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Environmental heterogeneity and population density affect the functional diversity of personality traits in small mammal populations

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Understanding factors affecting the functional diversity of ecological communities is an important goal for ecologists and conservationists. Previous work has largely been conducted at the community level; however, recent studies have highlighted the critical importance of considering intraspecific functional diversity (i.e. the functional diversity of phenotypic traits among conspecifics). Further, a major limitation of existing literature on this topic is the lack of empirical studies examining functional diversity of *behavioural phenotypes*—including animal personalities. This is a major shortcoming because personality traits can affect the fitness of individuals, and the composition of personalities in a population can have important ecological consequences. Our study aims to contribute to filling this knowledge gap by investigating factors affecting the functional diversity of personality traits in wild animal populations. Specifically, we predicted that the richness, divergence and evenness associated with personality traits would be impacted by key components of forest structure and would vary between contrasting forest types. To achieve our objective we conducted a fully replicated large-scale field experiment over a 4 year period using small mammal populations as a model system. We found that greater heterogeneity in the cover of shrubs, coarse woody debris and canopy cover was associated with a greater richness, lower divergence and lower evenness in personality traits. Greater population density was associated with greater functional richness and lower functional divergence and evenness of personality traits. To maintain a behaviourally diverse population and its associated functions, managers may promote heterogeneity in vegetation and increased population density, which we found to be the most important determinants driving functional diversity of personality traits.

1. Introduction

Defaunation leads to a loss of functional diversity in ecosystems [1]. While earlier studies have mostly focused on decreases in functional diversity caused by the loss of species, more recently researchers have highlighted the potential consequences of loss of intraspecific functional diversity [2,3], such as the loss of phenotypic traits associated with ecosystem functions. This phenomenon generates cryptic function loss [4], whereby a species is still present in an ecosystem but part of the functions associated with it are lost. Many cases of cryptic function loss have been documented such as eutrophication owing to decrease in the abundance of oysters, and lowered nutrient deposition and seed dispersal as consequences of reduction in seabird and bat abundances [4]. A possible source of cryptic function loss from ecosystems is the loss of certain personality types from a population. Personalities are defined as behavioural differences among individuals that are consistent over time and across contexts [5–7]. The personality composition of a population (i.e. the richness and the evenness of different

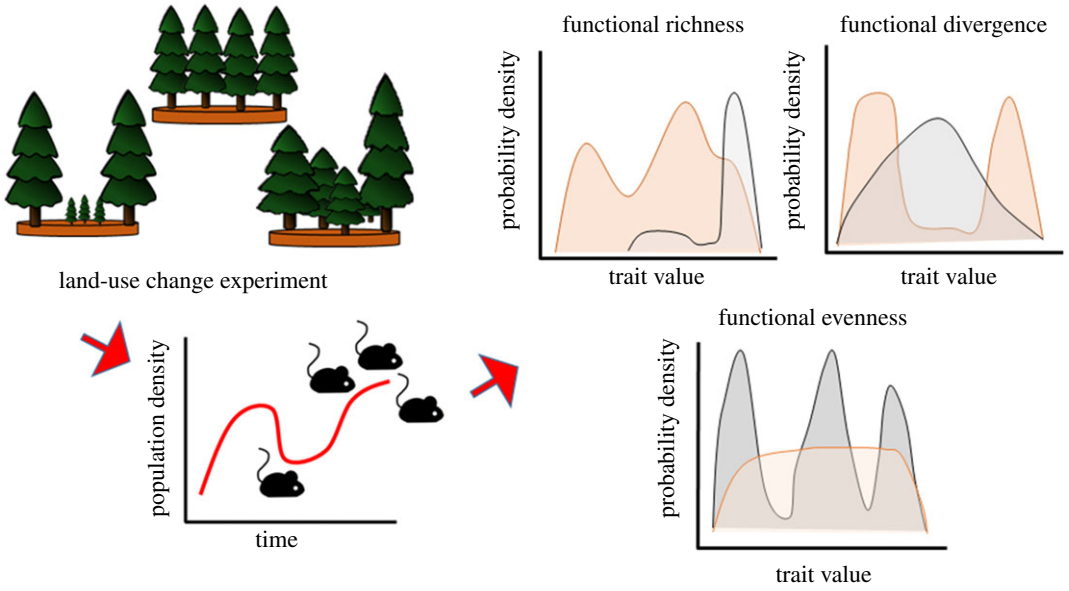

Figure 1. Conceptual overview of the project. Land-use change (silvicultural treatments) creates contrasting environmental conditions: variations in the structure and heterogeneity of vegetation which are coupled with variation in small mammal density over time and space (i.e. among treatments). We examined how variation in environmental conditions and demographics affected the functional diversity of behavioural (personality) traits. Graphs on the right show contrasting values of functional diversity: high (pink) versus low (grey) functional richness, high versus low divergence, high versus low evenness. (Online version in colour.)

personality types) is important and has ecological consequences [6,8]. As an example Brehm *et al*. [9] recently suggested potential seed dispersal impairment as a consequence of shifts in the personality composition of small mammal populations caused by habitat modifications.

Despite the recent surge in research investigating personalities in wild populations, studies focusing on the functional diversity of personality traits are lacking (but see [10,11] for other behavioural traits). Specifically, it is unclear how the diversity of personality traits in a population vary as a function of environmental characteristics such as the quality and heterogeneity of habitats, as well as population density. Understanding the determinants of behavioural diversity will help preserve, maintain and manage behaviourally diverse populations and the associated functions, thus allowing managers to integrate this ecological parameter into conservation actions. As an example, if functional behavioural diversity of populations increases with environmental heterogeneity, then this supports managing habitats to maintain heterogeneity [12]. The goal of this work is to contribute to filling this gap.

Theoretical work suggests that environmental heterogeneity increases variation in phenotypic traits, including behavioural traits such as personality [13–15]. Empirical work on personality traits partly supports this prediction. As an example Dubuc-Messier *et al*. [16] found divergent personality traits in blue tits inhabiting two habitat types that differed in the degree of heterogeneity, whereas Dochtermann *et al*. [17] did not find significant differences in a similar comparison focused on small mammals. Furthermore, empirical studies on habitat matching and behavioural type–environment correlations provide indirect support for theoretical predictions [18–20], as they support the idea that variation in environmental characteristics should be linked to variation in personality traits. Likewise several studies have shown that population density affects the personality composition of populations [21,22]. Specifically, both Le Galliard *et al*. [22] and Nicolaus *et al*. [21] found density-dependent selection on personality traits in the common lizard (*Zootoca vivipara*) and the great tit (*Parus major*).

These previous studies, however, did not explicitly test for a relationship between habitat structure and the richness, evenness and divergence of personality traits. The functional trait diversity approach [23,24] provides several advantages as it explicitly measures the trait space occupied by a species in a certain environment (functional richness), the distribution in abundance (i.e. evenness) and the overall divergence of the trait distribution [24,25] (figure 1). The objectives of this study are to: (i) test for a relationship between environmental characteristics and the functional diversity of personality traits in populations living in contrasting environments, and (ii) concurrently assess if and to what extent the behavioural diversity varies with population density.

To achieve our objectives we conducted a fully replicated large-scale field experiment over a 4 year period. Behavioural diversity of small mammal populations was assessed in three highly contrasting environments: two treatment areas characterized by intensive silvicultural management (even-aged forestry and two-stage shelterwood) and reference (unmanaged) areas. We focused on small mammals because methods to assess their personality traits are well established [26,27], their personality traits may have functional consequences on ecosystems [9] and, further, the density of small mammal populations fluctuates drastically over time, thus providing the experimental conditions for establishing a link between behavioural diversity and population density. In line with theoretical and empirical work on phenotypic trait variation, we predicted the richness and divergence of behavioural traits would increase with the amount and heterogeneity of key environmental resources [28,29] such as shrubs and coarse woody debris [30–32]. In addition, we predicted that an increase in population density (i.e. competition) would promote the richness and divergence of behavioural traits [15]. Specifically, we predicted that greater density would lead to greater trait richness because of a sampling effect (more individuals results in more different

phenotypes) and greater competition would increase the likelihood of disruptive selection [33] which would manifest as greater divergence among phenotypes.

2. Material and methods

(a) Study area and experimental design

The study was conducted in the Penobscot Experimental Forest (44°51′ N, 68°37′ W, Maine, USA), located in the transitional zone between the eastern broadleaf and boreal forests. Here units were chosen at random and logged separately with different silvicultural treatments (two independent replicates per treatment). Each replicate treatment used in this study averages 12.84 ha in area (range 8.32–17.49 ha) and two blocks of forest (25 total ha) have remained unmanaged since the late 1800s and serve as reference. For this study, we selected two treatments and one reference type that generated contrasting habitat types for small mammals. These include even-aged forest, two-stage shelterwood and unmanaged forest (the following descriptions are provided using [34]).

(1) Treatment 1: *even-age forest* (two replicate sites). This treatment is characterized by dense stands of trees that are all the same age-class. This type of forest is characterized by very sparse shrubby or herbaceous understory cover, with a dense canopy and low light-levels.

(2) Treatment 2: *two-stage shelterwood* (two replicate sites). This treatment is used in silviculture to increase growth and vertical structure, as well as provide downed wood and snags and is accomplished by retaining large trees from the older cohort and then applying an even-aged cut. The resulting forest is composed of a mosaic of mossy understory, downed woody material, open, grassy patches, small saplings, and large standing residual trees.

(3) Reference: *unmanaged forest* (two replicate sites). This forest type is characterized by large, individual overstory trees which die naturally and are replaced by understory trees. The resulting forest is very open (i.e. low shrub cover) with abundant downed woody material.

Common trees in the forest include red spruce (*Picea rubens*), balsam fir (*Abies balsamea*), eastern hemlock (*Tsuga canadensis*), eastern white pine (*Pinus strobus*), northern white-cedar (*Thuja occidentalis*), and hardwoods such as maples (*Acer* spp.), birches (*Betula* spp.) and red oak (*Quercus rubra*) [34]. The most abundant small mammal species which were included in this study are: deer mice (*Peromyscus maniculatus*), southern red-backed voles (*Myodes gapperi*) and northern short-tailed shrews (*Blarina brevicauda*).

(b) Small mammal trapping and handling

Within each of our six sites we positioned a 90 m × 90 m small mammal trapping grid using Longworth traps (10 m distance between traps, 100 traps total). Traps were baited with a mix of sunflower seeds, rolled oats and mealworms; cotton was provided for bedding. Traps were left active for three consecutive days and were checked twice in a 24 hour period.

Following capture, individuals were subject to behavioural measurements (detailed below) and then anaesthetized using Isoflurane. Animals were then 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). For each individual we recorded sex, body mass (using a Pesola Lightline spring scale), body length, tail length, age class (juvenile versus adult) and reproductive status. Individuals were released in the proximity of the site of capture.

Trapping was conducted monthly (June to October) at each grid from 2016 to 2019, for a total of 20 trapping sessions per grid. The mean distance between grids is approximately 1.47 km, and the mean distance between replicates (i.e. grid within the same treatment) is approximately 1.17 km. The area covered by each trapping grid (0.81 ha) was, at a minimum, less than 10% the area covered by each treatment and large enough to encompass multiple home-ranges of individual small mammals. Further details on methods are available in [9,26,35,36].

(c) Behavioural measurements

Personality of captured individuals was assessed using a standard *open-field test* [27,37], in which animals are recorded as they explore an arena. Test boxes (size: 46 × 46 × 50 cm) are placed on a level platform and underneath a tarp to control for light levels and canopy cover. We use software ANY-MAZE (V. 5.1; Stoelting Co., Wood Dale, IL) to automatically track animal movement and quantify behaviour. The test is conducted prior to marking animals and once per session (to avoid test habituation) on new and recaptured individuals (minimum interval between tests is one month). In our previous work [26,36] we showed that trap confinement does not affect our behavioural measurements and that personality does not affect trappability, thus demonstrating that our sample is not biased towards certain personality types.

(d) Microhabitat and heterogeneity measurements

At each trapping site, during the summer of 2017 (the midpoint of this study), we recorded microhabitat measurements within a 5 m radius of each trap site (100 sites per trapping grid, 600 sites total). Variables measured included: per cent cover of mosses, grasses and herbs, per cent cover of shrubs and saplings at two height categories, metres of coarse woody debris present and per cent canopy cover. More details are provided in the electronic supplementary material, table S1. For each of these variables we calculated the average value for each trapping grid and the coefficient of variation as a measure of heterogeneity [38,39].

(e) Data analysis

(i) Personality

Personality variables to be included were selected based on our previous work [9]; a repeatability analysis was conducted on the raw variables (electronic supplementary material, appendix S1 and table S2). Variables selected are described in detail in the electronic supplementary material, table S4 and include: proportion of time spent in the centre of the open field test (interpreted as an indicator of boldness), rear rate (interpreted as an indicator of vertical exploration and activity, proportion of time spent grooming (interpreted as an indicator of anxiety) and mean speed (a proxy for activity, electronic supplementary material, table S4). To account for variability in the behaviour measurements of each individual we calculated the individual's best linear unbiased predictor (BLUP) for each of the behaviour variables, after controlling for sex, body size, forestry treatment, trapping session and year as fixed effects and individual identity (ID) as random effect (as done for the repeatability analyses, electronic supplementary material, appendix S1 and table S2). We adopted the approach followed by [40–42] to minimize the risk of transferring BLUP errors into the functional diversity analyses [43,44]. We used the *sim* function in package arm [45] to simulate 1000 series of individual BLUPs and then used the mean as the behaviour score for each individual [40–42]. Subsequently we conducted a principal component analysis with varimax rotation on the mean BLUP for each of the four behaviours [42,46], to derive a more synthetic measure of the behaviour profile of each individual. The factor scores for the three derived components were then used to calculate the indices of functional behavioural diversity.

(ii) Functional behavioural diversity

Traditional approaches for measuring functional diversity in communities [25] have recently been adapted by Carmona *et al*. [24,47] for intraspecific trait variation. These methods are based on trait probability density functions (TPD), which reflect the probability of observing a given value for a variable [47] and are calculated through kernel density estimation. TPD's allow the estimation of several components of functional diversity such as functional richness, functional evenness and functional divergence. *Functional richness* is the amount of functional space occupied by a trait and it is equivalent to the sum of the hypervolumes of cells in which the TPD is greater than zero [47]. *Functional evenness* reflects the distribution of abundance within trait space (figure 1) and it is quantified by estimating the overlap between the TPD of the trait and a hypothetical trait distribution occupying the same functional volume with uniform probabilities (i.e. maximum possible evenness for a given functional volume). *Functional divergence* reflects the extent to which trait values are close to the centre of gravity of the distribution (i.e. with high functional divergence the trait is distributed towards the extremes of its functional volume [24,47]. Functional diversity measurements were calculated for each population (i.e. within a grid) for each species, using data from all 20 trapping sessions, thus they represent the cumulative richness, evenness and divergence of behavioural traits observed in a given grid on a given year (out of a total of 4 years of sampling). All calculations were performed using the R package TPD (https://CRAN.R-project.org/package=TPD).

(iii) Factors affecting functional behavioural diversity

To test for a relationship between the structure and heterogeneity of habitat variables and the behavioural diversity of small mammal personality traits, we used mixed effects models with grid as random effect (to account for potential dependence among all animals sampled in the same grid) [48]. The functional richness, diversity and evenness for each species that we observed in each grid on a given year ($n = 24$, six grids sampled for 4 years) were used as dependent variables, whereas explanatory variables included the microhabitat variables and their coefficients of variation (electronic supplementary material, table S1) and the number of individuals caught in the grid each year (a proxy for population density). To avoid collinearity all variables were screened for correlation prior to analysis (using $R < 0.7$ as threshold [49]). We conducted a preliminary analysis with mixed effect models to check whether the microhabitat variables were at all related with population abundance. The analysis showed that these are not related (i.e. the null model was always included in the top model set, electronic supplementary material, table S3). Because the variable treatment and microhabitat variables were linked by design, we decided to focus on the microhabitat variables as these are probably more directly related to the habitat features generating functional diversity in personality traits. We compared models through the Akaike information criteria corrected for small sample sizes (AICc) and obtained predictions through model averaging using top ranking models within 2 delta AICc [50]. To avoid over-parametrization we initially fitted models with single predictors and then fitted additive models with variables included within 2 delta AICc from the top model (only if the null model was not included in the top model set).

3. Results

We measured personality traits in a total of 1276 unique individuals in the period 2016–2019 (574 *Pe. maniculatus*, 470 *M. gapperi* and 232 *B. brevicauda*). During the 4 years of study, captures for all three species ($n = 3938$) peaked in 2018 ($n = 1872$) and were lowest in 2019 ($n = 376$).

Results for the principal component analysis are shown in the electronic supplementary material, table S5. For all three species the first component (PC1) was characterized a gradient of activity and exploration, with the two variables mostly contributing to the component being rear rate and mean speed. The second component (PC2) for *Pe. maniculatus* and *B. brevicauda* and PC3 for *M. gapperi* were highly related to the proportion of time spent in the centre of the arena (with high scores representing individuals passing higher amounts of time in the centre of the open field arena). The third component (PC3) for *Pe. maniculatus* and PC2 for *M. gapperi* were instead highly related to the proportion of time spent grooming (high scores being individuals grooming extensively). Individuals of *Blarina* did not groom, so this variable was not included in the principal component analysis for this species.

Results for the mixed effects models are shown in table 1 (main results for PC1 and PC2, additional results reported in the electronic supplementary material, table S6). The two most widespread predictors of the functional diversity of personality traits (i.e. based on inclusion in the top ranking model set) were population density and the heterogeneity of microhabitat (shrub cover, coarse woody debris and canopy cover; table 1, electronic supplementary material, table S6). The direction of the relationship between the heterogeneity of vegetation and functional richness and divergence was positive in most cases (greater richness and greater divergence with greater heterogeneity) (table 1 and figure 2), and it was negative for evenness in all cases but one (table 1 and electronic supplementary material, table S6). The direction of the relationship between population density and functional richness was always positive (greater richness with greater density), and it was negative for evenness and divergence in all cases but one (figure 3).

4. Discussion

Through a large-scale field experiment conducted over a 4 year period, we found that the functional diversity of personality traits in three target small mammal species was influenced by both the vegetation characteristics of the environment and by the population density. Specifically, we found that greater heterogeneity in the cover of shrubs, coarse woody debris and canopy cover was associated with a greater richness, lower divergence and lower evenness in the personality traits describing the mean speed and rearing rate, proportion of time grooming and proportion of time spent in the centre of the open-field arena. Greater population density was associated with greater functional richness and lower functional divergence and evenness of personality traits. As personality traits have ecological consequences [6,8,9] and can affect the demographics of populations [27,51,52] practitioners should incorporate the functional diversity of personality traits in conservation plans. Our results suggest that, where direct measurements are not possible, vegetation heterogeneity and population density may be used as proxies for functional behavioural diversity in wildlife populations. However, further studies are needed to assess the generality of this relationship.

(a) Microhabitat heterogeneity

The observed intraspecific relationship between heterogeneity and functional diversity matches a well-established pattern for interspecific data, particularly at the population and

Table 1. Results for mixed-effects models with the following response variables: functional richness, functional evenness and functional divergence of the personality traits examined (PC1 for all species, PC2 for *Myodes gapperi* and *Blarina brevicauda*). (Random effect was grid ID in all models. Fixed effects included microhabitat variables and their coefficient of variation (CV; listed in the electronic supplementary material, table S1) and population density. Model ranking according to ΔAICc (delta Akaike information criterion corrected for small sample sizes); only models <2 ΔAIC are shown, and results are not shown when the null model <2 ΔAIC. R^2 = conditional R^2 for the top ranked model (including fixed and random effects). For additive models, the direction of the relationship is the same for all fixed effects unless specified. $n = 24$ (six treatments sampled over 4 years). CWD, coarse woody debris.)

personality trait	functional diversity parameter	species	model	ΔAICc	R^2	direction of relationship	variance of intercept (grid ID)	variance of residual
PC1 (rear rate and mean speed)	functional richness	*Peromyscus maniculatus*	density (log)	0.00	0.38	+	(<0.001)	0.76
		Myodes gapperi	density (log)	0.00	0.35	+	(<0.001)	0.82
	functional evenness	*Peromyscus maniculatus*	density	0.00	0.51	−	0.001	0.001
		Myodes gapperi	density (log)	0.00	0.24	−	(<0.001)	0.005
			canopy cover+density (log)	0.08	0.32	−	(<0.001)	0.005
	functional divergence	*Peromyscus maniculatus*	CV shrubs <2 m + density	0.00	0.38	CV shrubs <2 m (+) density (−)	(<0.001)	0.002
		Blarina brevicauda	density (log)	0.00	0.27	density (−)	(<0.001)	0.002
PC2 (proportion of time centre)	functional richness	*Peromyscus maniculatus*	density (log)	0.00	0.34	+	(<0.001)	0.63
PC2 (proportion of time grooming)		*Myodes gapperi*	density (log)	0.00	0.33	+	0.05	0.48
			CV canopy cover + density (log)	0.07	0.38	+	(<0.001)	0.45
			CV canopy cover	1.21	0.23	+	(<0.001)	0.56
PC2 (proportion of time centre)	functional divergence	*Peromyscus maniculatus*	CV CWD + density (log)	0.00	0.44	CV CWD (+) density (log) (−)	(<0.001)	0.003
			density (log)	0.91	0.39	−	(<0.001)	0.003

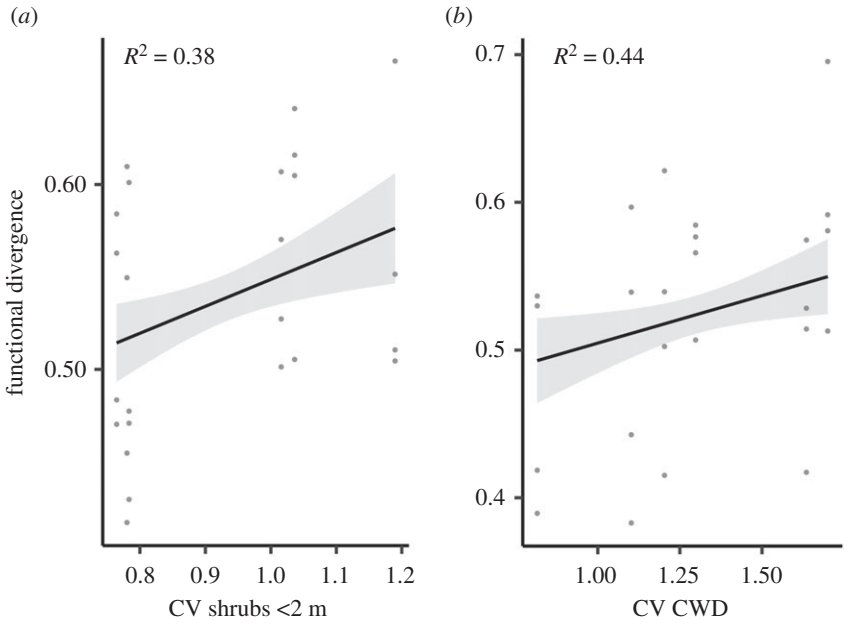

Figure 2. Model averaged predicted relationships (and 95% confidence interval (CI)) between functional behavioural diversity measurements (functional divergence) and vegetation heterogeneity ($n = 24$) in *Peromyscus maniculatus*. (*a*) shows the functional divergence in PC1 (rear rate and mean speed) predicted by the coefficient of variation (CV) of shrub abundance less than 2 m in height. (*b*) shows the functional divergence in PC2 (proportion of time spent in the centre) predicted by the CV of coarse woody debris (CWD) abundance. R^2 values shown are the conditional coefficients of determination for the top model. Data points represent observed values (one per session per trapping grid over a 4 year sampling period) of functional behavioural diversity (functional divergence) and vegetation heterogeneity (CVs of shrub abundance <2 m in height and CWD abundance).

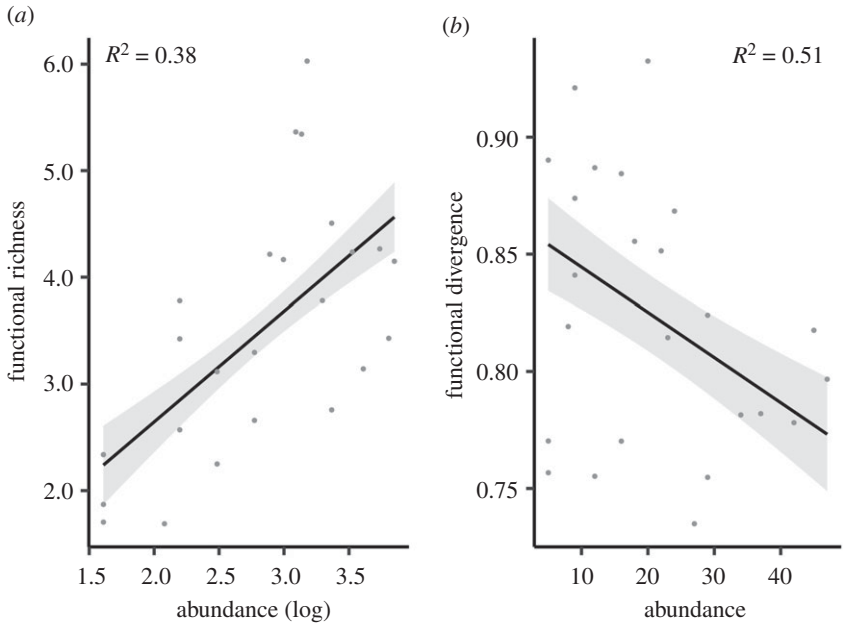

Figure 3. Model averaged predicted relationships (and 95% CI) between functional behavioural diversity measurements and population abundance of *Peromyscus maniculatus* ($n = 24$). (*a*) shows the relationship between functional richness in PC1 (rear rate and mean speed) and log-transformed population abundance. (*b*) shows the relationship between functional evenness in PC1 and population abundance. R^2 values shown are the conditional coefficients of determination for the top model. Data points represent observed values (one per session per trapping grid over a 4 year sampling period) of functional behavioural diversity (functional richness and evenness) and population abundance.

community levels [32,53–55]. Indeed the positive relationship between heterogeneity of key vegetation structures and the richness and divergence of personality traits are in line with our predictions. High vegetation heterogeneity corresponds to greater availability of potential niche space [39,54,55]. For example, relatively open areas may be preferred by risk-taking (i.e. bolder) individuals, whereas more dense areas may be preferred by more timid individuals [18,56]. Consequently, a highly heterogeneous environment allows for more individuals to be positioned in the most suitable microhabitat. We cannot untangle whether niche occupation is the result of habitat matching [18,19] or development (i.e. individuals growing in a specific microhabitat develop certain personality traits [7]). However, regardless of the

mechanism generating the observed patterns, the ecological implications are that a greater variety of behavioural phenotypes (and the associated ecological outcomes), should be expected in areas characterized by greater vegetation heterogeneity. As ecologists recognize the potential for intraspecific trait variation to impact community and ecosystem processes, a focus on the intraspecific niche has grown considerably in recent years [57], and interest in intraspecific behavioural variation is no exception [58]. Empirical studies that identify the drivers of trait variation (via functional diversity) in populations and that propose methods to promote variation are important avenues for further research.

The observed positive relationship between heterogeneity and divergence is in line with our expectations and with community level studies [59]. The highest values of vegetation heterogeneity are observed in areas with high contrasts, such as grids with both areas of high shrub density and very open areas with low density of shrubs. These grids may thus be characterized by niche space for animals with contrasting personality traits, such as highly exploratory versus less exploratory voles, or fast paced versus slow paced shrews, which probably determines the high divergence value (table 1). The negative relationship between evenness and heterogeneity is in line with community level studies [59]: more homogeneous environments are characterized by a more even distribution of traits.

Among the four heterogeneity measures considered, the two related to shrubs appeared more frequently in top ranking models. These findings are in line with existing knowledge on shrubs providing key habitat features for rodents, as these provide both shelter from predators (such as aerial predators) [30,31] and facilitate the interaction with seeds [60]. Furthermore, shrubs are directly linked to food resource abundance as many provide fruit that are consumed by small mammal species [61,62]. Likewise coarse woody debris and canopy cover are also known to be important habitat features for small mammals [31,63].

Vegetation heterogeneity and population abundance were not related in our study system. This was shown by preliminary analyses conducted with mixed effect models with abundance as dependent variable and microhabitat variables as predictors (electronic supplementary material, table S3). Future long-term investigations (i.e. more than 4 years of duration) are required to determine if a relationship exists over the long term.

We acknowledge that our microhabitat measurements were conducted once (halfway through the study), in line with other studies in the Penobscot Experimental Forest [34]. While more frequent measurements would have been ideal, inter-annual changes in the microhabitat structure of our temperate forest system are relatively slow, therefore it is unlikely that these affected our results (i.e. variation among treatments is much stronger than inter-annual variation within a treatment).

(b) Population density

The abundance of our small mammal populations varied strongly during the 4 year duration of the study, which is in line with the expected periodicity of small mammal population cycles in Maine [64]. The observed positive relationship between population density and both the functional richness and divergence of behavioural traits is in line with our predictions and may be interpreted in several non-exclusive ways. First, we need to take into account a 'sampling effect': more individuals simply means greater chances of observing a different phenotype (the variable is continuous so each individual has a unique score). The probabilistic nature of this relationship however, does not mean the relationship is an artefact. Indeed, it shows that at a given point in time and space (i.e. a 1 ha area of forest) the distribution of personality traits (and the associated ecological outcomes) will depend on the total number of individuals present in the area. In the case of small mammals this number will probably be less than 60–70 individuals ha^{-1} under many circumstances [65], consequently our results suggest that an increase in the abundance of individuals may be associated with a greater richness of personality traits and all the associated ecological outcomes.

Beyond the sampling effect, which is stochastic in nature, the relationship between functional diversity and population density is probably shaped in a more deterministic manner by other processes. As an example, greater population density may determine elevated competition among individuals which could lead to increased disruptive selection [33] and thus greater functional divergence. Contrary to predictions, we observed negative relationships between abundance and the functional divergence of multiple traits for all three species (table 1): that is higher abundance coincided with lower divergence. This result suggests that any sampling effect was probably minor, because otherwise we would have expected a neutral relationship between divergence and density. Our results thus suggest that stabilizing selection may occur with higher abundances. In these instances, mean values of the personality traits tend to be advantageous [66]. Further studies focusing on fitness estimation are required to clarify the processes generating the observed pattern.

5. Conclusion

We show that the richness, divergence and evenness of personality traits in wild populations are linked to key characteristics of the environment such as vegetation heterogeneity and a fundamental demographic parameter: population density. Maintaining functional diversity is widely considered a key conservation outcome [67,68] and our study provides evidence to suggest that conservation practitioners should consider vegetation heterogeneity and population density as key factors associated with high diversity of behavioural phenotypes.

Ethics. Experiments in this study were approved by the University of Maine's Institutional Animal Care and Use Committee (IACUC number A2015_11_02 and A2018_11_01).

Data accessibility. Data and scripts are available at the following link (Figshare site): https://figshare.com/s/317a6217b4ef013c31fb.

Authors' contributions. A.M. and A.M.B. conceived and designed the study; A.M. and A.M.B. collected and analysed the data; all authors contributed to manuscript preparation.

Competing interests. We declare we have no competing interests.

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