calculating the geodesic distance between each pair of GPS points that were taken 1 h apart. To identify seed harvesting and -caching sites, we followed a procedure implemented by Sorensen et al. (2022): We identified highly frequented sites for each bird using recursion analyses (Bracis et al., 2018), and then classified them as either harvesting or caching site (Sorensen et al., 2022, see Figure 1b,c for examples, and Table S1 in Supporting Information for additional details). For 19 birds, this resulted in two frequently visited sites: one harvesting- and one caching site. The sites were classified as either harvesting or caching site based on behavioural observations in the field, following the method implemented by Sorensen et al. (2022). In this earlier study, we verified that the observed movements represent actual seed dispersal flights using field observations at seed harvesting and seed caching sites (Sorensen et al., 2022). For 11 individuals, movement distances were so short that it was impossible to distinguish two sites. In these cases, a single site was identified for each bird and was considered to serve as both harvesting and caching site. In the case of one bird, three different locations were visited frequently, hence we identified three sites: two harvesting- and one caching site (see Table S1).

2.5 | Clustering into behavioural types

We used a Bayesian hierarchical Gaussian mixture model to cluster the birds into behavioural types based on their hourly displacements. We suspected two behavioural types a priori after a visual inspection of the data, which seemed to be divided into birds that fly short distances and birds that regularly fly long distances (Figure 1a, Figure S6). We therefore assumed our observed data, that is the hourly displacements, to be the result of two different normal distributions with distinct mean and variance, which we called clusters. The model estimated mean and variance for both clusters and assigned each bird to either cluster. The vector z served as an indicator variable that denoted which of the two clusters a bird's set of data points y_i was assigned to ($i = 1, \dots, N$; where N is the number of individuals). Assuming two clusters, each z_i could either be 1 or 2, which we modelled by using a multinomial distribution with $k = 2$ clusters. We also assumed two separate probabilities p_1 and p_2 (one for each cluster), which represent the probabilities of a bird belonging to either cluster. The two clusters were mutually exclusive, hence $p_1 = 1 - p_2$. Each observation y_i comprised all hourly displacements of individual i , allowing the model to assess a bird's entire dataset for the clustering. Each observation was generated as follows:

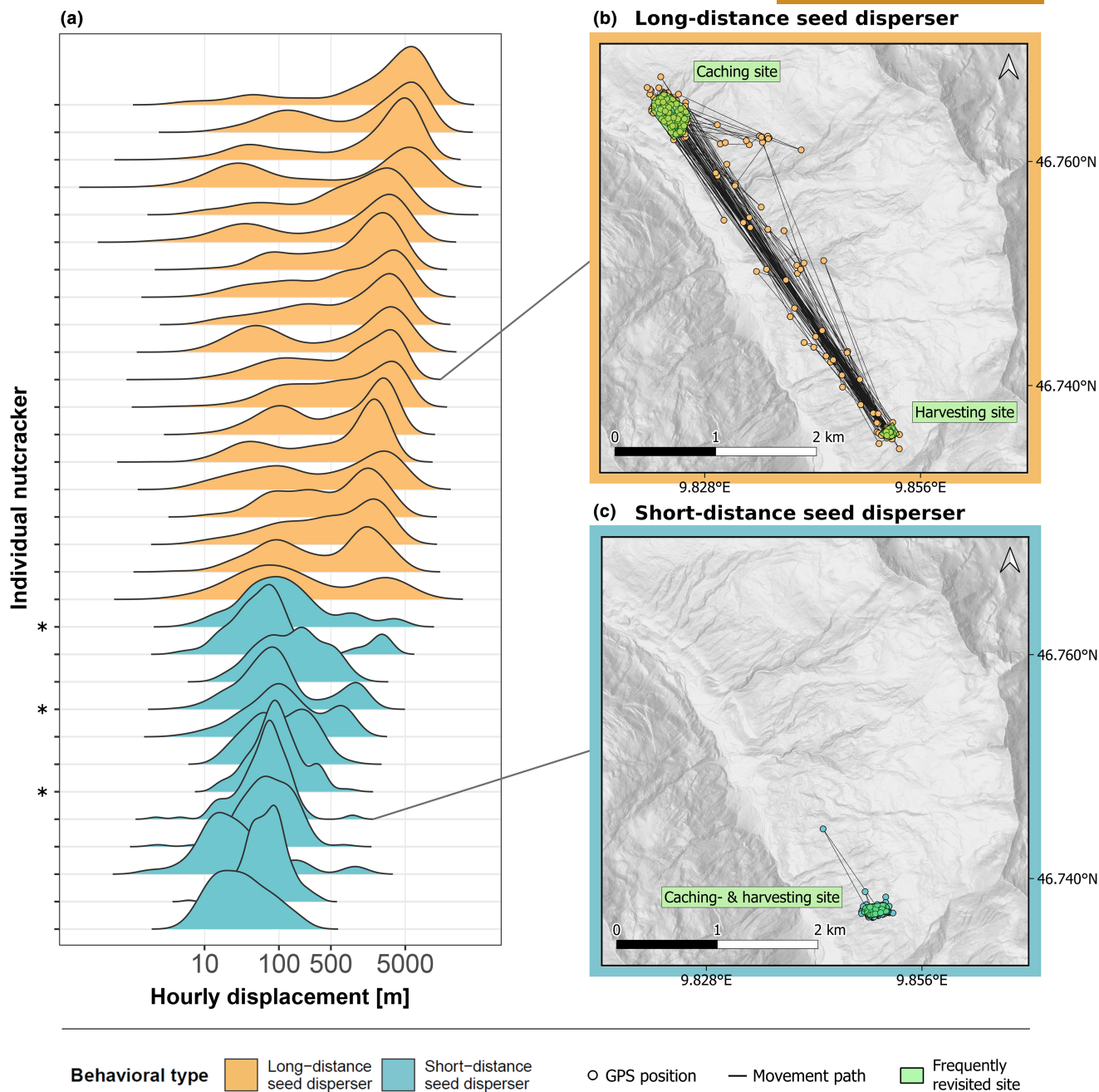


FIGURE 1 Daytime movement patterns of GPS-tagged seed-dispersing spotted nutcrackers. (a) Density of hourly displacement (geodesic distance calculated between hourly GPS locations) on a natural logarithmic scale, with one density curve per individual. Individuals on the y-axis are ordered by mean hourly displacement. Blue colour represents individuals classified as short-distance seed dispersers, and yellow colour represents long-distance seed dispersers. Asterisks (*) highlight birds with data pooled from two consecutive seasons. Maps show movement data of (b) a long-distance seed disperser and (c) a short-distance seed disperser with recorded GPS locations (points) connected in chronological order (lines). Green polygons show frequently revisited sites identified through recursion analyses.

$$y_{i[j]} \sim \text{Normal}(\mu_k, \sigma_k^2)$$

$$\mu_k \sim \text{Normal}(0, 10^{10})$$

$$\sigma_k^2 \sim \text{Scaled inverse gamma}(s, d, f.)$$

$$z_i \sim \text{Multinomial}(p_k)$$

$$p_k \sim \text{Dirichlet}(\alpha_k)$$

where $y_{i[j]}$ is the j th observation of individual i , modelled from a normal distribution with mean μ_k and variance σ_k^2 . We used an uninformative normal prior for mean μ_k , and a weakly informative

scaled inverse gamma prior with scale $s = \text{SD}(y)$ and two degrees of freedom ($\text{d.f.} = 2$) for the variance σ_k^2 . For the indicator variable z , we used a multinomial prior distribution with probability p_k , which itself was drawn from a Dirichlet hyperprior distribution with $\alpha_k = 1$, meaning that p_1 and p_2 were initially equal. In the modelling process, the indicator z_i was estimated along with each cluster's mean and variance (μ_k , σ_k^2), as well as a bird's probability of belonging to either cluster (p_1 , p_2). The model ran three chains for 21'000 iterations each, it was thinned by selecting every third iteration to facilitate convergence, and the first 4'000 iterations were discarded as burn-in. This resulted in each bird being categorized a total of 17'000 times. After accounting for autocorrelation among the posterior samples, the effective sample size (N_{eff}) was 16'998. Values of potential scale reduction factor indicated convergence (all $\hat{r}$ values < 1.05). To assess the certainty of a bird belonging to its assigned group, we calculated the proportion of that bird's posterior samples of z_i ($n = 16'998$) falling into each of the two clusters. For all individuals, this proportion was 16'998:0 (100%), indicating high model certainty (see Table S2 in Supporting Information). We performed a posterior predictive check based on a comparison of residual sums of squares of observed data versus simulated data. It resulted in a posterior p -value of 0.4986, indicating good model fit (Gelman et al., 1996). The analyses were performed using the package 'jagsUI' (v1.5.2; Kellner, 2015).

2.6 | Associations between behavioural types and bird traits

We tested whether behavioural types differed in bird-specific traits (i.e. body mass, relative wing length and sex). We fitted a generalized linear model with a binomial error distribution using *behavioural type* as a binary response variable and *body mass*, *relative wing length* and *sex* as explanatory variables. Relative wing length was calculated by dividing wing length by tarsus length. *Relative wing length* and *body mass* were scaled and zero-centred to improve comparability. A correlation test revealed no correlation between *relative wing length* and *body mass* (Pearson's $r < 0.1$). We fitted a full model with all possible combinations of two-way interaction effects between *body mass*, *relative wing length* and *sex*. We then conducted model selection with all possible combinations of fixed effects using the *dredge()* function of the 'MuMIN' package (v1.47.5; Barton, 2023). This led to the removal of all interaction effects.

2.7 | Associations between behavioural types and caching site conditions

We further tested whether seed caching sites of the two behavioural types differed in environmental conditions (i.e. overall forest cover, pine forest cover and elevation). For this, we calculated the area overlap of each bird's caching site with (i) overall forest cover

(i.e. mainly spruce, larch and/or pine forest) and (ii) Swiss stone pine forest cover only, using vector layers provided by local authorities ('Amt für Wald und Naturgefahren Graubünden'). Additionally, we determined the elevation above sea level for each caching site by calculating the mean elevation of all GPS datapoints within the site. We then performed three separate one-way ANOVAs with overall forest cover, pine forest cover and elevation as the respective response variables, each with behavioural type as the only explanatory variable. All statistical analyses were performed using R software (v4.2.3; R Core Team, 2022).

3 | RESULTS

3.1 | Behavioural types

Nutcrackers showed pronounced variation in movement behaviour. The Bayesian mixture model divided the 31 birds into long-distance seed dispersers (Figure 1b, yellow densities in Figure 1a [$n = 19$]), and short-distance seed dispersers (Figure 1c, blue densities in Figure 1a [$n = 12$]; see Table S3 for a model summary). The behaviour of long-distance seed dispersers was characterized by long hourly displacement, that is frequent flights over long distances. This group's mean hourly displacement was 1834 m, with the bird with the shortest flights moving a mean distance of 860 m every hour, and the bird with the longest flights a mean distance of 4004 m every hour. Further, long-distance seed dispersers showed high variation in mean hourly displacement with an average standard deviation of 1720 m. In contrast, the movement behaviour of short-distance seed dispersers was characterized by a high occurrence of short hourly displacements, with flights further than 1000 m being exceptions ($< 4\%$ of cases). The mean hourly displacement of this group was 179 m, with the shortest flier moving at an average of 45 m, and the longest flier at an average of 381 m every hour. The birds in this group showed low variation in their hourly displacement with an average standard deviation of 272 m.

3.2 | Bird traits associated with behavioural types

We found no significant associations between behavioural types and bird traits (Figure 2). The generalized linear model revealed no significant effect of body mass ($z = 1.012$, $p = 0.312$), relative wing length ($z = 1.157$, $p = 0.247$) and sex ($z = -1.020$, $p = 0.308$) on behavioural types.

3.3 | Environmental conditions at seed caching sites

Caching sites of short- and long-distance seed dispersers did not differ significantly in their percentage of overall forest cover, which

was high for both groups ($F_{1,30}=0.705$, $p=0.41$, Figure 3a). However, caching sites of long-distance seed dispersers had significantly lower Swiss stone pine cover ($F_{1,30}=14.6$, $p<0.001$) and were located at lower elevations ($F_{1,30}=15.59$, $p<0.001$) than caching sites of short-distance seed dispersers (Figure 3b,c).

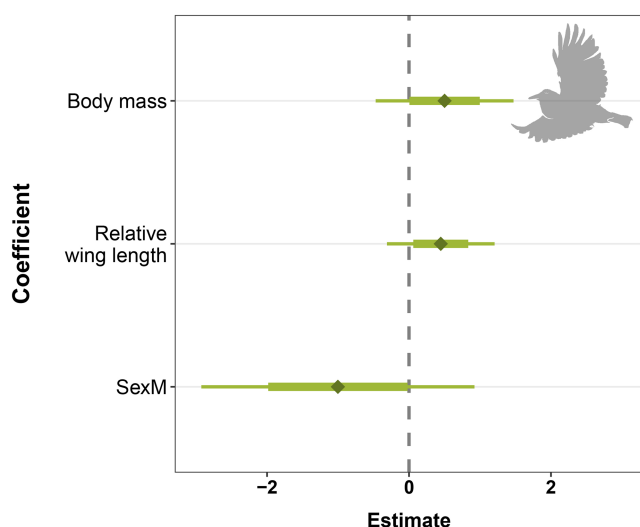


FIGURE 2 Effects of bird-specific traits on the probability of exhibiting long-distance seed dispersal. Estimates are shown as dark green diamonds together with their respective confidence intervals (thick whisker: 75% CI, thin whisker: 95% CI). Overlap of 95% CI with the dotted line (zero-line) indicates no significant effect for all estimates.

4 | DISCUSSION

The movement behaviour of seed-dispersing nutcrackers was characterized by pronounced variation between individuals. This variation was non-random but instead allowed for a separation of the birds into two behavioural types, that is short-distance and long-distance seed dispersers. The behavioural types were not significantly associated with the individuals' body mass, wing length, or sex. Importantly, short-distance seed dispersers deposited seeds predominantly in Swiss stone pine habitat at high elevations, while long-distance seed dispersers deposited seeds outside of Swiss stone pine habitat at lower elevations. The individual variation in seed dispersal movements therefore has implications for both birds and pines: Both behavioural types entail contrasting costs and benefits for the seed-dispersing nutcrackers, and they also affect the regeneration potential of Swiss stone pine.

We show that the two behavioural types, and thus, seed dispersal strategies found in this study lead to differences in the establishment potential of Swiss stone pine seedlings. Long-distance seed dispersers deposited seeds in habitats with no adult pine trees, indicating conditions unfavourable for pine regeneration (Figure 4). Previous studies on Swiss stone pine have indeed shown that the pine seedling establishment and survival increase with elevation and with increasing canopy openness (Neuschulz et al., 2015, 2018). This is likely the result of competition with other tree species, mainly Norway spruce (*Picea abies*, Appiah Mensah et al., 2021; Ulber et al., 2004) that dominates at the lower elevational range edge of Swiss stone pine. Hence, seeds transported by short-distance dispersers should have a better chance of successful establishment than

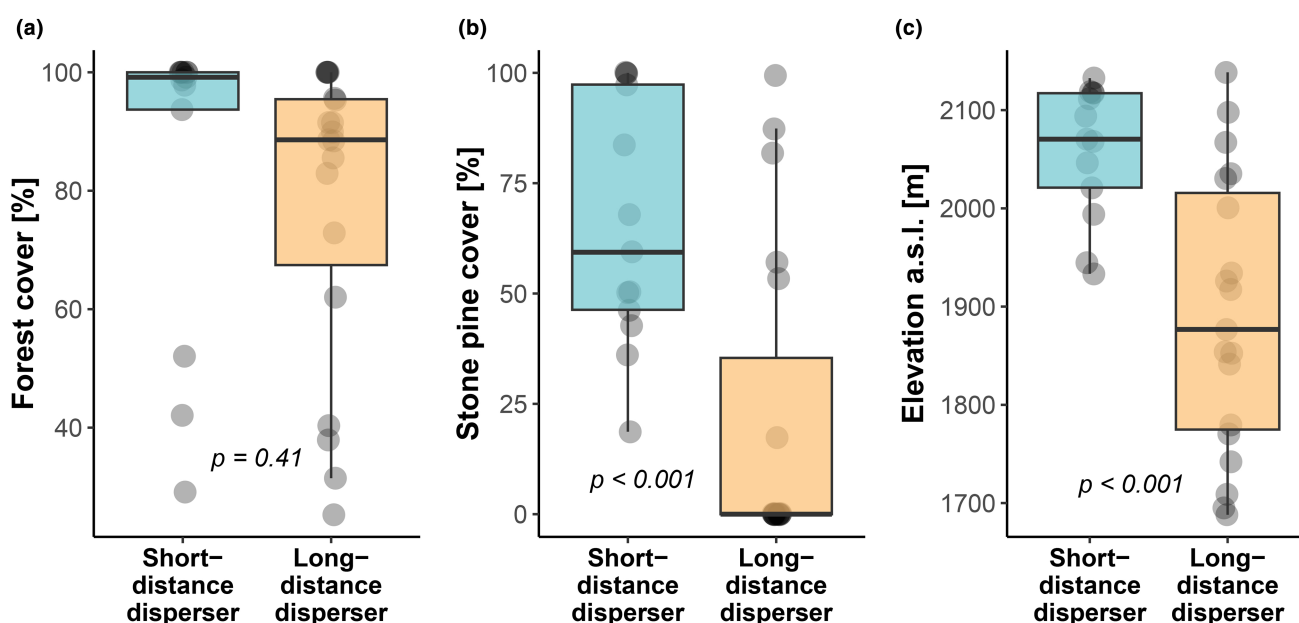


FIGURE 3 Environmental conditions at caching sites for short- and long-distance seed dispersers. (a) Percentage of overall forest cover, (b) percentage of Swiss stone pine forest cover and (c) mean elevation a.s.l. at caching site. Box margins indicate the 25% and 75% quartiles, the black line represents the median. Whiskers extend from the box margins to the furthest value still within 1.5 x the interquartile range, grey dots represent data points, with one dot per individual caching site.

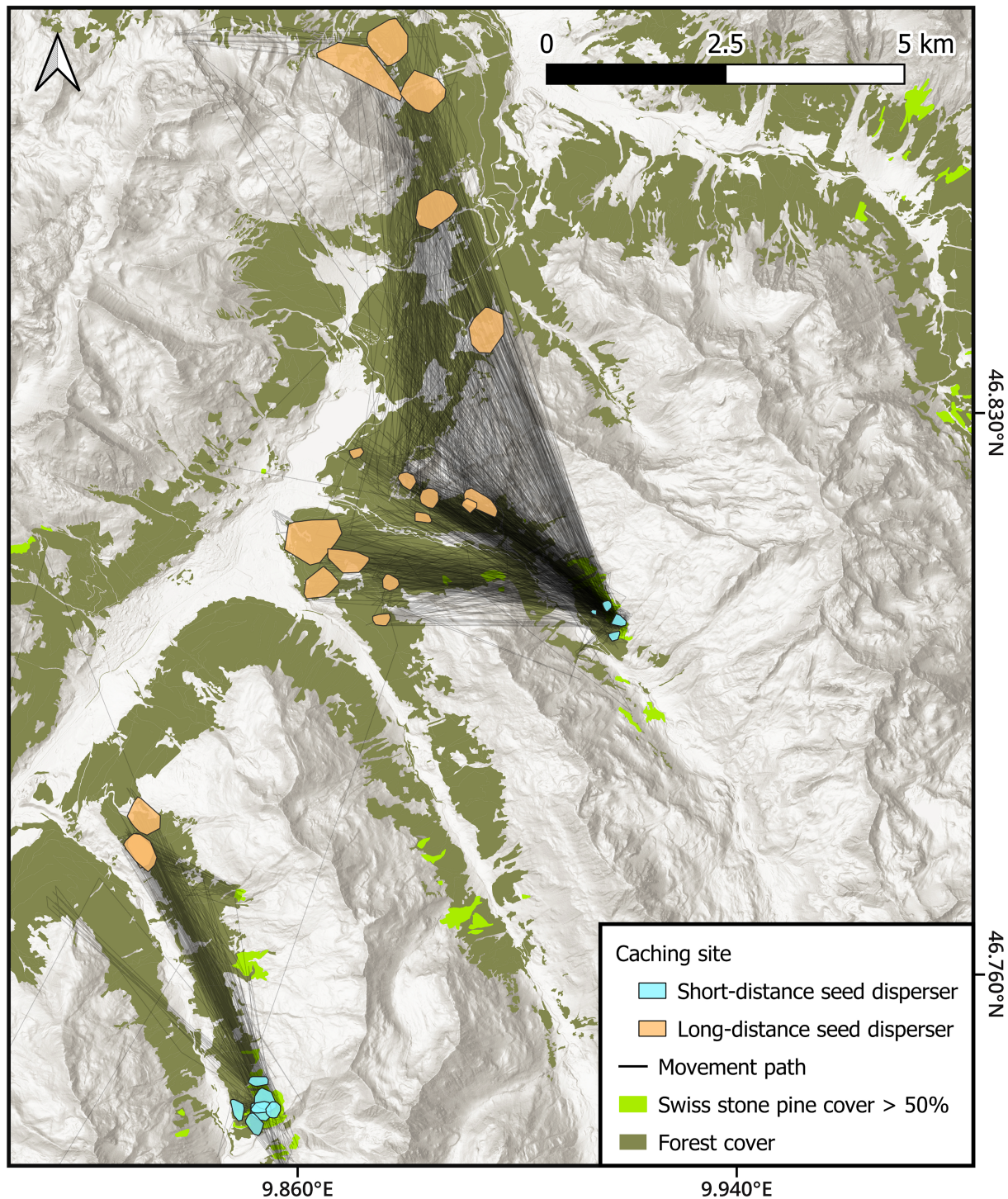


FIGURE 4 Map of the study area in Grisons, Switzerland. Individual seed caching sites of 31 spotted nutcrackers. Blue colour represents individuals classified as short-distance seed dispersers, and yellow colour represents long-distance seed dispersers. Black lines show nutcracker movements. Bright green areas represent forests dominated by Swiss stone pine (>50%), and dark green areas represent non-pine forests (mainly Norway spruce [*Picea abies*] and larch [*Larix decidua*]).

seeds deposited by long-distance seed dispersers in dense spruce forest at low elevations. Finally, the recruitment of Swiss stone pine seems to be constrained by a trade-off between dispersal distance and the probability of seedling establishment. However, estimating the extent to which short-distance seed dispersal is more beneficial for Swiss stone pine regeneration remains challenging, as it hinges

on additional factors like the microhabitat conditions at the seed caching site (e.g. above- and below-ground, Tomback, 1978), the degree of secondary dispersal and seed predation by birds and rodents at the caching location (Vander Wall et al., 2005; Zong et al., 2010), as well as the probability of seedlings to mature into adult trees (Loehle, 1988). Nevertheless, our results provide first evidence that

the individual behaviour of seed-dispersing nutcrackers has strong implications for population dynamics of Swiss stone pine. Similar patterns have been shown by Clark's nutcrackers (*Nucifraga columbiana*) that disperse seeds of whitebark pine (*Pinus albicaulis*). For these birds, long-distance flights of up to 22 kilometres have long been described (Vander Wall & Balda, 1977), and consequent studies found that many seeds were dispersed to lower elevations with a reduced reproductive potential for the plant (Lorenz et al., 2011; Tomback, 1978). Future studies should investigate pine seedling establishment and tree growth at known caching sites of both behavioural types to quantify the consequences of different seed dispersal strategies for pine regeneration.

The two seed dispersal strategies were not associated with differences in bird body mass or relative wing length, which is contrary to what has been found in previous studies of animal seed dispersers (Larsen & Burns, 2012; Todd et al., 2022; Wotton & Kelly, 2012). Thus, our results suggest that nutcrackers are not primarily limited by morphology for their seed dispersal behaviour and that the decision to pursue either behavioural strategy must be more strongly influenced by other factors. We also found no evidence for sex-specific differences driving seed dispersal strategies, although behavioural differences between males and females are widespread across animal taxa including birds (Kelley, 1988), mostly influencing mate choice and reproduction (Schlinger & Chiver, 2021). The lack of association between seed dispersal behaviour and sex indicates that seed caching behaviour is not primarily driven by bird-specific traits. Further, it could indicate that both males and females contribute equally to the rearing of offspring and hence, deposit seeds in a similar way.

Interestingly, the three individuals that were tracked over two consecutive summers maintained their unique caching locations and followed the same behavioural type during both seasons. This is the first indication that seed caching sites are used every year by the same individuals, and that individual seed dispersal strategies are consistent, repeated behaviours in adult nutcrackers. Although more data across individuals and years is needed to further investigate the consistency of individual behavioural types, it indicates that individual behaviours in seed dispersal may be inherent to specific nutcrackers. In the long term, these inherent seed dispersal behaviours could have important implications for the potential of the pine to locally adapt to changing environmental conditions. Previous work has shown that variation in individual behaviours exists across various taxa (Bolnick et al., 2003; Peña-Villalobos et al., 2020; Stearns, 1989) and entails consequences for individuals, populations and ecosystems (Shaw, 2020). Our study further underlines that behavioural types may have stronger implications for ecosystem functions than morphological traits, such as body mass, that usually are used to infer ecosystem functions (e.g. Donoso et al., 2020; Schleuning et al., 2020). We conclude that acknowledging behavioural types can improve our understanding of ecosystem functioning across various taxa and ecosystems.

For an individual, the limited availability of energy in ecosystems forces animals across taxa to allocate their resources optimally to

maximize their fitness (Boggs, 1992). This allocation often leads to trade-offs between different behaviours, where an investment in one behaviour may lead to a decrease in another behaviour. For scatter-hoarding animals, for instance, an optimum food-hoarding strategy should ideally maximize the amount of cached food resources, while minimizing the energy spent during food collection and storage. However, competition, predation risk, or the quality of foraging sites can constrain the foraging activity of animals (Laundré et al., 2001; Pays et al., 2012; Weterings et al., 2018). In our study system, short-distance seed dispersers spent a significant portion of the harvesting season in a small area of pine forest, where they harvested and cached seeds. They dispersed seeds over short distances and spent relatively little energy and time on seed dispersal flights. This likely allowed them to harvest and cache a high number of seeds in a short amount of time. However, their caching locations were located in high-elevation pine forests (around 2050 m a.s.l.), where snow cover lasts roughly from early October to late May. Thus, nutcrackers caching at these sites will have high energetic costs during winter time, as they need to dig through the thick snow cover to retrieve seeds (Mattes, 1982). In contrast, nutcrackers that dispersed seeds over long distances spent in comparison more energy during the seed harvesting time by moving seeds to their far away caching sites, mostly located in dense spruce forests and at lower elevations (around 1850 m a.s.l.). This energetic investment may, however, pay off during winter, as less snow accumulates in dense forest and at low elevations, facilitating the retrieval of cached seeds. In addition, previous studies have shown that seeds deposited in dense forest at low elevations are less likely to germinate and remain preserved and edible for a longer time (Neuschulz et al., 2015, 2018). Based on these results, we consider a trade-off between caching site quality and energy expenditure to be the main driver of the two behaviours. It remains unclear which of the two strategies is more beneficial for the birds and what the underlying drivers are that lead to these types, as the exact mechanisms shaping this dynamic are still unknown. Currently, both strategies entail costs as well as benefits for the birds, and both seem to be effective in providing them with a sufficient food supply throughout the year. Likely, the two behaviours are linked to each individuals' home range. If so, birds that occupy a home range in the pine forest would perform short-distance flights to harvest and cache pine seeds, whereas birds with a home range outside of the pine forest would need to undergo long-distance flights. Unfortunately, as we yet lack year-round data of nutcracker movements, we cannot infer year-round home ranges for spotted nutcrackers. However, previous studies on Clark's nutcracker have shown that the birds cached seeds near the centroids of their home ranges, thus making the geographic location of a home range a good predictor of seed dispersal distance (Lorenz et al., 2011; Lorenz & Sullivan, 2009).

5 | CONCLUSIONS

Using movement data of individual nutcrackers, we show how intraspecific variation in seed dispersers can alter the outcome of a

seed dispersal process and have potentially far-reaching consequences for both the plant and its animal disperser. The relationship between the two species is shaped by different trade-offs that could conceivably be thrown off-balance as temperatures continue to rise and environmental conditions change. In the future, climate change may gradually alter the profitability of the two behavioural types, with consequences for the dispersed pine seeds. There is concern about the pine's capacity to cope with rapidly changing climatic conditions due to its low genetic diversity, small and fragmented populations and slow life history (Brodbeck & Gugerli, 2010; Dauphin et al., 2021; Gugerli et al., 2009; Ulber et al., 2004). In the European Alps, rising temperatures over the last decades have decreased the duration and thickness of snow cover during winter (Gobiet et al., 2014; Klein et al., 2016). As Alpine winters become less severe, the retrieval of cached pine seeds might be facilitated for short-distance seed dispersers. Freed from the disadvantage of costly seed retrieval during winter, the short-distance strategy might become advantageous. This could lead to a potential shift towards more short-distance seed dispersal behaviour in the future. Consequently, more seeds would be deposited in suitable habitats at high elevations, making dispersal events beyond the tree line more likely. This could potentially aid the Swiss stone pine in shifting its range to higher elevations, and thereby enable it to better track its climatic niche. Although speculative, this example illustrates how changing climatic conditions may alter seed dispersal patterns in the future. This may not only apply to scatter-hoarders that actively deposit seeds at certain sites but also to other seed dispersal systems where the movements of seed dispersers are affected by changing environmental conditions (Auffret et al., 2017; Schleuning et al., 2020).

So far, only few empirical studies have focused on how climate change may alter the individual behaviours of moving animals (but see Aikens et al., 2020; Hill et al., 2021) and further studies are needed. Our results highlight the importance of considering individual variation in seed dispersers to better understand seed dispersal processes and how they are influenced by future climatic conditions. Our study also reveals important findings that go beyond the system of seed-dispersing animals. Moving animals are a central component of many ecosystem functions, such as pollination, pest control, or nutrient deposition (Bauer & Hoyer, 2014; Runge et al., 2014). Our findings support the notion that individual variation in animal movement behaviours may have major implications for the outcome of diverse ecosystem functions. Surprisingly, only very few studies have so far linked individual behaviours to ecosystem functions and services (Laskowski et al., 2022, but see Frølich et al., 2022; Hunter et al., 2022), although recently this has been done for nutrient deposition by reef fish (Allgeier et al., 2020). In particular, under changing environmental conditions, individual behaviours may help to maintain certain ecosystem functions that are otherwise at risk. Future studies should therefore focus on individual variation to better understand how individual behaviours may shape ecosystems in the future.

AUTHOR CONTRIBUTIONS

VG and ELN designed the study, collected and analysed the data and led the writing of the manuscript. MCS aided in data collection. TM, AGH and JA contributed to data analyses and interpretation of the results. All authors contributed critically to the drafts and gave final approval for publication. Our research unites authors from different countries, including scientists located in the country where the study was conducted. Local stakeholders were kept up to date through a regular newsletter written in local language with a non-scientific audience in mind. When applicable, we cited literature from scientists in the region, and we made efforts to consider relevant work published in the local language.

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CONFLICT OF INTEREST STATEMENT

All authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The datasets generated and analysed during the current study are available in the Movebank Data Repository, <https://doi.org/10.5441/001/1.324> (Graf et al., 2024).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Details of the recursion analyses for all individual nutcrackers.

Table S2. Posterior results of the Bayesian hierarchical mixture model.

Table S3. Summary of the Bayesian hierarchical mixture model.

Table S4. Summary of the generalized linear model for bird traits associated with behavioural types.

Table S5. Summaries of three separate ANOVAS testing for environmental conditions at caching sites.

Figure S6. Distribution and clustering of GPS tracking data.

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