Land-use change alters associations between personality and microhabitat selection

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Abstract. Ecologists commonly assess ecological patterns at the population level, focusing on the average response of all individuals within a population, but to predict how populations will respond to land-use change we must understand how changes to habitat differentially affect individuals within a population. For example, forest management is a widespread type of land-use that impacts wildlife through the loss of key habitat features, but individuals within a population may vary in their responses to this loss due to differences in habitat selection among individuals. Specifically, intraspecific variation in habitat selection has been linked to animal *personalities* (i.e., consistent behavioral differences among conspecifics), but previous research has not examined whether the relationship between personality and habitat selection is influenced by land-use change. To address this knowledge gap, we tested the hypothesis that land-use change alters the association between personality and microhabitat selection in small mammals. Specifically, we investigated two main questions: (1) To what extent are personality type and microhabitat selection correlated among conspecifics? (2) Does land-use change alter individual patterns of microhabitat selection? To answer these questions, we conducted a large-scale field experiment over 4 years, contrasting unmanaged forest (control) with managed forest (two silvicultural treatments) in Maine, USA. We examined the relationships between habitat selection and personality traits in deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*). We found that personality traits were correlated with microhabitat selection at multiple spatial scales. Furthermore, land-use change altered these patterns of selection; resulting in either the loss of personality-associated selection or in novel patterns of selection in managed forests. These findings suggest that promoting structural complexity at multiple spatial scales, such as by interspersing stands of mature forest with managed stands, may maintain a variety of intraspecific habitat selection patterns and the associated ecological outcomes.

Key words: animal personality; forest management; hierarchical habitat selection; intraspecific variation; microhabitat; small mammals.

INTRODUCTION

Land-use change alters the structure and connectivity of landscapes (Lindenmayer and Fischer 2007, Turner et al. 2007), resulting in substantial changes to the functioning of ecosystems worldwide (Steffen et al. 2004, Dirzo et al. 2014). Managed forests represent one of the most widespread land-uses, with roughly 71% of the Earth's forests actively managed for timber and other commodities (IPCC 2019). The management of forested land for timber, biofuels, and recreation involves changing forest stand structure and composition to meet management goals, often diminishing or degrading key habitat features for wildlife (Fisher and Wilkinson 2005, Zwolak 2009, Gasperini et al. 2016). The way wildlife populations respond to the loss or degradation of key habitat features is, in part, a culmination of the response of each individual in the population. Consequently, we must understand how land-use change alters individual-level resource use and behavior if we are to predict how populations and communities will respond to land-use change (Miranda et al. 2013, Sutherland et al. 2013).

For years, ecologists assumed that all individuals within a species moved throughout the landscape and utilized resources similarly, following the traditional ideas of resource partitioning (Hutchinson 1957, Schoener 1974). The niche variation hypothesis (Van Valen 1965, Roughgarden 1972), however, posits that populations can exhibit among-individual variation in resource use, and this topic has gained traction in recent years (Bolnick et al. 2003, Costa-Pereira et al. 2018). The ability of conspecifics to use different resources and occupy functionally different niches is likely to facilitate the response of populations under changing conditions (Moran et al. 2016). Therefore, identifying the effects of

TABLE 1. Mechanisms with the ability to generate behavioral correlations between personality and habitat selection across landscapes.

Mechanism	Description	Sources
Niche picking	Individuals of a certain personality type seek out certain habitats or features of the environment	Stamps and Groothuis (2010a, b), Sih et al. (2018), Schirmer et al. (2019)
Niche construction	Individuals of a certain personality type modify selective environments	Odling-Smee et al. (1996), Laland et al. (2016)
Matching habitat choice	The habitat chosen via niche picking is that which best "matches" an individual's abilities to use this environment	Edelaar et al. (2008)
The environment influences behavior	The environment itself can influence the behavior of individuals; for example, safe environments can encourage individuals to behave more boldly	Tuttle and Ryan (1982), Sharpe and Horne (1998), López et al. (2005), Webster et al. (2007), Peluc et al. (2008)
Habitat-specific mortality	Certain personality types are more or less likely to survive in specific environments; may be a result of matching habitat choice	Jaenike and Holt (1991), Edelaar et al. (2008)
Density-driven assortment	Certain personality types may seek out areas of high or low density	Pearish et al. (2013), Sih et al. (2018), Schirmer et al. (2019)
Congregating with similar individuals	Individuals may congregate in areas with similar personality types	Johnson et al. (2017)
Social networks	Conspecifics may distribute within social networks according to personality traits	Croft et al. (2009), Snijders et al. (2014), Best et al. (2015), Carter et al. (2015)

Notes: Provided are the mechanism, a brief description, and a non-exhaustive list of references. Note that these mechanisms are not all mutually exclusive.

a changing environment on intraspecific variation in habitat selection should be of great interest to ecologists and conservationists alike (Sih et al. 2011, Moran et al. 2016).

Several studies have highlighted the ecological importance of interindividual differences in resource use and spatial distribution (Araújo et al. 2011, Bolnick et al. 2011, Schreiber et al. 2016). Such differences can be driven by sex, age classes, morphometric differences, and individual specialization (Bolnick et al. 2003, Zwolak 2018). Notably, one driver of individual specialization shown to affect resource use and spatial distribution is animal personality (Boon et al. 2008, Kobler et al. 2009, Boyer et al. 2010, Pearish et al. 2013, Gharnit et al. 2020, Wat et al. 2020). *Personality* refers to consistent individual differences in the behavior of conspecifics (Gosling 2001, Sih et al. 2004, Stamps and Groothuis 2010b). A growing body of research highlights the existence of associations between personality types and habitat selection, in which individuals with certain personality types occur disproportionately in certain physical or social environments (for example, because certain personality types select specific microhabitats or select areas with high densities of similar personality types) (Wilson et al. 1993, Bergmüller and Taborsky 2010, Réale et al. 2010a, Stamps and Groothuis 2010b, Schirmer et al. 2019, 2020). This has been referred to as *spatial niche specialization* (Schirmer et al. 2019, 2020). A range of mechanisms may generate correlations between personality type and habitat selection across landscapes (Plomin et al. 1977, Stamps and Groothuis 2010a); eight are described in Table 1.

When anthropogenic changes alter structural characteristics of the environment, the capacity for individuals in a population to adapt will determine the ability of that population to persist. Ultimately, shifts in personality-associated habitat selection caused by land-use change may be an important mechanism affecting the response of populations and communities to global change. However, although a few studies have recognized the capacity for personality traits to influence habitat selection and resource use (Wilson et al. 1993, Bergmüller and Taborsky 2010, Réale et al. 2010a, Stamps and Groothuis 2010b, Schirmer et al. 2019, 2020), previous research has not assessed the extent to which land-use change might affect this process. This knowledge would provide novel justification for the importance of landscape complexity and heterogeneity. That is, it would show that by maintaining landscape complexity and heterogeneity we may maintain suitable habitat for varying personality types and contribute to fostering intraspecific trait diversity.

To address this knowledge gap, we tested the hypothesis that land-use change alters individual patterns of microhabitat selection by small mammals. Specifically, we investigated two main questions (Fig. 1): (1) To what extent are personality type and microhabitat selection correlated among conspecifics? and (2) Does land-use change (specifically, silvicultural practices) alter these individual patterns of microhabitat selection? We predicted to see correlations between personality traits (such as boldness and activity rates) and selection for major structural components in the forest such as the amount of vegetative cover or coarse woody debris (i.e., a mechanism referred to in the literature as niche picking; Table 1). Specifically, we expected that timid small mammals would select for areas with more vegetative cover than bolder individuals (Carrete and Tella 2010, Holtmann et al. 2017) as bold individuals often take more risks and suffer higher predation (Réale et al. 2010b,

Objective #1: Determine whether personality traits and microhabitat selection are correlated among individuals
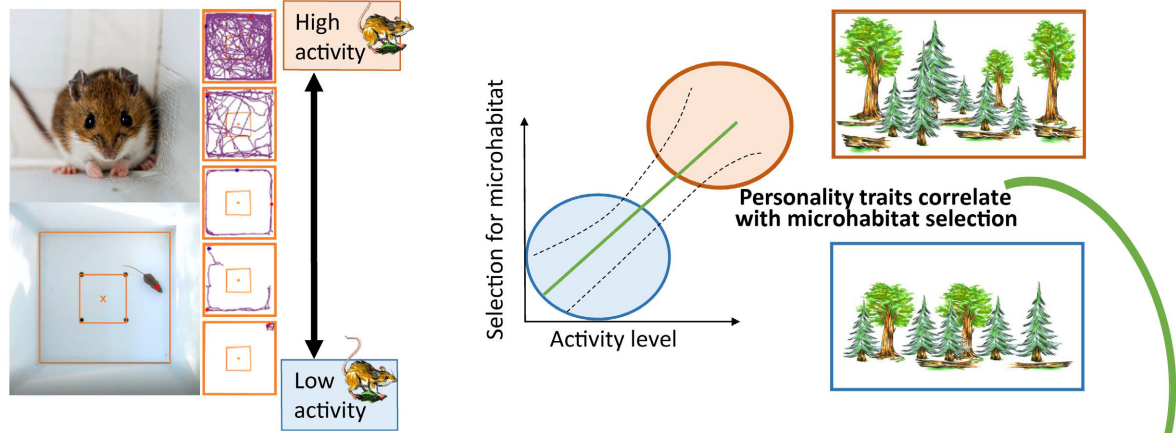
Objective #2: Identify whether silvicultural practices shift individual patterns of microhabitat selection

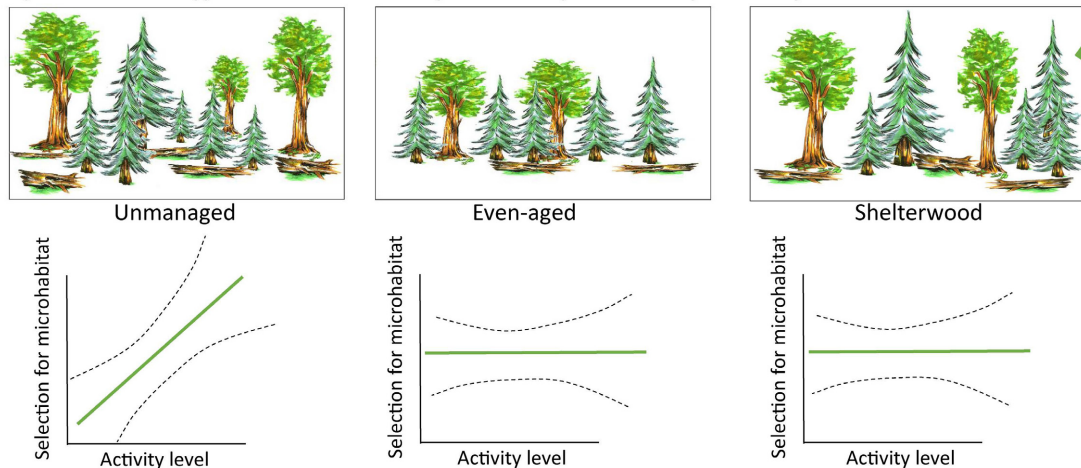Unmanaged   Even-aged   Shelterwood

FIG. 1. A conceptual diagram identifying the two main objectives of this study. Deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*) were trapped, individually marked, and personality traits were measured using three standardized tests (i.e., an emergence test, an open-field test, and a handling test. The open-field test is pictured here). We next identified correlations between personality traits (i.e., activity level, exploration, docility, and boldness) and selection for key microhabitat features. We predicted that personality traits such as activity level would correlate with the tendency to select for different microhabitat features (such as tree size, pictured here). Among-individual correlations between personality traits and microhabitat selection were compared across three forest types to assess whether silvicultural practices shift patterns of microhabitat selection.

Dammhahn et al. 2018) and that more active individuals would select areas with larger, cone-bearing trees due to increased metabolic needs (Biro and Stamps 2010).

Furthermore, as a primary mechanism thought to maintain personality variation within animal populations is fluctuating selection associated with environmental heterogeneity (Sih et al. 2004, Réale et al. 2010*b*, Le Cœur et al. 2015), we predicted that in forests treated with different silvicultural manipulations, there would be observable differences in the correlation between personality traits and selection for major structural components. We expected that these differences would be associated with the activity rates, docility, or boldness/risk-taking capacities of individuals and explained by variation in key resource availability between forest treatments. For example, we expected this selection to be

more prominent where important microhabitats are less abundant (i.e., that correlations between boldness/timidness and coarse woody debris would be stronger in managed forest types where these features are scarcer and only the more bold or aggressive individuals gain access). Additionally, as typically decisions made on broader scales have greater impacts on fitness (Rettie and Messier 2000, Dupke et al. 2017), we expected that patterns of selection would be stronger at coarser ecological scales (i.e., the selection of the home range vs. the selection of daily capture locations).

To achieve our objectives, we conducted a large-scale field experiment over 4 years in which we contrasted two replicates of unmanaged forest (control) with four areas of managed forest (two silvicultural treatments – two replicates each). The study was conducted in Maine

(USA); target species were the deer mouse (*Peromyscus maniculatus*) and the southern red-backed vole (*Myodes gapperi*). We used small mammals as model species because standard methods exist to assess their personalities (Carter et al. 2013, Brehm and Mortelliti 2018, Mazzamuto et al. 2018, Brehm et al. 2020) and microhabitat selection (Dueser and Shugart 1978, Longland and Price 1991, Mortelliti and Boitani 2007, Kellner and Swihart 2014).

METHODS

Study area and small mammal trapping

This study was conducted at the Penobscot Experimental Forest (44°51′ N, 68°37′ W) in Maine, USA. Here, different compartments have been logged separately, managed with contrasting silvicultural treatments, and replicated twice in a randomized experimental design. Approximately 25 ha of forest has been retained in two separate units and left unmanaged since the late 1800s to serve as a reference. The Penobscot Experimental Forest is a mixed conifer-deciduous forest (Brissette and Kenefic 2014) and is dominated by shade-tolerant conifers including balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), and Eastern hemlock (*Tsuga canadensis*) (Kimball 2014).

From June through October during 4 years consecutively (2016–2019) we implemented a large-scale capture-mark-recapture experiment in four areas (representing two contrasting silvicultural treatments) and used two areas of unmanaged forest as reference sites. The treatment areas used were as follows: treatment 1 (even-aged cut) and treatment 2 (shelterwood cut with reserves). Due to the contrasting silvicultural systems, these forest stands differ greatly in the understory density, diameter of trees present, light levels, and quantity of downed woody material and snags. These varying structural characteristics have generated highly contrasting habitat types for small mammals (for further information about the forestry treatments used, a brief description of each site, and photographs see Appendix S2: Table S1).

We trapped small mammals in six separate study grids (two control grids in reference areas and two grids in each of two replicated treatment areas). The area of the treatments used in this study was 12.8 ha on average (range: 9.49–19.39 ha). Each trapping grid was 0.81 ha in area and was positioned at or close to the center of the treatment area to minimize edge effects. The mean home range for *Peromyscus* in this study system was 0.34 ha (range: 0.08–1.01 ha), and for *Myodes* was 0.33 ha (range: 0.05–0.87 ha). Home-range calculations were estimated using the *getverticeshr* command from the *adehabitatHR* package in program R to extract the kernel home-range contours with a 75% home-range estimation (Calenge 2006). Trapping grids consisted of 100 flagged points spaced 10 m apart. The mean distance between grids was approximately 1.42 km, and the mean distance between duplicate grids of the same treatment was approximately 1.44 km. We placed one Longworth small mammal trap at each flagged point. We baited traps with a mixture of sunflower seeds, oats, and freeze-dried mealworms, and bedded traps with cotton stuffing. We checked Longworth traps twice per day (just after sunrise and in the late afternoon). We trapped at each grid for 3 consecutive days and nights each month for 5 consecutive months each year totaling over 35,000 trap nights (trap nights = number of active traps × number of nights).

Animal tagging and behavioral tests

Before animals were handled or tagged, we used three standardized tests to measure behaviors that would later be used to assess personality. An *emergence test* was used to assess boldness (Brown and Braithwaite 2004, Carter et al. 2013), an *open-field test* to measure activity and exploration in a novel environment (Walsh and Cummins 1976, Perals et al. 2017), and a *handling bag test* to measure docility and the response to handling by an observer (Martin and Réale 2008, Montiglio et al. 2012, Taylor et al. 2014). We performed behavioral tests once monthly to ensure that animals would not habituate to the tests. See Brehm et al. (2019, 2020) and Appendix S1 for detailed behavioral test procedures.

After the behavioral tests were complete, we anesthetized animals with isoflurane and inserted passive integrated transponder (PIT) tags (MiniHPT8, Biomark, Boise, Idaho, USA) subcutaneously at the midback. Animals were also marked with a small animal ear tag (Style 1005-1, National Band & Tag Co., Newport, Kentucky, USA). We recorded sex, body mass (measured using a 100 g Pesola Lightline spring scale), body length, tail length, and age class (juvenile, subadult, or adult; based on body size and pelage coloration). Animals were released at the site of capture post-processing.

To quantify behavior from videotaped emergence and open-field tests, recordings were played back in the laboratory. For emergence tests, an observer recorded whether or not the animal emerged (defined as all four feet having left the Longworth trap), the latency to emerge, and the total time spent at the end of the Longworth tunnel before emerging. When an individual did not emerge from the test after the three-minute cutoff, the latency to emerge was set to 1.25× the maximum test length. Open-field tests were analyzed using the behavioral tracking software ANY-maze© (version 5.1; Stoelting Co., Wood Dale, Illinois, USA). To assure the independence of response variables in our analyses, all behavioral variables were screened for correlation before analysis (using $R < 0.7$ as threshold) (Dormann et al. 2013). See Appendix S2: Table S2 for pairwise correlations between all behavioral variables used for each study species, and Table 2 (modified from Brehm et al. [2019]) for a complete list of the behaviors used, their

Table 2. Repeatable behavioral traits from three different behavioral tests performed on deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*).

Behavior	Personality trait	Behavioral test	Description	Notes about interpretation	Sources
Handling time	Docility	Handling bag	Total number of seconds of inactivity during a 1-minute handling bag test	Interpreted as a measure of docility or as a response to stressful confinement	Boon et al. (2007), Martin and Réale (2008), Montiglio et al. (2012), Taylor et al. (2014)
Latency to emerge	Bold/timid	Emergence	Latency (in seconds) to emerge from trap in the emergence test. An animal was considered to have emerged when all four feet left the trap	The latency to emerge from a shelter and into a novel or open environment is commonly assessed on a timid/bold continuum where increased latency signals increased timidness	Brown and Braithwaite (2004), Carter et al. (2013), Gracceva et al. (2014)
Time at end of tunnel	Bold/timid	Emergence	Total number of seconds spent at the end of the tunnel before emerging	We interpret increased time at the end of the tunnel as a sign of timidness. These individuals had a more timid/fearful behavioral tendency and required time to survey the arena before emergence	
Mean speed	Activity	Open field	Mean speed in the open-field test in (m/s). Calculated by dividing the total distance traveled in the test by the test duration	This is a direct measure of locomotion and activity in the open-field test	Carter et al. (2013), Gracceva et al. (2014)
Proportion time grooming	Anxiety/ stress	Open field	Proportion of test duration spent grooming	Grooming in small mammals is an indicator of anxiety and stress. In the deer mouse, a nocturnal species, the open-field test represents an environment of high aversiveness and increased grooming suggests lower anxiety and better coping. In contrast, for the vole (a more diurnal species) low to moderate grooming seems to signal coping, whereas high amounts of grooming indicate high anxiety	Choleris et al. (2001), Fernández-Teruel and Estanislau (2016), Kalueff et al. (2016)
Rear rate	Activity and exploration	Open field	Rate of rearing (rears/s). Rearing is defined as forelegs leaving the arena floor	Rearing is commonly assessed as correlating positively with activity, and represents part of the animal's *diverse* exploration, or the *search phase* of exploratory behavior	Choleris et al. (2001), Prut and Belzung (2003), Martin and Réale (2008), Tanaka et al. (2012)
Proportion time center	Bold/timid	Open field	Proportion of test duration spent in the center portion of the arena	Entering into the center, "unsafe" areas in the open-field arena signifies boldness and avoidance of these areas indicates fearfulness	Barnett (1976), Treit et al. (1989), Choleris et al. (2001), Gracceva et al. (2014)

Notes: These variables are considered personality traits, and this table provides a guide for their interpretation, a non-exhaustive list of citations supporting these interpretations, the behavioral test each trait was measured using, and a description of the behavior. This table was interpreted from Brehm et al. (2019), and a more thorough behavioral interpretation is provided there.

description and interpretation, and supporting sources. Briefly, we used the following variables: *handling time* (the number of seconds immobile in a handling test; note that the term *handling time* should not be confused with a term sometimes used in ecological literature to indicate the time spent handling, processing, and consuming food items), *latency to emerge* and *time at tunnel end* (from the emergence test), *mean speed* (in *Peromyscus*

only), *rear rate*, *proportion of time grooming*, and *proportion of time in the center* (from the open-field test).

Repeatability of behavior in standardized tests

To determine which behaviors could be considered personality, we calculated the adjusted repeatability and associated 95% confidence intervals for key behaviors performed in the standardized tests using the *rptR* package in R (Stoffel et al. 2017). Statistically, repeatability refers to the proportion of the total phenotypic variation that can be attributed to individual differences (Dingemanse et al. 2009, Nakagawa and Schielzeth 2010, Dingemanse and Dochtermann 2013). Practically, this means that repeatability equals the between-individual variance divided by the total phenotypic variance (between-individual variance + within-individual variance). The random effect of individual ID was included in the models and fixed effects included sex, body condition (calculated using the scaled mass index) (Peig and Green 2009), silvicultural treatment, and trapping session. In all models, we used 1,000 parametric bootstraps and 100 permutations. We used Box-Cox transformations on the response variable to approach normality when necessary (Box and Cox 1964, Yang et al. 2011) and we assessed normality by visually inspecting Q-Q plots and by plotting the fitted values against the residual values. Note that we use the term "repeatability" from this point forwards, but that these estimates are "adjusted repeatabilities" because they have been estimated from mixed models fit with fixed effects (Wilson 2018).

We considered any behavioral trait with a 95% CI for repeatability that excluded zero to be a personality trait (Nakagawa and Schielzeth 2010), but we emphasize that this classification as significantly repeatable does not say anything about the strength of repeatability. We used the raw behavioral variables themselves as measures of personality (Dingemanse et al. 2004, 2012), instead of using a principal component analysis (PCA) or similar dimensionality reduction technique (Boon et al. 2007, Martin and Réale 2008). We made this choice to maximize the variation in behavioral measurements, to remain consistent with our previous work (Brehm and Mortelliti 2018, Brehm et al. 2019, 2020), and because components retained from a PCA can sometimes become difficult to interpret biologically (Lever et al. 2017).

Microhabitat selection

Microhabitat selection refers to the disproportionate use of certain microhabitat features in relation to what is available in the environment (Johnson 1980, Jones 2001). The theory of habitat selection is well established, and it has been long recognized that selection occurs at multiple hierarchical orders (i.e., animals select for different habitat features at different spatial and temporal scales) (Johnson 1980, Krausman 1999, Manly et al. 2002, Mayor et al. 2009, McGarigal et al. 2016). This includes broad-scale selection of the geographic range to the fine-scale selection of microhabitat features. In this study, we were interested in selection occurring at the *second order*, or the selection of a home range (i.e., where an individual positions its home range), and selection at the *third order*, or the selection of microhabitat features within the home range (Fig. 2). For a glossary of terms associated with habitat selection and hierarchical orders, see Appendix S2: Table S3.

In July 2017, we recorded detailed microhabitat measurements within a 5 m radius of each trap site (100 sites per trapping grid, 600 sites total). Microhabitats include structural components of the environment such as fallen logs and woody vegetation cover. Structural components such as these can shift drastically following silvicultural disturbance and result in changes to microhabitat use by small mammals (Kellner and Swihart 2014). In line with previous literature on small mammal microhabitat use (Dueser and Shugart 1978, Price and Kramer 1984, Mortelliti and Boitani 2007, Hille and Mortelliti 2010, Fukasawa 2012), variables measured included: percent cover of mosses, herbs, and forbs, percent cover of shrubs and saplings at three height categories, meters of coarse woody debris present (in two size categories), percent canopy cover, and the diameter at breast height (DBH) of the largest tree. See Appendix S2: Table S4 for a brief description of each microhabitat variable and more detail about methods of measurement.

Fig. 2. Habitat selection by small mammals occurs at multiple spatial scales. Second-order selection (a): within the trapping grid, individuals select a home range. This home range may contain more or less of a specific habitat feature than is available on average in the trapping grid. Third-order selection (b): Within the home range, individuals may more frequently select sites that contain more of a specific habitat feature than is available on average in the home range.

We used a PCA to reduce the number of measured microhabitat variables and to create meaningful "components" which would explain the structural variation in our study areas. We used a simplimax rotation (Kiers 1998), which is a form of oblique rotation that optimizes for simplicity in the structure of the pattern matrix while minimizing the correlation between components. The Kaiser-Guttman criterion was used to select the number of principal components to retain (Kaiser 1991).

Third-order selection

For each microhabitat component, we calculated a variable that would encompass an individual's tendency to select for that component at the third order of selection (or selection for specific components of habitat within the home range) (Johnson 1980). To calculate the true selection of a resource, it is necessary to take the availability of that resource into account; as *selection* is defined as use that is disproportionate to a resource's availability (Johnson 1980, Mayor et al. 2009). To do this, we subtracted the mean microhabitat component value in the neighborhood of available traps from the component value at an individual's capture site. Through this subtraction, we were able to quantify whether an individual selected for higher or lower than average microhabitat features. Therefore, positive selection values indicate that the trap site of choice had a greater component value than was available on average, and negative values indicate the opposite. We *z*-standardized this value of selection by dividing by the standard deviation (meaning that the value would be given in units of standard deviation from the mean):

$$\text{Select PC1} = \frac{\text{PC1 capture site} - \text{PC1 neighborhood}}{\text{sd(neighborhood)}}$$

The neighborhood radius for each species was calculated by estimating the mean distance between consecutive capture locations, pooled over individuals (calculated using the *secr* package in R; Efford 2021). This rendered a species-specific estimate for daily activity per trapping grid, and we used the overall mean per species as the neighborhood radius. Within this neighborhood radius, we included only trap sites that were *available* (had no capture on the specific trap occasion). Neighborhood radii were as follows: *Peromyscus* (mean: 28.05 m, range: 21.56–46.11 m); *Myodes* (mean: 24.39 m, range: 10–47.89 m).

If daily selection for microhabitat is repeatable among individuals, this suggests limited behavioral plasticity. Therefore, using previously described methods for repeatability analysis, we assessed the extent to which individuals differed consistently in their daily microhabitat selection. We calculated the adjusted repeatability of the microhabitat selection variables using silvicultural treatment, sex, body condition, body mass, and trapping year as fixed effects, and including the random effect of individual ID.

Data used in third-order analyses included 1,716 observations from 570 individual deer mice and 1,383 observations from 475 individual southern red-backed voles (mean number of observations per individual deer mouse was 3.01 ± 2.89 [range 1–29] and per southern red-backed vole was 2.91 ± 2.61 [range 1–18]). See Appendix S2: Fig. S1 for plots showing the number of captures per individual used in these analyses.

Second-order selection

For each microhabitat component, we calculated a variable that would encompass an individual's tendency to select for that component at the second order of selection (or selection of the home range) (Johnson 1980, Krausman 1999). To do this, we removed all individuals who had fewer than four captures. Then, for the remaining individuals, we calculated the mean value of each microhabitat component across all of their capture locations. We then subtracted the mean value available in the trapping grid from each individual's mean component value following the same procedures as above (and *z*-standardizing once more). Positive values indicate that an individual's home range had a greater component value than was available on average in the trapping grid, and negative values indicate the opposite.

$$\text{Select PC1 home range} = \frac{\text{PC1 home range} - \text{PC1 grid}}{\text{sd(grid)}}$$

Because this analysis rendered one unique value per individual, no repeatability analysis was performed on the second-order selection values.

Data used in second-order analyses included 1,071 observations from 162 individual deer mice and 823 observations from 129 individual voles (mean number of observations per individual deer mouse was 6.61 ± 3.14 [range 4–29] and per southern red-backed vole was 6.38 ± 2.65 [range 4–18]).

Assessing correlations between personality traits and microhabitat selection

Finally, we determined whether personality traits and microhabitat selection at the third order were correlated using multiresponse Bayesian models fit with Markov chain Monte Carlo methods using the *MCMCglmm* statistical package for R (Hadfield et al. 2010). We estimated the correlation between the habitat selection variables described above and the behavioral variables as measured on the day of this habitat selection (i.e., on the day that each trap site was chosen). When an individual was captured on an occasion when a behavioral test was not performed (such as when weather conditions were too poor to perform behavioral tests) we used the

individual's most recent behavioral measurement. This gave us a repeated measures design and allowed us to measure the among–individual-level covariance between traits which can then be used to derive an among–individual-level correlation between these traits. We chose these methods as opposed to using the mean behavior or a best linear unbiased predictor (BLUP) (Houslay and Wilson 2017*b*).

We used non-informative (parameter expanded) priors for both the individual and residual variances of the personality variables and the microhabitat selection variables (prior specifications: R structure degree of belief (nu) = 0.002; G structure degree of belief = 2.0, alpha.mu = rep(0, 2), alphaV = diag(25^2, 2, 2)) (Hadfield 2015, Ólafsdóttir and Magellan 2016, Houslay and Wilson 2017*a*, Brehm and Mortelliti 2018). We scaled the response variables using the *scale* function in Base R to help with model fit and ease of interpretation. We fit an unstructured covariance matrix for the grouping variable of individual ID, which allowed us to calculate the variance in each response variable due to differences among individuals as well as the covariance between these variances. For the residual variation (or the within-individual variation), we constrained these to equal zero as, although both traits have repeated measures, they were not measured at the same time (Dingemanse and Dochtermann 2013, Hadfield 2015). Models were run with a burn-in of 25,000 and subsequent 1,000,000 iterations (thinning interval of 500). This resulted in Markov chain Monte Carlo (MCMC) sample sizes of 1,950. We inspected plots of traces and posterior distributions to confirm convergence (Hadfield et al. 2010) and confirmed that autocorrelation between samples was low using the R package *coda* (Monnahan et al. 2017). We performed analyses on each species separately, and we inspected the correlation between the response variables for each silvicultural treatment separately and compared these correlations among treatments. In all, we have run 14 models per treatment for *Peromyscus* (7 personality traits × 2 microhabitat components) and 12 models per treatment for *Myodes* (6 personality traits × 2 microhabitat components).

Fixed effects included sex, body condition (scaled and centered), body mass (scaled and centered—used as a proxy for age), and year. To obtain a posterior distribution of the correlation between the dependent variables, we standardized the bivariate model covariances on a scale from −1 to 1 by dividing the corresponding covariance between the two variables by the product of the square root of their variances (Houslay and Wilson 2017*a*). We assessed the 95% confidence interval of the correlation and considered intervals that excluded zero to signal significance.

We assessed whether the repeatable behavioral variables correlated with microhabitat selection at the second order following similar methods as above, however, as outlined by Houslay and Wilson (2017*a*), we fixed the within-individual variance in the non-repeated measures

to equal a very small positive number as a trait measured only once has no within-individual variance (Houslay and Wilson 2017*a*, Brehm and Mortelliti 2018). We included the same fixed effects as in the univariate models. For trace and density plots of all posterior distributions of the correlations between dependent variables see Appendix S3.

All research was conducted in accordance with and approved by the University of Maine's Institutional Animal Care and Use Committee (IACUC numbers A2015-11-02 and A2018-11-01).

RESULTS

Microhabitat structure

Following dimension reduction of the trap-level microhabitat characteristics with PCA, we retained two components (Appendix S2: Table S5). The third component was very close to the cutoff using the Kaiser-Guttman rule and so we decided to focus on the first two components (Appendix S2: Fig. S2). The first component (PC1) characterized a gradient ranging from areas with a dense ground cover (mosses, herbs, and forbs) and a more open canopy toward areas with less ground cover and a closed canopy and the second component (PC2) had the highest loadings for the abundance of coarse woody debris (CWD) present and the DBH of the largest tree. We, therefore, interpreted the first component to be a measure of ground cover and light levels and the second to represent key resource availability (seed-bearing trees and CWD).

Trapping and behavioral data

Over four trapping years in our study population (June through October 2016–2019) we obtained behavioral data (via standardized tests) from 577 individual deer mice and 473 individual southern red-backed voles. Both species showed repeatability for all behavioral variables measured. Mean repeatability was 0.346 for deer mice (mean CI = 0.26–0.45) and 0.221 for voles (mean CI = 0.12–0.37). See Appendix S2: Table S6 for all repeatability estimates and sample sizes.

Both behavioral data and microhabitat selection data (via capture site) were available for 3,099 observations from 1,045 total individuals from the two study species. We found selection at the third order for microhabitat characteristics to have low but significant repeatability in all instances (Appendix S2: Table S7).

Effects of land-use change on personality-associated microhabitat selection

Individual selection for certain components of microhabitat structure and one or more personality traits were significantly correlated across all individuals at one or both orders of selection in both study species. Moreover,

the strength and direction of the correlations differed among the unmanaged forest and silvicultural treatments (Table 3). For example, we commonly saw that relationships that were present in the unmanaged forest were lost in one or both silvicultural treatments. For instance, we observed a positive relationship between activity and exploration in an open-field test (based on the rate of rearing) and selection for areas within the home range (third-order selection) with increased ground cover and light levels (PC1) in both deer mice and southern red-backed voles (deer mice: mean correlation = 0.38, CI = 0.04–0.68; voles: mean correlation = 0.40, CI = 0.11–0.68), but this relationship was not significant in either the even-aged or shelterwood treatments (Fig. 3). In addition, out of seven relationships in the even-aged forest, five were unique to this treatment

and all four relationships seen in shelterwood forest were only present in that treatment.

In red-backed voles, we observed a correlation between docility level (based on handling time) and microhabitat selection at the second order (home-range selection), and our results showed that this effect was also present in one of the forest treatments (Fig. 4). In this instance, we found a negative relationship between docility level and selection for PC2 in the reference forest (mean correlation = −0.49, CI = −0.77 to −0.18). Higher values for this second component are representative of larger trees and therefore more abundant food resources (i.e. seeds) and increased structural attributes important for small mammals (runways via CWD). In the even-aged forest, this negative relationship was less strong, but still significant (mean correlation = −0.40,

TABLE 3. Correlations between repeatable behavioral variables and selection for two components of microhabitat structure at the second and third orders of selection in deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*).

Species	Order of selection	Corr. (x, y)	Reference		Even-aged		Shelterwood	
			Correlation	95% CI	Correlation	95% CI	Correlation	95% CI
Peromyscus maniculatus	Third order	(PC1, rear rate)	0.38†	0.04, 0.68	−0.12	−0.42, 0.19	−0.22	−0.68, 0.19
	Second order	(PC1, mean speed)	0	−0.30, 0.28	−0.32†	−0.58, −0.02	0.02	−0.24, 0.26
		(PC1, prop. groom)	0.2	−0.10, 0.47	0.37†	0.06, 0.65	−0.24	−0.50, 0.01
		(PC1, handling time)	−0.35†	−0.70, −0.01	0.1	−0.25, 0.43	0.17	−0.11, 0.48
		(PC1, time tunnel)	−0.35	−0.70, 0.01	0.36†	0.08, 0.62	−0.27	−0.56, 0.02
		(PC2, mean speed)	−0.08	−0.56, 0.44	−0.13	−0.41, 0.13	0.25‡	0, 0.52
		(PC2, handling time)	−0.03	−0.43, 0.34	0.11	−0.25, 0.46	−0.28†	−0.55, −0.01
Myodes gapperi	Third order	(PC1, rear rate)	0.4†	0.11, 0.68	−0.32	−0.76, 0.15	0.19	−0.26, 0.65
		(PC1, prop. groom)	−0.05	−0.36, 0.27	−0.19	−0.68, 0.33	0.44†	0.09, 0.83
		(PC1, latency emerge)	−0.37†	−0.69, −0.02	0.45‡	0, 0.94	−0.04	−0.53, 0.43
		(PC2, prop. groom)	−0.07	−0.58, 0.44	0.11	−0.51, 0.85	−0.34‡	−0.68, 0
		(PC2, handling time)	−0.67†	−0.98, −0.38	−0.25	−0.90, 0.35	−0.34	−0.72, 0.05
	Second order	(PC2, prop. groom)	−0.06	−0.38, 0.24	0.46†	0.12, 0.78	−0.07	−0.33, 0.20
		(PC2, handling time)	−0.49†	−0.77, −0.18	−0.4†	−0.77, −0.01	0	−0.30, 0.31
		(PC2, time tunnel)	−0.29	−0.62, 0.05	−0.51†	−0.83, −0.13	−0.09	−0.40, 0.21

Notes: Correlations were estimated as the posterior mean for a correlation based on Markov chain Monte Carlo (MCMC) Bayesian models controlling body mass, body condition, trapping year, and sex. Behavioral variables involved in significant correlations include mean speed in the open field, rears per second in the open field (rear rate), proportion of time grooming in the open field (prop. groom), latency to emerge from the emergence test (latency emerge), time spent at the end of the emergence tunnel (time tunnel), and seconds immobile in a handling test (handling time). Only results that were significant in at least one treatment are shown. Data used in third-order analyses included 1,716 observations from 570 individual deer mice and 1,383 observations from 475 individual southern red-backed voles (mean number of observations per individual deer mouse was 3.01 ± 2.89 [range 1–29] and per southern red-backed vole was 2.91 ± 2.61 [range 1–18]). Data used in second-order analyses included 1,071 observations from 162 individual deer mice and 823 observations from 129 individual voles (mean number of observations per individual deer mouse was 6.61 ± 3.14 [range 4–29] and per southern red-backed vole was 6.38 ± 2.65 [range 4–18]).
† 95% CI does not include or cross zero.
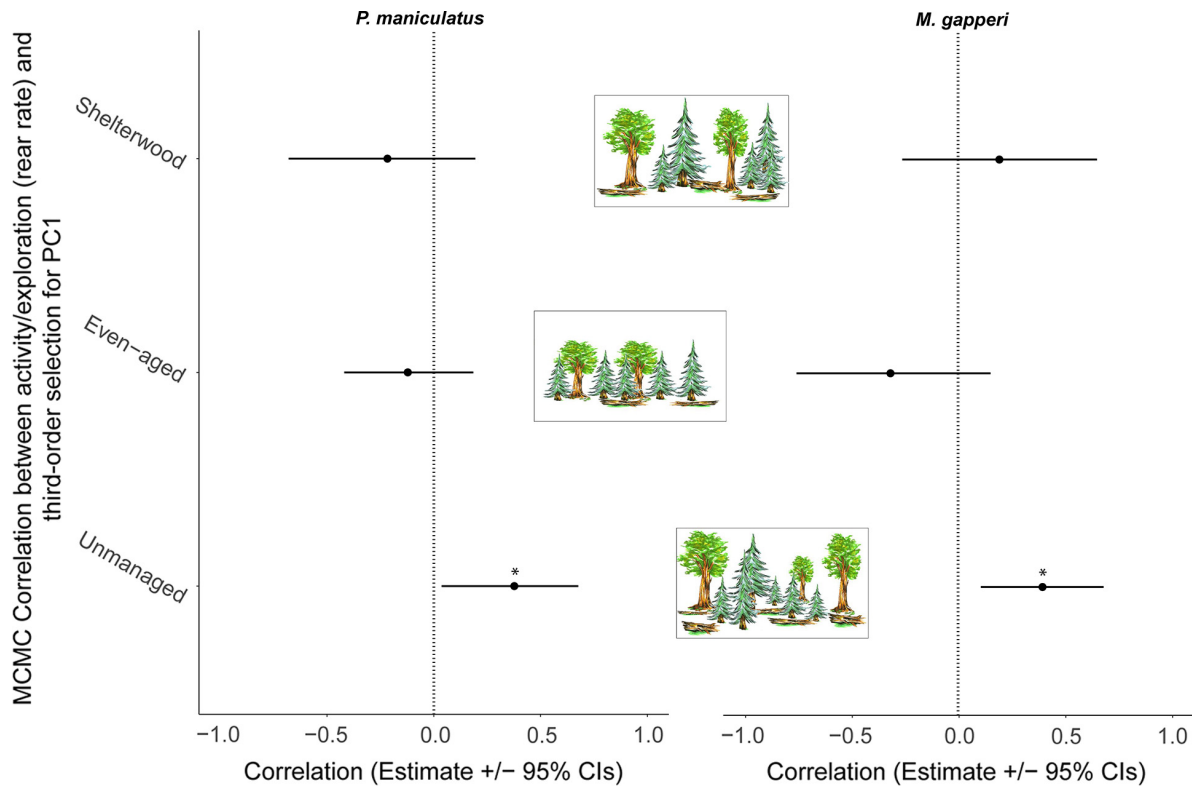‡ 95% CI includes, but does not cross, zero.

FIG. 3. Personality-microhabitat associations are altered by silvicultural practices in deer mice (*Peromyscus maniculatus*) and southern red-backed voles (*Myodes gapperi*). In unmanaged forests, more active and exploratory mice and voles select areas within their home range (third-order selection) with more ground cover and higher light levels (PC1) than less active and exploratory individuals, but this relationship was absent in all of the forest treatments. Activity/exploration was interpreted from the rate of rearing in an open-field test. Correlations were estimated as the posterior mean for a correlation based on Markov chain Monte Carlo (MCMC) Bayesian models controlling body mass, body condition, trapping year, and sex. Estimates in the unmanaged forest were as follows: (*Peromyscus maniculatus*) posterior mean = 0.38, 95% credible interval (0.04, 0.68); (*Myodes gapperi*) posterior mean = 0.40, 95% credible interval (0.11, 0.68).

CI = −0.77 to −0.01). Additionally, our results showed that docile red-backed voles also selected areas with less CWD and smaller trees than were available on average *within* their home ranges (third-order selection) compared with less docile, more aggressive individuals (mean correlation = −0.67, CI = −0.98 to −0.38). However, at this third order, the correlation was only significant in the unmanaged forest (Fig. 4).

DISCUSSION

Within a fully controlled and replicated field experiment performed over 4 years, we investigated the relationships between microhabitat selection and personality traits of individual deer mice and southern red-backed voles. By using MCMC correlation analyses we found that personality traits were associated with patterns of microhabitat selection at the second and third orders of selection. Furthermore, at both orders these patterns of selection varied depending on land-use differences; resulting in either the loss of personality-associated microhabitat selection or in novel patterns of selection in managed forests. These findings underpin a

novel mechanism that may contribute to affecting the response of species to global change and reinforce the need for understanding individual-level resource use to comprehend patterns within populations and communities.

The relationship between personality traits and fitness is well established (Smith and Blumstein 2008, Moiron et al. 2020), and personality-associated habitat selection is a key mechanism through which personality traits can affect fitness. In this study we show that, depending on the environment and the availability of preferred and non-preferred resources, selection patterns of individuals differ; probably allowing for favorable home-range placement and daily movement patterns. Specifically, contrasting silvicultural treatments result in dissimilar relationships between personality traits and habitat selection, which could drive fitness differences between habitats if, for example, certain personality types are more or less likely to survive in specific environments. This is a phenomenon that warrants further investigation in this study system as this could, in turn, influence the behavioral diversity of populations experiencing anthropogenic disturbance (Miranda et al. 2013, Mortelliti and Brehm 2020). Understanding how
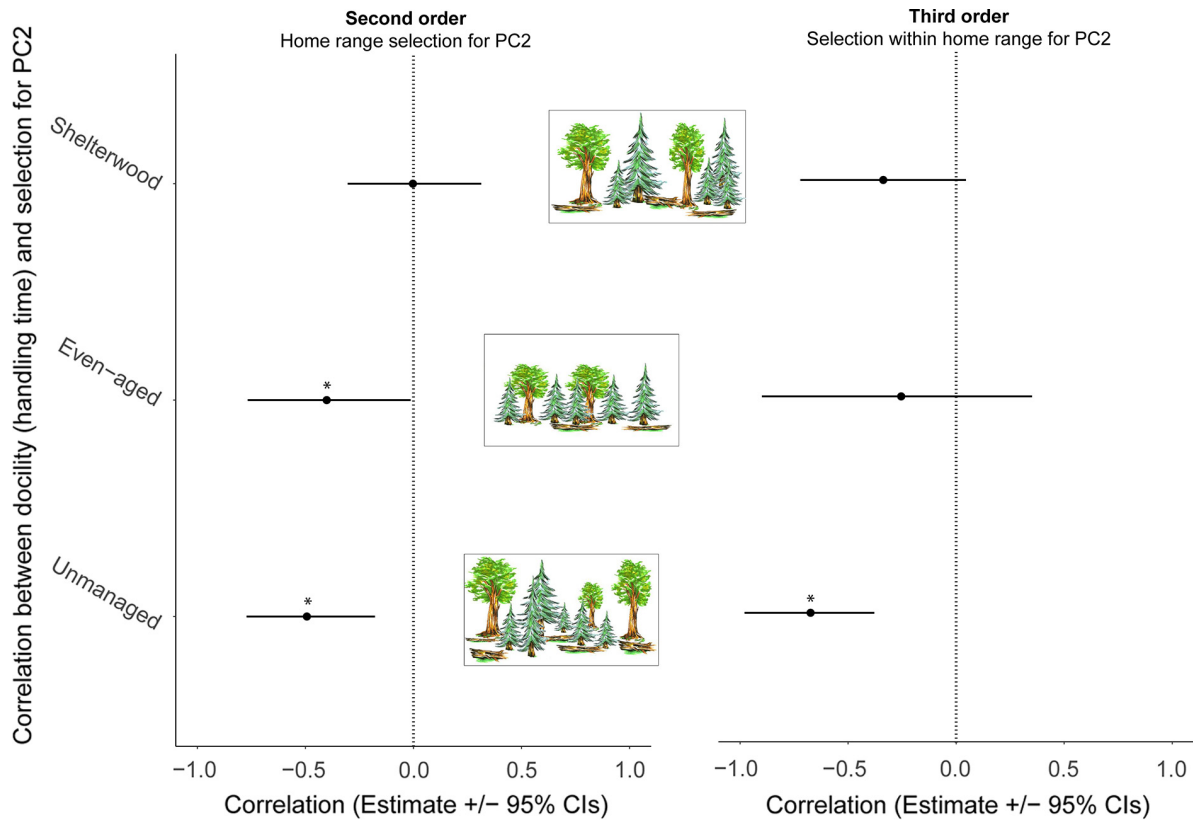
FIG. 4. Correlations between docility (in a handling bag test) and selection for PC2 at the second order and third order in southern red-backed voles (*Myodes gapperi*). Selection for tree size and coarse woody debris (PC2) decreases with increasing docility in the unmanaged forest at both the second and third orders of selection, and in the even-aged treatment at the second order only. Correlations were estimated as the posterior mean for a correlation based on Markov chain Monte Carlo (MCMC) Bayesian models controlling body mass, body condition, trapping year, and sex. (Second order) Unmanaged: posterior mean = −0.49, 95% credible interval (−0.77, −0.18); even-aged: posterior mean = −0.40, 95% credible interval (−0.77, −0.01). (Third order) Posterior mean = −0.67, 95% credible interval (−0.98, −0.38).

altering resource availability and habitat structure will influence future resource use by animal populations is fundamental if we are to predict how populations will be affected by land-use change and minimize our impact on ecosystem structure and function. We suggest that this study highlights one overlooked factor, personality-associated habitat selection, which may influence population and community responses to global change.

Personality traits and the selection for key resources

The second microhabitat component, characterized by the diameter of trees and the amount of CWD present, was a prominent variable correlated with the personality traits of both species at the second and third orders of selection. This component describes two forest features that are well known to influence small mammal habitat selection and are characteristic of older, less disturbed (especially logged) forests. As primary seed predators and dispersers in forest ecosystems (Vander Wall 1990, 2010, Jansen et al. 2004, Vander Wall et al. 2005), small mammals rely on mature, seed-bearing trees for a

substantial portion of their diet. Although many tree species begin bearing seeds between 5 and 25 years of age, optimal seed production does not occur until much later; age 20–30 years in Eastern white pines (*Pinus strobus*), 50+ years for red oaks (*Quercus rubra*), and over 100 years in others (Krugman and Jenkinson 1974, Perkey and Wilkins 2001, Bonner and Karrfalt 2008). As a result, mature trees are the primary contributors to a forest's seed bank and a central resource for granivorous rodents such as deer mice and red-backed voles.

The observed relationships between the selection of PC2 and personality traits may be influenced heavily by tree species composition and whether the dominant tree type of a forest stand is of a preferred or non-preferred food source. In fact, four out of six trends found between personality and selection for PC2 in voles may be explained by the selection or avoidance of the dominant tree species by individuals with docile or timid personality types. For example, we found that more docile or timid voles avoided areas with large seed-bearing trees, while bolder or more aggressive individuals selected these areas in the forest (as seen in Fig. 4 and Table 3).

These trends occurred in either the unmanaged forest or in the even-aged forest treatment where Eastern white pine is a dominant tree type. It is well established that Eastern white pine is an important and preferred food source for our study species (Abbott 1962, Abbott and Quink 1970, Duchesne et al. 2000, Boone and Mortelliti 2019). Conversely, Eastern hemlock and balsam fir are non-preferred food sources for both small mammal species (Abbott and Hart 1960, Duchesne et al. 2000, Boone and Mortelliti 2019), and these two tree species dominate the shelterwood forest treatment. It is possible that, in the forest stands where the white pine is dominant, docile and timid voles are avoiding the areas of the forest with large, cone-bearing white pine trees because of foraging competition with deer mice and the American red squirrel (*Tamiasciurus hudsonicus*). This finding may support the idea that there is a difference in competitive ability between docile or timid individuals and their aggressive and bolder counterparts, in which the timid and docile are actively displaced by the better competitors and instead are found in areas of lower competition (Schirmer et al. 2019).

Coarse woody debris (CWD) volume and tree diameter varied significantly across our reference sites and the treatments used in this study which could further explain some of the differences in personality-associated habitat selection across treatments. See Appendix S2: Figs. S3, S4 for kernel density plots showing the distribution of the microhabitat components across the study areas and a PCA plot showing PC1 vs. PC2 by treatment, respectively. The reference sites had more CWD available and trees were larger than in the two managed forest types. Just as mature, seed-bearing trees are critical for small mammals, woody debris in the form of downed trees and stumps is widely recognized as an important resource for these species. Our results are in line with previous research in which associations between woody debris and home range are well documented (Kaminski et al. 2007, Vanderwel et al. 2010, Fauteux et al. 2012). Indeed, CWD provides key structural complexity, nutrients, and substrate for a variety of plant and animal species and is crucial to the overall health of a forest ecosystem (Maser and Trappe 1984, Harmon et al. 1986, Fukasawa 2012) making it essential for the conservation of biodiversity (Johnson and O'Neil 2001, Lindenmayer and Franklin 2002). In many managed forests, the quantity of large living trees and dead wood has been greatly depleted as large trees are of important value for timber and wood products, and standing dead wood is often removed before it can cause damage to living trees (Hansen et al. 1991, Berg et al. 1994, Linder and Östlund 1998, Fraver et al. 2002, Gibb et al. 2005).

We also observed several relationships between personality traits and selection for the first microhabitat component (PC1), which described the quantity of herbaceous ground cover, mosses, and grasses that were present at a site, as well as the amount of light present (via canopy openness). This component shows a clear difference between the even-aged forest (which has less ground cover and less open canopy) and the reference/shelterwood forests (both of which have more ground cover and canopy openness) (Appendix S2: Fig. S4). Our results show a positive relationship between the level of activity and exploration and third-order selection for PC1 in the unmanaged forest by both deer mice and red-backed voles (Fig. 3). Sites with ample ground cover and a more open canopy were characterized by high scores for this microhabitat component. In other words, in both study species, when compared with less active and exploratory individuals, highly active and exploratory individuals were found at sites that had more ground cover and light than was available on average in the home range. As more active individuals have higher metabolic requirements (Biro and Stamps 2008, Careau et al. 2008, Réale et al. 2010*b*), our results may represent an example of personality-matching habitat choice (Table 1; Edelaar et al. 2008). Here, highly active and exploratory individuals may preferentially select for areas with highly caloric, seasonal food resources. In our study sites, these included wild raspberry (*Rubus occidentalis*), wild strawberry (*Fragaria vesca*), bunchberry (*Cornus canadensis*), and Canada mayflower (*Maianthemum canadense*), and these species are common to newly created forest gaps. PC1 was also characterized by the amount of mossy ground cover where moisture-loving insects (another important food source) may be abundant.

Another reason why relatively more active individuals may seek out areas with denser ground cover is for added protection from aerial predators (Longland and Price 1991). Several studies have linked personality traits such as activity and exploration to predation-associated mortality rates (Smith and Blumstein 2008, Rödel et al. 2015, Moiron et al. 2020), therefore it is likely that these differences in predation risk may drive individuals to select more or less strongly for sites of refuge. Furthermore, this could mean that individuals who take more risks offset increased predation-induced mortality through habitat selection, but further work is required to assess this phenomenon. Regardless of the mechanism driving the relationship between activity/exploration and selection for ground cover and light levels, the presence of this trend in both study species is noteworthy.

We found several instances in which the personality traits of deer mice and southern red-backed voles correlated significantly with selection for key habitat features at the population level. Interestingly, there were trends that we had expected to see that were not supported by our results. For example, we predicted that we may see an overarching trend between the degree of boldness and selection for vegetative ground cover (Carrete and Tella 2010, Holtmann et al. 2017, Schirmer et al. 2019). Instead, the majority of observed relationships with this habitat component involved activity level in both species.

In voles, there were two significant correlations between boldness/timidness (latency to emerge from an emergence test) and selection for ground cover, but this relationship was not uniform among treatments (Table 3). Instead, bolder voles selected home ranges with less ground cover in the unmanaged forest—consistent with the findings of Carrete and Tella (2010) and Holtmann et al. (2017)—but in the even-aged treatment this relationship was reversed, and bolder individuals selected home ranges with more vegetative cover (Table 3); the finding in this treatment was consistent with those of Schirmer et al. (2019). The apparent discrepancies between existing empirical studies may reflect differences in the history of land-use or forest management in a study area.

Additionally, we had expected to see stronger patterns of selection at coarser ecological scales (i.e., second order: home-range selection vs. third order: daily activity patterns), as decisions made on broader scales can have greater impacts on fitness (Rettie and Messier 2000, Dupke et al. 2017). We did see more patterns at the second order vs. the third order when looking at deer mice (six significant correlations vs. one), but in voles we saw six significant correlations at the third order compared with four at the second order and the strength of these correlations was comparable at both orders. The idea that more limiting factors drive habitat selection at coarse scales but are less influential at finer scales (Rettie and Messier 2000) has ambiguous support in the literature (as discussed by Dupke et al. 2017), and our study adds to those that do not show clear support for this hypothesis.

Management implications

In this study, we identified a system in which land-use change has altered patterns of personality-associated habitat selection and influenced the distribution of individuals across the population. The congregation of similar individuals in a population can potentially drive divergent selection (Rice 1987, Via 1999), influence patterns of transmission for diseases and parasites (Boyer et al. 2010, Dizney and Dearing 2013, VanderWaal and Ezenwa 2016, Sih et al. 2018), and could ultimately limit behavioral trait diversity on the landscape. Additionally, within-population differences in resource use or habitat selection could reduce intraspecific competition, perhaps having ecological consequences, for example by impacting patterns of species coexistence (Chesson 2000). Ultimately, these phenomena may influence which individuals persist in response to anthropogenic disturbance and knowledge of these processes should inform management actions (Merrick and Koprowski 2017).

It is well known that maintaining heterogeneity at multiple ecological scales is vital for fostering biodiversity (MacArthur and MacArthur 1961, Stein et al. 2014), however practitioners typically promote heterogeneity to maximize interspecific (rather than intraspecific) richness and diversity. A recent study by the authors showed that behavioral diversity is affected by heterogeneity in vegetation (Mortelliti and Brehm 2020), and here we add to this existing knowledge by showing that implementing silvicultural practices (such as even-aged or 2-stage shelterwood) across a landscape may create the conditions favored by only certain personality types, and are likely to play a role in shaping the personality composition of populations (with possible loss of intraspecific diversity). Indeed, previous research on the study system investigated here has shown that contrasting methods for managing forests have shifted the distribution of personalities present in different areas of the landscape (Brehm et al. 2019); something that can have both ecological and fitness consequences (Smith and Blumstein 2008, Sih et al. 2012, Wolf and Weissing 2012, Carere and Maestripieri 2013, Lapiedra et al. 2018). To support behaviorally diverse populations and their associated functions, habitat heterogeneity should be maintained at multiple ecological scales. Maintaining landscapes where mature forest stands are interspersed with managed stands may create suitable habitats for different behavioral types and therefore encourage intraspecific behavioral diversity (and its important ecological and evolutionary consequences).

Conclusions

The adoption of forest management techniques that maintain healthy, functioning ecosystems is a crucial step toward limiting anthropogenic effects on biodiversity. Landscape ecologists and conservation biologists must identify silvicultural methods that promote the maintenance of suitable habitat at multiple spatial scales by promoting connectivity, habitat heterogeneity, and stand structural complexity (Hunter 1990, Lindenmayer and Franklin 2002); this is vital to maintain not only interspecific diversity and richness, but to promote intraspecific behavioral diversity and its associated functions. In this study, we distinguished key patterns of microhabitat selection that are correlated with animal personalities at multiple scales. Our results show that, depending on the type of silvicultural system implemented, forest management can alter patterns of intraspecific habitat selection. This study provides a novel addition to the mechanistic underpinnings of species' responses in the face of global change.

Literature Cited

Abbott, H. G. 1962. Tree seed preferences of mice and voles in the Northeast. Journal of Forestry 60:97–99.

Abbott, H. G., and A. C. Hart. 1960. Mice and voles prefer spruce seeds. Northeastern Forest Experiment Station Paper No 153. US Department of Agriculture, Upper Darby, Pennsylvania, USA.

Abbott, H. G., and T. F. Quink. 1970. Ecology of eastern white pine seed caches made by small forest mammals. Ecology 51:271–278.

Araújo, M. S., D. I. Bolnick, and C. A. Layman. 2011. The ecological causes of individual specialisation. Ecology Letters 14:948–958.

Barnett, S. 1976. The rat – a study in behavior. Revised edition. ANU Press, Canberra, Australian Capital Territory, Australia.

Berg, A., B. Ehnstrom, L. Gustafsson, T. Hallingback, M. Jonsell, and J. Weslien. 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. Conservation Biology 8:718–731.

Bergmüller, R., and M. Taborsky. 2010. Animal personality due to social niche specialisation. Trends in Ecology & Evolution 25:504–511.

Best, E. C., S. P. Blomberg, and A. W. Goldizen. 2015. Shy female kangaroos seek safety in numbers and have fewer preferred friendships. Behavioral Ecology 26:639–646.

Biro, P. A., and J. A. Stamps. 2008. Are animal personality traits linked to life-history productivity? Trends in Ecology and Evolution 23:361–368.

Biro, P. A., and J. A. Stamps. 2010. Do consistent individual differences in metabolic rate promote consistent individual differences in behavior? Trends in Ecology and Evolution 25:653–659.

Bolnick, D. I., et al. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology and Evolution 26:183–192.

Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. American Naturalist 161:1–28.

Bonner, F. T., and R. P. Karrfalt. 2008. The woody plant seed manual. Agriculture Handbook, USDA Forest Service, Washington, D.C., USA.

Boon, A. K., D. Réale, and S. Boutin. 2007. The interaction between personality, offspring fitness and food abundance in North American red squirrels. Ecology Letters 10:1094–1104.

Boon, A. K., D. Réale, and S. Boutin. 2008. Personality, habitat use, and their consequences for survival in North American red squirrels Tamiasciurus hudsonicus. Oikos 117:1321–1328.

Boone, S. R., and A. Mortelliti. 2019. Small mammal tree seed selection in mixed forests of the Eastern United States. Forest Ecology and Management 449:117487.

Box, G. E. P., and D. R. Cox. 1964. An analysis of transformations. Journal of the Royal Statistical Society: Series B (Methodological) 26:211–243.

Boyer, N., D. Réale, J. Marmet, B. Pisanu, and J. L. Chapuis. 2010. Personality, space use and tick load in an introduced population of Siberian chipmunks Tamias sibiricus. Journal of Animal Ecology 79:538–547.

Brehm, A. M., and A. Mortelliti. 2018. Mind the trap: large-scale field experiment shows that trappability is not a proxy for personality. Animal Behaviour 142:101–112.

Brehm, A. M., A. Mortelliti, G. A. Maynard, and J. Zydlewski. 2019. Land-use change and the ecological consequences of personality in small mammals. Ecology Letters 22:1387–1395.

Brehm, A. M., S. Tironi, and A. Mortelliti. 2020. Effects of trap confinement on personality measurements in two terrestrial rodents. PLoS One 15:1–14.

Brissette, J. C., and L. S. Kenefic, editors. 2014. History of the penobscot experimental forest, 1950–2010. Pages 1–20 in Penobscot experimental forest: 60 years of research and demonstration in Maine, 1950-2010. GTR-NRS-P-123. USDA Forest Service, Newtown Square, Pennsylvania, USA.

Brown, C., and V. A. Braithwaite. 2004. Effects of predation pressure on the cognitive ability of the poeciliid Brachyraphis episcopi. Behavioral Ecology 16:482–487.

Calenge, C. 2006. The package adehabitat for the R software: tool for the analysis of space and habitat use by animals. Ecological Modelling 197:1035.

Careau, V., D. Thomas, M. M. Humphries, and D. Réale. 2008. Energy metabolism and animal personality. Oikos 117:641–653.

Carere, C., and D. Maestripieri. 2013. Animal personalities: behavior, physiology and evolution. University of Chicago Press, Chicago, Illinois, USA.

Carrete, M., and J. L. Tella. 2010. Individual consistency in flight initiation distances in burrowing owls: a new hypothesis on disturbance induced habitat selection. Biology Letters 6:167–170.

Carter, A. J., W. E. Feeney, H. H. Marshall, G. Cowlishaw, and R. Heinsohn. 2013. Animal personality: what are behavioural ecologists measuring? Biological Reviews 88:465–475.

Carter, A. J., A. E. G. G. Lee, H. H. Marshall, M. T. Ticó, G. Cowlishaw, H. H. Narshall, M. T. Ticó, and G. Cowlishaw. 2015. Phenotypic assortment in wild primate networks: implications for the dissemination of information. Royal Society Open Science 2:1–13.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. Annual Review of Ecology and Systematics 31:343–366.

Choleris, E., A. W. Thomas, M. Kavaliers, and F. S. Prato. 2001. A detailed ethological analysis of the mouse open field test: effects of diazepam, chlordiazepoxide and an extremely low frequency pulsed magnetic field. Neuroscience & Biobehavioral Reviews 25:235–260.

Costa-Pereira, R., V. H. W. Rudolf, F. L. Souza, and M. S. Araújo. 2018. Drivers of individual niche variation in coexisting species. Journal of Animal Ecology 87:1452–1464.

Croft, D. P., J. Krause, S. K. Darden, I. W. Ramnarine, J. J. Faria, and R. James. 2009. Behavioural trait assortment in a social network: patterns and implications. Behavioral Ecology and Sociobiology 63:1495–1503.

Dammhahn, M., N. J. Dingemanse, P. T. Niemelä, and D. Réale. 2018. Pace-of-life syndromes: a framework for the adaptive integration of behaviour, physiology and life history. Behavioral Ecology and Sociobiology 72:1–8.

Dingemanse, N. J., C. Both, P. J. Drent, and J. M. Tinbergen. 2004. Fitness consequences of avian personalities in a fluctuating environment. Proceedings of the Royal Society of London B: Biological Sciences 271:847–852.

Dingemanse, N. J., K. M. Bouwman, M. Van De Pol, T. Van Overveld, S. C. Patrick, E. Matthysen, and J. L. Quinn. 2012. Variation in personality and behavioural plasticity across four populations of the great tit *Parus major*. Journal of Animal Ecology 81:116–126.

Dingemanse, N. J., and N. A. Dochtermann. 2013. Quantifying individual variation in behaviour: mixed-effect modelling approaches. Journal of Animal Ecology 82:39–54.

Dingemanse, N. J., A. J. N. Kazem, D. Réale, and J. Wright. 2009. Behavioural reaction norms: animal personality meets individual plasticity. Trends in Ecology and Evolution 25:81–89.

Dirzo, R., H. S. Young, M. Galetti, G. Ceballos, N. J. B. Isaac, and B. Collen. 2014. Defaunation in the anthropocene. Science 345:401–406.

Dizney, L., and M. D. Dearing. 2013. The role of behavioural heterogeneity on infection patterns: implications for pathogen transmission. Animal Behaviour 86:911–916.

Dormann, C. F., et al. 2013. Collinearity: A review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46.

Duchesne, L. C., D. G. Herr, S. Wetzel, I. D. Thompson, and R. Reader. 2000. Effect of seed predation, shade and soil organic matter on the early establishment of eastern white pine and balsam fir seedlings. Forestry Chronicle 76:759–763.

Dueser, R. D., and H. H. Shugart. 1978. Microhabitats in a forest-floor small mammal fauna. Ecology 59:89–98.

Dupke, C., C. Bonenfant, B. Reineking, R. Hable, T. Zeppenfeld, M. Ewald, and M. Heurich. 2017. Habitat selection by a large herbivore at multiple spatial and temporal scales is primarily governed by food resources. Ecography 40:1014–1027.

Edelaar, P., A. M. Siepielski, and J. Clobert. 2008. Matching habitat choice causes directed gene flow: a neglected dimension in evolution and ecology. Evolution 62:2462–2472.

Efford, M. 2021. secr: Spatially explicit capture-recapture models. R package version 4.4.1. https://CRAN.R-project.org/package=secr

Fauteux, D., L. Imbeau, P. Drapeau, and M. J. Mazerolle. 2012. Small mammal responses to coarse woody debris distribution at different spatial scales in managed and unmanaged boreal forests. Forest Ecology and Management 266:194–205.

Fernández-Teruel, A., and C. Estanislau. 2016. Meanings of self-grooming depend on an inverted U-shaped function with aversiveness. Nature Reviews Neuroscience 17:591.

Fisher, J. T., and L. Wilkinson. 2005. The response of mammals to forest fire & timber harvest in the N-A boreal forest. Mammal Review 35:51–81.

Fraver, S., R. G. Wagner, and M. Day. 2002. Dynamics of coarse woody debris following gap harvesting in the Acadian forest of central Maine, U.S.A. Canadian Journal of Forest Research 32:2094–2105.

Fukasawa, Y. 2012. Effects of wood decomposer fungi on tree seedling establishment on coarse woody debris. Forest Ecology and Management 266:232–238.

Gasperini, S., A. Mortelliti, P. Bartolommei, A. Bonacchi, E. Manzo, and R. Cozzolino. 2016. Effects of forest management on density and survival in three forest rodent species. Forest Ecology and Management 382:151–160.

Gharnit, E., P. Bergeron, D. Garant, and D. Réale. 2020. Exploration profiles drive activity patterns and temporal niche specialization in a wild rodent. Behavioral Ecology 31:772–783.

Gibb, H., J. P. Ball, T. Johansson, O. Atlegrim, J. Hjältén, and K. Danell. 2005. Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. Scandinavian Journal of Forest Research 20:213–222.

Gosling, S. D. 2001. From mice to men: What can we learn about personality from animal research? Psychological Bulletin 127:45–86.

Gracceva, G., A. Herde, T. G. G. Groothuis, J. M. Koolhaas, R. Palme, and J. A. Eccard. 2014. Turning shy on a winter's day: effects of season on personality and stress response in *Microtus arvalis*. Ethology 120:753–767.

Hadfield, J. D. 2015. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. Journal of Statistical Software 33:1–22.

Hadfield, J. D., A. J. Wilson, D. Garant, B. C. Sheldon, and L. E. B. Kruuk. 2010. The misuse of BLUP in ecology and evolution. American Naturalist 175:116–125.

Hansen, A. J., T. A. Spies, F. J. Swanson, and J. L. Ohmann. 1991. Conserving biodiversity in managed forests. BioScience 41:382–392.

Harmon, M. E., et al. 1986. Ecology of coarse woody debris in temperate ecosystems. Advances in Ecological Research 15:133–302.

Hille, S. M., and A. Mortelliti. 2010. Microhabitat partitioning of *Apodemus favicollis* and *Myodes glareolus* in the sub-montane alps: a preliminary assessment. Hystrix 21:157–163.

Holtmann, B., E. S. A. Santos, C. E. Lara, and S. Nakagawa. 2017. Personality-matching habitat choice, rather than behavioural plasticity, is a likely driver of a phenotype–environment covariance. Proceedings of the Royal Society B: Biological Sciences 284:20170943.

Houslay, T. M., and A. J. Wilson. 2017*a*. Avoiding the misuse of BLUP in behavioural ecology: I. Multivariate modelling for individual variation (MCMCglmm tutorial). Behavioral Ecology 28:1–18.

Houslay, T. M., and A. J. Wilson. 2017*b*. Avoiding the misuse of BLUP in behavioural ecology. Behavioral Ecology 28:948–952.

Hunter, M. L. 1990. Wildlife, forests and forestry: Principles for managing forests for biological diversity. Prentice Hall, Englewood Cliffs, New Jersey, USA.

Hutchinson, G. E. 1957. Concluding remarks. Population studies: animal ecology and demography. *In Cold Spring Harbor Symposium on Quantitative Biology*.

IPCC 2019. Climate change and land: An IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems. Geneva, Switzerland. https://www.ipcc.ch/srccl-report-download-page/

Jaenike, J., and R. D. Holt. 1991. Genetic variation for habitat preference: evidence and explanations. American Naturalist 137:S67–S90.

Jansen, P. A., F. Bongers, and L. Hemerik. 2004. Seed mass and mast seeding enhance dispersal by a neotropical scatter-hoarding rodent. Ecological Monographs 74:569–589.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61:65–71.

Johnson, K. V. A., L. M. Aplin, E. F. Cole, D. R. Farine, J. A. Firth, S. C. Patrick, and B. C. Sheldon. 2017. Male great tits assort by personality during the breeding season. Animal Behaviour 128:21–32.

Johnson, D. H., and T. A. O'Neil. 2001. Wildlife-habitat relationships in Oregon and Washington. Oregon State University Press, Corvallis, Oregon, USA.

Jones, J. 2001. Habitat selection studies in avian eology: a critical review. Auk 118:557–562.

Kaiser, H. 1991. Coefficient alpha for a principal component and the Kaiser-Guttman rule. Psychological Reports 68:855–858.

Kalueff, A. V., A. M. Stewart, C. Song, K. C. Berridge, A. M. Graybiel, and J. C. Fentress. 2016. Neurobiology of rodent self-grooming and its value for translational neuroscience. Nature Reviews Neuroscience 17:45–59.

Kaminski, J. A., M. L. Davis, M. Kelly, and P. D. Keyser. 2007. Disturbance effects on small mammal species in a managed Appalachian forest. American Midland Naturalist 157:285–297.

Kellner, K. F., and R. K. Swihart. 2014. Changes in small mammal microhabitat use following silvicultural disturbance. American Midland Naturalist 172:348–358.

Kiers, H. A. L. L. 1998. Three-way SIMPLIMAX for oblique rotation of the three-mode factor analysis core to simple structure. Computational Statistics & Data Analysis 28:307–324.

Kimball, A. J. 2014. Penobscot Experimental Forest: resources, administration, and mission. Pages 21–30 in States Department of Agriculture Forest Service, editor. Penobscot experimental forest: 60 years of research and demonstration in Maine, 1950-2010. GTR-NRS-P-123. USDA Forest Service, Newtown Square, Pennsylvania, USA.

Kobler, A., T. Klefoth, T. Mehner, and R. Arlinghaus. 2009. Coexistence of behavioural types in an aquatic top predator: a response to resource limitation? Oecologia 161:837–847.

Krausman, P. R. 1999. Some basic principles of habitat use. Pages 85–90 in K. L. Launchbaugh, K. D. Sanders and J. C. Mosley, editors. Grazing behaviour of livestock and wildlife. Idaho Forest, Wildlife & Range Experiment Station, Moscow, Idaho, USA.

Krugman, S. L., and J. L. Jenkinson. 1974. Pinaceae—pine family. Page 1380 in Seeds of woody plants in the United States. Agricultural Handbook 450. USDA Forest Service, Washington, D.C., USA.

Laland, K., B. Matthews, and M. W. Feldman. 2016. An introduction to niche construction theory. Evolutionary Ecology 30:191–202.

Lapiedra, O., T. W. Schoener, M. Leal, J. B. Losos, and J. J. Kolbe. 2018. Predator-driven natural selection on risk-taking behavior in anole lizards. Science 360:1017–1020.

Le Cœur, C., et al. 2015. Temporally fluctuating selection on a personality trait in a wild rodent population. Behavioral Ecology 26:1285–1291.

Lever, J., M. Krzywinski, and N. Altman. 2017. Principal component analysis. Nature Methods 14:641–642.

Lindenmayer, D., and J. Fischer. 2007. Landscape modification and habitat fragmentation: a synthesis. Global Ecology and Biogeography 16:265–280.

Lindenmayer, D. B., and J. F. Franklin. 2002. Conserving forest biodiversity: A comprehensive multiscaled approach. Island Press, Washington, D.C., USA.

Linder, P., and L. Östlund. 1998. Structural changes in three mid-boreal Swedish forest landscapes, 1885–1996. Biological Conservation 85:9–19.

Longland, W. S., and M. V. Price. 1991. Direct observations of owls and heteromyid rodents: Can predation risk explain microhabitat use? Ecology 72:2261–2273.

López, P., D. Hawlena, V. Polo, L. Amo, and J. Martín. 2005. Sources of individual shy-bold variations in antipredator behaviour of male Iberian rock lizards. Animal Behaviour 69:1–9.

MacArthur, R., and J. W. MacArthur. 1961. On bird species diversity. Ecology 42:594–598.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Second edition. Springer, Dordrecht, The Netherlands.

Martin, J. G. A., and D. Réale. 2008. Temperament, risk assessment and habituation to novelty in eastern chipmunks, Tamias striatus. Animal Behaviour 75:309–318.

Maser, C., and J. M. Trappe. 1984. The seen and unseen world of the fallen tree. USDA Forest Service, Washington, D.C., USA.

Mayor, S. J., D. C. Schneider, J. A. Schaefer, and S. P. Mahoney. 2009. Habitat selection at multiple scales. Écoscience 16:238–247.

Mazzamuto, M. V., G. Cremonesi, F. Santicchia, D. Preatoni, A. Martinoli, and L. A. Wauters. 2018. Rodents in the arena: a critical evaluation of methods measuring personality traits. Ethology Ecology & Evolution 31:1–21.

McGarigal, K., H. Y. Wan, K. A. Zeller, B. C. Timm, and S. A. Cushman. 2016. Multi-scale habitat selection modeling: a review and outlook. Landscape Ecology 31:1161–1175.

Merrick, M. J., and J. L. Koprowski. 2017. Should we consider individual behavior differences in applied wildlife conservation studies? Biological Conservation 209:34–44.

Miranda, A. C., H. Schielzeth, T. Sonntag, and J. Partecke. 2013. Urbanization and its effects on personality traits: a result of microevolution or phenotypic plasticity? Global Change Biology 19:2634–2644.

Moiron, M., K. L. Laskowski, and P. T. Niemelä. 2020. Individual differences in behaviour explain variation in survival: a meta-analysis. Ecology Letters 23:399–408.

Monnahan, C. C., J. T. Thorson, and T. A. Branch. 2017. Faster estimation of Bayesian models in ecology using Hamiltonian Monte Carlo. Methods in Ecology and Evolution 8:339–348.

Montiglio, P. O., D. Garant, F. Pelletier, and D. Réale. 2012. Personality differences are related to long-term stress reactivity in a population of wild eastern chipmunks, Tamias striatus. Animal Behaviour 84:1071–1079.

Moran, E. V., F. Hartig, and D. M. Bell. 2016. Intraspecific trait variation across scales: implications for understanding global change responses. Global Change Biology 22:137–150.

Mortelliti, A., and L. Boitani. 2007. Patterns of interspecific and intraspecific microhabitat segregation of two rodents Praomys jacksoni (De Winton 1897) and Hylomyscus stella (Thomas 1911) (Rodentia) in an African rainforest subjected to various levels of anthropogenic disturbance. Tropical Zoology 20:163–186.

Mortelliti, A., and A. M. Brehm. 2020. Environmental heterogeneity and population density affect the functional diversity of personality traits in small mammal populations. Proceedings of the Royal Society B: Biological Sciences 287:20201713.

Nakagawa, S., and H. Schielzeth. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biological Reviews 85:935–956.

Odling-Smee, F. J., K. N. Laland, M. W. Feldman, J. F. Odling-Smee, K. N. Laland, and M. W. Feldman. 1996. Niche construction. American Naturalist 147:641–648.

Ólafsdóttir, G. Á., and K. Magellan. 2016. Interactions between boldness, foraging performance and behavioural plasticity across social contexts. Behavioral Ecology and Sociobiology 70:1879–1889.

Pearish, S., L. Hostert, and A. M. Bell. 2013. Behavioral type-environment correlations in the field: a study of three-spined stickleback. Behavioral Ecology and Sociobiology 67:765–774.

Peig, J., and A. J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos 118:1883–1891.

Peluc, S. I., T. S. Sillett, J. T. Rotenberry, and C. K. Ghalambor. 2008. Adaptive phenotypic plasticity in an island songbird exposed to a novel predation risk. Behavioral Ecology 19:830–835.

Perals, D., A. S. Griffin, I. Bartomeus, and D. Sol. 2017. Revisiting the open-field test: What does it really tell us about animal personality? Animal Behaviour 123:69–79.

Perkey, A. W., and B. L. Wilkins. 2001. Crop tree field guide – selecting and managing crop trees in the Central

Appalachians. USDA Forest Service, Morgantown, West Virginia, USA.

Plomin, R., J. C. DeFries, and J. C. Loehlin. 1977. Genotype-environment interaction and correlation in the analysis of human behavior. Psychological Bulletin 84:309–322.

Price, M. V., and K. A. Kramer. 1984. On measuring microhabitat affinities with special reference to small mammals. Oikos 42:349–354.

Prut, L., and C. Belzung. 2003. The open field as a paradigm to measure the effects of drugs on anxiety-like behaviors: a review. European Journal of Pharmacology 463:3–33.

Réale, D., N. J. Dingemanse, A. J. N. N. Kazem, J. Wright, J. A. Stamps, T. G. G. Groothuis, N. J. Dingemanse, A. J. N. N. Kazem, J. Wright, and S. Biologiques. 2010a. Evolutionary and ecological approaches to the study of personality. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365:3937–3946.

Réale, D., D. Garant, M. M. Humphries, P. Bergeron, V. Careau, and P. O. Montiglio. 2010b. Personality and the emergence of the pace-of-life syndrome concept at the population level. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365:4051–4063.

Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23:466–478.

Rice, W. R. 1987. Speciation via habitat specialization: the evolution of reproductive isolation as a correlated character. Evolutionary Ecology 1:301–314.

Rödel, H. G., M. Zapka, S. Talke, T. Kornatz, B. Bruchner, and C. Hedler. 2015. Survival costs of fast exploration during juvenile life in a small mammal. Behavioral Ecology and Sociobiology 69:205–217.

Roughgarden, J. 1972. Evolution of niche width. American Naturalist 106:683–718.

Schirmer, A., A. Herde, J. A. Eccard, and M. Dammhahn. 2019. Individuals in space: personality-dependent space use, movement and microhabitat use facilitate individual spatial niche specialization. Oecologia 189:647–660.

Schirmer, A., J. Hoffmann, J. A. Eccard, and M. Dammhahn. 2020. My niche: individual spatial niche specialization affects within- and between-species interactions. Proceedings of the Royal Society B: Biological Sciences 287:20192211.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 185:27–39.

Schreiber, S. J., R. Bürger, D. I. Bolnick, and I. Bolnick. 2016. The community effects of phenotypic and genetic variation within a predator population. Ecology 92:1582–1593.

Sharpe, P. B., and B. Van Horne. 1998. Influence of habitat on behavior of Townsend's ground squirrels (*Spermophilus townsendii*). Journal of Mammalogy 79:906–918.

Sih, A., A. M. Bell, J. C. Johnson, and R. E. Ziemba. 2004. Behavioral syndromes, an integrative overview. Quarterly Review of Biology 79:241–277.

Sih, A., J. Cote, M. Evans, S. Fogarty, and J. Pruitt. 2012. Ecological implications of behavioural syndromes. Ecology Letters 15:278–289.

Sih, A., M. C. O. Ferrari, and D. J. Harris. 2011. Evolution and behavioural responses to human-induced rapid environmental change. Evolutionary Applications 4:367–387.

Sih, A., O. Spiegel, S. Godfrey, S. Leu, and C. M. Bull. 2018. Integrating social networks, animal personalities, movement ecology and parasites: a framework with examples from a lizard. Animal Behaviour 136:195–205.

Smith, B. R., and D. T. Blumstein. 2008. Fitness consequences of personality: a meta-analysis. Behavioral Ecology 19:448–455.

Snijders, L., E. P. van Rooij, J. M. Burt, C. A. Hinde, K. van Oers, and M. Naguib. 2014. Social networking in territorial great tits: slow explorers have the least central social network positions. Animal Behaviour 98:95–102.

Stamps, J. A., and T. G. G. Groothuis. 2010a. Developmental perspectives on personality: implications for ecological and evolutionary studies of individual differences. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365:4029–4041.

Stamps, J., and T. G. G. Groothuis. 2010b. The development of animal personality: relevance, concepts and perspectives. Biological Reviews 85:301–325.

Steffen, W., et al. 2004. Global change and the Earth system: a planet under pressure. Springer-Verlag, New York, New York, USA.

Stein, A., K. Gerstner, and H. Kreft. 2014. Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. Ecology Letters 17:866–880.

Stoffel, M. A., S. Nakagawa, and H. Schielzeth. 2017. rptR: Repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods in Ecology and Evolution 8:1639–1644.

Sutherland, W. J., et al. 2013. Identification of 100 fundamental ecological questions. Journal of Ecology 101:58–67.

Tanaka, S., J. W. Young, A. L. Halberstadt, V. L. Masten, and M. A. Geyer. 2012. Four factors underlying mouse behavior in an open field. Behavioural Brain Research 233:55–61.

Taylor, R. W., S. Boutin, M. M. Humphries, and A. G. Mcadam. 2014. Selection on female behaviour fluctuates with offspring environment. Journal of Evolutionary Biology 27:2308–2321.

Treit, D., M. Fundytus, and A. M. Fundytus. 1989. Thigmotaxis as a test for anxiolytic activity in rats. Pharmacology Biochemistry & Behavior 31:959–962.

Turner, B. L., E. F. Lambin, and A. Reenberg. 2007. The emergence of land change science for global environmental change and sustainability. Proceedings of the National Academy of Sciences USA 104:20666–20671.

Tuttle, M. D., and M. J. Ryan. 1982. The role of synchronized calling, ambient light, and ambient noise, in anti-bat-predator behavior of a treefrog. Behavioral Ecology and Sociobiology 11:125–131.

Van Valen, L. 1965. Morphological variation and width of ecological niche. American Naturalist 99:377–390.

Vander Wall, S. B. 1990. Food hoarding in animals. University of Chicago Press, Chicago, Illinois, USA.

Vander Wall, S. B. 2010. How plants manipulate the scatter-hoarding behaviour of seed-dispersing animals. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365:989–997.

Vander Wall, S. B., P. Forget, J. Lambert, and P. Hulme. 2005. Seed fate: predation, dispersal, and seedling establishment. CABI Publishing, Wallingford, UK.

VanderWaal, K. L., and V. O. Ezenwa. 2016. Heterogeneity in pathogen transmission: mechanisms and methodology. Functional Ecology 30:1606–1622.

Vanderwel, M. C., J. R. Malcolm, J. P. Caspersen, and M. A. Newman. 2010. Fine-scale habitat associations of red-backed voles in boreal mixedwood stands. Journal of Wildlife Management 74:1492–1501.

Via, S. 1999. Reproductive isolation between sympatric races of pea aphids.I. Gene flow restriction and habitat choice. Evolution 53:1446–1457.

Walsh, R. N., and R. A. Cummins. 1976. The open-field test: a critical review. Psychological Bulletin 83:482–504.

Wat, K. K. Y., A. P. H. M. Herath, A. I. Rus, P. B. Banks, and C. Mcarthur. 2020. Space use by animals on the urban fringe: interactive effects of sex and personality. Behavioral Ecology 31:330–339.

Webster, M. M., A. J. W. Ward, and P. J. B. Hart. 2007. Boldness is influenced by social context in threespine sticklebacks (*Gasterosteus aculeatus*). Behaviour 144:351–371.

Wilson, A. J. 2018. How should we interpret estimates of individual repeatability? Evolution Letters 2:4–8.

Wilson, D. S., K. Coleman, A. B. Clark, and L. Biederman. 1993. An ecological study of a psychological trait. Journal of Comparative Psychology 107:250–260.

Wolf, M., and F. J. Weissing. 2012. Animal personalities: consequences for ecology and evolution. Trends in Ecology and Evolution 27:452–461.

Yang, Y., O. F. Christensen, and D. Sorensen. 2011. Analysis of a genetically structured variance heterogeneity model using the Box-Cox transformation. Genetics Research 93:33–46.

Zwolak, R. 2009. A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals. Forest Ecology and Management 258:539–545.

Zwolak, R. 2018. How intraspecific variation in seed-dispersing animals matters for plants. Biological Reviews 93: 897–913.

SUPPORTING INFORMATION

Additional supporting information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/eap.2443/full

OPEN RESEARCH

Data and scripts are available on the Figshare Repository (https://doi.org/10.6084/m9.figshare.14488626).