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Genotypic covariance between the performance of a resident species and community assembly in the field

Arthur M. Riedel[1] (iD) | Keyne Monro[2] | Mark W. Blows[1] | Dustin J. Marshall[2] (iD)

[1]School of Biological Sciences, University of Queensland, Brisbane, Queensland, Australia

[2]School of Biological Sciences, Monash University, Clayton, Victoria, Australia

Correspondence
Arthur Riedel
Email: arthur_riedel@mac.com

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Abstract

1. Genetic variation in resident species can influence the assembly and dynamics of communities, but the potential for these genetic effects to persist across generations is largely unresolved. In principle, persistent, directional changes in communities are only predicted when community properties covary genetically with the fitness of resident species.

2. Estimates of genetic covariance between the fitness of a resident species and its community are therefore necessary to "close the eco-evolutionary loop" in studies of community genetics, but such estimates are rare. Emulating community genetics experiments in plants, we used clonal replicates of 21 genotypes of a resident species (the encrusting bryozoan, *Hippopodina*) to investigate the magnitude of genotypic variance contributing to assembly of a marine benthic community.

3. Genotypes explained up to 35% of variation in community assembly. Critically, the performance of *Hippopodina* genotypes covaried both with the evenness of communities and with the abundances of some individual species, representing an indirect genetic effect that creates the potential for multigenerational interactions between *Hippopodina* and co-existing species. Our results suggest that different genotypes will associate with different community members consistently across generations, and such non-random associations can give rise to specialization. Further interactions between species other than *Hippopodina* itself may also be altered by effects of genetic variation in the focal species.

4. Furthermore, species in the community other than *Hippopodina* itself will interact more commonly in the presence of some genotypes over others.

5. Our results support the potential for genetic variation in one species to have deterministic effects on the dynamics of ecological communities.

KEYWORDS

community/ecosystem genetics, direct–indirect genetic covariance, eco-evolutionary feedbacks, genetic variation, indirect genetic effects, interspecific interactions, marine invertebrates, Robertson–Price Identity

1 | INTRODUCTION

The role that genetic variation in one resident species plays in shaping the properties of associated communities, often referred to as community or ecosystem genetics (Haloin & Strauss, 2008; Johnson & Stinchcombe, 2007; Whitham et al., 2006), is a key issue at the interface of ecology and evolutionary biology. There is increasing evidence that community assembly in a range of systems is influenced by

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genetic variation, but the potential for these effects to persist remains unclear. An elegant study by Agrawal, Hastings, Johnson, Maron, and Salminen (2012) provided the first evidence for real-time eco-evolutionary feedbacks between a resident species and its community under field conditions (Agrawal et al., 2012), but such demonstrations are exceedingly rare, and may not be accessible in many systems. As such, identifying direct and enduring links between community assembly and genetic variation within populations more broadly remains an ongoing challenge.

The central observation underlying ecosystem genetics is that the genotype of a resident species can affect other members of the associated community. In this regard, ecosystem genetics has paralleled theory addressing indirect genetic effects. Indirect genetic effects (IGEs) are generated when heritable variation among individuals of one species influences trait expression in other individuals (Moore, Brodie, & Wolf, 1997; see Figure S1). Indirect genetic effects in the context of a single species are well established (Petfield, Chenoweth, Rundle, & Blows, 2005; Wolf, Brodie, Cheverud, Moore, & Wade, 1998; Wolf, Mutic, & Kover, 2011). They occur when genetic variation among individuals modifies the environment for other unrelated individuals, leading to indirect genetic variation in phenotype/fitness among these latter individuals (Wolf, 2003). In a community context, the effect of heritable trait variation in a resident species on community properties is termed an interspecific indirect genetic effect (IIGE) (Genung et al. 2011). Often, IIGEs are reported as estimates of community heritability, or how much of the variation in a community property is due to genetic variation among individuals of a resident species. For example, IIGEs have been commonly reported in plants and include the effect of host-plant genotype on the assembly of its arthropod community, and influences on above-ground and below-ground interactions (Dungey, Potts, Whitham, & Li, 2000; Genung, Bailey & Schweitzer 2011; Johnson & Agrawal, 2005; Rowntree, Cameron, & Preziosi, 2011; Whitham et al., 2006).

The pattern and magnitude of the genetic basis to multi-trait variation in a population is summarized in **G**, a matrix whose diagonal elements are the additive genetic variances (or in this instance, genotypic variances) of traits, and whose off-diagonal elements are the genetic (or broad-sense genotypic) covariances of these traits; thus, G_1 is the genetic variance in trait 1, and G_{12} is the genetic covariance between traits 1 and 2:

$$\mathbf{G} = \begin{bmatrix} G_1 & G_{12} & G_{13} & \dots & G_{1n} \\ & G_2 & G_{23} & \dots & G_{2n} \\ & & G_3 & \dots & G_{3n} \\ & & & \dots & \\ & & & & G_n \end{bmatrix} \tag{1}$$

The value of modelling **G**, bringing insights from evolutionary processes to bear on ecological dynamics, lies in the ability to predict change in community properties (Ridenhour & Nuismer, 2014); however our methods differ in that, instead of evaluating **G** and its corresponding selection gradient to estimate change, we here evaluate the covariance of fitness-associated traits with community properties, as described below. In the context of IIGEs, **G** enables

examination not only of the indirect effects of a resident species on individual taxa but also of further alteration to the relationships among those taxa in the community. Notwithstanding limitations to the stability of **G**, which can change over multiple generations due to selection or drift (McGuigan, Chenoweth, & Blows, 2005), most comparative studies find that **G** matrices estimated from experimental and natural populations are predominantly stable geometrically (Arnold, Bürger, Hohenlohe, Ajie, & Jones, 2008). Given the reasonable assumption of stability, **G** matrices can be reliably used to estimate that part of ecological interaction among species that derives from genetic variation.

While the existence of IIGEs of a resident species on its associated community suggests that community properties may respond to evolutionary changes in the resident species, it does not inevitably follow that the genetic variation in the species driving the IIGE is associated with fitness. This distinction is critical because only that part of the genetic variation in the resident species that covaries with fitness is predicted to cause multigenerational changes in the community properties influenced by that species. More formally, the response to selection on any trait (including the traits of resident species that may influence community properties) is predicted by that trait's genetic covariance with fitness (Robertson, 1966):

$$\Delta z = \text{cov}_G(z, \omega) \tag{2}$$

where Δz is the change in trait value from one generation to the next, and ω is fitness. Applied to community genetics, Δz is the change in the community property from one generation to the next, and ω is the fitness of the resident species. An IIGE on a community is therefore predicted to have persistent and directional consequences for that community only when the fitness of individuals in the resident species and the properties of the community covary genetically (Johnson, Vellend, & Stinchcombe, 2009). The genetic covariance between the fitness of individuals in a resident species and its associated community should predict, therefore, whether any effects of that species on its community will persist across generations. In the absence of this genetic covariance (sometimes referred to as direct–indirect covariance in quantitative genetics), there is no potential for genetic effects in one species to influence the trajectory of community assembly, or for eco-evolutionary feedbacks between the species and its surrounding community (Haloin & Strauss, 2008). Without this potential, the indirect genetic effects generated among genotypes of a resident species on associated communities should vary stochastically from generation to generation as certain genotypes become more or less common. Each generation will influence assembly anew, but there is no potential for deterministic genetic effects to be transmitted from one generation to the next. Applied to IIGEs, this is the equivalent of genetic drift (Vellend, 2010), in that variation in abundances of other species in the community would subsist through generations without being influenced by the evolution of fitness in the resident species.

Despite mounting evidence for IIGEs, studies that link them to fitness remain rare. Here, under field conditions, we explore the relationship between community properties and heritable variation in

the fitness-related traits of a resident species, the encrusting bryozoan *Hippopodina iririkiensis*. Community properties were quantified in two ways: (1) common metrics of community species diversity (diversity, evenness and coverage), and (2) the species composition and abundances within the communities. We estimate a derivation of the **G** matrix, the direct–indirect covariance matrix, which summarizes the indirect effects of genotype on community properties, the covariances among these indirect effects which amount to altered species interactions, the direct genetic effects of genotype on performance. Critically, we further estimate the genetic covariance between the performance (fecundity and size) of *Hippopodina* with its indirect effect on communities assembling in the field. Our examination of the covariation between fitness-related traits in our resident species *Hippopodina* and the genotypic effects on community assembly enables us to determine the potential of IIGEs to influence persistent, directional change in communities.

2 | MATERIALS AND METHODS

2.1 | Study system and resident species

Epifaunal marine communities occur worldwide and are composed largely of filter-feeding species within the same trophic level. The assembly of such communities is influenced by factors that act both before and after settlement. Pre-settlement effects include the direct predation of immigrant larvae (Nydam & Stachowicz, 2007) and allelopathic chemical interactions between residents and immigrants (Jackson & Buss, 1975; Koh & Sweatman, 2000; Thacker, Becerro, Lumbang, & Paul, 1998). Post-settlement, residents may limit the growth of neighbours or overgrow them entirely (Buss, 1979; Osman & Whitlatch, 1995; Russ, 1982). Larger individuals are better spatial competitors (Buss, 1979), but interactive networks, rather than hierarchies, may exist, whereby no single species dominates all others (Buss & Jackson, 1979). In these systems, moreover, species distributions and abundances are also influenced by non-contact competition for oxygen (Ferguson, White, & Marshall, 2013), food (Svensson & Marshall, 2015), as well as the sizes of feeding structures in neighbours (Davis & Marshall, 2014). Some species can have lasting impacts by altering their environment profoundly, while others can simply change the availability of resources for others (Jones, Lawton, & Shachak, 1994). Variation in the identity of resident species is known to generate variation in community assembly, within (Sutherland, 1978) and among (Estes & Palmisano, 1974) trophic levels. In contrast, the role of variation *within* a resident species is poorly understood.

As resident species, we used the encrusting bryozoan *Hippopodina iririkiensis* (Tilbrook, 1999; hereafter referred to by genus). *Hippopodina* grows by the repeated budding of modular subunits, or zooids, of identical genotype. Sexually produced offspring, each of them genetically unique, are brooded in specialized zooids with conspicuous brood-chambers (known as ovicells), prior to release as larvae. Larvae swim briefly (minutes to hours) in the plankton before permanently attaching to a substrate and metamorphosing into settlers that form new

colonies (Eitan, 1972). Colony size is major component of fitness in *Hippopodina* (as it is in many colonial organisms; Jackson & Coates, 1986) because larger, faster-growing colonies can outperform smaller, slower-growing competitors and, critically, have higher fecundity due to the positive association of colony size with number of ovicells, which develop within a few weeks. Ovicell number is, therefore, an appropriate assay of fecundity. Each colony derived from a single settler is a unique genotype that can be replicated clonally via fragmentation, and the ability to follow clonal replicates in the field through time permits the traits and communities associated with resident genotypes to be assayed simultaneously in different environments or experimental treatments. This use of fragmentation has been used repeatedly for clonal plants (Nyquist & Baker, 1991), seaweeds (Monro & Poore, 2009) and colonial marine invertebrates (Monro & Marshall, 2013; Yund, Marcum, & Stewart-Savage, 1997), like *Hippopodina*, to estimate the broad-sense heritabilities of measured traits (Falconer & Mackay, 1996).

Hippopodina colonizes available space early in the summer season, when benthic communities where it is found show increased settlement and growth. It is a regular and persistent species, and consequently co-exists with all sessile species found in this system without often dominating it. Moreover, the longevity and generation time of *Hippopodina* (weeks) is equivalent to that of most co-occurring species, such that IIGEs of *Hippopodina* can potentially influence current and new generations of community members (Hairston, Ellner, Geber, Yoshida, & Fox, 2005). Importantly, we have previously shown that the presence of *Hippopodina* influences community assembly at our study site (Riedel, Monro, Blows, & Marshall, 2014).

2.2 | Collection and cultivation of resident genotypes

Roughened A4 acetate sheets were fastened to ten PVC backing panels (250 × 450 × 4 mm) and suspended face down, *c.* 1 m below the water surface at Manly Boat Harbor, Queensland (See Figure S2). Panels were spaced widely among pontoons to minimize relatedness among recruits. After 13 days of natural recruitment, resident settlers of *Hippopodina* were sampled from distant panels and brought to the laboratory. There, they were gently stamped out with a small (8 mm) hole-punch, retaining them on a circular fragment of acetate. Settlers were then glued to new acetate sheets, returned to the field and attached to backing panels (590 × 590 × 4 mm), then cultivated to maturity as single colonies within a common garden setting (within metres of each other). These colonies cultivated from settlement were our resident genotypes. Each was genetically distinct and at most shared parents with others in the sample, though our sampling strategy minimized this possibility. We deal later, in the data analysis stage, with the potential for persistent environmental effects affecting later growth stages that a common garden setting may have created. Growing colonies were maintained weekly, removing surrounding organisms and debris that might interfere with lateral growth. At the end of this cultivation phase, when colonies had grown to *c.* 100 mm diameter (over *c.* 14 weeks), they were returned to the laboratory for use in the experiment proper.

2.3 | Experimental design and deployment

The experiment was a nested block design, using separate equipment to the cultivation phase just described. Four clonal replicates from each of 21 resident genotypes were distributed across two panels (experimental blocks). Thus, panels were nested within genotype (allowing genotypic variation to be partitioned from spatial variation among panels), and two clonal replicates per panel formed the basis for estimating residual variation (21 genotypes × 2 panels × 2 replicates). Clonal replicates were obtained by cutting fragments of approximately equal size (c. 100 mm^2) from each colony, and gluing each replicate via its acetate base alone onto a rigid PVC settlement plate (110 × 110 × 4 mm). Plates were returned to the field site within 48 hr, where they were again attached to PVC backing panels. Panels were suspended underwater, as previously, in random order along one side of a single pontoon. The experiment lasted 8 weeks, during which communities were permitted to assemble freely.

2.4 | Data collection

Initial fragment size was recorded from digital photographs taken at the start of the experiment, and final colony size was recorded from another set of photographs taken at its conclusion 8 weeks later. For each clonal replicate, two components of fitness were evaluated: final colony size, and the density of brood chambers in two 100 mm^2 subsamples of each final colony (a relative measure of fecundity independent of total colony size). In marine biofouling communities, larger colonies can have a substantial advantage in competitive interactions (Buss, 1979). The initial size of clonal replicates (99.59 mm^2, SD = 37.17) did not differ systematically among genotypes (ANOVA, $F_{20,60}$ = 1.51, p = .11). Nevertheless, to control for slight differences in initial size in our subsequent estimates of colony growth or available space, final colony size was regressed on initial fragment size, and the residuals retained as estimates of growth (Final mm^2 = 1063.153 + (17.497 × initial mm^2), R^2 = 0.548, $F_{1,79}$ = 95.6, p < .001); similarly, the mean densities of ovicells were regressed on initial size (in mm^2), and the residuals retained to estimate fecundity (Fecundity = 1.237 + (0.037 × initial mm^2), R^2 = 0.047, $F_{1,79}$ = 3.935, p = .05).

Using a dissecting microscope and digital image analysis of the final photographs, the abundances and sizes of community members on each plate were also recorded. We composed two datasets of (1) community metrics commonly used in ecology, and (2) the abundances of individual species. For organisms that did not vary substantially in size (e.g. polychaete worms and sponges), we estimated abundance as numerical counts. The polychaetes, *Hydroides diramphus* and *Janua pagenstecheri* were extremely abundant and counts were estimated from the mean of three subsamples of 100 mm^2. We did counts across whole settlement plates for *Balanus balanoides* (a common barnacle), *Bugula stolonifera* (an erect, branching bryozoan) and erect, non-encrusting sponges of the genus *Sycon* (for which we are unable to obtain greater taxonomic resolution). In these cases, counting individuals was most efficient and pilot studies indicated that counts and coverage were highly correlated (Table S1). For encrusting bryozoans (*Watersipora subtorquata*, *Celleporaria* sp., *Schizoporella* sp., an unidentified encrusting bryozoan, and conspecific *Hippopodina*), and the solitary ascidian *Microcosmus squamiger* (all referred to by genus hereafter), size variation was considerable, and we therefore estimated abundance as the cumulative area of cover on the plate.

To assay the community on each plate in comparable units, we estimated the density of each species by dividing all measures by the area unoccupied by the resident colony. We excluded the densities of *Janua* and *Hydroides* from this standardization, given these counts were already independent of any direct effect of resident colony size having already been estimated on space free of the resident species colony.

2.5 | Community metrics

Three standard community metrics were calculated from the abundance of each species, excluding measures of the resident genotype of *Hippopodina*: community coverage, Shannon–Wiener diversity (H'), and its derivative, Pielou's Evenness (J'). In order to use data of similar units, we converted all count data to estimates of coverage, using regressions of area on counts for the relevant species (Table S1). H' was calculated as:

$$H' = -\sum_{i=1}^{S} (p_i \ln (p_i)), \tag{3}$$

where S is the number of species, N is the coverage of the whole community on each settlement plate and p_i is the relative density of species i (calculated as the coverage of a given species on space free of the resident genotype colony: n_i/N. Pielou's Evenness (J') was calculated as H'/H_{max}, where $H_{max} = \ln(S)$.

2.6 | Community composition

We combined the encrusting bryozoans into a single group for analysis, based on their functional and morphological similarity, and the fact that our statistical model (see below) would not converge when the five species were analysed separately (most likely due to a low level of variation in the abundances of at least one of them). Some 25% of settlement plates attracted new recruits of our resident species, *Hippopodina*, but we could easily distinguish between these new (very small) settlers and our focal clonal fragments. The final dataset comprised counts and coverage of seven taxa, including the summed coverage of encrusting bryozoans, but excluding assay of the resident genotype.

2.7 | Data analysis

As the variables (growth and fecundity of resident *Hippopodina* genotypes, plus counts and surface-area measures for associated communities) were of different units and scales, we standardized all data for multivariate analysis. For each variable, data were centred on zero by

subtracting their mean, and then scaled to a variance of one by dividing them by their standard deviation (Quinn & Keough, 2001).

To visualize the communities associated with different genotypes, we computed a Bray-Curtis dissimilarity matrix from the community composition data and derived an ordination plot using non-metric dimensional scaling (NMDS; Figure 1). To analyse these patterns, we then fitted a multivariate (multi-response) model in SAS 9.2, treating genotype and panel as random effects:

$$\mathbf{y}_{ijk} = \mathbf{\alpha} = \mathbf{X}_{jk}b + \mathbf{Z}_{jk(g)}\mathbf{\delta}_{jk(g)} + \mathbf{Z}_{j(k)}\mathbf{\delta}_{j(k)} + \mathbf{\varepsilon}_{ijk} \qquad (4)$$

where $\mathbf{X}$ and $\mathbf{Z}$ are the matrices of fixed and random effects, respectively, the jth plate (replicate) is nested within the kth panel (block) and replicate panels are nested within genotype (g). At each of these levels, of plate, panel and genotype, we estimated trait variation and covariation using restricted maximum likelihood with an unstructured covariance matrix, treating variation among plates within panels as residuals. In a first application of the model, we treated three community metrics and two measures of performance in our resident species as the response variables; the second application of the model replaced the three community metrics with the abundances of seven taxa. Our primary interest lay in the components of variance and covariance at the level of genotype (**G**), as these represent the direct genetic effects on performance in *Hippopodina*, the indirect effects on species in the community, and the direct–indirect covariance of performance in the resident species on community assembly. The significance of each component of **G** was tested using a log-likelihood ratio test by comparing the full model to a reduced model in which the component of interest was held at zero as a null hypothesis (Littell, Milliken, Stroup, Wolfinger, & Schabenberger, 2006). Tests had one degree of freedom and were one-tailed for variances and two-tailed for covariances.

We developed the two models (one for the interaction of *Hippopodina* with community metrics, and one for its interaction with seven individual taxa) taking a multivariate approach to characterize

the genetic direct–indirect covariance between *Hippopodina*'s performance and community composition. Although testing for genetic covariances between community traits and fitness components of the resident species is readily accomplished using the original models, there is no reason to expect that each species will respond to genetic variation in *Hippopodina* independently from the others, and so the genetic variance in trait combinations is often more informative than the bivariate genetic covariances of multiple traits (Blows, 2007; Walsh & Blows, 2009). We used factor analytic modelling (Hine & Blows, 2006) to establish the effective dimensionality of the variance–covariance matrix estimated at the broad-sense genetic level (**G**) in each model above. Starting with a model in which **G** was assumed to be full rank (i.e. have as many dimensions as traits), we used log-likelihood tests to compare nested models in a stepwise model reduction strategy. The effective dimensionality of **G** was identified as the number of dimensions to which it could be reduced without significant loss of model fit. We then extracted the appropriate reduced-rank matrix from our model output and viewed its statistically supported dimensions as principal components (PCs). Each PC had an eigenvalue describing the amount of variation in **G** that it explained, plus a loading describing the strength of its association with each trait. We ascribed salience to loadings (Table S3) comprising at least 50% of the largest value for each PC (Jolliffe, 2002). Using this approach, we could characterize the multi-trait relationships underlying the majority of genetic effects on community structure generated by *Hippopodina*.

3 | RESULTS

As evident in the NMDS (Figure 1), variation among communities exceeded variation within communities: the overall spread of NMDS scores in each dimension was greater than that among communities identified by individual genotypes. Therefore, the communities

FIGURE 1 Ordination plot (NMDS), representing the dissimilarities of communities associated with clonal replicates of the resident species, *Hippopodina*. The centroid for the community associated with each genotype is shown as a larger filled circle, with replicate communities of individual genotypes (plates) marked as empty circles. Colours for genotypes are arbitrary, as are letters, solely to aid graphic differentiation
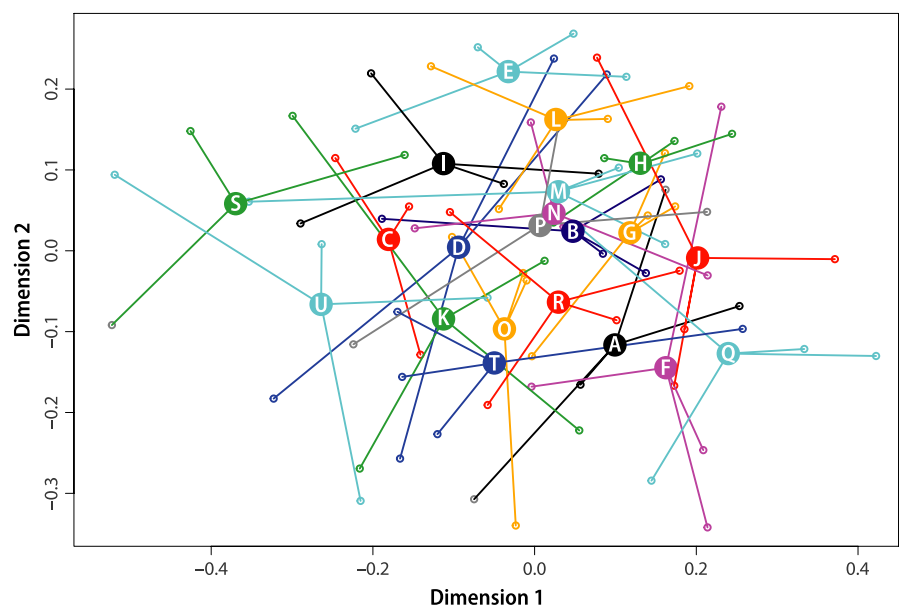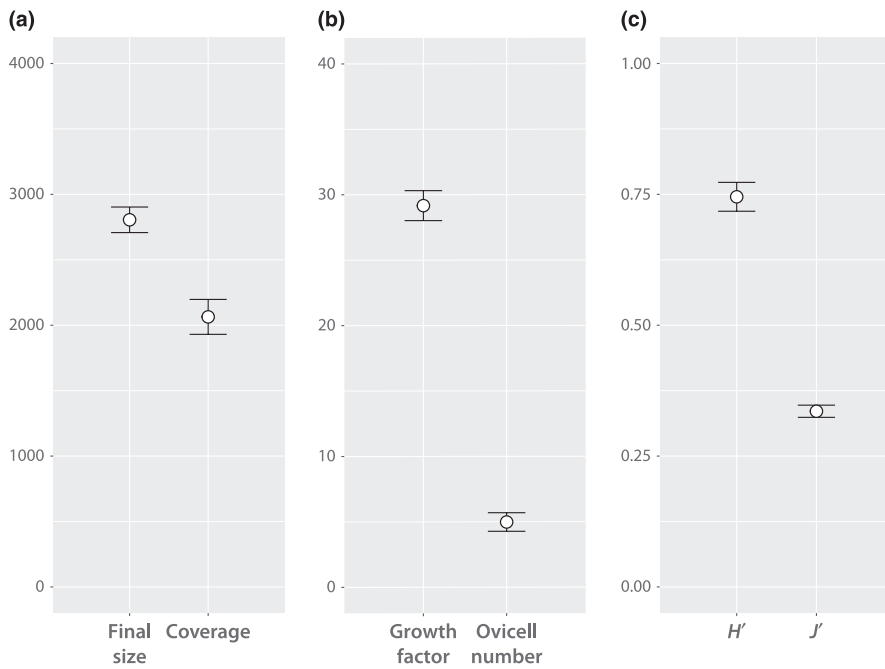
FIGURE 2 Mean values (±*SE*) for (a) final resident colony size and estimated coverage (mm²) by assembled communities; (b) growth factor of resident colonies and number of ovicells; (c), community metrics among resident genotypes of *Hippopodina* (Shannon–Wiener Diversity (*H'*), Pielou's Evenness (*J'*))
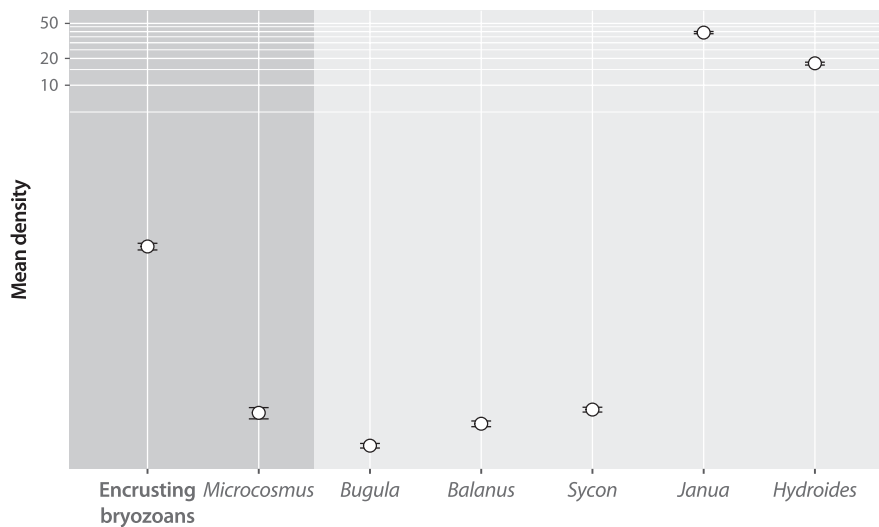
FIGURE 3 Mean densities (±*SE*) for species composition in communities associated with resident genotypes of *Hippopodina* (per 100 mm²): two species groups by surface area (in darker box), five by abundances

associated with clonal replicates of the same genotype were, on average, more similar to each other than to the communities associated with other genotypes.

Of the area available on settlement plates (12,100 mm²), the mean coverage by resident genotypes was 23%, whereas mean community coverage was 17% (Figure 2a). Therefore, resident genotypes typically occupied more available space than the communities they were associated with; however, none were associated with an absence of community assembly. Resident genotypes grew to *c.* 30 times their original size over the 8 weeks that communities had to assemble; mean ovicell density was high but variable (mean: 4.96 per 100 mm², *SD*: 6.38) (Figure 2b). Community composition was dominated by encrusting bryozoans, occupying a mean 12% of settlement plates; *Janua* and *Hydroides* were the most numerically abundant group, whereas *Bugula*, *Sycon* and *Balanus* were least abundant (Figure 3).

3.1 | Community metrics

Estimates of indirect genetic variance for most community metrics, as well as for the direct genetic effects of growth and fecundity were significant (Table 1). Indeed variation among genotypes explained 35% of the variation in growth and 45% of the variation in fecundity, with a (non-significant) covariance of 0.18. There was significantly positive genetic covariance between indirect genetic effects on community coverage and the estimate of diversity, meaning that the larger communities generated by some genotypes were also more diverse. We found diversity to have similarly positive covariance with evenness. Critically, the significantly positive genetic covariance between direct effects on growth of resident genotypes and indirect effects on evenness were uncovered, though not between growth and diversity.

TABLE 1 Complete covariance matrix for community metrics: genetic variances (on the diagonal) and covariances (below the diagonal) for three indirect effects on community metrics (community density/biomass, Shannon–Wiener Diversity (*H′*), and Pielou's Evenness (*J′*), shown above the horizontal line) and two direct effects on fitness-related traits (growth and fecundity, shown below the horizontal line) of the resident species, *Hippopodina*

	Coverage	Diversity	Evenness	Growth	Fecundity
Coverage	0.145				
Diversity	**0.210**	0.28			
Evenness	0.192	**0.27**	0.258		
Growth	0.179	0.234	**0.243**	0.348	
Fecundity	0.081	0.131	0.139	0.179	**0.459**

The direct–indirect covariance matrix, derived from the Robertson–Price Identity (2), is highlighted in grey. *p* ≤ .05 in bold.

TABLE 2 The statistically supported dimensions of the matrix in Table 1. Each dimension (or PC) has an eigenvalue that indicates the degree of variance that it accounts for, and each element of the eigenvector indicates the product (direction and magnitude) of its relationship with each variable. Salient loadings in bold (see text for details)

	PC1
Eigenvalue	1.009
Variance explained	100%
Coverage	**0.306**
Diversity	**0.422**
Evenness	**0.429**
Growth	**0.543**
Fecundity	**0.501**

Genotype explained considerable proportions (14%–27%) of the variation in community metrics, and as much as 45% of the total variation in performance traits of the resident species *Hippopodina*. Factor analytic modelling of **G** for these five traits supported a reduction from five dimensions to one dimension (moving from one dimension to none: $\chi^2_5 = 11.089$, *p* < .05), implying that multiple traits shared genetic relationships that may be overlooked by simply inspecting the individual elements of **G** in Table 1. As **G** is one-dimensional here, all such relationships can be summarized in a single PC (Table 2) (factor loadings, all approximating to one, are detailed in Table S3). Community metrics and fitness components all loaded strongly and positively on this PC, indicating that larger genotypes were more fecund, and also generated denser, more diverse, and more even communities.

That *Hippopodina* genotypes were initially cultivated in one environment only raises the possibility that variation among genotypes during our experiment may have derived from response to discrete microenvironments on individuals. In part, we dealt with this by reducing microenvironmental variation: we minimized interactions with resident genotypes by removing any other settlers at least once weekly. To determine the possible influence of this early environmental variation inflating variation among genotypes during our experiment, we examined the among-replicate variances for the two fitness components of our resident genotypes at the level of our blocking factor (i.e. panels). These variance components represent microenvironmental variation in the cultivation environment, which should be comparable to microenvironmental variation

that acted during the assembly experiment. We found the percentage of the total variation contained in this microenvironmental component was 0% for growth and 15% for fecundity, compared to the *c.* 37% for growth and 45% for fecundity explained by genotypic variation, suggesting that it was not the predominant source of variation among genotypes.

3.2 | Community composition

Considerable variation in community composition occurred among genotypes compared to within genotypes (Figure 1). We found significant genetic variances for the assembly of four of the seven taxa. In the resident species, growth and fecundity also displayed significant levels of genotypic variation (Table 3); variation among genotypes accounted for 38% of the variation in growth, whereas variation among panels accounted for none. Similarly, 56% of the variation in fecundity was explained by genotype, whereas only 18% was explained by spatial variation among panels. With regard to indirect genotypic effects on community composition, the abundances of encrusting bryozoans showed a positive genetic association with that of the ascidian, *Microcosmus*. The direct genetic effects of performance (in terms of growth) showed a negative correlation with the indirect genetic effects on abundances of *Sycon* and *Balanus*. In other words, communities associated with faster-growing genotypes had fewer sponges and barnacles.

Variation among genotypes accounted for up to 42% of variation in species abundances among all communities. Factor analytic modelling of **G**, in this case, indicated that three dimensions (of a possible nine) were sufficient to account for all genetic relationships among the seven species abundances and two *Hippopodina* performance measures (moving from three dimensions to two dimensions: $\chi^2_8 = 15.21$, *p* = .033). The first PC explained 48.5% of the variance in relationships between community composition (in terms of the abundances of seven taxa) and fitness-related traits (fecundity and growth) of the resident species, while 31% and 21% of this variance was explained by the second and third dimensions respectively (Table 4). The two largest dimensions both provided evidence for direct–indirect genetic covariance between performance in *Hippopodina* and community phenotype (Table 4 and Figure 4). On the first PC, growth and fecundity were positively associated with the abundances of encrusting bryozoans and *Microcosmus*, but negatively associated with the abundances of *Bugula*, *Sycon* and

TABLE 3 Complete covariance matrix for community composition: genetic variances (on the diagonal) and covariances (below the diagonal) for indirect effects on community composition (in terms of the abundances of seven major taxa, shown above the horizontal line) and direct genetic effects on two fitness-related traits (growth and fecundity, shown below the horizontal line) of the resident species, *Hippopodina*

	Bryozoans	Balanus	Sycon	Hydroides	Janua	Microcosmus	Bugula	Growth	Fecundity
Bryozoans	**0.43**								
Balanus	−0.081	0							
Sycon	−0.244	0.107	**0.358**						
Hydroides	−0.088	−0.099	−0.150	0					
Janua	0.106	−0.064	−0.048	0.159	**0.385**				
Microcosmus	**0.422**	−0.005	−0.246	−0.067	0.0279	0			
Bugula	−0.213	−0.167	0.159	−0.107	−0.027	−0.055	0.42		
Growth	0.118	**−0.333**	**−0.324**	−0.085	−0.118	0.0122	0.088	**0.387**	
Fecundity	0.086	0.049	−0.240	0.014	0.097	−0.041	0.052	0.176	**0.452**

The direct–indirect covariance matrix, derived from the Robertson–Price Identity (2), is highlighted in grey. *p* ≤ .05 in bold.

TABLE 4 The statistically supported dimensions of the matrix in Table 3. Each dimension (or PC) has an eigenvalue that indicates the degree of variance that it accounts for, and each element of the eigenvector indicates the product (direction and magnitude) of its relationship with each variable. Salient loadings in bold (see text for details)

	PC1	PC2	PC3
Eigenvalue	1.13	0.714	0.484
Variance explained	48.5%	30.7%	20.8%
Encrusting bryozoans	**0.44**	**0.347**	−0.0578
Balanus	**−0.167**	**0.265**	0.007
Sycon	**−0.599**	0.052	0.058
Hydroides	0.068	0.092	**0.29**
Janua	0.112	**0.322**	**0.793**
Microcosmus	**0.17**	**0.274**	−0.096
Bugula	−0.167	**−0.604**	**0.443**
Growth	**0.421**	**−0.479**	−0.135
Fecundity	**0.411**	−0.159	0.24

Balanus. On the second PC, in contrast, growth was negatively associated with the abundances of encrusting bryozoans, *Janua*, *Balanus*, and *Microcosmus*, but positively associated with the abundance of the erect bryozoan *Bugula*.

4 | DISCUSSION

Heritable variation in *Hippopodina* had widespread indirect genetic effects on both the ecological properties of communities and on the abundances of individual taxa. Most importantly, the covariance between the direct effects in performance and the indirect effects on community properties provides evidence that one species may influence the properties of a community across generations in a deterministic way. The potential for non-random communities to develop is an indirect response to selection of this resident species. Specifically, at least under the experimental conditions used here, our results predict that the proliferation of higher performing genotypes would see some species (e.g. *Sycon*) become rarer, while others (e.g. encrusting bryozoans) would become more common. Genotypic variation in our resident species has strong and pervasive indirect genetic effects on subsequent community assembly and structure. Covariance among indirect genetic effects highlighted that genetic variation in our resident species also precipitates non-random interactions among other species, such that different genotypes of the resident species have discernible emergent effects on species interactions within the communities they generate. Direct effects of genotype on focal species traits accounted for almost half of the variation in the performance of resident colonies.

Within generations, smaller scale patterns (within this system, likely metres rather than kilometres) caused by IIGEs on community assembly are likely to affect the nature of competition in communities (Aarssen, 1989; Fridley, Grime, & Bilton, 2007). In the marine environment, competition is intense at small spatial scales, particularly among adjacent individuals where overgrowth interactions are common (Buss, 1979). Our results suggest that some genotypes are consistently associated with some species more than others, and that certain genotypes may compete with some species more often than others. This underscores the importance of individuals not being ecologically equivalent (Bolnick et al., 2011; Wilson & Swenson, 2003): the competitive environments experienced by individuals of the same species may differ dramatically. Our results suggest that different community members may also interact non-randomly among themselves, due to genetic variation in the resident species. In the presence of high-performing *Hippopodina* genotypes, for example, *Microcosmus* is more likely to co-occur with high densities of encrusting bryozoans, and less likely to encounter the sponge *Sycon*. More broadly, non-random competitive interactions are likely in a range of systems where genotype affects community assembly (Fridley et al., 2007; Whitlock, Bilton, Grime, & Burke, 2011), but the eco-evolutionary dynamics of such interactions have yet to be explored.

Across generations, the ecological consequences of IIGEs on community assembly may differ according to spatial scale (Chase, 2003). At
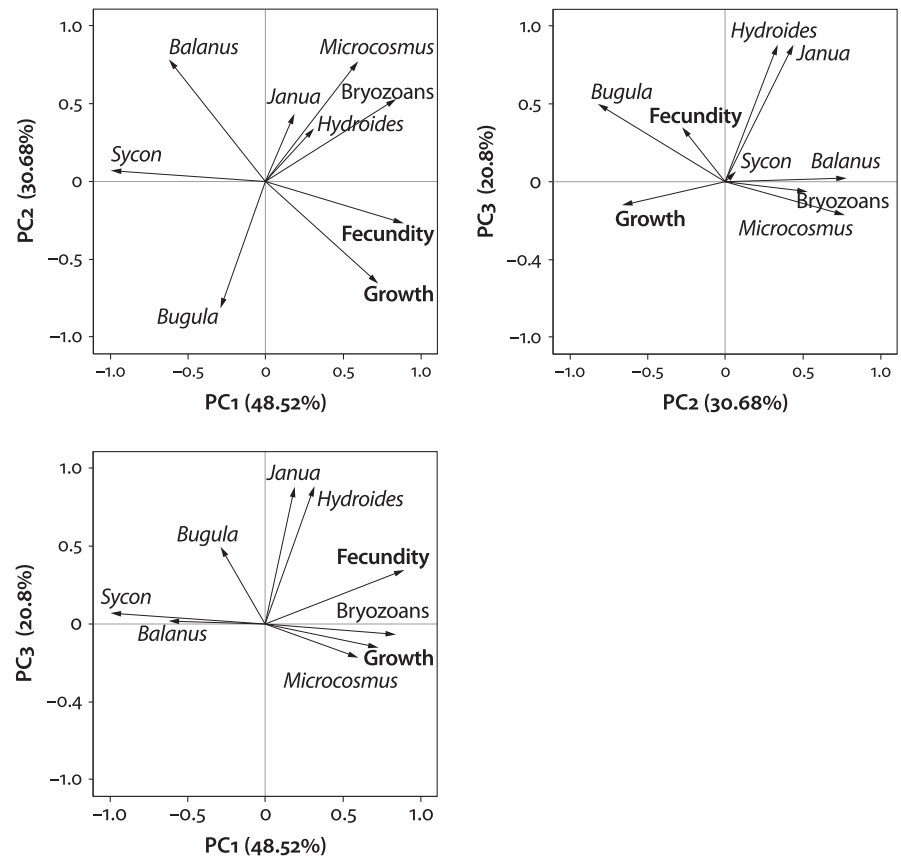
FIGURE 4 Biplots of factor loadings for the three statistically supported dimensions of genetic variance relating community composition (in terms of the abundances of seven major taxa) to fitness-related traits (fecundity and growth) of the resident species, *Hippopodina*

smaller scales, for example, genetic variation within populations of the resident species may shape local communities (α-diversity), even if the overall composition of the regional species pool (γ-diversity) were to remain constant. At larger scales, local communities may vary in accordance with genetic variation among populations of this species. How genetic variation in a resident species is distributed geographically may, therefore, affect the distribution of other species, both within and among communities. If *Hippopodina* evolves as predicted by our results, then variation among genotypes and their associated communities could potentially generate a geographic mosaic of species distributions and abundances (β-diversity; Thompson, 1999). The broader implication is that patterns of β-diversity are influenced by genetic variation within species, which may in turn be affected by community context, thus forming the basis for a potential eco-evolutionary feedback loop (Wade, 2007).

A key limitation of the approach we have taken is our ability to measure total fitness under field conditions. While we measured two key components of individual fitness (particularly for sessile colonial organisms like *Hippopodina*), other unmeasured fitness components include survival, settlement and mating success. We detected substantial levels of genetic variance in our fitness components (consistent with the general pattern that such components vary more genetically than traits under weaker selection; Houle, 1992), but would expect genetic variation in *total* fitness to be lower because selection should deplete it (Blows & Walsh, 2009). Thus, we may have overestimated total variance in fitness, and therefore the strength of the IIGEs in our system. Alternatively, genetic variation in fitness may be maintained in

Hippopodina by spatial or temporal variation in selection (Johnson & Stinchcombe, 2007; Thompson, 1999), thereby maintaining variation in communities associated with different genotypes (to the extent that the two covary).

It is unclear by what mechanism genetic variation in *Hippopodina* affected community assembly. In principle, the availability of space will always be a limiting factor to community assembly. In established marine benthic communities, primary uninhabited space is rare and transitory in a setting characterized by competition for space (Buss, 1979; Sutherland, 1978). Because genotypes systematically differed in their growth, and therefore in the amount of space they left available for colonization by others, variation in size among genotypes may well have influenced community assembly. Typically, larger individuals will reduce the amount of area that is available to others (Hughes, 1984). Our methods standardized community metrics as a proportion of the remaining available space, decoupling the simple effect of area on community metrics. Though we precluded any artefactual effect of colony size in our measures of communities, it may have influenced community assembly indirectly: marine invertebrates can recruit differentially to patches of free space that vary in size (Keough, 1984), creating variation in the assembly and trajectory of sessile marine communities. While we cannot eliminate the effect of different growth rates among genotypes as the driver of our results, there are also other mechanisms that may explain the community patterns that we found. For instance, variation in morphological traits related to feeding affects what resources are available to others (Okamura, 1992), and may influence patterns of

community assembly. In the communities observed here, the effects of different genotypes were more similar for species with similar morphologies: genetic variances for the two polychaete species that share similar feeding habits (*Janua* and *Hydroides*) remain closely correlated in all three dimensions of the PCA. Genetic variances for *Balanus* are unrelated to those for the encrusting bryozoans. Interestingly, *Balanus* grows up and away from the substratum and the only species which is showed any correlation with was *Sycon*, another species that grows vertically away from the substrate. Differential chemical interactions between genotypes and their communities are another possible mechanism for the effects seen here. Chemical-based interactions (e.g. allelopathy, induced defences and offences, settlement cues) within and among species are well established in marine ecology (Pawlik, 2000), suggesting that benthic sessile communities are likely to be influenced by a complex chemical landscape (Zimmer & Butman, 2000).

Ecological communities are characterized by complex patterns and cycles of recruitment that may cause levels of genetic variance to vary in time and space (Frédéric & Whitlock, 2007). Consequently, the stability of **G** across multiple generations in nature remains unclear (Arnold et al., 2008). In the case of *Hippopodina*, the establishment of new recruits may be expected to alter the magnitude and specificity of genetic effects on community assembly. Furthermore, given we predict that some genotype/community combinations will have higher fitness than others, genetic variance is expected to deplete over time as such genotypes increase in abundance. While **G** has limitations as a predictive tool, it may nonetheless show conservation of its geometry (Jones, Arnold, & Bürger, 2007), remaining stable for many trait combinations (Jones, Arnold, & Bürger, 2003) even after population divergence (Hine, Chenoweth, Rundle, & Blows, 2009). From a pragmatic perspective, despite uncertainty over its stability, **G** remains the best tool for predicting evolutionary change across generations (Blows & Walsh, 2009).

It has long been recognized that the identity and density of resident species can influence subsequent community assembly, particularly in the marine environment (Sutherland, 1978). Notwithstanding our limitations in understanding the mechanism driving our results, it is clear that genotypes and communities covary significantly. Notably, that such covariance further involves the performance of those genotypes offers rare evidence that communities may change in response to evolutionary change in a resident species. Further, if species influence the assembly of communities about them, then they also influence the environments where they evolve and which evolve about them (Moore et al., 1997), suggesting that opportunities for feedbacks between ecology and evolution may be complex but widespread.

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AUTHORS' CONTRIBUTIONS

A.R., K.M., M.B. & D.M. conceived the experiment and methodology; A.R. collected the data; A.R. & K.M. analysed the data; A.R. & D.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data deposited in the Dryad Digital Depository: https://doi.org/10.5061/dryad.30dg0 (Riedel, Monro, Blows, & Marshall, 2017).

ORCID

Arthur M. Riedel [iD] http://orcid.org/0000-0002-3297-7209

Dustin J. Marshall [iD] http://orcid.org/0000-0001-6651-6219

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SUPPORTING INFORMATION

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