Evolvability and macroevolution of colony-level traits in two species of bryozoans

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Abstract: The evolution of trait variation among populations of animals is difficult to study due to the many overlapping genetic and environmental influences that control phenotypic expression. But, in a group of animals called bryozoans, it is possible to isolate genetic contributions to phenotypic variation, due to the modular nature of bryozoan colonies. Each bryozoan colony represents a snapshot of the phenotypes that correspond to a single genotype, which can be summarized as a phenotypic distribution. We test whether these phenotypic distributions are evolvable across a generation of colonies in two sister species of the bryozoan *Stylopoma*, grown and bred in a common garden breeding experiment. We find that components of phenotypic distributions, specifically median trait values of colony members, are evolvable between generations of colonies. Furthermore, this evolvability has macroevolutionary importance because it correlates with the morphological distance between these two species. Because parts of the phenotypic distributions are evolvable, and this evolvability corresponds to evolutionary divergence between species, we infer that these distributions can shift and change shape over macroevolutionary timescales. Such changes to phenotypic distributions across many generations of colonies may underpin the emergence of colony-level traits, like division of labor in colonies.

Introduction

In a group of colonial animals called cheilostome bryozoans, colonies are composed of genetically identical individuals, termed zooids, that possess a wide range of phenotypic variation (McKinney and Jackson, 1991; Lidgard, 1990). This variation is expressed among zooids (Cheetham et al., 1993), so that colonies represent a snapshot of the phenotypic variation that stems from a single genotype (Cheetham et al., 1995). At its most extreme, this variation within colonies is expressed as differentiated body types, called polymorphs, which serve different functions in the colony. How polymorphism in bryozoans evolved is unknown (Taylor, 2020), but it is impossible to resolve without first understanding whether phenotypic variation within colonies is actually evolvable across colony generations.

Cheilostome bryozoans have a complex life cycle with distinct asexual and sexual modes of reproduction (Taylor, 2020; McKinney and Jackson, 1991). Asexual reproduction allows for a single colony to grow larger by increasing the number of zooids in a colony. The sexual stage of the cheilostome bryozoan life cycle leads to the formation of new colonies, via the release of gametes from colony members (Lidgard and Jeremy, 1989; McKinney and Jackson, 1991; Taylor, 2020). The larvae formed by sexual reproduction between colonies found new, genetically-distinct colonies upon settling.

The structure of phenotypic variation (V_P) present within a colony is neither the result of trait similarity between asexually-budded zooids (Simpson et al., 2020) nor environmental change along axes of colony growth (Okamura, 1992). However, species of bryozoans have measurable zooid-level differences from each other (Jackson and Cheetham, 1990). Therefore, there must be some mechanism that allows for zooid morphologies to evolve. If phenotypic variation present among zooids within colonies stems from additive genetic variances (V_A) passed across the sexual stage of reproduction (Fig. 1), then zooid-level traits are evolvable as colony-level phenotypic

distributions. The evolvability of these distributions would support existing explanations for the evolution of division of labor in bryozoan colonies, because polymorph types are believed to be derived from preexisting body types within colonies (Taylor, 2020; McKinney and Jackson, 1991).

In this study we assessed trait distributions of parent-offspring colony pairs in two *Stylopoma* species to test the hypothesis that trait variation in colonies is evolvable. These same specimens were used in a series of pioneering studies on quantitative genetics of bryozoans during the 1990s (Cheetham et al., 1993, 1994, 1995). However, these studies focused on zooid-level traits and did not consider colony-level evolution. Here we use new measurements on these same specimens to quantify the evolvability (sensu Houle 1992) of colony-level traits, and therefore their evolutionary potential.

Methods

Specimens

We used colonies from two species of the bryozoan genus *Stylopoma*. These specimens were originally used in several studies on skeletal morphology and the assessment of morphological difference between species of *Stylopoma* (Jackson and Cheetham, 1990; Cheetham et al., 1993, 1994, 1995). Colonies were grown in the 1980s from a larval stage to adulthood in a common environment at the Smithsonian's field station in the San Blas islands in Panama. The experimental design was based on Maturo's protocol (Maturo Jr, 1973) to isolate maternal colonies with a clean substrate for their larvae to settle. Once offspring colonies were established, they were reintroduced into a common environment. More details on the rearing of these specimens can be found in Jackson and Cheetham 1990; Cheetham et al. 1993; Simpson et al. 2020.

We used a total of 93 parent-offspring colony pairs of *Stylopoma species 1* (42 pairs) and

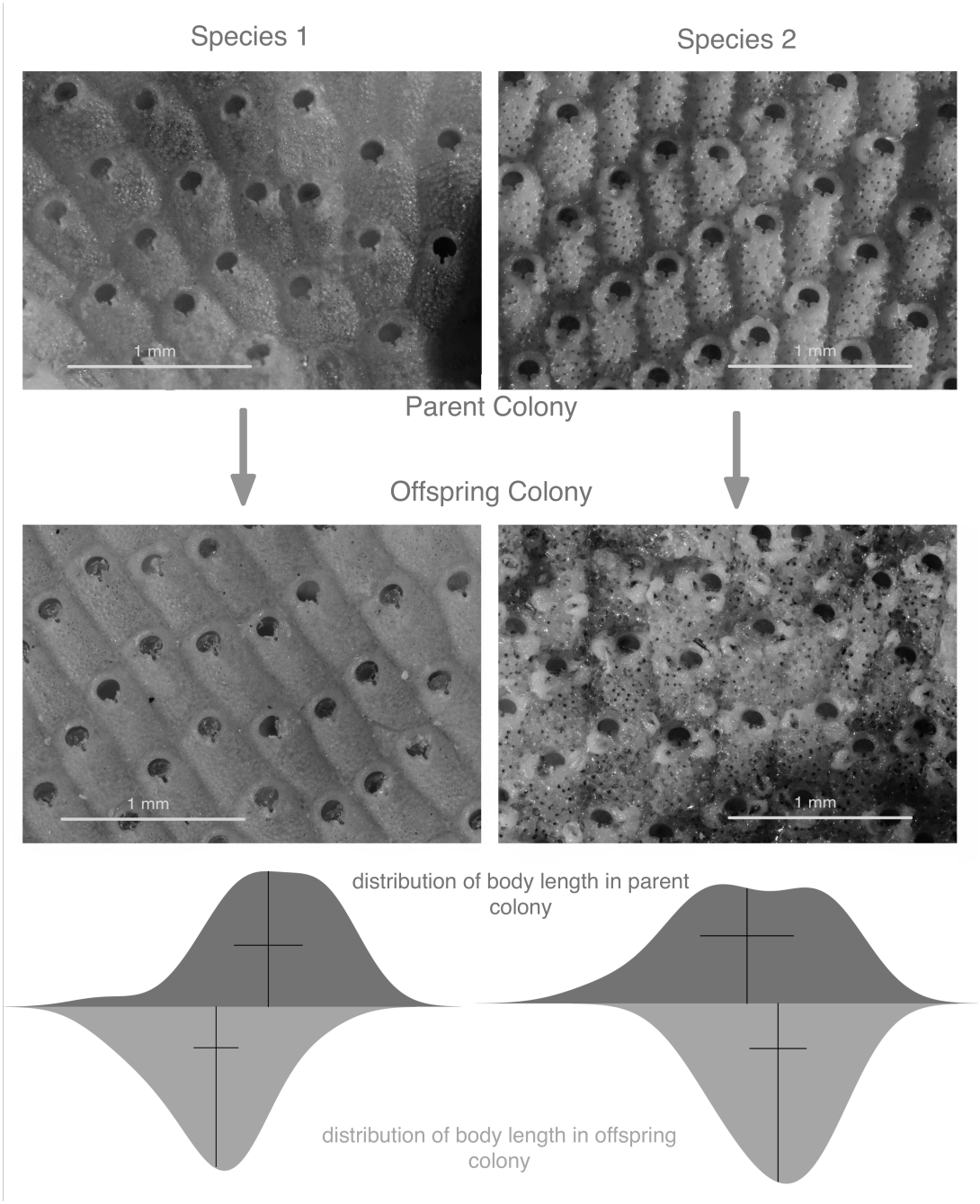

Figure 1: **An example of aggregate phenotypic similarity across a colony generation.** We show an example of two colony generations from two species of *Stylopoma*. The resulting distributions of length values are displayed below each maternal and its offspring colony. To quantify the distributions, we measure two aspects of these distributions: central tendency with the median (vertical black lines) and dispersion around the median with median absolute deviation (MAD, horizontal black lines). The analysis in this study measures parent-offspring covariation by comparing the medians and median absolute deviations of traits across colony generations.

Stylopoma species 2 (53 pairs).

Quantifying aggregate colony-level traits

We measured two summary statistics of the distributions of five autozooid traits in digitized mother and offspring colonies. To digitize colonies, we used a stackshot rail, a Canon EOS camera, and Helicon Remote software to generate image stacks of colonies, and we used Helicon Focus software to stitch together our image stacks, yielding high-resolution photographs for measurement. We evaluated this technique for error by repeatedly measuring the same zooids in a colony photographed at different angles. We found that at extreme angles, we had an error of ±20, but for our flat speciemens the error was much less. Within each colony, we selected thirty autozooids at random and measured four of their skeletal traits: zooid length, zooid width, orifice length, orifice width. A fifth trait, frontal pore density, was quantified using a subset of five zooids. We selected these traits because they are taxonomically significant in *Stylopoma*, as they allow for the morphological distinction of these two species (Simpson et al., 2020; Jackson and Cheetham, 1990). To assess the measurement error for these traits, we measured each trait on a single zooid from each species ten times. The ranges of the measurements in each species were calculated and divided by with the mean measured value in each species. The resulting error estimates were averaged between the two species, yielding single estimates of measurement error for each trait. The resulting error values were 3.8% for zooid length, 4.0% for zooid width, 4.1% for orifice length, 2.8% for orifice width, and 4.9% for frontal pore density. Since the calculation of summary statistics relies on measured individual traits, the error for median values and MAD values of traits are comparable to the error in individual measurements.

The colony-level traits we selected are based on two summary statistics that quantify the phenotypic distributions of constituent zooids. We first quantified the median phenotype (a measure of central tendency) of each trait in each colony. Then, we quantified dispersion among

zooids within a colony by calculating the median absolute deviation (MAD). We chose these two summary statistics as proxies for the mean and variance because they are robust to small sample sizes (Whitley and Ball, 2001; Leys et al., 2013; Kashif et al., 2017) and if the data are normally distributed, these values are estimators of the mean and variance. Given the large number of measurements ($> 25,000$) required for this study, we prioritized measuring more colonies over sampling more zooids within a colony. The use of the median and MAD values ensures that central tendency and dispersion in the dataset are adequately captured. Of course, it is possible that evolution can occur at higher moments (skew and kurtosis) (Rice, 2004) of the distributions, but for this analysis we are focusing on first and second moments.

Measuring colony-level aggregate trait evolvability

There are generally two types of colony-level traits: aggregate traits, which are summary statistics of traits in colony members, and emergent traits, which are only expressed at the colony-level (Grantham, 1995; Okasha, 2014; Lloyd and Gould, 1993). Evolutionary potential of these traits has rarely been assessed, with the exception of some studies (e.g., Jablonski 1986 and Jablonski and Hunt 2006). In bryozoans, emergent colony-level traits, such as the position and orientation of polymorphs relative to other zooids in colonies, are known to have evolutionary potential (Simpson et al., 2020). As far as we know, while the sorting of aggregate traits has been subject to some prior study (e.g., Lloyd and Gould 1993), the evolutionary potential of aggregate traits has never been assessed. Here we assess the evolutionary potential of aggregate traits in bryozoan colonies.

We follow Schluter (Schluter, 1996) to calculate a G-matrix using parent-offspring pairs, and Hunt (Hunt, 2007) to calculate evolvabilities. Traditionally, evolutionary potential is measured by a quantity termed heritability (h^2), which is the proportion of total phenotypic variation that

is underpinned by additive genetic variance ($h^2 = \frac{V_A}{V_P}$). However, heritability has fallen out of favor because $\frac{V_A}{V_P}$ is a measure that scales with the degree of phenotypic variance, and is therefore not an adequate quantitative prediction of evolutionary change across multiple traits (Houle, 1992). Instead, we scale additive genetic variance (V_A) by the mean trait value squared, yielding a measure called evolvability (Houle, 1992; Hansen and Houle, 2008; Love et al., 2021).

To estimate evolvability, first we calculated the covariances of these median and MAD values across parent and offspring colony generations to form a parent-offspring covariance matrix (Fernandez and Miller, 1985; Rice, 2004; Falconer and Mackay, 1996). Since these colonies are sexually produced, we doubled this covariance matrix to estimate additive genetic covariances and variances of traits (Falconer and Mackay, 1996). To deal with the natural asymmetry of a parent-offspring covariance matrix, we took the mean of entries across the diagonal (Schluter, 1996). Any entries that fell below zero were set to zero, since they tend to have low r^2 values (Cheetham et al., 1995). This results in two matrices, one for *S. species 1* and one for *S. species 2*. The dimensions of these matrices correspond to the ten colony-level aggregate traits we measured: the median and MAD values of zooid length, zooid width, orifice length, orifice width, and frontal pore density. To calculate evolvabilities from the G-matrix of each species, we scaled entries by dividing them with the squared mean value for each trait (Hansen et al., 2011; Houle, 1992). For off-diagonal values, we use the product of the two trait means instead of a single trait squared mean. Scaling the G-matrix in this way yields evolvabilities (Houle, 1992), which can be interpreted as a maximum percent change per generation.

We calculated the standard error in our estimates of trait evolvability using the method outlined by Lynch and Marsh (Lynch and Walsh, 1998). To follow this method, we first found the standard deviation of our large sample variance for each trait and then we divided that standard deviation value by the trait mean squared (Lynch and Walsh, 1998; Garcia-Gonzalez et al., 2012). The resulting values is the standard error of each evolvability estimate.

Calculating Directions of Evolutionary change

Since these two species of *Stylopoma* are sisters (Jackson and Cheetham, 1994), we have the opportunity to understand how our measured evolvability values correspond to the pattern of trait divergence between these species. To do this, we first transformed our data by the natural log (Schluter and McPhail, 1992) to remove the large differences in trait variance and to reduce skew in the dataset. Then we calculated the deviation between the species trait means as a vector connecting the two centroids of the species trait distributions (Hopkins, 2016), pointing from *Stylopoma species 1* to *Stylopoma species 2*. We computed the components of this vector by taking the difference in the ln-transformed trait means, with each entry corresponding to a different trait. We then decomposed the resulting divergence vector into components corresponding to each of the 10 traits.

To evaluate the structure of variation in each species, we calculated the eigenvectors and corresponding eigenvalues of the evolvability matrix for each species. We used the first eigenvector for our analysis (Schluter, 1996). Historically, the angle between the first eigenvector of each species and the divergence vector between species is used to evaluate how the structure of variation in a species corresponds to the direction of divergence between species (Schluter, 1996). This method has been subject to criticism in the past for focusing exclusively on the major axis of variation in a species (Hunt, 2007). Hunt (2007) suggested calculating the variance ("projected variance") of the entire covariance matrix onto the divergence vector between species to remedy this problem (see (Hunt, 2007) for details). This method is useful in analysis across multiple species when the first eigenvector of the G-matrix does not capture most of the additive genetic variance. Since our analysis focuses on two species, we have the opportunity to look at trait-specific patterns of divergence.

In our case, we want to understand how each trait relates to the pattern of divergence observed between species. Since the first eigenvector of our evolvability matrices covers most

of the variation in each species (51% of the additive genetic variance of *Stylopoma sp1* and 83% of the additive genetic variance of *Stylopoma sp2*), we focus only on the first eigenvector of each scaled G matrix for this analysis. We therefore estimated the angle between the first eigenvectors of each species (Hansen and Houle, 2008) and the decomposed divergence vector. To do this, we computed the arcosine of the inner product of the first eigenvector for each species and each component of the divergence vector. The resulting angles represent the deviation between the first eigenvector of each evolvability matrix and the amount of divergence for each trait. This provides insight into how the direction of evolutionary divergence in each trait between the species corresponds to the structure of variation within each species.

We compared the angles (which we call θ_i, for traits 1 through i) calculated from the procedure above with the trait evolvabilities as well as the distance between species. For each comparison, we calculated correlations to assess the significance of the relationship. To assess the direct relationship between trait evolvabilities and trait divergence between the species, we took the mean evolvability value for each trait across the two species and compared those mean evolvabilities with trait divergence between the species. We measured a correlation to evaluate the strength of this relationship.

Estimating rates of species divergence

Our calculated evolvability values can provide a lower bound on the number of generations required for divergence between *Stylopoma species 1* and *Stylopoma species 2*. Evolvability values represent maximized phenotypic change per generation. Thus, assuming stability of the G matrix on macroevolutionary timescales and stability of a selective gradient, we take our smallest calculated evolvabilities and estimate the maximum rate of change for the phenotypes of *Stylopoma species 1* to converge at the phenotypes of *Stylopoma species 2*. Both species experience stasis (Jackson and Cheetham, 1999), so we estimate minimal divergence time to

represent the number of generations for *Stylopoma species 1* to match *Stylopoma species 2*.

Results and discussion

The evolvability of colony-level phenotypic distributions

Our measures of evolvabilities have the advantage of being interpreted as percentages, ranging from 0.1% to 15% per generation. These evolvability measures (Tables 1 and 2, Fig. 2), at least for median trait values, complement the findings from Cheetham et al.'s 1993 study of *Stylopoma* quantitative genetics (Cheetham et al., 1993). We find that aggregate traits of colonies are evolvable. Because median and MAD traits are evolvable at the colony level, sexual reproduction among colonies allows colonies to maintain and evolve these parts of their phenotypic distributions.

In traits that have evolvabilities of zero, evolution may still be possible through covariation with other traits. For example, the median trait value of orifice width is not evolvable in either species. However, the median orifice width value has a positive covariance with other traits across generations of colonies (Tables 3 and 4). The covariation across traits in the G-matrix may explain how traits with no evolvability may still diverge across species.

The macroevolutionary impact of evolvable distributions

The angle between the first eigenvectors of *Stylopoma species 1* and *Stylopoma species 2* correlates negatively with the trait evolvability and the components of trait deviation between species ($-0.95 < r^2 < -0.45$ across all analyses; Fig. 2 A and B). These results show that smaller angles of deviation between each first eigenvector and each component of the species divergence vector correspond to traits with higher evolvabilities and higher divergence between

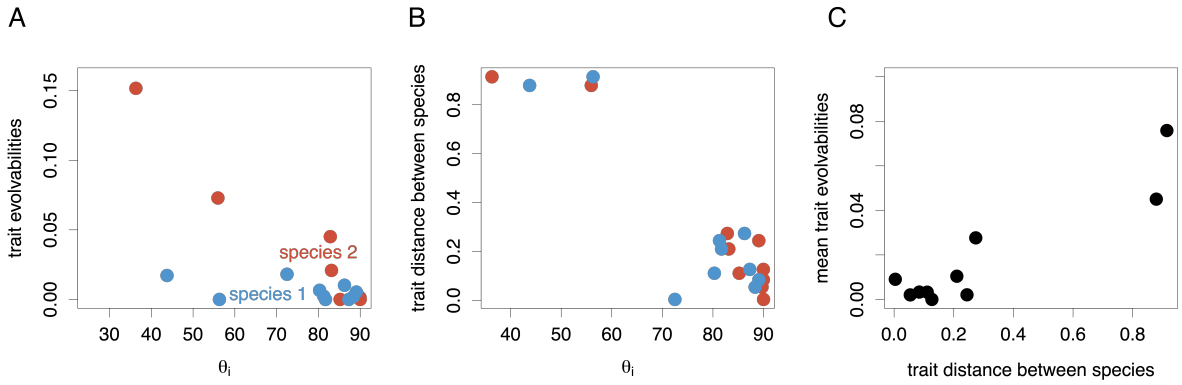

Figure 2: **Macroevolutionary impact of colony-level evolvability. A:** Angle between each component of the mean trait divergence vector and the first eigenvector of median trait values in each species (θ_i) plotted against trait evolvabilities (r^2_{sp1} = -0.45, r^2_{sp2} = -0.97). **B:** Angle between each component of the mean trait divergence vector and the first eigenvector of trait values in each species plotted against the trait divergence vector (r^2_{sp1} = -0.87, r^2_{sp2} = -0.96). **C:** Averaged trait evolvabilities plotted against mean trait divergence (r^2=0.92).

Table 1: **Trait evolvability in *Stylopoma species 1*.** Evolvability values for five trait medians and five trait MADs. ol=orifice length, ow=orifice width, pd=pore density.

	evolvability value	standard sample error
median length	0.0019	±0.000094
median width	0.0053	±0.00020
median ol	0.0023	±0.00069
median ow	0.00	±0.00038
median pd	0.017	±0.0029
MAD length	0.0065	±0.0058
MAD width	0.018	±0.0041
MAD ol	0.00	±0.033
MAD ow	0.010	±0.035
MAD pd	0.00	±0.050

the species.

Furthermore, traits with higher evolvability tend to be more divergent between species (Fig. 2 C). Our measure of evolvability between colonies and trait divergence between species complements the previously observed positive correlation between trait variance in a population

Table 2: **Trait evolvability in *Stylopoma species 2*.** Evolvability values for five trait medians and five trait MADs. ol=orifice length, ow=orifice width, pd=pore density.

	evolvability value	standard sample error
median length	0.0021	±0.00012
median width	0.0013	±0.00019
median ol	0.0019	±0.00074
median ow	0.00	±0.00028
median pd	0.073	±0.011
MAD length	0.00	±0.0050
MAD width	0.00	±0.0043
MAD ol	0.021	±0.037
MAD ow	0.045	±0.032
MAD pd	0.15	±0.14

and trait divergence between species, termed evolution along lines of least resistance (Schluter, 1996). In fossil species of ostracods (Hunt, 2007), in extant species of fiddler crabs (Hopkins et al., 2016), and in stickleback fish (Schluter, 1996), macroevolutionary change of organism-level traits occurs preferentially in directions of maximum phenotypic variance. In *Stylopoma*, we find that this pattern is also observable for colony-level aggregate traits.

The connection between the microevolution and macroevolution of phenotypic variation remains unclear (Erwin, 2000). As with the other bryozoan *Metrarabdotos*, species of *Stylopoma* exhibit punctuated equilibrium (Jackson and Cheetham, 1994). *Stylopoma species 1* diverged rapidly from *Stylopoma species 2* around 3 million years ago, and both species exhibit morphological stasis (Jackson and Cheetham, 1994, 1999). We find that the direction of speciation matches the direction of maximum evolvability across colonies, establishing a link between microevolutionary potential and microevolutionary pattern.

Cheetham et al. (Cheetham et al., 1994), following Lande (Lande, 1976), estimated the selection and drift needed to produce the observed pattern of stasis in *Stylopoma*. Assuming that selection and drift are involved in punctuated speciation, we can therefore complement

Table 3: **Trait evolvability matrix in *Stylopoma species 1*.** Evolvability matrix values for five trait medians and five trait MADs. ol=orifice length, ow=orifice width, pd=pore density. The diagonal of this matrix contains the evolvability values shown in Table 1.

	med length	med width	med ol	med ow	med pd	mad length	mad width	mad ol	mad ow	mad pd
med length	0.0019	0.0026	0.00075	0.00070	0	0.0042	0.0012	0	0	0
med width		0.0053	0.0019	0.0011	0	0.0014	0	0	0	0
med ol			0.0023	0.00036	0.0022	0.0099	0.011	0	0	0
med ow				0	0	0.00593	0.00359	0	0	0
med pd					0.017	0	0.0030	0.0027	0	0.0345
mad length						0.0065	0.0157	0	0	0
mad width							0.0181	0.0082	0.0078	0
mad ol								0	0	0.0040
mad ow									0.010	0
mad pd										0

Table 4: **Trait evolvability matrix in *Stylopoma species 2*.** Evolvability matrix values for five trait medians and five trait MADs ol=orifice length, ow=orifice width, pd=pore density. The diagonal of this matrix contains the evolvability values shown in Table 2.

	med length	med width	med ol	med ow	med pd	mad length	mad width	mad ol	mad ow	mad pd
med length	0.0021	0.00065	0	0.00040	0	0.0050	0.00045	0	0.0057	0
med width		0.0013	0	0	0	0	0.0012	0.0010	0	0
med ol			0.0019	0.00021	0.0040	0	0	0.0046	0.0055	0
med ow				0.00000	0	0	0.00085	0	0.00088	0
med pd					0.073	0.0064	0	0.033	0.025	0.090
mad length						0	0	0	0.030	0.013
mad width							0	0	0	0
mad ol								0.021	0.039	0
mad ow									0.045	0
mad pd										0.15

Cheetham et al.'s estimate for stasis by estimating the minimum number of generations needed for punctuated speciation to occur. Our observed evolvabilities (Tables 1-4), which are interpretable as the maximum possible phenotypic change per generation, allow us to estimate a minimum time of speciation. Only 27 generations are needed to produce the phenotypic distance observed between species. Not only is the rate of punctuated speciation geologically rapid (Jackson and Cheetham, 1994), but it also may occur over short evolutionary time.

The role of evolving phenotypic distributions in the emergence of division of labor

The evolvable nature of colony-level phenotypic distributions provides a mechanism for the evolution of zooid traits that are not evolvable across asexual generations. The evolution of colony-level phenotypic distributions also underpins a hypothesis which proposes that polymorphs, or morphological division of labor in bryozoan colonies, are derived from preexisting body types within colonies as an expansion of that phenotypic distribution (Cheetham, 1973; Cheetham et al., 2006; Boardman et al., 1973). These body types are thought to diverge gradually, so that unimodal phenotypic distributions become bimodal.

Trait distributions are evolvable across generations of colonies; they can shift and change shape over time, leading to an array of phenotypic expressions within colonies. On a macroevolutionary timescale, the evolution of phenotypic distributions may underpin the origin of division of labor within colonies. The origin of division of labor in bryozoans is often linked to the current function of polymorph types (Schack et al., 2019; Silen, 1977; Lidgard et al., 2012). However, functions change over evolutionary time (Gould and Vrba, 1982), so we do not know the ancestral functions of polymorphs. We do know that polymorphs such as avicularia are derived from autozooids (Carter et al., 2010), and that their origination is tied to the evolution

of multimodal zooid phenotypic distributions from unimodal ones (Cheetham, 1973). Since we find that these distributions are evolvable, the key to understanding the origin of division of labor is to study how these distributions change over time.

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Author Contributions

S.L. and S.J-T. digitized all available specimens for analysis and collected measurement data. S.L. performed the data analysis. S.L. and C.S. wrote the manuscript.

Competing Interests Statement

The authors declare that they have no competing interests.

Data Accessibility

All data needed to evaluate the conclusions in the paper are present in the paper and/or Supplementary Materials. Additional data related to this paper may be requested from the authors.

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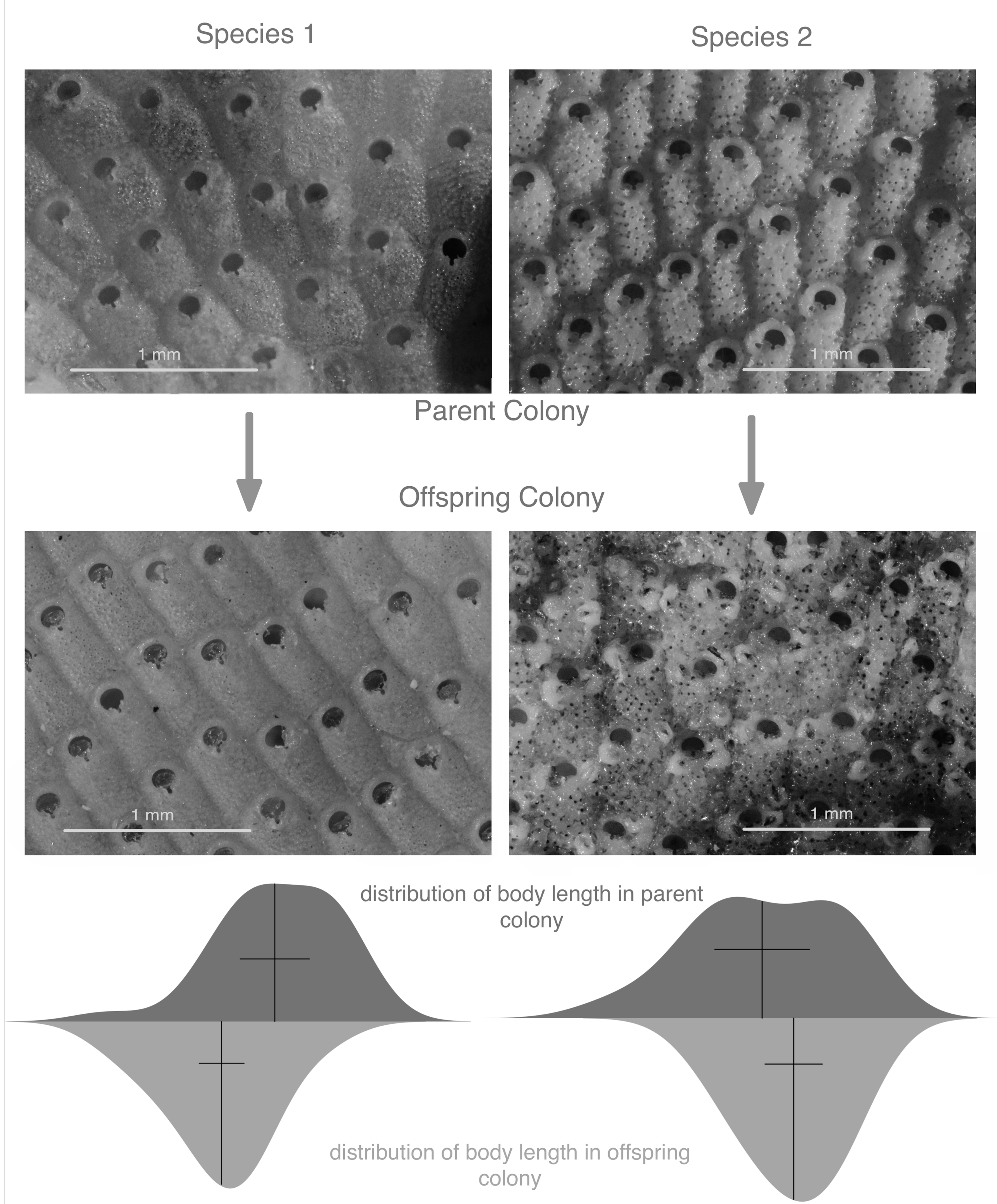
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Species 2
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Parent Colony
Offspring Colony
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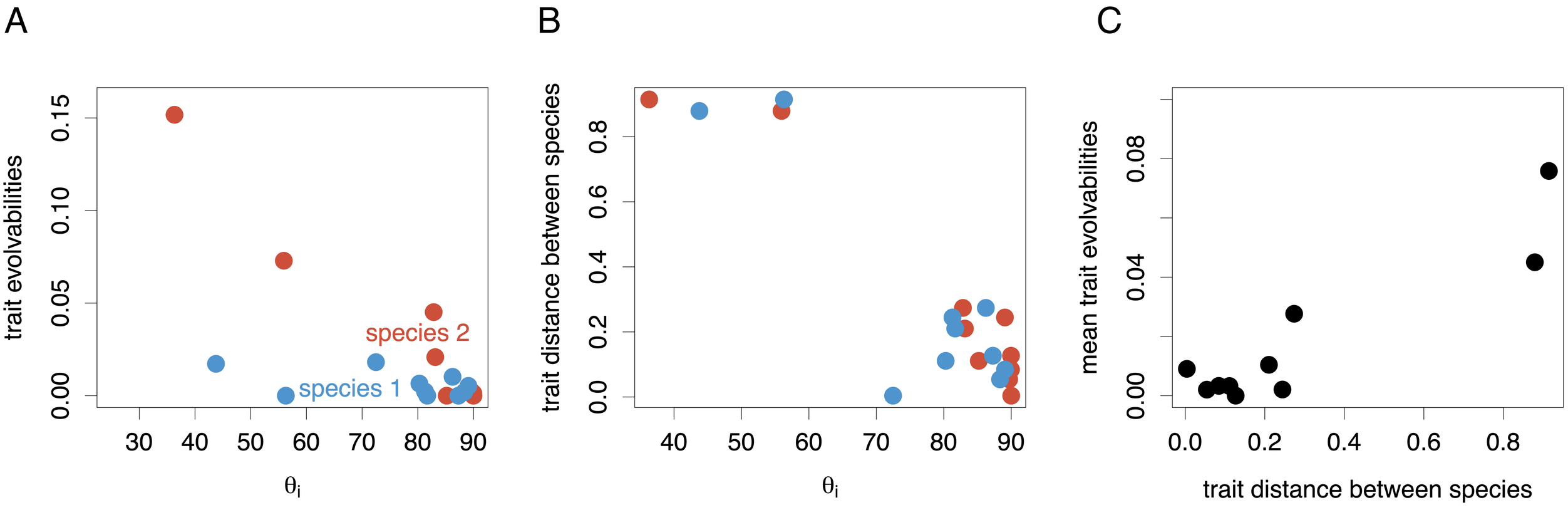
distribution of body length in parent colony
distribution of body length in offspring colony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0.15
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species 1
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B
trait distance between species
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0.2
0.4
0.6
0.8
40
50
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θi
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