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LETTER

Land-use change and the ecological consequences of personality in small mammals

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Abstract

Many plants rely on animals for seed dispersal, but are all individuals equally effective at dispersing seeds? If not, then the loss of certain individual dispersers from populations could have cascade effects on ecosystems. Despite the importance of seed dispersal for forest ecosystems, variation among individual dispersers and whether land-use change interferes with this process remains untested. Through a large-scale field experiment conducted on small mammal seed dispersers, we show that an individual's personality affects its choice of seeds, as well as how distant and where seeds are cached. We also show that anthropogenic habitat modifications shift the distribution of personalities within a population, by increasing the proportion of bold, active, and anxious individuals and in-turn affecting the potential survival and dispersal of seeds. We demonstrate that preserving diverse personality types within a population is critical for maintaining the key ecosystem function of seed dispersal.

Keywords

Behavioural syndrome, cache site, dispersal distance, individual variation, seed consumption, seed dispersal, seed selection, silvicultural practices.

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INTRODUCTION

All plants rely on dispersal mechanisms to carry their seeds to germination sites, with an estimated 50–90% of seed producing plants relying upon animals for dispersal (Howe & Smallwood 1982). *Scatter-hoarding* mammals are one such group of seed dispersers: by caching surplus seeds in small hoards, they promote dispersal (Jansen *et al*. 2004; Vander Wall 2010). Scatter-hoarding behaviour involves several key decisions (Fig. 1): which seed to select, whether to consume it immediately or cache it for later consumption, how far to disperse it, and where to cache it to maximise retrieval (Lichti *et al*. 2015). Surprisingly, although variation among individuals is a prerequisite for evolution, little is known about the impact of individual variation in scatter-hoarding behaviours on seed dispersal.

Understanding individual-level variations in small mammal seed dispersal is critical (Zwolak 2018) because these are pervasive seed predators and dispersers, harvesting up to 95% of preferred seeds in their territory (Lobo 2014). This exerts selective pressures on certain seed attributes that result in community-level changes in plant species composition and drive the evolution of seeds (Jansen *et al*. 2002; Vander Wall 2010). If certain individuals contribute disproportionately to seed dispersal or provide rare outcomes (i.e., through selection of larger seeds or further dispersal) (Nathan 2006), this will alter our general understanding of the mechanistic foundations of seed dispersal and the importance of individual variation to selection (Bolnick *et al*. 2011).

Research has primarily examined how seed characteristics and environmental attributes influence seed dispersal at interspecific levels (Lichti *et al*. 2015); but see Zwolak (2018) for a review of the effects of sex, ontogenetic shifts and individual specialisation on intraspecific variation. However, previous research has failed to examine the variation in seed dispersal due to *personality* (Zwolak 2018), or consistent differences in behaviour among conspecifics (Sih *et al*. 2004). This is surprising because personalities are ubiquitous across taxa (Pennisi 2016) and result in consistent behavioural differences that ultimately affect individual fitness and ecological parameters (Smith & Blumstein 2008; Sih *et al*. 2012; Wolf & Weissing 2012; Carere & Maestripieri 2013; Lapiedra *et al*. 2018). Consequently, small mammal personalities likely influence important decisions during seed dispersal because personality encapsulates an individual's unique way of behaving and responding to life's challenges (Réale *et al*. 2010); such as the challenge of collecting and maintaining seed caches.

If personalities influence seed dispersal, certain individuals may be more important for maintaining ecosystem functioning than others (Zwolak 2018). Thus preserving behavioural diversity within populations could be critical for protecting this vital service to ecosystems (Dirzo *et al*. 2014). Furthermore, previous studies have shown that land-use change may modify the distribution of personalities present within populations (Miranda *et al*. 2013), therefore, habitat alteration could have unexpected consequences on seed dispersal through the selection of certain individual seed dispersers. We examined the relationship between personality traits and four key decisions made during seed dispersal (Fig. 1) and tested whether these relationships varied across forests

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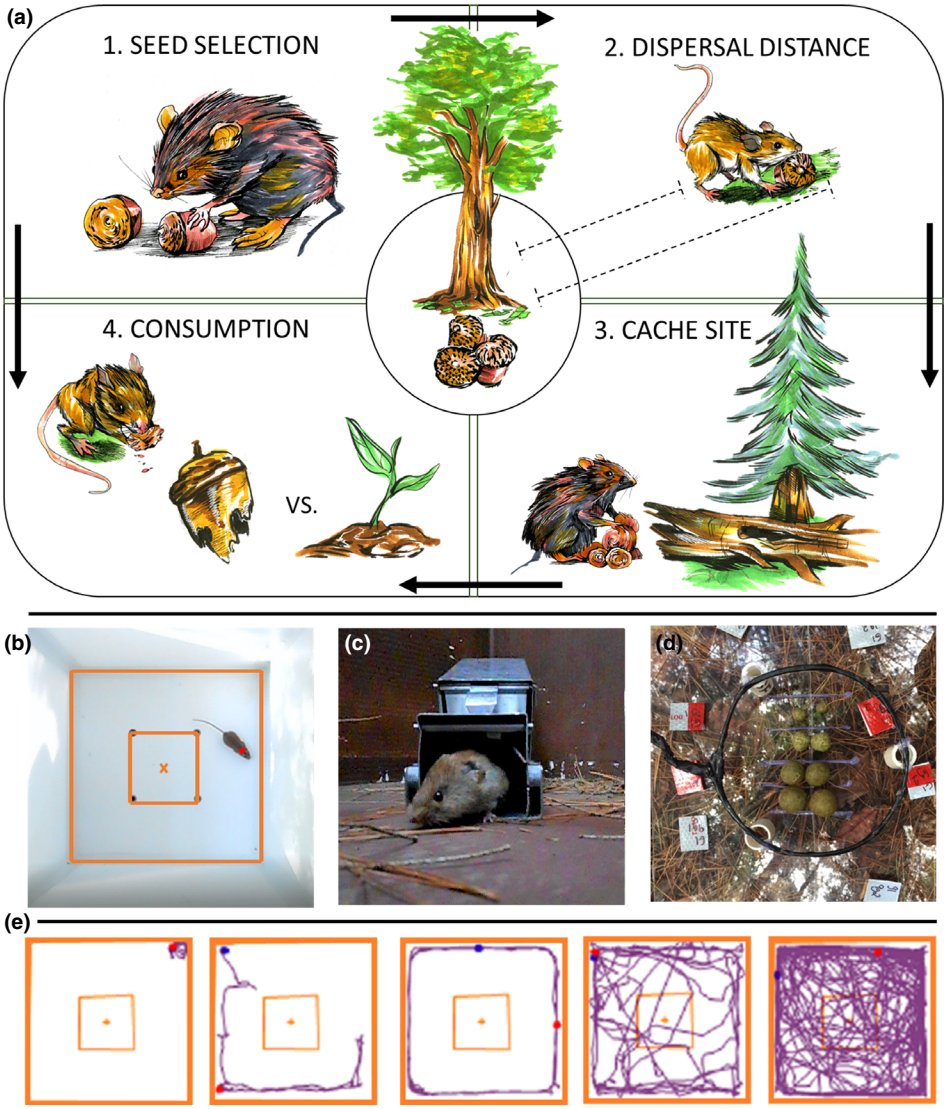

Figure 1 Key features of the study. (a) Four key decisions made by small mammals during seed dispersal are observed: seed selection, dispersal distance, cache site and consumption (i.e., seed consumed or cached intact). Arrows represent decision pathways where, for example, the decision to select a seed must occur before the decision to disperse or the decision to consume/cache. (b) In an open-field test, personality is measured and analysed using ANY-maze© software. (c) Latency to emerge from a trap (emergence test) measures boldness/timidness in small mammals. (d) Marked individuals are identified while choosing between seeds of varying masses, seeds are then tracked to show effects of personality on dispersal. (e) Tracks of five individuals show differences in activity and exploration (95% of behavioural traits are significantly repeatable, Tables S1 and S4).

manipulated with different silvicultural treatments. We conducted a large-scale field experiment wherein we trapped three different small mammal species in three forest types: two sites in unmanaged forest (reference), two sites in even-aged forest (treatment 1) and two sites in shelterwood forest (treatment 2) (See Fig. S1). Using mark-recapture techniques, we used three standardised tests and behavioural tracking software to measure personality in 648 free-ranging individuals from three study species: the deer mouse (*Peromyscus maniculatus*), the southern red-backed vole (*Myodes gapperi*) and the northern short-tailed shrew (*Blarina brevicauda*). Previous work on these study populations confirms that our trapping is not biased towards certain personality types (Brehm & Mortelliti 2018). In a seed predation experiment (Fig. S2), we then observed interactions with artificial seeds (to control for mass, shape and odour) (Jansen *et al.* 2004; Steele *et al.* 2014) and assessed whether personality traits influenced key decisions including: seed selection (dependent on mass), dispersal distance, cache site, and whether or not to consume the seed. Lastly, we assessed personality types present in the forest treatments to determine whether habitat modification shifts the distribution of personality traits, thus directly influencing seed dispersal.

METHODS

Study site and small mammal trapping

We conducted this study in the Penobscot Experimental Forest (PEF, 44°51' N, 68°37' W) which is located in east-central

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Maine, USA (Fig. S1). The PEF is an experimental forest where units were chosen at random and logged separately with different silvicultural treatments (minimum of two replicates per treatment). Management units average 8.5 ha in area (range 8.1–16.2 ha) and nearly 25 ha of forest has remained unmanaged since the late 1800s and serves as reference (Brissette & Kenefic 2014; Brehm & Mortelliti 2018).

As part of a fully controlled and replicated field experiment, we implemented a large-scale mark-recapture study on six trapping grids: two reference and four experimental. Reference grids were in the unmanaged forest and experimental grids were located in either even-aged forest or two-stage shelterwood with retention (each with two replicates) (Brehm & Mortelliti 2018). Each trapping grid was 0.81 ha in area and consisted of 100 flagged points spaced 10 m apart. We positioned Longworth traps at each flagged point, bedded traps with cotton and baited traps with a mixture of sunflower seeds, oats and freeze-dried mealworms. Grids were positioned close to the centre of the management unit to minimise edge effects (mean distance between grids was 1.44 km and mean distance between duplicate grids was 1.45 km; greater than the movements of our target species). We trapped at each grid for 3 consecutive days and nights and grids were revisited after 1 month (five trapping sessions in total each year). We analysed data collected from individuals over two trapping seasons (June–October 2016, 2017).

Behavioural tests

We used three standard behavioural tests to measure personality in trapped individuals: an *emergence test* to measure boldness (Carter *et al*. 2013), an *open-field test* to assess activity and exploration in a novel environment (Walsh & Cummins 1976; Perals *et al*. 2017) and a *handling bag test* to measure docility and the response to being handled (Montiglio *et al*. 2012; Taylor *et al*. 2014). At a base area in the home grid of the focal individual, we performed all tests in the order above before handling or marking. Details on each test are provided in Appendix S1. Once behavioural tests were complete, animals were anaesthetised with isoflurane and marked with passive integrated transponder (PIT) tags (Biomark MiniHPT8, 134.2 kHz) and either a small animal ear tag or a distinctive haircut (i.e., for shrews, which have no external auricle). We recorded the sex, mass (measured using a 100 g Pesola Lightline spring scale), body length, tail length, age class and reproductive status. Reproductive status was classed as either reproductive (with enlarged testes, or showing signs of pregnancy, lactation or a perforated vagina) or not. Animals were released at the exact site of capture. Behavioural tests were performed once monthly to ensure that animals would not habituate to the tests.

To analyse the recorded emergence tests, we assessed if the animal emerged (defined as all four feet having left the trap), the latency (in seconds) to emerge, and the total time spent at the end of the Longworth tunnel before emerging. Open-field tests were analysed using the behavioural tracking software, ANY-maze© (version 5.1; Stoelting CO, USA). See Table S1 for a complete list of the behaviours measured and Fig. 1e for an example of tracks.

Seed experiments

To record observations of seed choice in our marked populations, we performed a detailed seed experiment (Fig. S2) during the months of July–October (2017 only); when seeds are naturally available. After the three-consecutive day/night trapping period was completed each month, we deployed seed experiment stations in our trapping grids (106 total; *c*. 18 stations per trapping grid). At each seed station, we mounted a trail camera (Bushnell 119740 14MP Nature View HD) 1 m above the ground and directed it towards the forest floor. We placed a 30 × 30 cm piece of transparent plexiglass on the forest floor, and atop this plexiglass we presented artificial seeds of four controlled masses (Wang *et al*. 2009). This allowed us to control for shape, odour and quality (Smallwood & Peters 1986; Wang *et al*. 2013). Artificial seeds were made using raw organic pumpkin seeds pulverised into powder and a mixture of pure gelatin powder and water. The four seed masses were 1, 3, 6 and 9 g, which represent a range of options from relatively light (1 g) to a mass of ~ 60% of the study species' body weight (9 g), because previous research has shown that at ~ 60% of an animal's body weight, seed selection decreases significantly (Muñoz & Bonal 2008). Each artificial seed was formed into a ball of consistent shape and size. Two seeds of each mass were placed at the station, and we randomly rotated the location of these seeds at each experiment station (Fig. S2).

To allow for specific behavioural observations and seed choices to be associated with the individual who made them, we utilised a permanent radio frequency identification (RFID) reader to scan and identify individuals marked with PIT tags (RFIDLOG dual animal tag rfid data logger). Mounted atop the plexiglass was an antenna (Priority1 rfidcoil – 160a) which attached to the reader located in a dry bag 1 m away. These antennas were built for an operating frequency of 134.2 kHz. Records were automatically stored on an SD memory card along with the exact date and time of the detection. To allow for easy relocation of dispersed seeds, we connected a 10 cm long thin piece of copper thread to each seed, and at the end of the thread we attached a flag made of DOT-C2 grade reflective tape. Each flag was uniquely labelled and each seed's location on the plexiglass was recorded for ease of identification in videos. It has been shown that similar tagging methods have little to no effect on the decision by small mammals to consume or disperse seeds (Xiao *et al*. 2006; Kempter *et al*. 2018), and because all seeds were tagged using this method, we assume any influence to be negligible.

Each morning, an observer visited the seed experiment stations and recorded which seeds had been removed and which remained untouched at the site. Seeds that had been consumed at the site were recorded and removed. Seeds that had been removed from the site were relocated with the aid of a flashlight. The exact location of recovery was recorded by measuring the direct distance and bearing from the centre of the seed station. We noted the location of recovery as being: at the seed station, on the ground relatively in the open, at the base of a tree, down a hole, underneath or next to coarse woody debris (CWD) or underneath or next to fine woody debris (FWD). Each recovered seed was visually classified as

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either ≥ 50% consumed, or < 50% consumed (including 100% intact seeds). Seed stations were left active at a site for an average of 3 days and nights but were removed early if no seeds remained.

Analysis of seed videos

From seed experiment videos, we recorded the following variables of interest: the size of the first choice seed, whether the seed was eventually removed from the site or consumed at the site, and the size of the removed seed. We then combined these observations with corresponding data obtained in the field (i.e., the distance that the seed was removed, the cache site, and the fate of the seed), and matched observations with visits by known individuals (via PIT reads).

Statistical analyses

Personality and seed choice

First, we performed a repeatability analysis to determine which behavioural variables could be considered personality (Appendix S1). Then, to assess whether personality influenced seed dispersal decisions, we used a conservative nested hypothesis testing approach (Burnham & Anderson 2002) using mixed effects models in R package *lme4* (Bates *et al.* 2015; R Core Team 2017). We ran models on each species separately. When the dependent variable was numeric (such as the distance of seed dispersal), we assessed the residuals of the fitted model for normality and log10 transformed when necessary. Binomial variables were examined using generalised linear mixed effects models with a binomial family and a logit link. Count variables were examined using generalised linear mixed effects models with a poisson family. Numeric predictor variables were z-standardised.

We ran models using the variables obtained from the seed experiments (e.g., seed mass preference and distance seed is removed) as dependent variables. We used random intercept models with individual identity as a random effect. To assess whether a random effect of trapping grid was necessary, we compared the AICc scores of models with and without this effect (Zuur *et al.* 2009). Throughout our analysis, models within 2.0 ΔAICc of the top model were considered to have equal support (Buckland *et al.* 1997; Burnham & Anderson 2002). Random slope models were not fitted, because the predictor variables were not repeated measures. First, in a base model we tested covariates with known potential to influence the response variable of interest (such as the availability of each seed size, which changed upon subsequent small mammal visits) (Cooper & Millspaugh 1999; Manly *et al.* 2002; Richardson *et al.* 2013). See Table S2 for a full list of these covariates. We checked whether models containing the added covariates fit the data better than those without by comparing AICc scores. The necessary added covariates were retained throughout the rest of the model selection process.

Next, we ran a model set composed of six models: a base model (including necessary control variables), and one including each of the following: sex, body condition, reproductive status (either reproductively active or not), trapping session and silvicultural treatment. If two or more models showed better support than the base model, we tested for an additive effect of these variables. We retained the top model from this model set and tested it against six new models, adding one new microhabitat variable to each (Appendix S1 and Table S3).

We tested the top model from this model set against new models, each containing the additive effect of one personality variable: handling time, latency to emerge, time at end of tunnel, mean speed, rear rate, proportion time grooming, and proportion time centre (Table S1). By using this method, we intended to control for as much variability in the data as possible before introducing the personality covariates. We did not use BLUPS, because much criticism surrounds this method (Houslay & Wilson 2017). Instead, the personality measurement used was the one taken during the trapping session just prior to the seed experiment. We also tested for non-linear effects of personality (specifically, quadratic, exponential and logarithmic) (Pinheiro & Bates 2000; Chavel *et al.* 2017) and used the linear effect if it was within 2.0 ΔAICc of any non-linear effect. Last, we tested the hypotheses that the relationship between personality and seed decisions would vary depending on sex, trapping session and silvicultural treatment. To do this, we ran models including interactions between these variables. We retained all models within 2.0 ΔAICc of the top model and used model averaging (Burnham & Anderson 2002) to obtain model predictions and confidence intervals.

We examined the two categorical response variables of cache site and mass of the first choice seed using multilevel, multinomial logistic regression models (Koster & McElreath 2017). These models were fitted and plotted using *Rstan* (the interface to software Stan) and *rethinking* packages for R (McElreath 2015; Stan Development Team 2018). *Rstan* uses Hamiltonian Monte Carlo methods for parameter estimation. This is a preferred method for complex models because it allows adequate mixing of the posterior distribution in relatively fewer iterations of the chains (Monnahan *et al.* 2017). To facilitate good mixing of the Hamiltonian Monte Carlo chains, we provided weakly informative priors for the fixed effect parameters and variance-covariance matrices (McElreath 2015; Koster & McElreath 2017). For all models, we used three chains of 2000 iterations (including 1000 warm-up iterations) (McElreath 2015; Koster & McElreath 2017). We evaluated model convergence and adequate mixing by inspecting traceplots and checking the number of effective samples (n_eff) and the Gelman-Rubin convergence diagnostic (Rhat) (McElreath 2015). We used the same model selection process as described for *lme4*, using the Widely Applicable Information Criterion (WAIC) (McElreath 2015) and a threshold of 2.0 ΔWAIC. When dealing with multinomial multilevel models, interpretation of coefficients is not straightforward and may be misleading (Koster & McElreath 2017), therefore we based our inference on the final probability of selection and its 89% percentile intervals (see McElreath, 2015 for a discussion on 89 vs. 95% percentile intervals).

Personality distributions

To assess whether the distribution of personality traits differed between silvicultural treatments, we examined the

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probability density function of each personality trait for individuals present in each of the three distinct forest types. We performed non-parametric Kruskal–Wallis tests to test the hypothesis that the population distributions were identical. Further, we calculated the phenotypic distance between the two populations using the Δp method (a non-parametric distance measure which is calculated based on a joint cumulative distribution function) (Safran *et al*. 2012).

Finally, based on the top models obtained from our nested hypothesis testing, we calculated model-averaged predictions for response variables when personality variables were present in the top models. This allowed us to examine the extent to which a shift in the distribution of personality types results in a shift in the predicted seed dispersal behaviours. Using the mean value of all other fixed effects and the values of the personality variable present in each of the silvicultural treatments (i.e., considering all species for which a given personality trait predicted the interaction with seeds), we predicted the distribution of the response variable in each of the three forest types – allowing us to illustrate the ecological consequences of these personality traits under differing silvicultural pressures.

RESULTS

We examined behavioural data from standardised tests for 705 observations from 295 deer mice, 646 observations from 244 southern red-backed voles and 246 observations from 109 northern short-tailed shrews and found significant repeatability for 90% of behaviours (Table S4) indicating personality (Dingemanse & Dochtermann 2013) (mean number of repeat tests per individual was 2.4, 2.6, and 2.3, respectively). These personality traits were the key predictors in the top model(s) at all four stages of seed dispersal (Fig. 1; Table S5). Personality variables appeared in 63% of top models, and model fit for the top model was moderately high overall (mean $R^2 = 0.31$).

Our results demonstrate that personality affects four key decisions during seed dispersal: seed selection (seed mass preference), dispersal distance (distance seed is removed), cache site, and seed consumption (or the probability of consuming a seed). Personality influenced seed mass preference in mice and voles (Fig. 2; Table S5 and Fig. S3). The distance of seed dispersal was affected by anxiety (time grooming) in mice and timidness/boldness (time in the centre) in voles (Fig. 3) and docility (handling time) predicted cache location in voles (Fig. S4). Last, the probability of consuming a seed was influenced by activity levels (rear rate) in mice (Fig. 2) and anxiety (time grooming) in voles. Personality also influenced other variables such as the probability of removing a seed from the site (Table S5; Fig. 2). See Fig. S5 for partial residuals from Fig. 2 and Fig. 3, and Table S6 for information about the direction of effects in top models. Personality variables were not present in the top models for shrews, but future work may inform this relationship. While shrews are known to consume and store seeds for winter months when preferred foods are scarce (Smith & Reichman 1984), a majority of their diet consists of insects, amphibians, and other small mammals. This may have affected visitation rates at seed stations. Consequently, our sample size for shrews was substantially smaller than for mice and voles and the lack of results may be due to an issue of power.

Additionally, the distribution of these personality traits predicting key decisions differed between populations living in distinct forest types (Fig. 4; Table S7). As an example, in even-aged forest, a larger proportion of mice were bold (time at end of tunnel) compared to the reference and shelterwood forests ($\Delta p = 22.59$, $P = 0.05$, indicating marginal significance; and $\Delta p = -22.59$, $P < 0.05$, respectively). Mean levels

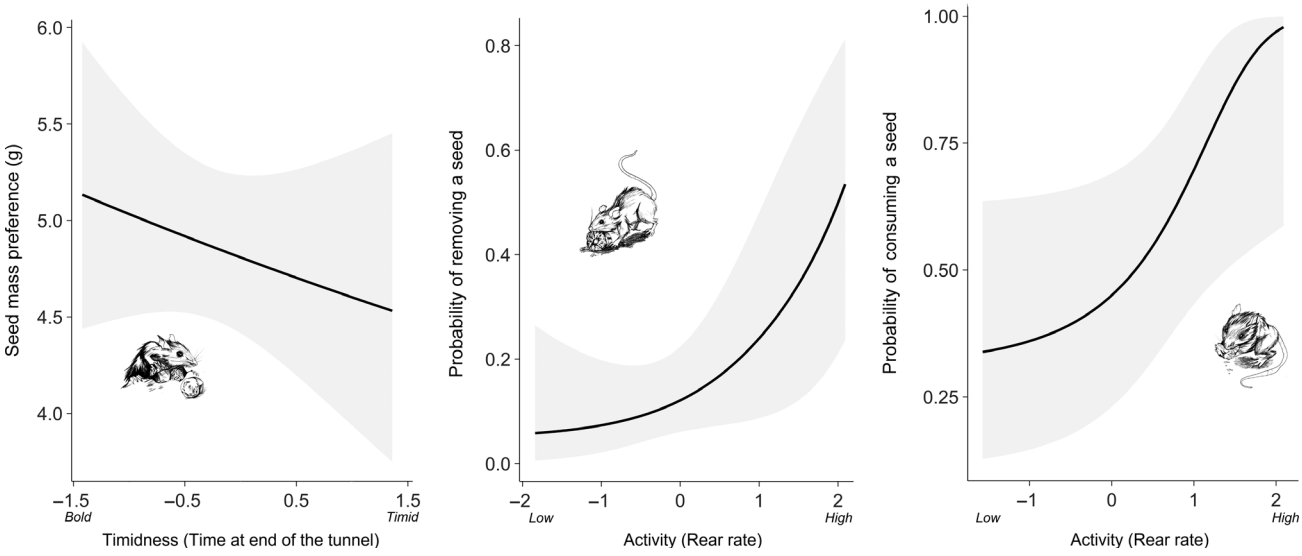

Figure 2 Effects of personality (x-axes) on three different seed dispersal decisions (y-axes) in *P. maniculatus*. Bold mice prefer seeds of greater mass (left), active mice have a higher probability of removing a seed from the experiment (middle), and active mice are more likely to consume a seed (right). Predictions were obtained from generalised linear mixed effects models; model-averaged 95% CIs are shown. Behaviours on the x-axes have been z-standardised. Predicted probabilities of removing and consuming seeds are shown for Session 3.

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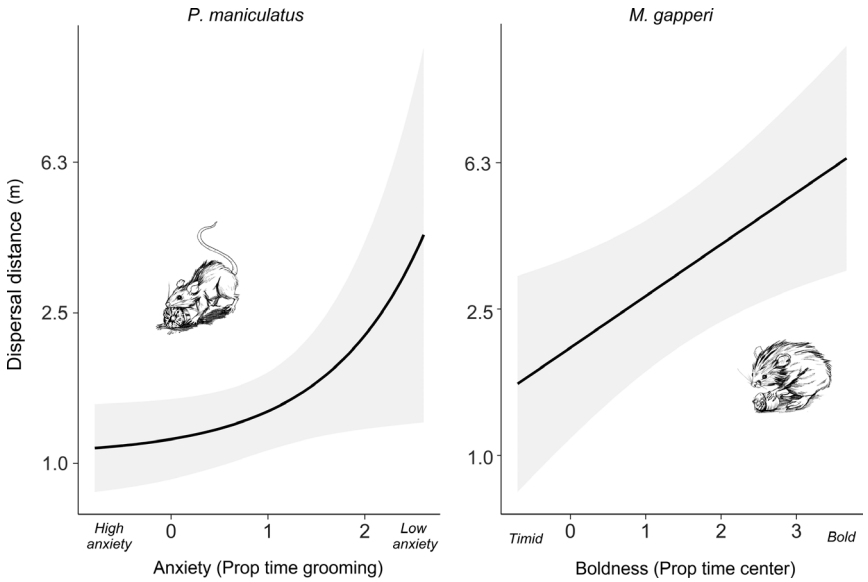

Figure 3 Effects of personality (x-axes) on seed dispersal distance (y-axes). Anxiety decreases dispersal distance in *P. maniculatus* (left) and boldness increases dispersal distance in *M. gapperi* (right). Results were obtained from linear mixed effects models; model-averaged 95% CIs are shown. Behaviours on the x-axes have been z-standardised. Y-axes are on a log10 scale and labels have been transformed into metres.

of boldness (latency to emerge) differed between vole populations living in the different forest types (Kruskal–Wallis $\chi^2 = 6.36$, $P < 0.05$). Mean activity levels (rear rate) differed between mice living in the different forest types (Kruskal–Wallis $\chi^2 = 6.63$, $P < 0.05$), and populations living in even-aged forest had a greater proportion of highly active individuals when compared to the reference ($\Delta p = -18.01$, $P < 0.05$). The same was true for voles, who were significantly more active (mean speed) in shelterwood forest than in the reference forest ($\Delta p = -20.00$, $P < 0.05$), and mean activity levels (rear rate) differed between the populations (Kruskal–Wallis $\chi^2 = 12.97$, $P < 0.05$).

Finally, after predicting the distribution of seed dispersal behaviours based on the composition of personality types present in the three different forest types (Fig. 4; Table S7), we found that dispersal distance of seeds is predicted to be farther on average in shelterwood forests than in reference and even-aged forests ($\Delta p = -15.21$, $P < 0.05$), the probability of a seed being consumed is predicted to differ between the three forest types (Kruskal–Wallis $\chi^2 = 6.63$, $P < 0.05$) and is lower in reference forests than in even-aged forests ($\Delta p = -18.01$, $P < 0.05$), and slightly larger seeds are selected for in even-aged forest than in reference and shelterwood ($\Delta p = 22.59$, $P = 0.05$ and $\Delta p = -22.59$, $P < 0.05$, respectively) (Fig. S6).

DISCUSSION

Through a large-scale field experiment conducted in Maine (USA), we found that personality traits in small mammals have consequences on all key decisions made during seed dispersal. As an example, we found that bolder mice tend to select larger seeds; docile voles are likely to cache them in optimal germination sites and bold voles disperse seeds farther from the mother tree than do timid ones. Furthermore, we show that anthropogenic habitat modifications (such as those inflicted by different silvicultural practices) ultimately affect seed selection, seed predation and seed dispersal by shifting the distribution of personalities present in populations. For example, we found that even-aged silvicultural practices increase the proportion of highly active mice. Because active mice show an increased probability of consuming seeds rather than leaving them intact, this suggests an unexpected, negative consequence of land-use change; one which may have potential cascade effects on the whole ecosystem by limiting the local recruitment of seeds.

A scatter-hoarder's preference for seed mass is related to nutrient content and metabolic requirements (Jansen *et al.* 2004), handling time (Muñoz & Bonal 2008) and predation risk (Lichti *et al.* 2015). We show that in addition to these factors, an individual's personality plays a role in this decision (Fig. 2; Fig. S3). Boldness in mice influenced seed mass preference, with timid mice removing smaller seeds than bolder ones. Selecting large seeds can increase predation risk due to the costs of longer handling times and a limited ability to be vigilant. We would expect, therefore, that the boldest individuals (i.e., those willing to exit the emergence test with less time spent assessing the external surroundings) would be more likely to take these associated risks, and this is in line with our findings. The relationship between boldness and mass preference implies differing selective pressures on large or small seeds depending on the personality types present within a population. We found that in even-aged forest, a larger proportion of mice are bold compared to the reference and shelterwood forests (Fig. 4; Table S7), suggesting that seeds of greater mass are being selected for disproportionately in this forest type (Fig. S6C). This study used artificial seeds so that mass, shape, quality and odour could all be controlled for. Investigating this relationship using real seeds is warranted in future studies.

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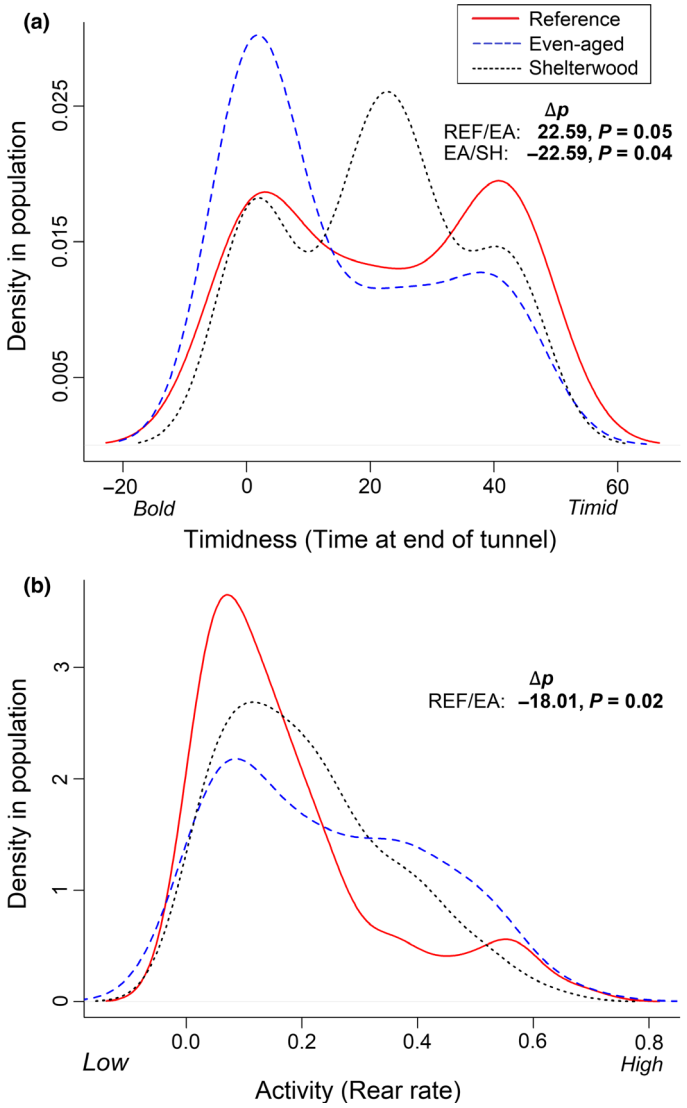

Figure 4 Examples of probability density plots showing the distributions of timid (a) and active (b) personality types present in three different forest types (REF – reference, EA – even-aged, and SH – shelterwood) for *P. maniculatus*. Δp values (Safran *et al.* 2012) and associated *P*-values were used to calculate the distance between each trait distribution among the three forest types. Significant Δp values are shown. Timidness predicts seed mass preference and activity predicts the probability of removing and consuming seeds (Fig. 2). Additional results are shown in Table S7.

Activity level influenced several seed dispersal decisions. Specifically, highly active deer mice (those who showed increased rates of rearing in the open-field test) were more likely to remove seeds from the retrieval site and consumed greater proportions of the seed (likely due to higher metabolic requirements) (Table S5). We show that mean activity levels differed between mice living in the different silvicultural treatments (Fig. 4; Table S7), and our models predict that these populations differ in terms of the proportion of seeds that are predated vs. cached intact. Populations with many highly active individuals (such as the mice living in even-aged forest) predate a greater proportion of available seeds contributing less to dispersal (Fig. S6B). These results add to a growing body of literature showing the influence of personality on species interactions as well as predator–prey interactions (reviewed by Sih *et al.* 2012). Interestingly, even-aged silvicultural treatments are used to create stands of trees that are all of the same age class and size (Brissette & Kenefic 2014). The result is often a dense canopy, where stem density is high but individual tree diameters stay smaller due to competition for resources. As a result, the number of large, seed-bearing trees is limited in a stand of this type. This increased competition for resources is possibly one of the factors contributing to the abundance of highly active mice in this forest type. Dispersal distance of seeds is influenced by several factors of the environment, seed and disperser (Jansen *et al.* 2004; Muñoz & Bonal 2008; Lichti *et al.* 2015) and is critical to plant recruitment (Nathan 2006; Dirzo *et al.* 2014; Jansen *et al.* 2014). Our results provide evidence that dispersal distance for mice and voles is personality driven (Fig. 3). Timid voles (i.e., those who avoid the centre of the open-field test) contribute far less to dispersal than bold ones. In fact, our predictions suggest that timid voles move seeds less than half the distance compared to bold voles. Our results show that land-use change increases the proportion of the population with a bold personality type (Table S7), which results in increased dispersal distances in shelterwood forests due to the slightly bolder population of voles (Table S7, Fig. S6A.). This may have disproportionate effects on gene flow of plants, regeneration rates and plant range expansion (Nathan 2006; Zwolak 2018). Our results also suggest that less anxious mice (i.e., those who show moderate levels of grooming in the open-field test, indicating the ability to cope with stress) disperse seeds at farther distances than do more anxious mice (grooming behaviours are discussed in Table S1). Because previous research suggests relationships between the size/quality of seeds and dispersal distance (Xiao *et al.* 2005; Cao *et al.* 2016; Wang & Corlett 2017), we tested for this effect during our model selection process, but we found no evidence for this. Regardless, these results suggest that the populations of mice in shelterwood forest are less anxious and show better coping than those in reference forest and therefore are dispersing seeds at farther distances than those in reference forest (Table S7). Although our results show that different personality traits predict dispersal distance in mice than they do voles, these findings are not surprising because these species, although filling similar ecological roles have very different evolutionary histories and have been shown to utilise and select for different resources and microhabitats within the forest ecosystem (Miller & Getz 1977).

Local dispersal (such as that provided by scatter-hoarding mammals) is crucial for local plant recruitment and population growth. Our findings highlight evidence that the personality composition of a population can impact the effectiveness of local dispersal. One previous study has observed a relationship between the spatial pattern and distance between caches and a behaviour termed 'boldness' (Dochtermann & Jenkins 2007); however, it remains unclear whether these measurements constituted personality because repeatability was not assessed (Dingemanse & Dochtermann 2013). Our results suggest that a complex relationship exists between land-use change and the efficacy of local dispersers because depending

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on the silvicultural treatment imposed, dispersal distance of seeds may be increased by the proportion of bolder voles and lower anxiety mice. However, seed predation rates in human-altered forests may negate these positive effects by increasing the overall activity level of the individuals present, thereby increasing rates of consumption. Further investigation of this complex relationship using metrics such as seed dispersal effectiveness (Schupp *et al*. 2010) and following dispersed seeds until eventual germination may prove informative.

The location of a cached seed depends on the risk of cache pilferage (Steele *et al*. 2014) and seed characteristics (Wang & Corlett 2017). Small mammals can often increase germination probability by transporting seeds to optimal germination sites (Vander Wall 2010). We show that docile voles are more likely to cache seeds among coarse woody debris (Fig. S4), which offers several benefits to seedlings and provides important refuge to small mammals (Fauteux *et al*. 2012; Fukasawa 2012). By contrast, less docile individuals are more likely to transport seeds to the base of a tree, where density-dependent seedling mortality is common (Jansen *et al*. 2014).

We foresee two major outcomes of our study. First, we show that personality traits in scatter-hoarding small mammals influence critical stages of seed dispersal because certain personality types are more likely to select larger seeds, cache them in optimal germination sites or disperse them farther from the mother tree. Second, we show that anthropogenic habitat modifications shift the distribution of personalities within a population by modifying the proportion of bold, active and anxious individuals. Our models predict that this may impact the survival and dispersal of seeds which could lead to cascading effects on ecosystems by modifying the structure and composition of forests. Ecological consequences of personality on seed dispersal are asymmetric among individuals, indicating a need for a paradigm shift towards promoting behavioural diversity within populations as a target for the conservation of ecosystems.

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AUTHORS' CONTRIBUTIONS

A.M.B. and A.M. conceived the study; A.M.B., A.M., G.A.M. and J.Z. designed the study, A.M.B. and A.M. collected and analysed the data; all authors contributed to manuscript preparation. The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data available from the Figshare Repository: https://doi.org/10.6084/m9.figshare.8144489.v1.

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

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