Social groups with diverse personalities mitigate physiological stress in a songbird

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Social groups often consist of diverse phenotypes, including personality types, and this diversity is known to affect the functioning of the group as a whole. Social selection theory proposes that group composition (i.e. social environment) also influences the performance of individual group members. However, the effect of group behavioural composition on group members remains largely unexplored, and it is still contentious whether individuals benefit more in a social environment with homogeneous or diverse behavioural composition. We experimentally formed groups of house sparrows (*Passer domesticus*) with high and low diversity of personality (exploratory behaviour), and found that their physiological state (body condition, physiological stress, and oxidative stress) improved with increasing group-level diversity of personality. These findings demonstrate that group personality composition affects the condition of group members and individuals benefit from social heterosis (i.e. associating with a diverse set of behavioural types). This aspect of the social life can play a key role in affiliation rules of social animals, in the evolutionary coexistence of different personalities in nature and has implications for human teams and animal welfare.

Keywords:

affiliation, group composition, personality, physiology, social environment, social heterosis

Subject Category:

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1. Introduction

Social groups were once considered aggregates of similar individuals, but more recently are viewed as a mixture of members with diverse phenotypes [1]. Variation within group can occur in morphology (e.g. size), behavioural traits (e.g. reactive and proactive behavioural types [2], or social roles (e.g. leaders/followers in human teams [3], or producers/scroungers in sparrow flocks [4]). Group composition has implications for emergent group-level processes such as decision-making, which ultimately drive group functioning (reviewed in [1,5]). Ethnic diversity can, for instance, have a positive effect on research teams' scientific performance [6].

Personality, the consistent among-individual differences in behavioural phenotype [7], has strong relevance for social life [8]. Social groups can largely differ in their personality composition [1]. Groups' personality composition can have effects at both the level of group as a whole ('upstream effects') and the level of individual group members ('downstream effects'). The group-level consequences of groups' personality composition have mostly been assessed in human teams [9,10], where personality composition may affect team performance, albeit in an inconsistent manner [11–13]. In non-human organisms, group personality composition influences within-group social network structure, collective behaviour, and group performance [5,14–17]. Although individual-level aspects of sociality, e.g. rank in the dominance hierarchy, have been shown to influence the state of individual members (reviewed by [18,19]), the downstream effects of group behavioural composition on individual state is surprisingly little scrutinised [1]. This happens despite that social selection theory postulates that the fitness of an individual is contingent upon the phenotype of those with whom it affiliates (i.e. social environment; [15,20]).

Health state can have a strong influence on the individual's performance [21] and, at the same time, is moulded by changes of individual's social environment [19]. Therefore, it is

reasonable to assume that physiological condition (e.g. body condition, stress physiology, oxidative stress, and immune capacity) of group members is also influenced downstream by the personality composition of their group. Correlative studies on human work teams found that age and gender composition can be associated with subjective self-reported health impairment [22], but human studies with experimental manipulation of group composition and actual health measurements are still lacking. Earlier animal studies mostly assessed how individuals' position within the social structure (e.g. rank in dominance hierarchy, an individual-level social attribute) affected their health or physiology (reviewed by [18,19]). Experimental studies on animals that tested directly whether group behavioural composition (a group-level social attribute) affects the stress level and condition of group members are very scarce and each involve livestock species (pigs; [23,24]). No experimental study addressed this question in wild animals.

We conducted an experimental study to explore whether manipulated personality composition of groups *per se* or in interaction with individual personality type affects the physiological condition of group members. Given that diverse groups might have advantages for group functioning (see above) and potentially there is less aggression in behaviourally diverse groups [23], we predicted that individuals in groups with more diverse personality composition would improve their physiological condition as compared with individuals in groups with more homogeneous personality composition. In this case, improved physiological condition of group members is a legacy of being part of a diversely composed and better functioning group and each group member shares this legacy. We do not know whether this potential benefit is indeed uniform for each member. Alternatively, some members might harvest more the benefits of better group-level functioning to the detriment of other group members. We assessed this prediction by testing whether personality diversity of the groups interact with individual personality type to

influence physiological condition. A significant interaction might suggest that individuals that either match or mismatch the group's personality composition benefit more than other group members do.

2. Material and methods

(a) Study protocol

The study is based on a large sample of 240 house sparrows. We captured 40 sparrows (1:1 sex ratio) per each of the six study replicates (Table S1). These 40 birds were divided into four treatment groups (see below) consisting of 10 birds each, which yielded 24 social groups for the entire study (four treatment groups per study replicate × six study replicates). There was no significant difference in sex ratio between the treatment groups in any of the study replicates (χ^2 test, all $p > 0.362$).

The study timeline was identical in each study replicate as follows. Upon capture (day 0), birds were marked with an aluminium ring, and their sex and body mass was recorded. Then they were housed in indoor aviaries for 18 days at the campus of Babeș-Bolyai University, Cluj-Napoca, Romania. On days 5–7, we recorded exploratory behaviour as a well-established and ecologically relevant axis of personality [25] following the novel environment test of Dingemanse and co-authors [26]. At day 9, we measured the body mass and tarsus length of the birds, and took pre-treatment blood sample. Then the birds were allocated according to an *a priori* defined protocol into one of four social treatment groups of 10 birds each: 'random' (random subsample of birds of a given replicate), 'low exploratory' (only birds with low exploratory scores), 'high exploratory' (only birds with high scores), and 'variable' (mixture of

birds with either low or high scores). To further characterise the birds' social environment, we calculated the Shannon diversity index of exploratory behaviour for each group by dividing exploration values into 10 ordered categories of roughly equal sizes. The social treatment period lasted nine days until day 18, when we measured again the body mass and took a second blood sample to measure the post-treatment physiological condition. Physiological state was characterised by measuring the within-individual change in body condition (scaled body mass index, SMI), heterophil-to-lymphocyte (H/L) ratio (an indicator of glucocorticoid-mediated stress response; [27]), oxidative stress (damage to lipids – malondialdehyde concentration, MDA), and innate immune capacity (natural antibodies – agglutination score; complement system – lysis score). There was no significant difference among social treatment groups in the pre-treatment values of the five physiological response variables (all $p > 0.225$). Within-individual change in physiological condition was computed as the difference between the post-treatment and pre-treatment values. We provide a more detailed description of study timeline, captivity conditions, measurement of exploratory behaviour, assignment to social treatment groups, blood sampling and physiological measurement methods in the *SI Appendix*.

(b) Statistical procedures

Malondialdehyde level was log-transformed to normalize its distribution. Changes in each physiological trait during the social treatment period were analysed in separate models as dependent variables. These change variables were calculated by subtracting the pre-treatment values from the post-treatment values. Exception from this are the scores of haemagglutination and haemolysis that were highly zero-inflated. Therefore, we converted these variables into binary variables (0 for absence and 1 for presence of agglutination or lysis), and scored the

change during treatment at a 4-point scale by considering all four possible transitions: 0 for 1 → 0 transition ("immune depression"); 1 for 0 → 0 transition ("stable weak immunity"); 2 for 1 → 1 transition ("stable good immunity"); 3 for 0 → 1 transition ("immunity improvement").

The explanatory variables were the same in all models as follows: sex and social treatment were set as fixed factors with two and four levels, respectively, and individual exploratory score as a continuous predictor with log(x+1)-transformation. In addition, all second-order interactions between the three explanatory variables were also tested. Study replicate (six levels) and group ID (24 levels) nested within study replicate were entered as random factors. Within each model, the continuous response variables (i.e. body condition, heterophil-to-lymphocyte ratio and malondialdehyde concentration) and exploration score were Z-transformed to zero mean and unit standard deviation [28]. We used linear mixed-effects models with normal error distribution (LMMs; 'lmer' function of the R package 'lme4'; [29]) for change in body condition, heterophil-to-lymphocyte ratio and malondialdehyde, while we used cumulative link models (CLMMs; 'clmm' function of the R package 'ordinal'; [30]) for change in agglutination and lysis scores. The assumption of homogeneity of variances among treatment groups were met for each response variable of the LMM models (Levene test, all $p > 0.22$). We assessed the fulfilment of model assumptions by graphical diagnosis; all assumptions were met for each model. Each model was simplified to obtain minimal adequate models (MAMs) containing only significant main effects or their interactions by sequentially dropping predictors with non-significant ($p > 0.05$) effects using the 'drop1' R function. Table 1 presents the type II Anova results of MAMs, while Table S2 presents the parameter estimates of both the full models and the MAMs.

To assess the relationships between groups' Shannon diversity of personality and changes

in physiological state, we computed the group-level mean of change in physiological variables for each of the 24 groups by averaging the 10 group members' physiological change values. These relationships were tested using LMMs with normal error distribution. In all models, the group-level mean of change in physiological parameter was entered as dependent variable, groups' Shannon diversity of exploration as a continuous predictor, and study replicate was entered as a random factor. Both the dependent variables and the exploration diversity values were Z-transformed. For all the statistical models the reported significance levels were calculated using type II Wald Chi-square tests using the 'Anova' and 'Anova.clmm' functions of the R packages 'car' [31] and 'RVAideMemoire' [32], respectively.

3. Results

The groups in the four experimental treatments differed in the mean, variance and Shannon diversity index of their personality composition (Fig. 1A–C; statistics in Social treatment section of Materials and Methods in *SI Appendix*). Treatment groups also clearly differed in within-individual change in body condition (Fig. 1D), heterophil-to-lymphocyte ratio (Fig. 1E) and oxidative stress (damage to lipids – malondialdehyde concentration; Fig. 1F), but not in change in the activity of constitutive innate immunity (natural antibodies – agglutination score, and complement system – lysis score; Fig. 1G and Fig. 1H) (Table 1). The differences in physiological condition among treatment groups (Fig. 1D–F) are mostly congruent with the group differences in personality diversity (cf. Fig. 1C) rather than with the mean or variance of personality of the groups (cf. Fig. 1A–B). Individuals' personality was not associated with the change in physiological condition by itself, but it was in interaction with social treatment in case of agglutination and lysis: changes in agglutination scores increased with exploration in the low

exploratory groups, while changes in lysis scores decreased with exploration in the random groups (Table 1; see also additional results in *SI Appendix* and Table S2).

To assess the role of personality diversity of experimental social groups, we tested whether the calculated Shannon diversity predicts the physiological responses to social treatment. Because the Shannon diversity index is a group-level metric (i.e. one value for a 10 birds group, hence 24 values in total), we computed the group-level mean of within-individual change in each physiological trait by averaging the change values of the 10 birds per group and assessed their association with groups' Shannon diversity of personality. We found that in groups with higher personality diversity body condition increased more (β = 0.515, s.e. = 0.152, t = 3.380, p < 0.001; Fig. 2A), while heterophil-to-lymphocyte ratio (β = –0.279, s.e. = 0.128, t = 2.174, p = 0.030; Fig. 2B) and oxidative damage to lipids (i.e. malondialdehyde; β = –0.464, s.e. = 0.189, t = 2.457, p = 0.014; Fig. 2C) became lower. Mean change in agglutination and lysis scores were not related to group personality diversity (agglutination: β = 0.058, s.e. = 0.188, t = 0.310, p = 0.757; lysis: β = –0.034, s.e. = 0.131, t = 0.263, p = 0.792).

4. Discussion

In the realm of human psychology, it is a long-standing debate whether uniformly or diversely composed teams perform better [11,12], but almost nothing has been known about whether group behavioural composition affects the physiological condition of group members either in humans or other animals. Pigs housed in groups of uniform behavioural composition or in groups with a mixture of behavioural types did not differ in their glucocorticoid stress response or weight gain [23,24]. Here we showed that "variety is delighting," as condition improved, and levels of

glucocorticoid-mediated stress response and oxidative stress was lower for house sparrows living in a social environment with diverse personalities. Therefore, living in social groups with diverse composition can provide benefits in terms of reduced physiological stress and superior health state. The finding of no significant interactions between social treatment and individual's exploration, at least in cases of physiological variables that improved in diversely composed groups, suggests that all individuals in diverse groups enjoy the benefits.

Diverse groups provide more opportunities for specialization [1,33] and are more likely to host keystone individuals, which are influential individuals with disproportionately large effect on other group members and/or overall group functioning [34]. Both role specialization and keystone individuals can lead to superior group-level performance (upstream effect). Indeed, great tit affiliations consisting of diverse personalities show the most effective coordinated action when exploring a habitat patch [5]. Note that the group compositions simulated in this modelling study [5] are highly similar to our experimental setup. Similarly, a mixture of shy and bold fish can be advantageous in reducing the trade-off between exploring novel foraging tasks and antipredator vigilance [16]. The minority of keystone individuals can also substantially affect group-level behaviour and performance [14]. Finally, groups with diverse behavioural composition might experience less aggression [23]. These group-level advantages of diversely composed groups can bring about higher individual performance (downstream effect) in terms of either fitness or condition [17] by reducing stress exposure and ultimately leaving group members in better physiological condition. Note that we found a positive effect of social diversity on health in a set-up where food was unlimited. This suggests that this benefit of diversity might arise because of the innate working of the group (e.g. the type and intensity of interactions between members) rather than being the consequence of more obvious benefits like improved

foraging success, habitat exploration, defence against predators, and decision-making. Therefore, preference for bonding with dissimilar individuals (i.e. heterophily), and in turn, the better health state of individuals in diverse groups might reinforce the improved group-level outcomes creating a positive feedback loop [35] between group-level and individual-level performances. Such a feedback loop can then drive the evolutionary maintenance of heterophily [36].

Consistency of personality traits places a constraint on individuals because one is either more reactive (shy, neophobic, less exploratory, less aggressive) or more proactive (bold, novelty seeking, more exploratory, more aggressive) [2]. However, if different personalities affiliate, they can share mutual benefits; a concept termed social heterosis [37]. Social heterosis in associations of dissimilar personalities thus can explain why behavioural (and genetic) diversity can evolutionarily persist [37]. Negative frequency-dependent selection is another evolutionary explanation for the existence of behavioural polymorphisms (producers–scroungers, hawks–doves, and leaders–followers), and has been shown to maintain diversity in group personality composition [38]. Our results provide a physiological mechanism that could also be responsible for the evolutionary maintenance of behavioural diversity in social groups. Behavioural diversity is a requisite for the evolution of leadership [39], cooperation [40], and social responsiveness, which in turn is necessary for the evolution of personality [41]. Our findings, thus, bring helpful insight into the study of social evolution, which is a fundamental question in biology and has implications for human work teams in particular and for human society in general. Although the role of group composition in human team performance is still contentious [10], there is some evidence showing that heterophily is advantageous in project groups that are less stable in time and are engaged in creative tasks, but disadvantageous in production groups that are stable in time and are engaged in routine tasks [12]. If humans also may gain health benefits from

belonging to a diversely composed team as sparrows do, the fact that homophily is still the rule of thumb in humans [42] poses a challenge on the health benefits of heterophily, and thus deserves more attention

Ethics. None of the birds died during the study and all of them were released at the site of capture in good health on day 18. The study complies with the ethical guidelines of the Babeș-Bolyai University (permit no. 30792) and the European laws regarding animal welfare, and adheres to the ASAB guidelines for the use of animals in behavioural research.

Data accessibility. Should the manuscript be accepted, all data supporting the results will be provided as *SI Appendix* or deposited in Dryad repository.

Authors' contributions. C.I.V., A.F., and Z.Ba. conceived and designed the study. C.I.V., A.F., P.L.P., O.G., J.P., and Z.Be. performed research. C.I.V., J.P., O.G., and Á.Z.L. contributed new reagents/analytic tools. C.I.V., A.F., and Z.Ba. analysed data. C.I.V., A.F., and Z.Ba. drafted the manuscript with major input from Á.Z.L. and P.L.P. All authors contributed revisions and approved the final version of the manuscript. The authors declare no conflict of interest.

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Tables

Table 1. Minimal adequate models containing predictors of changes in individual physiological state of house sparrows during the social treatment period. Statistically significant effects are marked in bold. Scaled Mass Index is a measure of body condition, heterophil-to-lymphocyte ratio is an indicator of glucocorticoid-mediated stress response, malondialdehyde reflects the oxidative damage to lipids, and personality refers to exploratory behaviour.

response	fixed effects	χ^2	df	*p*
scaled mass index	sex	6.52	1	**0.011**
	treatment	17.15	3	**< 0.001**
heterophil-to-lymphocyte ratio	treatment	7.94	3	**0.047**
malondialdehyde	sex	0.13	1	0.719
	treatment	13.34	3	**0.004**
	sex × treatment	8.35	3	**0.039**
agglutination	treatment	0.32	3	0.955
	personality	0.05	1	0.831
	treatment × personality	9.53	3	**0.023**
lysis	treatment	1.13	3	0.770
	personality	1.78	1	0.182
	treatment × personality	10.74	3	**0.013**

Figure legends and Figures

Figure 1. Behavioural and physiological differences among the social treatment groups. Treatment groups differ according to (A) mean, (B) variance and (C) Shannon diversity index of personality (i.e. exploration score), change in (D) body condition (SMI), (E) heterophil-to-lymphocyte ratio (H/L ratio, an indicator of glucocorticoid-mediated stress response), (F) oxidative damage to lipids (i.e. malondialdehyde, MDA), and (G–H) constitutive immune capacity, as expressed through agglutination score (G) and lysis score (H). Means ± s.e. are shown; raw data on panels A–C and model-predicted values on panels D–H. Different lowercase letters denote significant differences ($p \leq 0.05$), while similar but italicized letters denote marginal differences ($p < 0.1$) between social treatment groups based on pairwise comparisons with Tukey-adjusted *p*-values. Male house sparrow drawing credit: Márton Zsoldos.

Figure 2. Physiological condition improved in social groups with diverse personalities. Relationships between personality diversity in social groups of house sparrows and mean change in (A) body condition (SMI), (B) heterophil-to-lymphocyte (H/L) ratio, and (C) oxidative damage to lipids (MDA) during the social treatment period. Dots are group-level means, regression lines are model-predicted slopes with 95% confidence intervals (shaded area).

Fig. 1

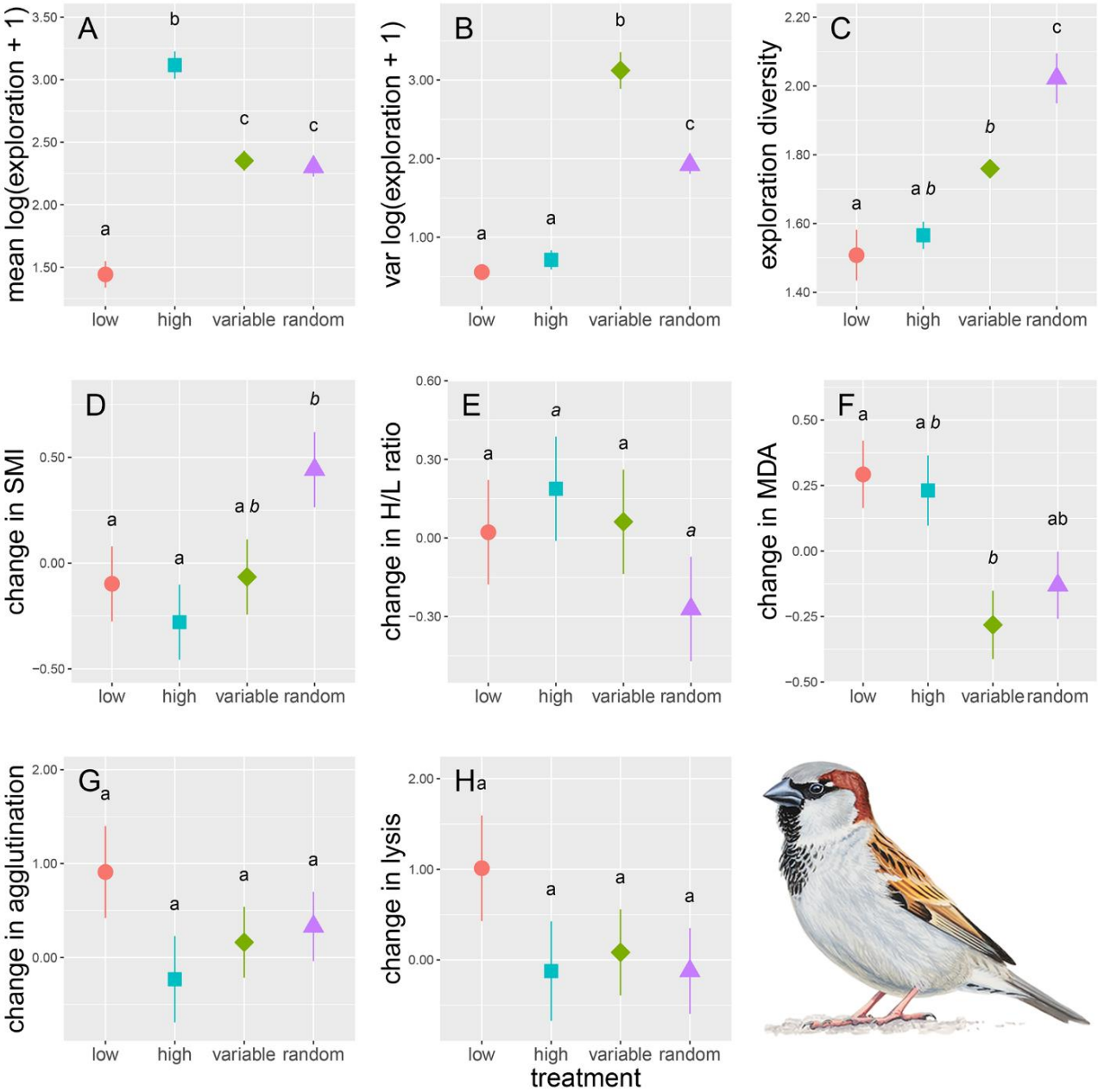
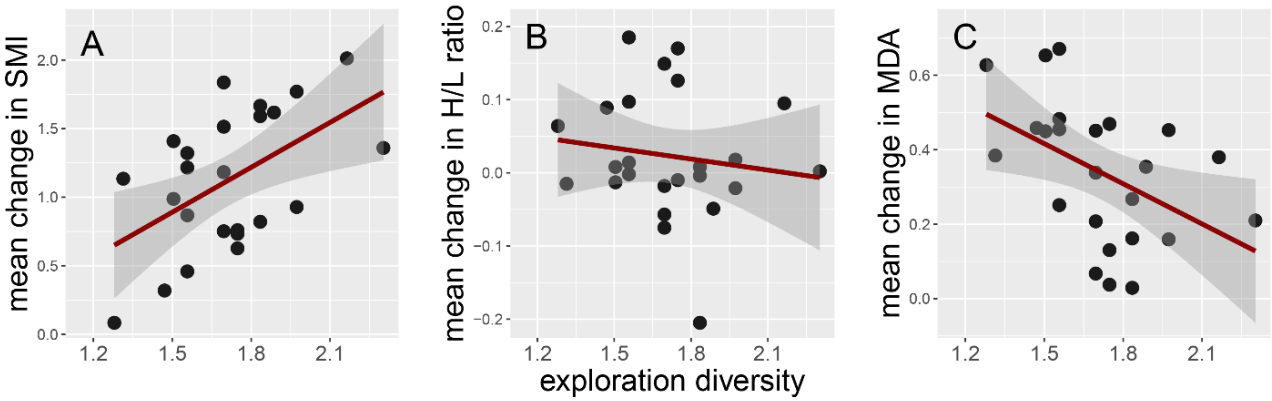

A
mean log(exploration + 1)
3.50
3.00
2.50
2.00
1.50
a
b
c
c
low
high
variable
random
B
var log(exploration + 1)
3.00
2.00
1.00
a
a
b
c
C
exploration diversity
2.20
2.00
1.80
1.60
1.40
a
a b
b
c
D
change in SMI
0.50
0.00
−0.50
a
a
a b
b
E
change in H/L ratio
0.60
0.30
0.00
−0.30
a
a
a
a
F
change in MDA
0.50
0.25
0.00
−0.25
−0.50
a
a b
b
ab
G
change in agglutination
2.00
1.00
0.00
a
a
a
a
H
change in lysis
2.00
1.00
0.00
a
a
a
treatment

Fig. 2


A
mean change in SMI
2.0
1.5
1.0
0.5
0.0
1.2
1.5
1.8
2.1
B
mean change in H/L ratio
0.2
0.1
0.0
−0.1
−0.2
1.2
1.5
1.8
2.1
exploration diversity
C
mean change in MDA
0.6
0.4
0.2
0.0
1.2
1.5
1.8
2.1