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Journal

Ecology, 106(1)

Authors

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Publication Date

2025

DOI

10.1002/ecy.4505

Peer reviewed

ARTICLE

An experimental test of eco-evolutionary dynamics on rocky shores

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Funding information

Division of Ocean Sciences, Grant/Award Number: OCE-1851462

Handling Editor: A. Randall Hughes

Abstract

A growing body of theoretical studies and laboratory experiments has focused attention on reciprocal feedbacks between ecological and evolutionary processes. However, uncertainty remains about whether such eco-evolutionary feedbacks have an important or negligible influence on natural communities. Thus, recent discussions call for field experiments that explore whether selection on phenotypic variation within populations leads to contemporaneous effects on community dynamics. To help fill this gap, in this study, we test the hypothesis that selection on consumer traits in a population of predatory drilling snails can drive eco-evolutionary dynamics in a rocky intertidal community in California, USA. We first conducted a laboratory selection experiment to raise newly hatched dogwhelks (*Nucella canaliculata*) on four diet treatments encompassing a range of prey species and shell thicknesses. Snails that survived to adulthood under these diet treatments differed in their capacity to drill thick-shelled mussels. Dogwhelks from these treatment groups were then outplanted to intertidal field cages for 1 year to test whether groups experiencing selection differed in their effects on mussel bed succession. As expected, succession proceeded most rapidly in the reference treatment with dogwhelks excluded. However, successional patterns differed minimally among dogwhelks raised under the different diet treatments. Thus, although our laboratory results suggest that prey can impose selection that leads to rapid adaptation and divergent consumer traits, these feedbacks were not strong enough to result in clear community effects in the field. We propose that a limited range of variation in functional traits within populations, moderate strengths of selection, and a background of substantial abiotic and biotic variation may all act to dampen the potential for strong eco-evolutionary dynamics in this and many other natural communities.

KEYWORDS

eco-evolutionary feedbacks, *Mytilus californianus*, *Nucella canaliculata*, predator-prey interaction, rocky intertidal community, succession

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INTRODUCTION

Increased recognition that evolution can proceed rapidly (Boag & Grant, 1981; Reznick & Ghalambor, 2001) has resulted in the emerging field of eco-evolution dynamics. Despite growing attention to eco-evolutionary feedbacks (Fussmann et al., 2007; Hendry, 2017; Pelletier et al., 2009), it is still unknown whether these feedbacks are consequential in natural communities (Hendry, 2019; Schoener, 2011). Most studies of eco-evolutionary dynamics have been conducted in the laboratory or in mesocosms (but see Agrawal et al., 2013; Farkas et al., 2013; Reznick & Travis, 2019), with relatively few experimental tests conducted in nature, particularly at the scale of a community or ecosystem (but see Bassar et al., 2010; Palkovacs et al., 2009). Field experiments are needed to determine whether eco-evolutionary feedbacks are swamped or amplified by external factors in more complex, natural environments (Hendry, 2019). In addition, existing experimental studies of eco-evolutionary dynamics have generally compared two or more locally adapted populations that have evolved under spatially divergent selection (Des Roches et al., 2013; Farkas et al., 2013; Fukano et al., 2022). While such studies provide proof of principle that evolutionary processes can influence ecological dynamics, this approach often relies on substantial phenotypic variation that has evolved through divergent selection imposed on separate populations over extended periods (e.g., decades to a century or more). In contrast, there have been increased calls for studying the dynamics of systems where there is no separation in time between the evolutionary and ecological processes under consideration (Bassar et al., 2021; Hersch-Green et al., 2011; Tack et al., 2012). One promising approach is to explore whether abiotic and biotic variation acting over rapid time-scales (e.g., months to years) might impose selection on existing within-population variation in functional traits that are linked to community dynamics (Hughes et al., 2008; Reusch et al., 2005; Whitham et al., 2003). However, to date, few field studies have tested whether ecological processes might be altered by feedbacks with contemporaneous selection on the phenotypic variation present within a local community (but see Agrawal et al., 2013; Carvajal-Endara et al., 2020; Schoener et al., 2017).

Evaluating the importance of such eco-evolutionary dynamics will ultimately require a body of field studies that span a range of ecosystems. However, a logical starting point is to seek evidence of eco-evolutionary dynamics in natural communities where these effects are expected to be particularly strong. Given that predator–prey interactions can be tightly coupled (Thompson, 1999a), and often lead to strong top-down control of communities (Menge & Branch, 2001), it is not surprising that many

studies of eco-evolutionary dynamics have focused on these interactions (Reznick & Travis, 2019; Yoshida et al., 2003). One might also expect eco-evolutionary feedbacks to be strong in communities where a predator has: (1) substantial intrapopulation variation in foraging traits that have a heritable basis and are linked to community dynamics; and (2) a relatively fast generation time and exposure to substantial environmental variation, high mortality, and the potential for strong selection.

Study system

Intertidal communities have long served as testing grounds for ecological theory (Menge & Branch, 2001), in part because species interactions in these systems are often strong and easily manipulated. In the northeast Pacific, dogwhelks (*Nucella* spp.) are important rocky intertidal predators that feed by drilling a tiny hole through their barnacle and mussel prey (Carriker, 1981). Beds of the mussel *Mytilus californianus* dominate the mid-intertidal zone, providing habitat for diverse species and exhibiting a well-documented sequence of succession following disturbance (Dayton, 1971; Paine & Levin, 1981). Prior work indicates that *Nucella* spp. can alter the rate of succession by consuming early colonizing space holders (Berlow, 1997; Wootton, 2002, 2013), and perhaps *M. californianus* later in succession (Sanford et al., 2003; Sanford & Worth, 2009, 2010). *Nucella* spp. produce benthic egg capsules with crawl-away young that are dependent on small, newly recruited prey (barnacles and/or mussels) that are spatially and temporally variable in their abundance, and potentially their shell properties (e.g., shell thickness). Mortality of juvenile *Nucella* in the field can reach 90%–99% during the first 2 months of life (Spight, 1975). Thus, seasonal and interannual variability in prey and other environmental factors might impose strong selection on *Nucella* phenotypes during the juvenile phase when mortality is especially high (Spight, 1982).

Previous work indicates that populations of the channeled dogwhelk, *Nucella canaliculata*, differ geographically in the length and thickness of *M. californianus* mussels that can be drilled (Longman & Sanford, in review; Sanford & Worth, 2009). Drilling phenotypes in this species persist after two generations in common laboratory conditions, establishing a genetic basis for this variation (Sanford & Worth, 2009). The *N. canaliculata* population on the Bodega Marine Reserve (BMR) in northern California, USA, is particularly interesting as it contains a mix of drilling phenotypes that vary both among and within *N. canaliculata* families (Sanford & Worth, 2009). The processes that generate and maintain this variation are unknown, but might include greater than expected gene flow from nearby populations. Alternatively, BMR is

located within a coastal region that has oceanographically driven seasonal and interannual variation in prey recruitment (Morgan et al., 2009, 2012) and mussel shell thickness (Kroeker et al., 2016), which could impose temporally fluctuating selection.

Collectively, prior work in this system suggests the potential for temporal variation in prey to impose strong selection on within-population variation in drilling phenotypes in *N. canaliculata*, a predator known to influence mussel bed succession. Although we focus on pairwise interactions and the potential for prey to impose selection on consumer traits, we acknowledge that selection imposed by multispecies interactions in natural communities is likely far more complex (De Meester et al., 2018; Govaert et al., 2021; Strauss & Irwin, 2004). For example, *N. canaliculata* partially overlaps in its intertidal distribution and diet with the dogwhelk *Nucella ostrina* (Wieters & Navarrete, 1998). These congeners might compete for prey and thus variation in the density of *Nucella ostrina* could impose selection on the drilling traits of *N. canaliculata*. Similarly, *Nucella* spp. are subject to predation, especially by cancrid crabs, and variation in crab predation may impose selection on the foraging behavior of *N. canaliculata* (Neylan et al., 2024).

Nevertheless, the potential for variation in prey to select for drilling traits in *Nucella* is one of the most plausible pathways for strong eco-evolutionary feedbacks to occur in this study system. Thus, in this study, we first hypothesized that variation in early-life diet would select for specific drilling phenotypes in dogwhelks. To test this hypothesis, we conducted a laboratory selection experiment to rear newly hatched dogwhelks on four prey treatments. Second, we hypothesized that the resulting divergence in predator phenotypes would alter the trajectory of mussel bed succession, with an increased frequency of strong drilling phenotypes slowing succession relative to weaker drillers. To test this hypothesis, we outplanted snails from the selection experiment to field enclosures to quantify their effects on community succession over 1 year.

METHODS

Laboratory rearing and selection experiment

Given the high mortality experienced by newly hatched *Nucella*, we hypothesized that variation in prey would lead to nonrandom survival of drilling phenotypes in the BMR population (38°19'24" N, 123°4'43" W). Dogwhelks were hatched and raised in the laboratory on four diet treatments: a control diet of *Mytilus trossulus* collected from Bob Creek Wayside, OR (44°14'39" N, 124°6'49"

W); *M. californianus* from Soberanes Point (SBR; 36°26'50" N, 121°55'44" W); *M. californianus* from BMR; and barnacles (*Chthamalus dalli*) (Figure 1). These diet treatments simulated natural scenarios where cohorts of newly hatched *Nucella* encounter pulses of different prey associated with spatial and temporal variation in recruitment (Broitman et al., 2008; Morgan et al., 2009). In addition, evidence suggests that the shell thickness of mussel recruits at BMR varies through time with oceanographic conditions (Rivest et al., unpublished data). To test the potential effects of such variability, *M. californianus* recruits from two populations were used as diet treatments because previous research has shown that adult *M. californianus* from BMR have thicker shells than those from SBR (Sanford, unpublished data). We hypothesized that the diet of *M. californianus* from BMR would impose the strongest selection for strong drilling phenotypes. In addition to dogwhelks from BMR, we raised a smaller number of dogwhelks from SBR as a control. Previous research has shown that after two generations on a common laboratory diet, the BMR population had a mixture of strong and weak drilling phenotypes, whereas the SBR population consisted of individuals with uniformly strong drilling (Sanford & Worth, 2009). If phenotypic plasticity was important, we expected snails from both populations to vary among diet treatments in their drilling phenotypes. Alternatively, if selection was the primary driver of variation, we expected the diet treatments to generate greater divergence in the BMR population than in the SBR population.

In summer 2020, we collected 18 sets of *N. canaliculata* egg capsules from BMR and four sets from SBR. Egg capsule from the same cluster, hereafter referred to as a "family," were held in small mesh-sided containers (~180 µm openings) with flowing seawater. Dogwhelks were hatched at Bodega Marine Laboratory and snails from each family were split with ~80 individuals added to each of four mesh-sided containers (Appendix S1: Section S1). For the first 3 weeks, all dogwhelks were fed a control diet of *M. trossulus* recruits, which is known to support high survival (Sanford & Worth, 2009). This 3-week diet period was necessary since pilot studies indicated that raising dogwhelks in the laboratory from hatching on *M. californianus* resulted in mortality that was too high. After this initial phase, we switched dogwhelks onto the four experimental diet treatments for a 3-month "selection phase." Food was replaced weekly with dogwhelks given progressively larger prey and any dead dogwhelks were removed. At the end of this period, total mortality was quantified, and all dogwhelks were switched to a common diet of *M. trossulus* and reared for ~6 months to adult size (>18 mm length).

We assessed variation in shell thickness among the three types of mussel recruits across the size range of

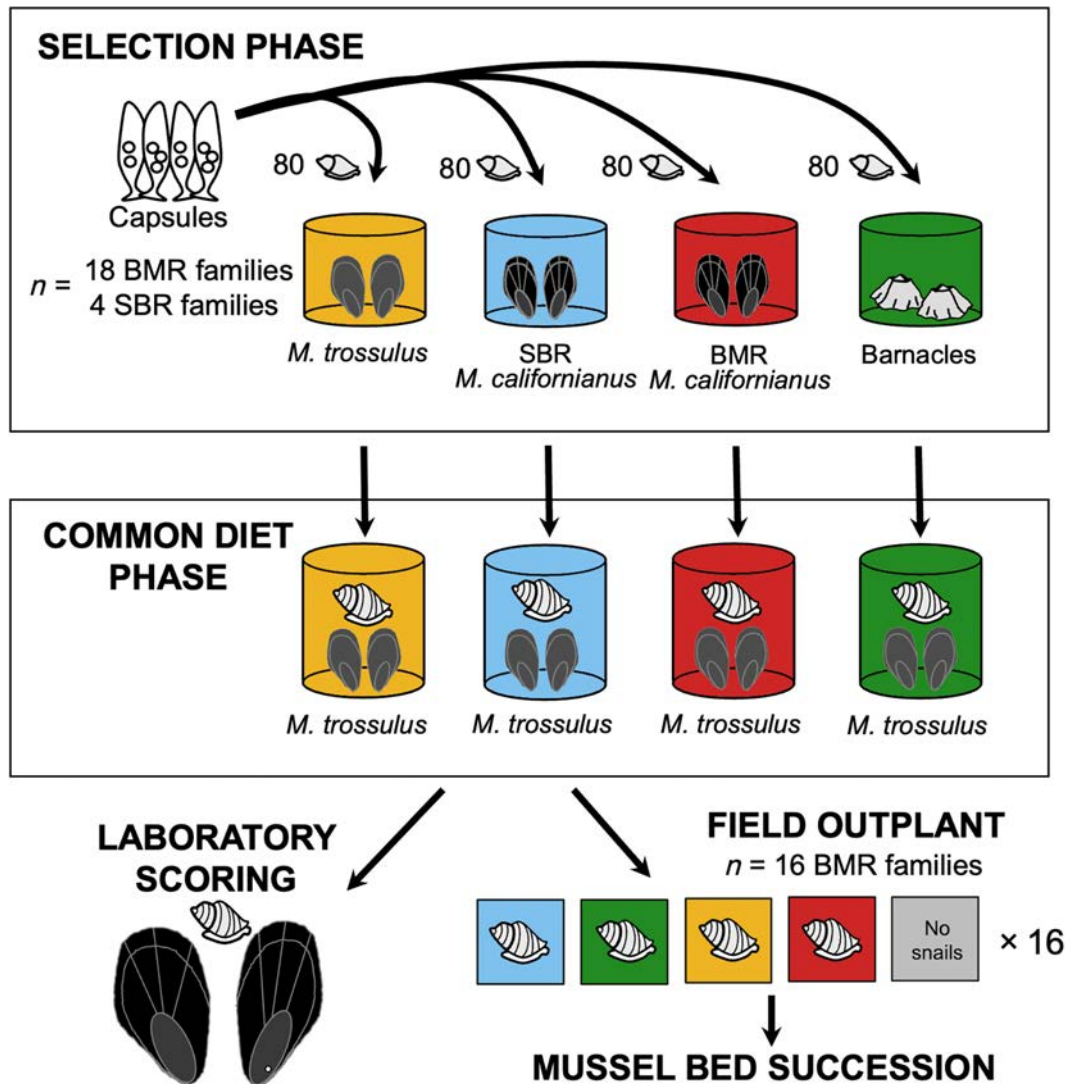


FIGURE 1 Experimental design testing whether early-life diet imposes selection on predatory dogwhelks (*Nucella canaliculata*), with cascading effects on rocky shore communities. During the “selection phase” (3 months), newly hatched dogwhelks from two populations (Bodega Marine Reserve [BMR] and Soberanes Point [SBR]) were raised in the laboratory on four early-life diet treatments. These included barnacles, the mussel *Mytilus trossulus*, and the mussel *Mytilus californianus* from two sources (SBR and BMR). All dogwhelks were then reared on a diet of *M. trossulus* during the “common diet phase.” The drilling capacity of adult dogwhelks was then quantified during a “laboratory scoring” experiment. Lastly, snails from the diet treatments were outplanted to field cages to test for effects on the trajectory of mussel bed succession.

mussels used during the selection phase ($n = \sim 55$ recruits per type) as we assumed this would contribute to selection for variation in drilling capacity. The total dry weight of both mussel valves divided by the total projected area was measured as a proxy for mussel shell thickness (Gaylord et al., 2018; Appendix S1: Section S2).

Laboratory scoring experiment

To quantify dogwhelk phenotypes, we scored adult *N. canaliculata* (12 snails from each family \times treatment) for their ability to drill mid-sized *M. californianus* during a 15-week experiment (Appendix S1: Table S1). At the start of

the experiment, snail length was measured with digital calipers and each dogwhelk was given two mussels (5–7 cm long) from BMR (Appendix S1: Section S3). Checks were performed every 3 weeks, and any drilled mussels were recorded and replaced. Successful drilling was defined as a snail that drilled a complete borehole through the shell of at least one mussel during the 15 weeks. The total number of mussels drilled by each snail was also recorded.

Field outplant experiment

To test whether variation in drilling phenotypes arising from the selection experiment would have ecological

consequences for mussel bed communities, we outplanted adult dogwhelks to field cages and quantified their effects on succession. In May 2020, all organisms were scraped away from sixteen $\sim 0.35 \text{ m}^2$ rectangular sections of mid-intertidal rock at BMR. Organisms were allowed to recolonize these bare areas naturally for the next year until the plots contained a mid-successional community with a mix of acorn barnacles, gooseneck barnacles, and a few small mussels. In May 2021, stainless steel mesh cages (dimensions = $20 \times 20 \times 7 \text{ cm}$, $L \times W \times H$) with removable lids were installed in these 16 areas (Appendix S1: Section S4). Cages were set in a block design with five cages placed within each of the 16 larger areas (80 total cages; Appendix S1: Figure S1A). Each block represented snails from the same family, with each cage randomly assigned to contain snails from one of the four diet treatments, plus a reference cage with no dogwhelks. The tidal height of each cage relative to mean lower low water (MLLW) was quantified with a rotary laser level (DeWalt DW071).

In July 2021, we placed five adult dogwhelks (18.1–20.5 mm in length and labeled with small tags, Floy Tag, Seattle, Washington, USA) from the 16 BMR family \times diet treatments in each treatment cage. This reflected a natural density of *N. canaliculata* in mid-successional habitats at this site (mean density \pm SE = 7.2 ± 5.2 snails/ 0.04 m^2). Snails outplanted to the field were assumed to have drilling capacities that matched those of other snails in the same diet treatment. Snails used as outplants were not scored as the 15-week scoring trials would likely have influenced the nutrition, size, and subsequent behavior of these individuals.

Every ~ 8 weeks for the next year, the lids of the cages were removed, and the caged plots were photographed to assess percent cover of sessile species (see Appendix S1: Figure S1B for example of successional sequence). During each survey, as many of the outplanted snails as possible were located; any dead tagged dogwhelks ($n = 15$) were replaced with another snail from the same family \times treatment. The experiment ended in August 2022 for a total of eight surveys, which included an initial community survey prior to the snail addition. Percent cover of sessile species was determined using image analysis of the photographs (ImageJ, Java 1.8.0_172; Appendix S1: Section S4). For percent cover analyses, species were clustered into seven functional groups: bare rock, acorn barnacles, gooseneck barnacles, mussels, other sessile animals, coralline algae, and other algae/surfgrass (Appendix S1: Table S2). At the completion of the experiment, the dogwhelks and all organisms within the cages were collected. Organisms were sorted in the laboratory by species and all mussels ($>10 \text{ mm}$ long) were counted and measured in each cage.

Analyses

The proxy for shell thickness of the mussel recruits was analyzed using a linear model with mussel length as a covariate and mussel type as a fixed effect. To fit model assumptions, the shell thickness metric was square root transformed prior to analysis. Snail mortality after the first 3 months on the experimental diet treatments was analyzed using a generalized linear mixed model (GLMM) assuming a binomial distribution and logit link function. The model included diet treatment, population, and their interaction as fixed effects, and family as a random effect nested within population. The significance of fixed effects was determined by analysis of deviance, Type II Wald chi-square tests using the “Anova” function from the “car” package (Fox & Weisberg, 2019) in R (version 3.5.1; R Core Team, 2022). Pairwise contrasts for linear and generalized linear mixed models were analyzed with the “emmeans” package. Models were run using the “lme4” package (Bates et al., 2015).

Both laboratory drilling responses were analyzed to determine whether early-life diet impacted adult dogwhelk phenotype. Due to the nested structure of the data with individuals nested within families nested within populations and the high level of phenotypic variation between populations, Bayesian hierarchical models were used to analyze the laboratory scoring data using the R package “brms” (Bürkner, 2017) since these models can handle maximal varying effect structure and highly homoscedastic groups (McElreath, 2018; Veenman et al., 2024). Population, treatment, and their interaction were fixed effects, family was a random effect nested within population, and initial size was included as a covariate. The binary drilling response and the number of mussels drilled per dogwhelk were modeled with a Bernoulli distribution and a negative binomial distribution, respectively. Weakly informative Gaussian priors were set for the global intercept and slope parameters centered on 0 with a SD of 5, and a half-Cauchy prior centered on 0 was set for the SD of the by-family varying intercepts. Median estimates and highest posterior density intervals (HPDI) were calculated using the packages “emmeans” and “bayestestR.” The log odds contrasts were calculated for each diet treatment combination within each population (significance determined if the HPDI of a given contrast did or did not include 1).

The effect of diet treatment on succession was compared using nonmetric multidimensional scaling (NMDS) ordinations and PERMANOVA on Bray–Curtis dissimilarity matrices of the percent cover data using the package “vegan” (Oksanen et al., 2022), as well as time series of the seven functional groups. Community data were analyzed using a two-way PERMANOVA (treatment \times time point). Model selection was performed to determine

the best fit model using the package “AIC_cPermanova” (Corcoran, 2023). PERMANOVAs were conducted using 10,000 permutations and permutations were constrained within blocks. Follow-up univariate linear mixed models with a similar model structure to the best fit PERMANOVA were used to assess the effects of treatment on each of the seven functional groups. The models for some functional groups violated assumptions; however, we prioritized keeping the model structure to match the PERMANOVA, since Gaussian models are robust to non-normality, especially if sample sizes are large (Knief & Forstmeier, 2021). An adjustment for multiple inference was made with a Bonferroni correction.

The number and length of mussels in each cage at the end of the experiment were analyzed with linear mixed models with cage tidal height as a covariate, cage treatment as a fixed effect, and block as a random effect.

RESULTS

Laboratory rearing and selection experiment

M. trossulus recruits used in the laboratory experiment were thinner than *M. californianus* (Appendix S1: Figure S2; one-way ANCOVA, “mussel type”, $F_{2,169} = 34.854$, $p < 0.001$), and shell thickness was strongly dependent on mussel length (one-way ANCOVA, “length,” $F_{1,169} = 1506.584$, $p < 0.001$). However, the thickness of *M. californianus* recruits from the two sources, BMR versus SBR, did not differ (Tukey’s honestly significant difference (HSD), $p = 0.354$).

Mortality of dogwhelks varied among the diet treatments after the 3-month selection phase (Appendix S1: Table S3; GLMM, binomial, “diet,” $\chi^2 = 86.859$, $p < 0.001$), with snails raised on BMR *M. californianus* having the greatest mortality (Figure 2). Mortality did not differ between the two snail populations (Appendix S1: Table S3; GLMM, binomial, “population,” $\chi^2 = 0.301$, $p = 0.583$), nor did the effect of diet treatment on mortality differ between the two populations (Appendix S1: Table S3; GLMM, binomial, “diet × population,” $\chi^2 = 1.216$, $p = 0.749$).

Laboratory scoring experiment

Dogwhelks from the four diet treatments were scored in the laboratory on their ability to drill mussels to test the potential effects of selection imposed by early-life diet. SBR dogwhelks had a much higher frequency of successful drilling than those from BMR (Figure 3; Appendix S1: Table S4; “population,” binary drilling ability 95%

HPDI = [3.08, 13.25], number of mussels drilled per dogwhelk 95% HPDI = [0.57, 1.24]). Early-life diet did not modify the drilling ability of SBR dogwhelks (Appendix S1: Table S5). This result is consistent with previous research showing little variation in drilling phenotypes within the SBR population (Sanford & Worth, 2009).

In contrast, early-life diet had substantial effects on the percentage of surviving BMR snails that were strong drillers. Drilling success was highest for BMR snails raised on BMR *M. californianus* for both the binary drilling response (Figure 3A; Appendix S1: Table S4; “BMR *M. californianus*” 95% HPDI = [0.712, 0.867]) and the number of mussels drilled per snail (Figure 3B; “BMR *M. californianus*” 95% HPDI = [2.14, 2.94]). The odds that a dogwhelk raised on BMR *M. californianus* drilled at least one mussel was 2.48, 1.90, and 2.70 times greater than for a dogwhelk raised on *M. trossulus*, SBR *M. californianus*, and barnacles, respectively (Appendix S1: Table S5). There were no differences in drilling capacity among dogwhelks raised on the other three diets (Appendix S1: Table S5). These results are consistent with the hypothesis that selection imposed by the diet of thick-shelled *M. californianus* favored the survival of more capable drilling phenotypes.

Field outplant experiment

Dogwhelks from the four diet treatments were outplanted to experimental cages to test whether selection on drilling phenotypes influenced mussel bed succession. Our predictions were that (1) dogwhelks would slow succession compared to plots with dogwhelks excluded; and (2) dogwhelks with a greater proportion of strong drilling phenotypes, identified as those raised on BMR *M. californianus* in the laboratory, would drill more and larger mussels and slow succession.

As predicted, the presence of dogwhelks slowed succession relative to the dogwhelk exclusion (reference) plots. However, dogwhelks raised under the four diet treatments did not differ in strong or predictable ways in their effects on succession (Table 1; Appendix S1: Table S6; Figure 4; Appendix S1: Figure S3). Ordination plots illustrate that community composition did not differ among treatments at the start of the experiment (July 2021; Figure 4). Over the course of the next year, trajectories of succession diverged most clearly in the reference cages with no dogwhelks (gray ellipses). Although there were some differences in community composition among the treatment groups with snails (colored ellipses), there was substantial overlap and no clear differences in successional trajectories (Figure 4). Model comparison identified the best fit PERMANOVA as

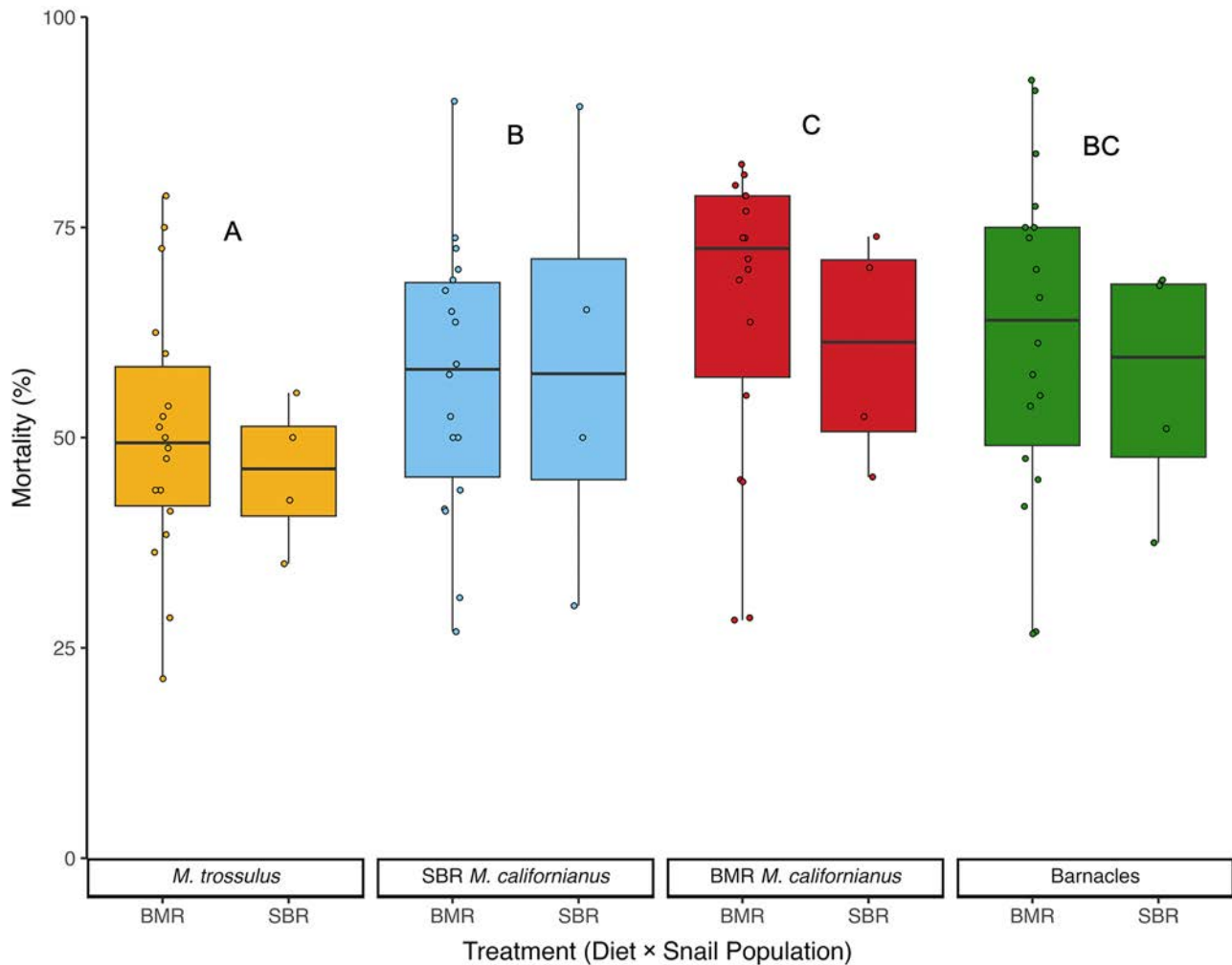


FIGURE 2 Percent mortality of *Nucella canaliculata* juveniles from two populations (Bodega Marine Reserve [BMR] and Soberanes Point [SBR]) after 3 months on the four early-life diet treatments. Points depict mortality at the level of the dogwhelk family, although statistical analyses were run on individual mortality data. Mortality differed among diet treatments, but did not differ between the two populations. Shared letters indicate treatments that did not differ (Tukey’s honestly significant difference [HSD], $p > 0.05$). See Figure 1 for explanation of diet treatments.

containing treatment and time period (Appendix S1: Table S6; difference in corrected Akaike information criterion between models [ΔAIC_c] = 53.66); thus, this structure was used for downstream models. The community composition differed based on the time period surveyed (Appendix S1: Figure S3; Appendix S1: Table S7; PERMANOVA, pseudo- $F = 21.488$, $p < 0.001$) and cage treatment (PERMANOVA, pseudo- $F = 8.424$, $p < 0.001$).

To identify differences among treatments, univariate models were run on each of the seven functional groups (Table 1; Appendix S1: Figure S3). Cage treatment influenced the percent cover of five of the seven functional groups. The reference cages contained more mussels than the four treatments with dogwhelks, had less bare space than the *M. trossulus* treatment, and fewer gooseneck barnacles than the SBR *M. californianus* and barnacle

treatments (Table 1). Contrary to our predictions, snails raised on BMR *M. californianus* did not slow the increase in mussel cover (Appendix S1: Figure S3). There were some subtle differences among diet treatments for the other functional groups; for example, cages containing dogwhelks raised on barnacles and SBR *M. californianus* had the highest cover of gooseneck barnacles (Table 1).

Given the lab results, we predicted that cages containing dogwhelks raised on BMR *M. californianus* would have fewer and smaller mussels than the other three diet treatments. At the end of the field experiment, the number of live mussels held within each cage differed among treatments (Figure 5A; one-way ANCOVA, $F_{1,60.70} = 7.157$, $p < 0.001$), with the reference cages with no dogwhelks containing more mussels than treatments with dogwhelks (Figure 5A). However, mussel abundance did

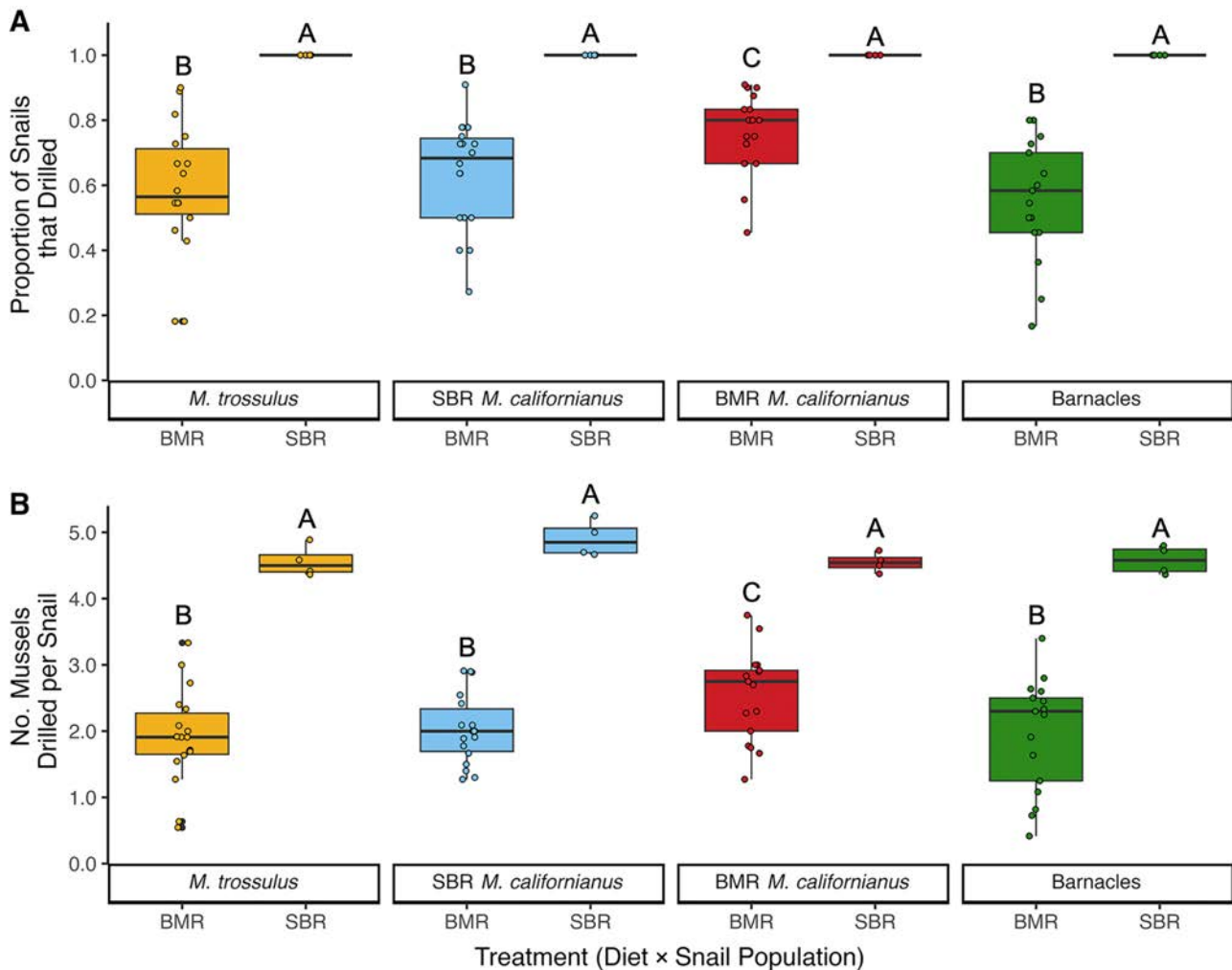


FIGURE 3 (A) Proportion of snails (*Nucella canaliculata*) from each family by diet treatment for the two dogwhelk populations—Bodega Marine Reserve (BMR) and Soberanes Point (SBR)—that drilled at least one 5–7 cm *Mytilus californianus* mussel over the course of the 15-week laboratory scoring experiment. (B) Mean number of mussels drilled per snail for each family × diet combination. Color represents the four early-life diet treatments. Values that extend beyond 1.5 times the interquartile range are plotted both as raw data points (in color) and as gray points on the box plots. See Figure 1 for explanation of diet treatments. Shared letters indicate groups that were not significantly different based on individual level models (Appendix S1: Table S5).

not differ among the four early-life diet treatments (Tukey's HSD, $p > 0.05$). Mussel length did not differ among the five cage treatments (Appendix S1: Figure S4A; one-way ANCOVA, $F_{4,56.99} = 1.109$, $p = 0.361$). Cages that were lower in the intertidal zone had more mussels (Figure 5B; one-way ANCOVA, $F_{1,52.89} = 4.622$, $p = 0.036$) and larger mussels (Appendix S1: Figure S4B; one-way ANCOVA, $F_{1,15.67} = 15.171$, $p = 0.001$).

DISCUSSION

Empirical field studies of the community-level effects of eco-evolutionary feedbacks are rare. As a result, uncertainty remains about whether such effects are

ecologically important or relatively trivial (Hendry, 2017, 2019; Schoener, 2011). Our experiments focused on a study system where there were compelling reasons to suspect that eco-evolutionary dynamics might be important. Previous research had shown that the drilling traits of *N. canaliculata* varied strongly both across its species range and within the focal population for this study (Sanford & Worth, 2009, 2010). When we raised snails in the laboratory under different prey regimes mimicking the natural seasonal and interannual variation in recruitment of prey at this focal site (Morgan et al., 2009, 2012; Sanford & Worth, 2010), mortality was highest in hatchling snails raised on BMR *M. californianus*, creating the potential for strong selection. Indeed, this treatment showed the highest frequency of strong drillers suggesting

TABLE 1 Differences in communities that developed during the year-long field experiment; cages contained dogwhelks (*Nucella canaliculata*) raised under different early-life diet treatments in the laboratory selection experiment.

Functional group	F-statistic (numerator and denominator df)	p value	Treatment comparisons
Bare rock	Treatment (4, 612): 15.57 Time period (7, 612): 4.147	$p < 0.001$ $p = 0.0025$	***Reference— <i>Mytilus trossulus</i> : $-9.37, t_{612} = -7.00$ *** <i>M. trossulus</i> —SBR <i>Mytilus californianus</i> : $8.52, t_{612} = 6.35$ *** <i>M. trossulus</i> —barnacles: $7.09, t_{612} = 5.29$
Acorn barnacles	Treatment (4, 612): 2.374 Time period (7, 612): 89.34	$p = 0.714$ $p < 0.001$	
Gooseneck barnacles	Treatment (4, 612): 23.80 Time period (7, 612): 7.475	$p < 0.001$ $p < 0.001$	***Reference—SBR <i>M. californianus</i> : $-13.7, t_{612} = -6.25$ ***Reference—barnacles: $-17.2, t_{612} = -7.87$ *** <i>M. trossulus</i> —SBR <i>M. californianus</i> : $-11.91, t_{612} = -5.45$ *** <i>M. trossulus</i> —barnacles: $-15.4, t_{612} = -7.07$ ***BMR <i>M. californianus</i> —barnacles: $-12.2, t_{612} = -5.57$
Mussels	Treatment (4, 612): 34.35 Time period (7, 612): 107.6	$p < 0.001$ $p < 0.001$	***Reference— <i>M. trossulus</i> : $18.1, t_{612} = 10.0$ ***Reference—SBR <i>M. californianus</i> : $16.7, t_{612} = 9.20$ ***Reference—BMR <i>M. californianus</i> : $14.0, t_{612} = 7.73$ ***Reference—barnacles: $17.0, t_{612} = 9.38$
Other sessile animals	Treatment (4, 612): 18.24 Time period (7, 612): 11.25	$p < 0.001$ $p < 0.001$	***Reference— <i>M. trossulus</i> : $-2.62, t_{612} = -7.13$ *** <i>M. trossulus</i> —SBR <i>M. californianus</i> : $2.10, t_{612} = 5.72$ *** <i>M. trossulus</i> —Barnacles: $2.67, t_{612} = 7.28$
Coralline algae	Treatment (4, 612): 3.097 Time period (7, 612): 9.365	$p = 0.215$ $p < 0.001$	
Algae and surfgrass	Treatment (4, 612): 9.521 Time period (7, 612): 13.54	$p < 0.001$ $p < 0.001$	***Reference— <i>M. trossulus</i> : $-1.98, t_{612} = -5.69$ * <i>M. trossulus</i> —barnacles: $1.56, t_{612} = 4.49$

Note: Table results show follow-up univariate analyses of the seven functional groups. Linear mixed models included both cage treatment and time period, following the structure of the best fit PERMANOVA. For significant treatment contrasts, post hoc pairwise comparisons were run to identify treatments driving the pattern. Effect sizes, t-ratios, and degrees of freedom are listed for all univariate drivers with significant effects (p values Bonferroni corrected; "*" if $p < 0.05$, "****" if $p < 0.001$).

that selection can rapidly modify this predator–prey interaction. However, despite well-established links between dogwhelk predation and succession (Sanford & Worth, 2010; Wootton, 2002), divergence in drilling traits generated by our laboratory treatments did not lead to clear community-level effects on succession. This suggests that, at least in this well-studied system, eco-evolutionary feedbacks were relatively weak in a natural field setting, perhaps due to the dampening effects of environmental and biotic variation, a restricted range of within-population phenotypes, and incomplete selection.

Eco-evolutionary feedbacks may often be swamped in the field by the overriding effects of substantial spatial variation in environmental conditions and the complex dynamics of biotic processes. In our study, fine-scale physical variation, including the vertical tidal gradient, was a primary driver of mussel cover with lower plots progressing more rapidly in succession toward competitive dominance by mussels. Trajectories of mussel bed succession are also dependent on patterns of recruitment of barnacles and mussels, which can vary strongly over small spatial and temporal scales (Berlow, 1997). The

effects of *Nucella* predation on succession in a given plot can in turn be strongly affected by these stochastic rates of prey recruitment (Berlow, 1997). Rates of succession in mussel bed communities can also be influenced by a range of other species interactions, including both facilitation and competition (Berlow, 1997; Navarrete, 1996; Wootton, 2002). Against this backdrop of substantial environmental variation and the noise-amplifying effects of complex biotic networks, the influence of intrapopulation variation in drilling traits on rates of succession may be comparatively minor.

A second factor that may weaken eco-evolutionary feedbacks in nature is a limited range of within-population variation available for selection to act upon. Polymorphism and genetic variation in behavior and other functional traits are common within populations (Smith & Blumstein, 2008; Wilson, 1998), and selection on this variation can have ecological consequences (Hughes et al., 2008; Whitham et al., 2003). Within-population variation can be maintained by fluctuating selection, gene flow from other populations, or genetic drift (Star & Spencer, 2013). However, the range of functional variation in ecologically important traits

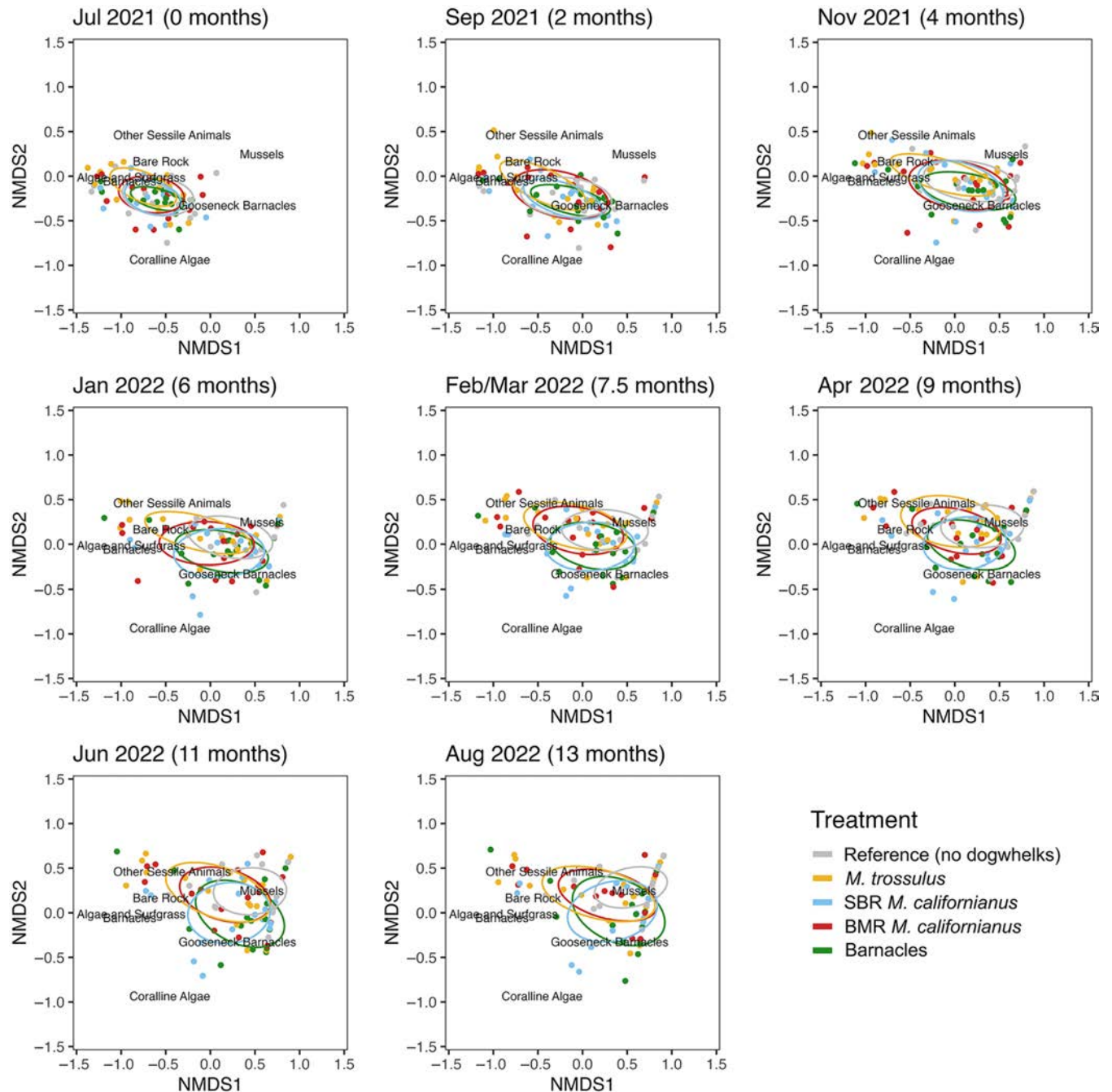


FIGURE 4 Trajectories of succession through time in experimental field cages with predatory dogwhelks (*Nucella canaliculata*) raised under four different early-life diet treatments and reference cages with dogwhelks excluded. Plots are nonmetric multidimensional scaling (NMDS) ordinations of the multivariate percent cover community data through time using Bray–Curtis dissimilarity (stress: 0.1137). Each panel represents a point in time, going from the initial time point before outplanting snails (top left), to the final time point when the experiment was concluded (bottom middle) with the approximate number of months elapsed from the initial survey (check 0). Each point represents the community in a given caged plot at that time point. Points and 95% ellipses are color coded by the five cage treatments. See Figure 1 for explanation of diet treatments. BMR, Bodega Marine Reserve; SBR, Soberanes Point.

within a population is generally small compared to that found across populations (Tack et al., 2012). Theories about eco-evolutionary dynamics have typically been tested by comparing the effects of locally adapted populations or divergent ecotypes (e.g., Des Roches

et al., 2013; Farkas et al., 2013; Fukano et al., 2022). An analogous approach has been common in the field of plant community genetics where plants are collected from distant, diverged populations and their effects on insects are quantified in a common garden environment

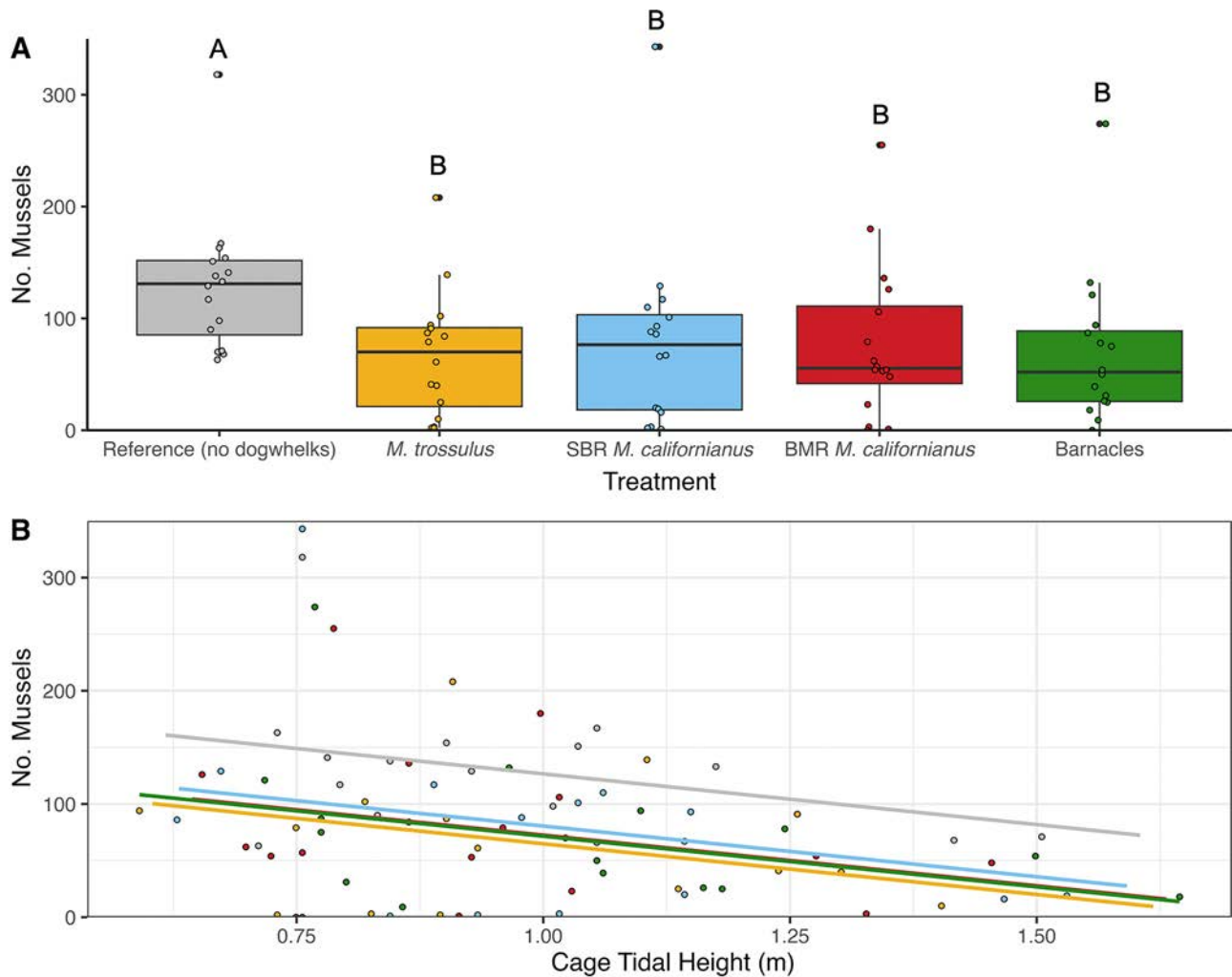


FIGURE 5 Number of live mussels present in each cage treatment at the end of the field experiment. (A) The final number of mussels in cages with dogwhelks (*Nucella canaliculata*) raised in the laboratory under different diet treatments. The gray box plot represents results from reference cages, which excluded all dogwhelks. Values that extend beyond 1.5 times the interquartile range are plotted both as raw data points (in color) and as gray points on the box plots. See Figure 1 for explanation of diet treatments. Shared letters indicate groups that were not significantly different (Tukey’s honestly significant difference [HSD], $p > 0.05$). (B) Variation in the number of live mussels with tidal height. Each point represents a caged plot. Predicted regression line from linear mixed effects model shown for each treatment. Tidal heights are expressed as meters above mean lower low water (MLLW). BMR, Bodega Marine Reserve; SBR, Soberanes Point.

(Hersch-Green et al., 2011). These approaches often create a mismatch in the spatial scales used to test the relative importance of genetic versus environmental influences on community processes (Tack et al., 2012; but see Hughes & Stachowicz, 2004; Reusch et al., 2005; Tack et al., 2010). This mismatch raises concerns that comparing the effects of distant populations in a common environment may inflate genotypic and phenotypic variation and its importance within a community (Bassar et al., 2021; Hersch-Green et al., 2011; Tack et al., 2012). Nevertheless, few studies of eco-evolutionary dynamics have assessed whether temporal variation in selection within a population causes contemporaneous genetic/phenotypic changes that ultimately have ecological

consequences (Bassar et al., 2021; but see Carlson et al., 2011; Carvajal-Endara et al., 2020; Schoener et al., 2017).

In our study system, the range of variation in drilling capacity within our focal population (BMR) is substantially less than that encompassed by geographically separated populations; populations of *N. canaliculata* from California can drill mussels 3.4 times thicker than populations from Oregon (Longman & Sanford, in review). Previous studies indicate that *Nucella* spp. are weak drillers in the Pacific Northwest with minimal impacts on *M. californianus* (Sanford & Worth, 2009) and that these snails facilitate the rate of succession by removing early primary space holders (Wootton, 2002).

In contrast, our study of a California population of *N. canaliculata* indicated that snails slowed and inhibited succession via their predation on *M. californianus*, the primary species that dominates later in succession. Had we outplanted snails from populations with highly divergent drilling phenotypes, the California populations would likely have slowed succession whereas Oregon snails may have accelerated succession. This approach would have highlighted the influence of intraspecific phenotypic variation on ecological processes. However, to assess the importance of eco-evolutionary feedbacks within a community, we prioritized studying the effects of intrapopulation variation to minimize the amount of separation between evolutionary and ecological processes (Bassar et al., 2021).

Lastly, eco-evolutionary feedbacks might be weaker than expected in nature if selection on a population is not strong enough to produce extreme divergence in functional traits. The existence of wild populations comprised of phenotypically diverse individuals suggests that past selection, even if relatively strong, has not been strong enough to eliminate variability in traits under more realistic selection regimes (Carlson et al., 2011; Grant & Grant, 2002). If selection on variation within a population tends to result in moderate shifts in the frequency of different functional traits, the community-level consequences of this selection may be dampened relative to comparisons of highly divergent ecotypes selected from separate populations (Tack et al., 2012). Our selection treatments mimicked natural variation in prey abundance and tested the community consequences of selection on functional variation within a consumer population. Bodega Marine Reserve lies within a strong coastal upwelling region that is known for high levels of seasonal and inter-annual variability in larval supply and recruitment (Morgan et al., 2012; Wing et al., 2003). These fluctuating food sources may select for different drilling phenotypes of *N. canaliculata* within and among years, ultimately maintaining a mix of phenotypes in the population. Although our BMR *M. californianus* treatment did select for a higher frequency of stronger drillers (Figure 3), there were likely still some strong drillers in all of the diet treatments outplanted to the field cages. The maintenance of this variability in consumer traits likely dampens eco-evolutionary effects in this and other natural communities.

The laboratory portion of our experiment relied on artificial selection, which can have unintended phenotypic consequences due to genetic linkage with the focal trait or experimentally imposed conditions (Conner, 2003). These inadvertent outcomes can subsequently impact an individual's fitness under natural conditions (Baskett & Waples, 2013) and may have influenced the ecological effects of *Nucella* once they were outplanted to the field. It

is also possible that some component of variation in drilling ability in our laboratory treatments arose from phenotypic plasticity rather than selection. In the few cases where plasticity in gastropod feeding structures has been documented, morphological variation appears to be a response to recent diet, as snails completely replace their radula over a span of 3–4 weeks (Padilla, 1998). In our study, after dogwhelks were subjected to the selection phase, they were raised on a common diet for 6 months before their drilling abilities were scored (to minimize any effects of plasticity). In addition, previous research has shown that SBR, BMR, and other populations vary in drilling phenotypes after being reared in the laboratory on a common diet (*M. trossulus*) through two generations, thus establishing a genetic basis to this trait variation (Sanford & Worth, 2009). The SBR population consists of uniformly strong drillers (Sanford & Worth, 2009), and the drilling ability of dogwhelks in this population was unaffected by the early-life diet treatments. In contrast, the BMR population (comprised of a mix of drilling phenotypes; Sanford & Worth, 2009) responded strongly to the diet treatments, consistent with the hypothesis that phenotypic variation was a result of differential mortality and selection. Although the SBR population exhibited no phenotypic plasticity in response to the diet treatments, we cannot completely rule out the possibility that plasticity contributed to phenotypic variation in the BMR population. Additional studies are underway to explore genomic differences underlying variation in drilling traits in *N. canaliculata* (Longman et al., unpublished data).

Overall, we suspect that all three of the factors discussed in this section—environmental and biotic variation, restricted within-population variation in phenotypes, and relatively modest levels of selection—contributed to weaken eco-evolutionary feedbacks in this rocky intertidal community. Experimental designs that use divergent populations from distant locations are common yet likely inflate the importance of genotypic/phenotypic variation in functional traits (Bassar et al., 2021; Hersch-Green et al., 2011; Tack et al., 2012). Although such an experimental design would have been consistent with the approach of many studies of eco-evolutionary dynamics to date, we agree with recent syntheses highlighting the need to study feedbacks where there is no separation in time between ecological and evolutionary dynamics (Bassar et al., 2021). In our view, this distinction lies at the heart of the debate about the relative importance of eco-evolutionary feedbacks. There is a long history of studies demonstrating that spatially divergent selection on geographically separated populations can lead to local adaptation and altered species interactions, with community-level impacts (Foster & Endler, 1999; Thompson, 1999b). However, the novel and pressing

question for the field of eco-evolutionary dynamics is whether selection on variation in important functional traits within populations influences the dynamics of natural communities in a consequential way. In our study system, many aspects of natural history, phenotypic variation, selection, and food web structure were aligned to create the potential for strong eco-evolutionary feedbacks. However, the effects of these feedbacks on community dynamics in the field ultimately proved to be weak. Although similar studies are required across many communities to assess the generality of our results, we suggest that a broad range of factors may often constrain and dampen the strength of eco-evolutionary dynamics in natural communities.

ACKNOWLEDGMENTS

Thanks to Michael Brito, Sarah Merolla, and Audrey Deutsch for assisting in raising the dogwhelk hatchlings and Anna Lee for help with the laboratory scoring. We thank A. Lee, J. Rajerison, J. Fosnight, G. Ng, S. Walkes, K. Monuki, M. Delgado, I. Neylan, Z. Brumbaugh, Z. Kimball, C. Kapsiak, S. Jung, S. Beckert, L. Carrasco, S. Allen, S. Harry, A. Kalmezola, S. Rogerson, J. Quan, L. Hsia, S. Moheed, L. Cabling, E. Dean, M. Prado-Zapata, T. Gouin, and J. Sones for assistance with the implementation, maintenance, and breakdown of the field experiment. This paper was improved by helpful suggestions from Rachael Bay, Keira Monuki, Jay Stachowicz, and Sam Walkes. This research was funded by NSF grant OCE-1851462, the Mathias Graduate Student Research Grant Program, and the Bilinski Fellowships at Bodega Marine Laboratory. Research for this project occurred under California scientific collecting permit: S-191200004-19122-001 and Oregon scientific taking permit: 25545.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Longman & Sanford, 2024) are available in Zenodo at <https://doi.org/10.5281/zenodo.13372138>. Datasets are also published by the Biological and Chemical Oceanography Data Management Office (BCO-DMO) under “Project: Coastal mosaics of local adaptation and the eco-evolutionary dynamics of a marine predator-prey interaction” at <https://www.bco-dmo.org/project/811409>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Longman, Emily K., and Eric Sanford. 2025. "An Experimental Test of Eco-Evolutionary Dynamics on Rocky Shores." *Ecology* 106(1): e4505. <https://doi.org/10.1002/ecy.4505>