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Phenotypic plasticity can reverse the relative extent of intra- and interspecific variability across a thermal gradient

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Intra- and interspecific variability can both ensure ecosystem functions. Generalizing the effects of individual and species assemblages requires understanding how much within and between species trait variation is genetically based or results from phenotypic plasticity. Phenotypic plasticity can indeed lead to rapid and important changes of trait distributions, and in turn community functionality, depending on environmental conditions, which raises a crucial question: could phenotypic plasticity modify the relative importance of intra- and interspecific variability along environmental gradients? We quantified the fundamental niche of five genotypes in monocultures for each of five ciliate species along a wide thermal gradient in standardized conditions to assess the importance of phenotypic plasticity for the level of intraspecific variability compared to differences between species. We showed that phenotypic plasticity strongly influences trait variability and reverses the relative extent of intra- and interspecific variability along the thermal gradient. Our results show that phenotypic plasticity may lead to either increase or decrease of functional trait variability along environmental gradients, making intra- and interspecific variability highly dynamic components of ecological systems.

1. Introduction

Understanding how biological diversity is generated and maintained at various levels of biological organization, from genes to ecosystems or from local to global scales, is at the core of ecological and evolutionary research. In principle, all habitats differ in their abiotic and biotic conditions, and every organism holds a unique history. As a result, the structuring, dynamics and functioning of biological systems across landscapes could be as diverse as the diversity of life forms itself. However, general patterns exist, with for instance higher species diversity in the tropics [1], or the scaling of metabolism and abundance with body size [2]. Identifying how the processes shaping biodiversity can lead to either common or divergent patterns across multiple scales is thus imperative to reach an integrated comprehension of biodiversity functioning and dynamics [1].

The comprehension of biological patterns across multiple scales is the focus of a great body of research, with an important emphasis on spatial scaling [1,3]. On the organizational scale, intraspecific variability has been relatively overlooked [4–8]. Intraspecific variability is however the nexus of any eco-evolutionary dynamics [9,10] and is now recognized by ecologists as key for community and ecosystem functioning [4,5,11–13]. For instance, intraspecific variability can allow niche complementarity and favour the stability of populations and communities [5,11,13–15], similarly to species richness favouring functional diversity [16,17]. Intraspecific variability can promote species coexistence by buffering environmental effects [18]. A recent meta-analysis showed that the effect size of intraspecific variability on communities (i.e. species abundance and diversity) and ecosystems (decomposition rate, element cycling, primary productivity and respiration) can be as important as the effect size of interspecific variability [13].

A key property of intraspecific diversity is that it permits rapid evolutionary changes, with the rapidity of such response to environmental changes that depend on the underlying mechanisms. A first mechanism is the sorting by natural selection of (epi)genetic heritable variants matching a given environmental condition over generations. However, the same assemblage of individuals may also lead to different phenotypic assemblages, and thus ecosystem functions, depending on the environmental context. Indeed, while the expression of traits can be entirely genetically based (full canalization of phenotypic variance), it can also vary depending on the environmental context as a result of phenotypic plasticity (reviewed for instance in [19–22]). Plastic variation, when one genotype modifies its phenotype depending on environmental conditions [19–21], can buffer perturbation effects and increase the range of conditions organisms can deal with through reversible trait changes within a single or a few generations [23,24], and therefore affect population dynamics and species interactions [25,26]. Across generations, heritable genetic variation for phenotypic plasticity can allow the selection of adaptive reaction norms [27,28]. Because phenotypic plasticity can rapidly modify how organisms interact with their environment and allow for broad fundamental niches, it is a major mechanism underlying modifications of species interactions and community composition at very short timescales [25,29,30]. How much of the variability in functional traits results from phenotypic plasticity, and whether the relative importance of plastic and genetically based variation differs among species are thus important current matters of investigation in community ecology [5,11,25,29,31–33].

Phenotypic plasticity, the ability of a genotype to lead to multiple phenotypes depending on the environment, generates changes of phenotypic traits along with environmental gradients. However, phenotypic reaction norms can differ among species, individuals and even traits (e.g. [34–36]). This makes one crucial question emerge: depending on how reaction norms vary within and among species, could phenotypic plasticity modify the relative importance of intra- and interspecific variability along environmental gradients? For instance, in the case of temperature gradients (i.e. thermal plasticity [36]), does warming increase phenotypic variability because of intra- and interspecific variability in thermal plasticity? Or alternatively, may differences in plasticity lead to reduced phenotypic variance in some environmental contexts, as would be expected if stronger phenotypic canalization occurs at higher temperatures? This might for instance underlie patterns of context dependence of covariations between intra- and interspecific variability, as found in plants [37]. Despite vast evolutionary literature on the origin, extent and consequences of phenotypic plasticity [19–22,33], and ecological literature on the extent of intra- versus interspecific variability [4,5,11–13,37,38], whether phenotypic plasticity may mediate the relative extent of intra- and interspecific variability along with environmental gradients is to our knowledge unanswered.

Here, we aimed at experimentally quantifying the extent of intra- and interspecific variability in multiple phenotypic traits across a meaningful thermal gradient, and at determining the part of trait variation that is genetically based or results from phenotypic plasticity. We used laboratory microcosms housing different genotypes and species isolated in replicated and standardized conditions to quantify the fundamental niches across a wide thermal gradient. Our aim was to disentangle the importance of plasticity and genetic differences in trait variation along with environmental gradients, a prerequisite to improve our mechanistic understanding of trait and niche variation [8,39,40]. We used five clonal genotypes for each of five species of heterotroph ciliates from the genus *Tetrahymena*, including the model species *Tetrahymena thermophila* and *Tetrahymena pyriformis* [41]. We measured multiple ecologically relevant traits in monoclonal cultures exposed for 2 h (i.e. within one generation) to a wide thermal gradient, including cell size, shape, movement and growth rate. From these thermal reaction norms, we first quantified the importance of genetic background and plasticity in traits' variability. Second, we quantified the extent of intra- versus interspecific trait variability, and tested whether their relative importance varies between traits and along with the temperature gradient. According to recent ecological literature, we predict that variation within species should be at least as important as interspecific variability [4,7,11–13]. We also predict that the relative importance of intra- and interspecific variability should vary along the thermal gradient if the form of reaction norms and the relative extent of plastic compared to genetically based variability differ within and/or between species. Contrastingly, the relative importance of intra- and interspecific variability should stay constant along with the thermal gradient if reaction norms are conserved within and across species.

2. Methods

(a) Culture conditions, species and genotypes

Tetrahymena sp. are 20 to 50 µm unicellular ciliated micro-eukaryotes naturally living in freshwater ponds and streams [42,43]. Five species of the genus *Tetrahymena* naturally co-occurring in North America freshwater lakes and ponds were used in the present study: *T. thermophila*, *T. pyriformis*, *Tetrahymena americanis*, *Tetrahymena borealis* and *Tetrahymena elliotti* [43]. Genetically distinct strains reproduce clonally in laboratory conditions, meaning that, for a given clonal strain, differences in trait values between replicated environmental conditions in a timeframe of less than one asexual generation result from the expression of phenotypic plasticity (e.g. [44,45]). We used five genotypes per species, originally sampled from different locations in North America (electronic supplementary material, table S1). Cells were maintained in axenic liquid growth media (0.6% Difco proteose peptone, 0.06% yeast extract) at 23°C. All manipulations were performed in sterile conditions under a laminar flow hood.

(b) Morphological and movement traits along a thermal gradient

To quantify the reaction norms of phenotypic traits across temperature, five replicates of one-week-old cultures (around asymptotic density) for each genotype of each species were exposed for 2 h to six different temperatures: 15, 19, 23, 27, 31 and 35°C. The temperature range was defined to cover a maximum of the viable temperature range of the species *T. thermophila*, known as tolerant to a very large temperature gradient [41,46]. Exposure time was set to 2 h (i.e. below the maximal generation time across the whole temperature range [47]; this paper). As all genotypes and species were bred under the same standard laboratory conditions, parental effects in response to environmental variation at the previous generations should have limited effects on phenotypic variance.

Immediately after the 2 h exposure to each temperature, we used a standardized procedure to measure phenotypic traits.

From each culture, we pipetted two samples (10 µl each) into multichambered counting slides (Kima precision cell) and immediately took 20 s videos from each chamber under dark-field microscopy to measure cell morphology and movement characteristics using the *BEMOVI* R-package [48]. This package tracks moving particles and quantifies cells phenotypic traits through an image processing workflow.

We quantified two morphological and two movement traits. *Cell size* was computed as the cell surface area, and *cell elongation* as the ratio of cell major/minor axis [49]. The *velocity* of cells is defined as the total distance travelled by cells divided by the duration of the trajectory, and *linearity* is the ratio between the net distance travelled (Euclidean distance between start and end positions) and the total distance effectively moved through a more or less tortuous way, such that higher values indicate straighter trajectories. We used the average trait values over the two samples in the analyses. In this study, morphological traits were not significantly correlated with movement traits (all $p > 0.4$). Cell size was correlated to cell shape (estimate ± s.e. = − 1198.47 ± 536.79; $t_{1,19} = -2.23$; $p = 0.038$; $R^2 = 0.125$), and movement velocity was correlated to linearity (400.71 ± 102.93; $t_{1,19} = 3.89$; $p = 0.001$; $R^2 = 0.231$). Given these relatively low levels of correlation between traits, which suggests different mechanisms underlying most of their variation across environmental gradients, we analysed them separately.

(c) Performance along a thermal gradient

In parallel to the quantification of traits and their thermal plasticity, we reconstructed the thermal niche of each genotype by quantifying population growth rate from a small number of cells (approx. 100) along with the entire viable thermal gradient (11, 15, 19, 23, 27, 31, 35 and 39°C) to accurately describe the thermal niche [46,47]. Cells were inoculated in 96-well plates filled with 250 µl growth media, with five replicates per genotype. Population growth was quantified through absorbance measurements at 550 nm performed twice a day until populations reached their maximal density (about 10 days to 3 weeks) using a microplate reader (Tecan Infinite Spectrophotometer). To avoid any bias owing to slight variability in absorbance measures, and thus allow the predicted logistic growth curves to accurately match the observed data, we smoothed the absorbance data using a general additive model (*gam* package), a non-parametric method that does not require any assumption regarding the shape of the curve. We then used the *grofit* package (*gcfit* function) to fit a spline-based growth curve and compute the *growth rate* as the maximum slope of population growth through time (i.e. maximal population growth rate [46,47]). We here choose to use population growth rate instead of per capita growth rate because: (i) Allee effects are well known in *Tetrahymena* sp. ([50,51]; see also [52]), and (ii) per capita growth rates are estimated at low density, meaning close to the detection threshold of optical density, and show no repeatability in this system ($R = 0.023$; $p = 0.118$) while the population growth rate is highly repeatable ($R = 0.833$; $p < 0.001$). The thermal niche of each genotype was computed from the relationship between growth rate and temperature fitted with a *gam*.

(d) Statistical analyses

For morphological and movement traits (cell size, elongation, velocity and linearity), we computed: (i) the average of phenotypic values over all tested temperatures, and (ii) the slope of the relationship between phenotype and temperature, as a measure of its thermal plasticity. Since some of the reaction norms obtained appear to deviate from the linear assumption (i.e. 17.8% are significantly quadratic), we additionally quantified phenotypic plasticity through the coefficient of variation (CV) of trait values along with temperature, which did not qualitatively modify our conclusions (electronic supplementary material, figure S1). It is noteworthy that excluding the 17.8% of quadratic reaction norms from the whole dataset did not change the results (data not shown). From the thermal niches, we computed: (i) *performance at optimum*, which is the maximum growth rate attained across temperature; (ii) *thermal optimum* as the temperature at the maximum growth rate; and (iii) *niche width* (i.e. the width of the thermal tolerance curve) as the temperature range containing 80% of the thermal niche (i.e. total tolerance range; [46]).

To disentangle the contribution of genetic and plastic mechanisms (i.e., respectively, genotype and temperature effects) underlying phenotypic variability, we quantified within each species, and for all phenotypic and performance trait, the relative extent of genetic (G), environmental (E) and gene by environment interaction following a G × E framework: traits were separately included as dependent variables in linear models (*lm*, *stats* R-package), with genotype identity and environment as explanatory variables (including the quadratic effect) and their interaction. Variance partitioning of the effects of genotype, temperature and their interaction on traits was performed using *calc.relimp* (*relaimpo* R-package with *lmg* metric) on models implemented using *lm* (*stats* R-package).

The contributions of intraspecific (variability among genotypes) and interspecific (variability among species) levels for total variability of mean traits and their plasticity were quantified using a repeatability estimation from linear mixed models fitted by restricted maximum likelihood, implemented in *rptGaussian* (*rptR* R-package). Genotype nested in species were included as grouping factors to compute the amount of variation (R^2) explained at the intra- and interspecific levels. Standard errors of contributions were estimated by parametric bootstrapping of mean traits and slope (1000 parametric bootstraps). For morphological and movement traits, we computed intra- and interspecific variability for both the mean traits across temperatures, and for the slope of thermal reaction norms as an index of phenotypic plasticity (patterns were similar when using the CV across temperature instead of the slope as a proxy of plasticity; see the electronic supplementary material, figure S1). For thermal niches, we partitioned the variance for the three descriptors: performance at optimum, thermal optimum and niche width. Finally, we tested for changes in the importance of intra- versus interspecific variability across temperature by partitioning the variance in phenotypic and performance traits at each temperature using the same method as exposed above.

3. Results

(a) Genetic versus plastic variation in traits

The analysis of thermal reaction norms through a Genotype by Environment statistical framework revealed that the variance in morphological and movement traits resulting from differences among genotypes, independently from thermal conditions, strongly differs between traits and species: the genotype effect G was significant for all traits in all species and explained between 8.0% and 91.6% of total trait variance across species (mean ± s.e. = 50.8 ± 21.0%; figure 1*a*). Cell size and linearity were the traits for which the genotypic effect G was the most important and consistent across species.

Morphological and movement traits showed patterns of thermal plasticity, as shown by the part of total variance significantly explained by the environment, again to different degrees depending on traits and species (environmental effects, mean ± s.e. = 13.4 ± 6.8%; range: 0.02 to 62.3%). Thermal reaction norms differed both between genotypes

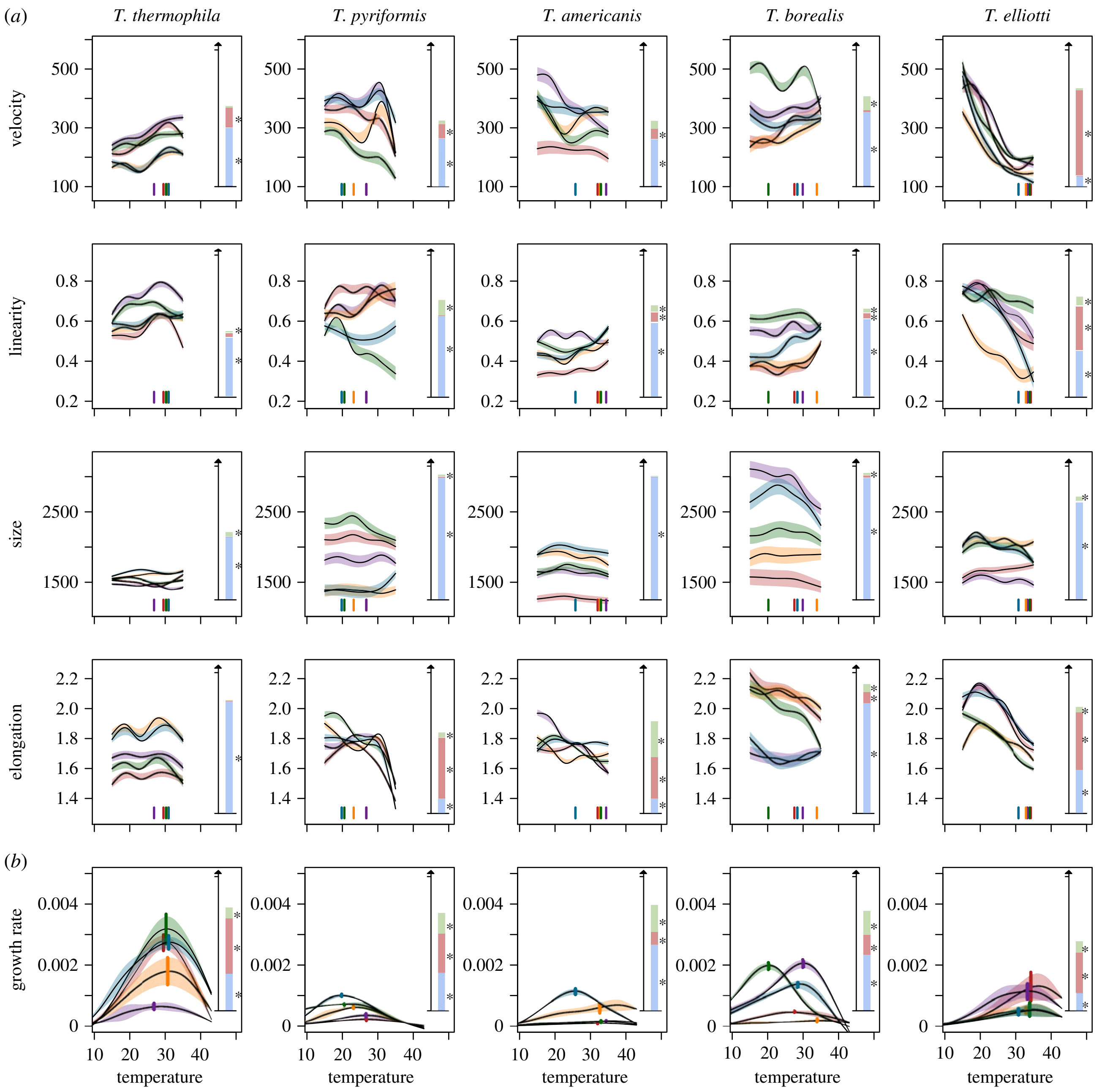

Figure 1. Thermal reaction norms of morphological, movement and performance traits in the genus *Tetrahymena*. (*a*) Thermal plasticity of morphological and movement traits after 2 h of exposure to six different temperatures (smoothed reaction norms ± s.e. using *gam* are shown). Coloured bars along the *X*-axis illustrate the position of the thermal optimum for each genotype. Inside graphs represent the contributions to the total variance in traits of genetic (in *blue*; 'G' variance explained by genotype identity), thermal plasticity shared among genotypes (in *red*; 'E' environment effect), and thermal plasticity that differ among genotypes (in *green*; 'G × E'). Significant contributions are annotated using asterisks (for $p < 0.05$). (*b*) Thermal niches of each genotype within each species, computed from the relationship between growth rate and temperature smoothed with a *gam*. Coloured bars show the position of the thermal optimum for each genotype. (Online version in colour.)

of each species (significant G × E interactions, mean ± s.e. = 5.1 ± 2.9%; range: 0.4% to 25.6%; figure 1) and among species (qualitative differences in figure 1 are further analysed quantitatively below; see section 'Intra- versus interspecific variability' and figure 2*a*). Interestingly, both the extent of plasticity and whether plastic responses are shared or different among genotypes of a species were trait- and species-dependent (figure 1). For instance, variability in velocity is mainly genetically determined in four species (higher G than E or G × E contributions), but almost entirely plastic in *T. elliotti* (high E; figure 1*a*). Cell elongation was mostly plastic in *T. pyriformis*, *T. americanis* and *T. elliotti*, and on the contrary mostly genetically determined in *T. thermophila* and *T. borealis*. Furthermore, intraspecific variability in phenotypic plasticity (G × E in figure 1*a*) varied between traits and species. For instance, thermal plasticity in movement velocity appeared highly similar among genotypes in *T. elliotti*, while it showed strong intraspecific variability in *T. borealis*. Although the extent of plasticity in cell size appeared small, we found significant G × E effects in four of the five species.

Performance (measured here through growth rate) differed significantly among genotypes within all five species (G effects, mean ± s.e. = 32.2 ± 13.1%; range: 0.13% to 49.3%; figure 1*b*). However, and contrary to morphological and movement traits, variance in performance resulted equally from genetic factors and plasticity (figure 1*b*). The temperature effects on performance (E, mean ± s.e. = 24.9 ± 10.2%; range: 9.5% to

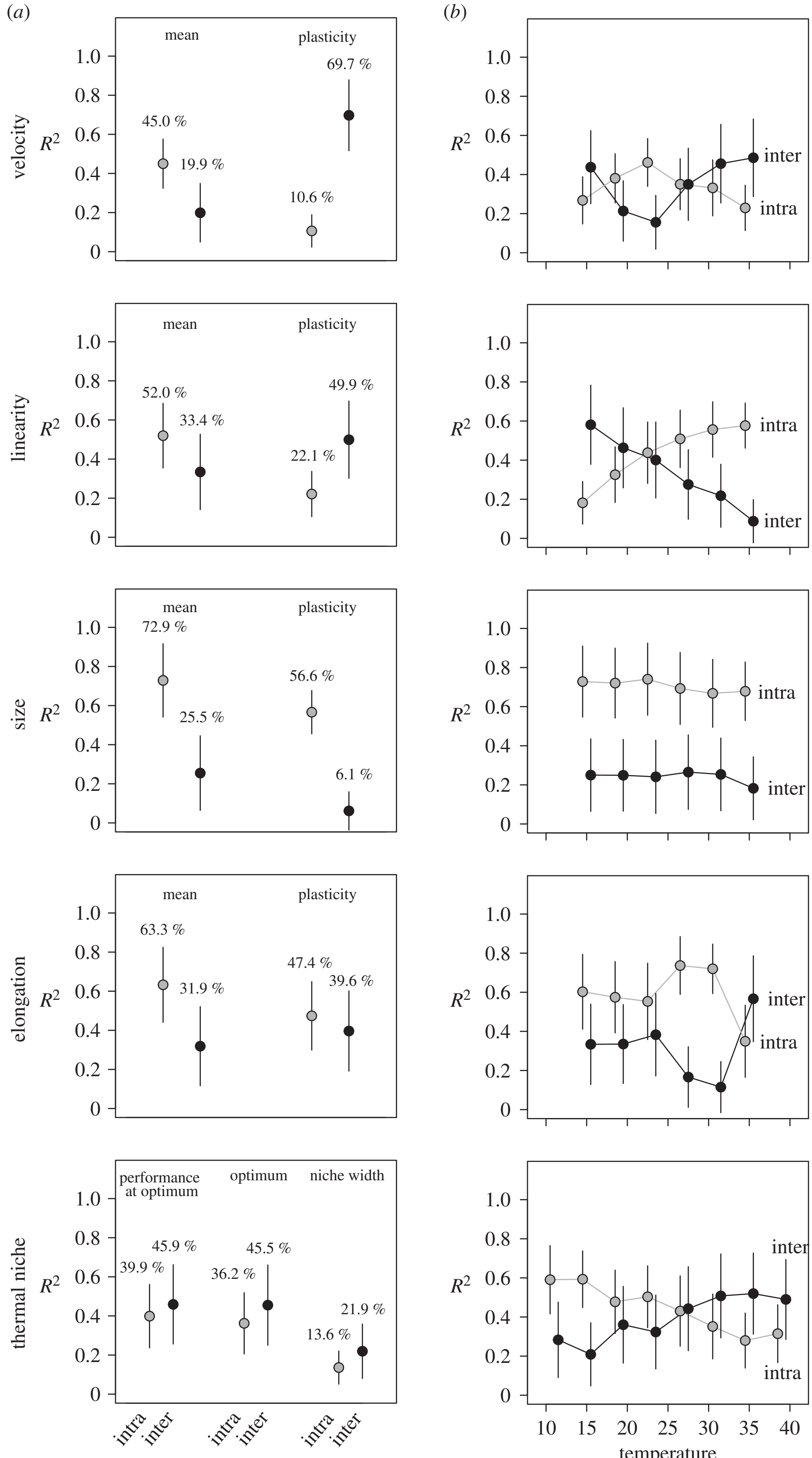

Figure 2. Intra- and interspecific variability of mean traits and plasticity along a thermal gradient in the genus *Tetrahymena*. (*a*) Contributions of intraspecific (among genotypes of a species; grey points) and interspecific (among species; black points) levels for the total variability in mean phenotypic traits (left) and in thermal plasticity (slope along with temperature; right). For thermal niches, intra- and interspecific variability are shown for three key descriptors: performance at optimum, thermal optimum and niche width. (*b*) Changes of intra- and interspecific variability along temperature. Mean ± s.e. are shown.

41.0%) differed both within (G × E, mean ± s.e. = 13.8 ± 5.6%; range: 8.0 to 19.9%; figure 1*b*) and among species (figure 1*b*; see below for quantitative analyses).

(b) Intra- versus interspecific variability

Investigating the extent of intra- and inter-specific variability for mean morphological and movement trait values (i.e.

averaged trait values across all six tested temperatures), we found that all traits differed among the five species, with species identity explaining 20 to 32% of the variance in mean phenotypic traits (dark points in the left panels of figure 2*a*). Interestingly, we found that the extent of intraspecific variability can equal and even outweigh interspecific variability for the four traits: differences among genotypes within species explain 45 and 52% of total variance in movement traits (respectively velocity and linearity), and 63.3 and 72.9% of total variance in morphological traits (respectively, elongation and size; grey points in figure 2*a*).

While intraspecific variability equalled or outweighed interspecific variability for mean morphological and movement trait values, the relative extent of intra- and interspecific variability in plasticity (as measured by the slope of reaction norms, see Methods) was trait-dependent (see also the electronic supplementary material, figure S1). Variability of plasticity in movement traits was lower within than between species, with 10.6 and 22.1% of the variance within species, respectively, for velocity and linearity, and 69.7 and 49.9% between species (figure 2*a*). Intraspecific variability in cell elongation plasticity was comparable to interspecific variability (respectively, 47.4 and 39.6%). Finally, while cell size was the less plastic trait in this study, we found that 56.6% of this plasticity was owing to differences between genotypes within species and only 6.1% to differences between species (figure 2*a*).

The variabilities of thermal niche descriptors (see Methods) were comparable within and between species (figure 2*a*). Especially, we found 39.9 and 36.2% of the variance in performance at optimum and thermal optimum at the intraspecific level, while 45.9 and 45.5% occurred at the interspecific level. For thermal niche width, differences between genotypes explained 13.6% of the variance while differences between species explained 21.9%.

(c) Changes of intra- and interspecific variability along the thermal gradient

We found that the relative importance of intra- and interspecific variability changed along with the thermal gradient (figure 2*b*), except for cell size where intraspecific outweighed interspecific variability at all temperatures. For instance, intraspecific variability of movement velocity outweighed interspecific variability at intermediate temperatures, while the pattern reversed at the warm margin of the thermal gradient (figure 2*b*). On the contrary, movement linearity was more variable between species than within at low temperatures and turned almost exclusively variable at the intraspecific level at warmer temperatures (figure 2*b*). Interestingly, the variability of performance also showed temperature-dependent patterns, with a decrease of intraspecific variability when temperature increased, while interspecific variability increased with temperature (figure 2*b*).

4. Discussion

Intraspecific variability is now recognized not only as the essential material for evolution, but also as a main component of ecological dynamics [4,5,11–13,38]. In this study, we aimed at quantifying the origin (genetic versus plastic) and extent of intra- versus interspecific variability of several morphological, movement and performance traits measured in monocultures of five closely related ciliate species along a wide thermal gradient. As expected, we found that variability in all traits resulted from both genetic background and phenotypic plasticity, and that the variability of these traits at the intraspecific level can equal or even outweigh interspecific variability [4,5,11–13,38]. Furthermore, we showed that phenotypic plasticity, by strongly modifying the amount of trait variation within species observed at different temperatures, can reverse the relative importance of intra- and interspecific variability along the thermal gradient. We discuss below the potential implications of these results for both ecological and evolutionary dynamics.

(a) Importance of genetic background and plasticity in trait variability

Variability among populations and species can have major implications for ecological and evolutionary dynamics (e.g. rate of adaptation, colonization efficiency, community stability and ecosystem services), but these consequences can differ depending on the mechanisms underlying such variability [5,11,19,31,32]. While heritable genetic variability allows adaptation through generations, phenotypic plasticity can result in rapid but non-heritable trait changes (see however *transgenerational plasticity* [53]), which might help organisms to rapidly deal with a wide range of environmental conditions. Phenotypic plasticity can indeed have major effects on population dynamics and species interactions [25,26,32]. Using experimental microcosms, we showed that, while an important part of the variability in phenotypic traits results from the genetic background, phenotypic plasticity can explain an important part of the variance in morphological and movement traits (up to two-thirds; figure 1). Similarly, changes in performance across the temperature gradient, therefore linked to expected fitness, equalled or even exceeded differences among genotypes.

Variability of trait expression in response to temperature variation is a ubiquitous phenomenon studied for decades in a diversity of taxa and traits (e.g. [36,54,55]). While general patterns of reaction norm shapes can be drawn like the unimodality of thermal performance, protists remain a poorly studied group compared to others [36]. Thermal performance has been measured in several protist species [56,57], but other traits (i.e. morphological, behavioural and physiological) are more rarely investigated (e.g. [58,59]). Here we show that changes in temperature induce the expression of plasticity in all tested traits in five *Tetrahymena* species. However, except for the classical performance thermal curve, no general pattern emerged across species, and the G × E interaction was often significant, meaning that variability in thermal reaction norms are common within species. This latter result might be common, since similar patterns were found for instance in *Drosophila* and plant species [60–62]. Such variation of traits along environmental gradients through phenotypic plasticity means that the relationship between genetic and phenotypic diversity (and by extension trait functionality and potentially complementarity) can greatly change, even at small temporal and spatial scales. These questions the ability of biodiversity indices based on genetic diversity to generally reflect functionality across situations (see an interesting development of such metrics in [63]). We suggest that plastically generated diversity could explain cases where genetically based indices fail to fully explain functionality, and that phenotypic diversity indices could potentially help to scale-up the effect of intraspecific diversity on ecological dynamics.

We found that the relative extent of genetic versus plastic variation can differ among traits and species, highlighting the importance of extending investigations of trait evolution and ecological functions beyond single-trait approaches [64,65]. Cell size for instance showed very low levels of plasticity, with almost all its variability resulting from genetic effects. On the contrary, variabilities in movement velocity and cell shape, two traits related to foraging and dispersal ability in ciliates [66,67], were almost entirely owing to plasticity in some species. On one side, weakly plastic traits, like cell size in this study, might provide reliable estimates of functional diversity across environmental conditions, as usually done in trait-based ecology [2,39,68]. On the other side, high plasticity of traits such as mobility might result in changes of trait diversity along with environmental conditions. Extrapolating trait values from measurements performed in a restricted range of environmental conditions might thus lead to under- or over-estimation of functional diversity in other environmental conditions. Therefore, our results confirm that obtaining accurate quantification of the influence of environmental variation on the expression of phenotypic plasticity and the level of intraspecific variability across species is an important challenge for our understanding of the functioning and stability of ecosystems [25,29]. One crucial step will be to estimate the (non)genetic heritability of the measured traits. Indeed, depending on the part of the heritable variation of each trait, the observed reaction norms, and thus the partition of intra- and interspecific diversity, could change across generations. The higher heritability is, the more consistent reaction norms should be over time. In this study, we measured trait values 2 h after exposure to thermal treatments, meaning less than one generation in our culture conditions. Transgenerational effects from previous generations are therefore not involved in the reaction norms quantified here. Whether observed phenotypic changes can reverse within the same generation (e.g. labile versus developmental plasticity) or affect subsequent generation through later transgenerational effects is an important next step in the comprehension of the origin and consequences of phenotypic plasticity in these species. Differences among traits in the type of phenotypic plasticity and the timing required to elicit plastic changes might partly explain why some traits appear more plastic than others.

Whether there is a convergence or divergence of reaction norms within and between species, owing to shared evolutionary history or trade-offs, remains poorly studied [69]. Reaction norms are expected to be more similar at the intra- than interspecific level, presumably owing to shorter divergence time [69]. Beyond providing evidence for thermal plasticity of multiple traits (E effects; figure 1), here we showed that reaction norms differed significantly among genotypes for all the traits investigated (G x E effects; figure 1), as previously found in other species (e.g. [27,28,57,70]). Such genetic variation within species in thermal plasticity may allow rapid evolution of plasticity facing environmental changes. These results point out once again that the integration of intraspecific variability into ecological community theories should consider not only the genotypic and species composition of communities, but also their composition in reaction norms [71]. Indeed, phenotypic plasticity and its intraspecific variability might generate changes of community function along environmental gradients independent of changes in community composition.

(b) Intra- versus interspecific variability along environmental gradients

Whether genotypes within a species can bear as much trait and functional variability as different species is an important and timely question [5,12,72]. Recently, there has been a general call in community ecology to consider intraspecific diversity with the same interest as interspecific diversity, because their effects can be as important for ecological dynamics [13], pushing them in similar or opposite directions. For instance, in bacteria forming biofilm communities, intra- and interspecific diversity can be functionally substituted to tolerate chemical stress [73]. Conversely, tree species richness promotes tree growth and has no effect on herbivory while family diversity within species mixtures reduces growth and increases herbivory [74]. Here we showed that intraspecific variability measured for five ecologically relevant traits can equal or outweigh interspecific variability across five ciliate species. For instance, the least plastic trait cell size, a key trait in community ecology analogous to body size in multicellular organisms [75], showed almost three times higher intraspecific than interspecific variability across all environments (72.0 and 25.5%, respectively; figure 2*a*). Similarly, velocity and cell elongation, two traits linked to foraging and dispersal and thus of major importance for both ecological and evolutionary dynamics [76], were twice as more variable at the intra- compared to interspecific level. These results point out the importance of understanding the effects of intraspecific variability, either genetic or plastic, for competition, niche complementarity and the width of realized niches (see below; [25,29,77,78]).

Beyond the overall levels of intra- and interspecific variability, we showed that their relative importance can change, and even reverse, along a temperature gradient owing to phenotypic plasticity (figure 2*b*). For instance, while intraspecific variability in movement linearity was lower than interspecific variability at low temperature, their importance reversed to six times more intraspecific than interspecific variability of movement when temperature rises (figure 2*b*). Inversely, variability of growth rate (a common proxy of fitness) goes from intra- to inter-dominated with warmer temperatures (figure 2*b*). This result suggests that intra- and interspecific thermal variability can be dynamic components of ecological systems that depend on variability in phenotypic plasticity between genotypes and species. Increased temperatures may therefore either lead to a convergence of traits within species (as for velocity and fitness here) or on the contrary to increased phenotypic and functional diversity.

One limitation of our study could be the limited phylogenetic diversity considered. We indeed used five ciliate species that belong to the same genus *Tetrahymena* and occupy similar positions in food chains. This limited sampling of species might explain the high levels of intraspecific variability we found when compared to interspecific variability. However, the five species are widely distributed in the *Tetrahymena* genus, a genus that originated approximately 300 Ma, about the origin time of amniotes [79]. This means that important evolutionary divergence exists between these five species, and that the extent of differences of mean traits and plasticity we found should thus be considered in this context of a long evolutionary history. Noteworthy, the large intraspecific variability observed in this study might partly result from genotypes being maintained isolated: the absence of competition among genotypes or species might inflate intraspecific variability compared to what would be expected under competition. Alternatively, competition within or between species might in itself result in phenotypic changes favouring a divergence of realized niches and thus in an increased intraspecific diversity (e.g. [29,30,80]). One important development will be to determine if and how the extent of phenotypic plasticity differs depending on intra- and interspecific competition, and whether it can shape changes in the relative importance of intra- and interspecific variability along other environmental gradients, and across trophic position or food chains.

5. Conclusion

Temperature is among the most studied abiotic factor defining habitats, and current global warming makes the accumulation of data on ecological and evolutionary response to increased temperatures urgent [81]. Our results highlight that neglecting intraspecific variability, both in terms of genetic diversity and phenotypic plasticity, could strongly bias the estimation of functional diversity and complementarity in populations and communities [4–7,11–13,38,82]. In the future, one key point will be to determine if climate warming will lead to a convergence of functional traits, or else to an increase of phenotypic variability, and what will be the consequences of thermal plasticity on species adaptiveness.

The classical focus on a few traits to summarize the functionality of species could restrict our understanding and ability to forecast ecological dynamics [39,64,68]. Integrating multiple key traits like thermal tolerance and dispersal, and identifying the mechanisms underlying their variability, is crucial given the role of these traits for organisms' performance in our spatially and temporally variable world. Especially, populations, communities and ecosystems are interconnected through fluxes of matter and organisms (e.g. [83]). Investigating how intraspecific variability in traits and their plasticity affect these fluxes is therefore crucial for our comprehension of metapopulations, metacommunities and metaecosystems [84–86].

Finally, genetic and plastic changes usually occur at different timescales. As described here, phenotypic plasticity can provoke immediate, extensive and potentially beneficial remodelling of functional trait values along with environmental gradients. Even in a few generations, such extensive remodelling of functional diversity is unlikely to occur repeatedly through genetic changes, although plasticity itself can enhance adaptation (e.g. [33,87]). However, depending on the homogenizing effect and costs of plasticity [88], it could also accelerate species extinction. Predictive models of biodiversity response to global change considering intraspecific variability could therefore have totally different outcomes depending on the source of variation.

Data accessibility. The data supporting the findings of this study is available from the Dryad Digital Repository: https://dx.doi.org/10.5061/dryad.s1rn8pk73 [89]. The data are provided in the electronic supplementary material.

Authors' contributions. S.J.: conceptualization, data curation, formal analysis, funding acquisition, investigation, methodology, project administration, resources, software, validation, visualization and writing—original draft; D.L.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, validation, visualization, writing—review and editing. Both authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Competing interests. The authors declare no conflict of interest.

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