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Biotic resistance or invasional meltdown? Diversity reduces invasibility but not exotic dominance in southern California epibenthic communities

Ryan A. Beshai · **Danny A. Truong** ·
Amy K. Henry · **Cascade J. B. Sorte**

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Abstract High community diversity may either prevent or promote the establishment of exotic species. The biotic resistance hypothesis holds that species-rich communities are more resistant to invasion than species-poor communities due to mechanisms including greater interspecific competition. Conversely, the invasional meltdown hypothesis proposes that greater exotic diversity increases invasibility via facilitative interactions between exotic species. To evaluate the degree to which biotic resistance or invasional meltdown influences marine community structure during the assembly period, we studied the development of marine epibenthic "fouling" communities at two southern California harbors. With a focus on sessile epibenthic species, we found that fewer exotic species established as total and exotic richness increased during community assembly and that this effect remained after accounting for space availability. We also found that changes in exotic abundance decreased over time. Throughout the assembly period, gains in exotic abundance were greatest when space was abundant and richness was low. Altogether, we found greater support for biotic resistance than invasional meltdown, suggesting that both native and exotic species contribute to biotic resistance during early development of these communities. However, our results indicate that biotic resistance may not always reduce the eventual dominance of exotic species.

Keywords Biotic resistance · Invasional meltdown · Diversity · Epibenthic · Dominance · Community assembly

Introduction

As the number of established exotic species increases worldwide (Seebens et al. 2017), it is increasingly important to understand the role of community diversity in promoting or hindering future invasions. Two competing invasion hypotheses make divergent predictions about the relationship between community diversity and the likelihood of establishment or spread of exotic species. The biotic resistance hypothesis holds that species-rich communities are more resistant to invasion than species-poor communities due to more efficient resource use, leading to fewer available resources and greater interspecific competition (Elton 1958; Levine and D'Antonio 1999). Conversely, the invasional meltdown hypothesis proposes that greater exotic diversity increases invasibility via facilitative interactions between exotic species, resulting in the increased probability of establishment or

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R. A. Beshai (✉) · D. A. Truong · A. K. Henry · C. J. B. Sorte
Department of Ecology and Evolutionary Biology, University of California, Irvine, CA 92697-2525, USA
e-mail: rbeshai@uci.edu

spread of exotic species (Simberloff and Von Holle 1999; Simberloff 2006). Here, we evaluated the degree to which biotic resistance or invasional meltdown influence community assembly, particularly the establishment and dominance of exotic species, in a marine epibenthic community.

Invasional meltdown and biotic resistance both have broad support in the literature even though they predict opposing responses of invasive establishment to community diversity. Recent reviews have found that the majority of studies—up to 77%—provide support for invasional meltdown (Jeschke et al. 2012; Braga et al. 2018) and positive relationships between exotic diversity and exotic establishment. Invasional meltdown has been studied across a variety of ecosystems, with empirical evidence coming from terrestrial plant, vertebrate, and invertebrate communities (Relva et al. 2010; Green et al. 2011; Ackerman et al. 2014; Collins et al. 2020), as well as freshwater plants and vertebrates (Ricciardi 2001; Meza-Lopez and Siemann 2015; Crane et al. 2020), and marine invertebrate communities (Grosholz 2005; Freeman et al. 2016). At the same time, biotic resistance (decreased exotic establishment in more diverse communities) has also been demonstrated in terrestrial (Levine et al. 2004; Beaury et al. 2020; Zhang et al. 2020), freshwater (Fitzgerald et al. 2016; Liew et al. 2016), and marine (Stachowicz et al. 1999; Stachowicz and Byrnes 2006; Kimbro et al. 2013; Marraffini and Geller 2015) communities.

Both hypotheses suffer from key knowledge gaps. Evidence for invasional meltdown at the community level remains relatively scarce in marine communities (Papacostas et al. 2017; Braga et al. 2018). For biotic resistance, studies have questioned if negative relationships are in fact driven by diversity and resource availability or are instead driven by spatial heterogeneity (Davis et al. 2005; Peng et al. 2019), productivity (Sandel and Corbin 2010), disturbance regimes (Davis et al. 2000; Sandel and Corbin 2010; Hill and Fischer 2014), or environmental stress gradients (Von Holle 2013). Finally, most studies examining biotic resistance or invasional meltdown have done so in developed or manually-assembled communities. There is a paucity of information about how these processes may influence exotic establishment during community assembly, such as during initial establishment in new habitat or reestablishment following extreme disturbance events.

Marine epibenthic communities are model systems for diversity–invasibility studies (Stachowicz et al. 2002; Stachowicz and Byrnes 2006; Marraffini and Geller 2015) and ideal for testing the role of biotic resistance and invasional meltdown during community assembly. Epibenthic communities occur on hard surfaces, including subtidal rocky reefs and infrastructure such as piers and docks. These communities are typically composed of sessile invertebrates such as ascidians (Phylum Chordata; hereafter referred to as chordates), bryozoans, poriferans, and polychaetes (Lord 2017). Epibenthic communities are ideal model systems for studying invasion dynamics during community assembly due to the high diversity of both native and exotic species (Sellheim et al. 2010; Lord 2017), relatively rapid community development (Sutherland and Karlson 1977), and the presence of a known, strongly-limiting resource given that these communities are characterized by sessile species: available space (Osman 1977; Sebens 1987). Several studies have highlighted the potential for invasional meltdown to occur in this system (Floerl et al. 2004; Freeman et al. 2016; Gavira-O'Neill et al. 2018). Facilitation within epibenthic communities that could lead to invasional meltdown includes the provisioning of resources such as food (Krüger et al. 2018), shelter (Floerl et al. 2004), additional space (Stachowicz and Byrnes 2006), or settlement cues (Wieczorek and Todd 1997; Dunstan and Johnson 2004). It is also possible that high turnover rates allow for opportunistic colonization by exotic species with life history traits that favor rapid establishment and growth (Sakai et al. 2001; Dunstan and Johnson 2004). However there is also evidence that biotic resistance can be important in this ecosystem, with more diverse assemblages preventing invasion due to more consistent occupation of primary space (Osman 1977; Stachowicz et al. 1999, 2002).

We tested the biotic resistance and invasional meltdown hypotheses by examining whether diversity decreased or increased exotic establishment, respectively, during assembly of epibenthic communities at two southern Californian sites. Importantly, we focused primarily on interactions between organisms of the same trophic level, although biotic resistance and invasional meltdown can also occur via across-trophic level interactions (Stachowicz 1999; Floerl et al. 2004; Kimbro et al. 2013; Papacostas et al. 2017). We evaluated the relationships between richness (total or exotic) and (1) the subsequent establishment of exotic species and (2) the subsequent changes in the abundance of exotic species, as well as (3) trends in exotic dominance over time. We predicted that if invasional meltdown plays a role in community assembly, we would observe the following: (1) higher exotic richness at time *t* would lead to greater increases in richness between *t* and *t+1*; (2) higher exotic richness would lead to greater relative increases in exotic abundance between times *t* and *t+1*; and (3) ratio of exotic to native cover (i.e., exotic dominance) would increase over time. In contrast, if biotic resistance were more important in determining the trajectory of community assembly, we predicted negative relationships between richness of established species and changes in exotic richness and abundance, and a saturation in exotic dominance over time.

Methods

Study locations

We tested the relationship between diversity and exotic species establishment during community assembly in two southern California sites: Huntington Harbor, Huntington Beach, California (33°43′18.90" N, 118° 04′20.60" W) and Newport Harbor, Newport Beach, California (33°37′09.70" N, 117° 53′45.90'' W). Huntington Harbor (3.63 km^2; hereafter referred to as Huntington) is fed by Anaheim Bay and receives runoff from the surrounding urban areas of Long Beach and Huntington Beach. Huntington is composed of five man-made islands and provides numerous hard, artificial settlement spaces. Newport Harbor (3.39 km^2; hereafter referred to as Newport) is a natural bay located approx. 20 km south of Huntington; it opens directly into the ocean in Corona del Mar and receives both heavy drainage from San Diego creek and urban runoff (Lambert and Lambert 2003). Both Huntington and Newport experience heavy use from recreational boaters.

Experimental approach

At each site, we mounted 8 clean, 10 × 10 cm PVC plastic plates approx. 1 m beneath the surface of the water (2 sites × 8 plates = total of 16 plates). We deployed the plates in August 2018 and allowed communities to assemble over a 4 month period until December 2018. During the assembly period, we assessed community development in a nondestructive manner by removing the plates from the water briefly (<5 min) and photographing the sessile invertebrate cover with a Nikon D90 DSLR camera (with Nikon AF-S DX NIKKOR 18–55 mm f/3.5–5.6G VR II lens with the lowest f-stop value and the capture mode set to aperture-priority auto-exposure). Photographs were taken weekly for the first 5 weeks post-deployment and then every 2 weeks through the end of the 18-week assembly period. For our statistical analysis, we removed weeks 1 and 3 and we calculated all of our response variables over 2 week intervals for consistency.

We estimated the proportional abundance of each species using point classifications generated by the web-based automated annotation tool, CoralNet (Beijbom et al. 2012, 2015; Beijbom 2015; https://coralnet.ucsd.edu/). We began by visually inspecting our photographs, conducting a microscopic analysis of species that were difficult to distinguish morphologically, and identifying all species to the lowest possible taxonomic resolution. We used this species identification list to generate a set of image classification labels to be used in the CoralNet analysis. We then submitted our photographs and classification labels to the software and superimposed a uniform 30 × 30 point grid (for a total of 900 points) on each of the photographs. We trained the software by allowing it to automatically classify the cover directly underneath each point (as either a species identification, bare primary space, or biofilm) and then confirming or correcting each of the classifications, resulting in increasingly accurate automatic classifications over time. Once we reached 80% classification accuracy, we allowed the tool to run automatically for the remaining photographs. We then conducted a visual inspection of all photos and verified or corrected any misidentified classifications. The software was retrained as communities developed to ensure that accuracy did not decrease over time. Though such a macro-scale assessment may not detect the smallest settlers unless they become established (i.e., grow), this semi-automated approach has been demonstrated to reduce classification variability compared to a fully-automated approach (Beijbom et al. 2015). We observed that both native and exotic species frequently settled directly on exposed oyster valves and that oysters never overgrew other organisms, so oyster cover was considered equivalent to available space. We did not include other calcareous species in this classification due to concerns about the quality of secondary settlement surfaces that they provide and due to the apparent resistance to overgrowth by some taxa. We therefore calculated the total available space on each plate as the sum of bare space, biofilm, and oyster cover. Available space averaged 48.07 ± 2.1% (mean ± SE) cover across all observations. For each species (Table 1), we determined its biogeographic status (i.e., native versus exotic) based on its classification in southern California according to the National Exotic Marine and Estuarine Species Information System (Fofonoff et al. 2018). If a species was not present in the database or did not have a record for southern California, we conducted a thorough literature search to find records of the species' native range or consulted expert opinion. We classified the species as "unresolved" when invasion status could not be determined (e.g., species-level identification was not possible and a genus consists of a mix of native and exotic species) or "cryptogenic" if the species was of uncertain provenance (i.e., the native range for the species is not resolved), sensu Carlton [1996]), respectively. Of 29 total taxa identified on the plates, 1 was classified as unresolved and 1 as cryptogenic.

Table 1 Taxa identified on our plates. Taxa were identified to the lowest possible level (species or genus)

Phylum	Name	Biogeographic status	Presence (yes/no)	
			Huntington	Newport
Porifera	*Halichondria bowerbanki*	Exotic	Y	Y
Cnidaria	*Anthopleura artemisia*	Native	Y	Y
Mollusca	*Ostrea lurida*	Native	Y	Y
Bryozoa	*Celleporella hyalina*	Cryptogenic	Y	Y
Bryozoa	*Amathia verticillata*	Exotic	Y	N
Bryozoa	*Bugulina stolonifera**	Exotic	Y	Y
Bryozoa	*Cryptosula pallasiana*	Exotic	Y	N
Bryozoa	*Schizoporella* spp.	Exotic	Y	Y
Bryozoa	*Tricellaria inopinata*	Exotic	N	Y
Bryozoa	*Watersipora* spp.	Exotic	Y	Y
Bryozoa	*Diaperoecia californica*	Native	Y	Y
Bryozoa	*Membranipora* spp.	Native	N	Y
Bryozoa	*Thalamoporella californica*	Native	Y	Y
Polychaeta	*Demonax* sp.	Exotic	Y	N
Polychaeta	*Hydroides elegans*	Exotic	Y	Y
Polychaeta	*Spirorbid* sp.	Unresolved	Y	Y
Chordata	*Ascidia zara*	Exotic	Y	N
Chordata	*Botrylloides diegensis*	Exotic	Y	Y
Chordata	*Botrylloides violaceus*	Exotic	Y	Y
Chordata	*Botryllus schlosseri*	Exotic	Y	Y
Chordata	*Ciona robusta*	Exotic	Y	N
Chordata	*Ciona savignyi*	Exotic	Y	Y
Chordata	*Didemnum vexillum*	Exotic	Y	Y
Chordata	*Diplosoma listerianum*	Exotic	Y	Y
Chordata	*Molgula manhattensis*	Exotic	Y	N
Chordata	*Styela clava*	Exotic	Y	Y
Chordata	*Styela plicata*	Exotic	Y	Y
Chordata	*Aplidium californicum*	Native	Y	Y
Chordata	*Metandrocarpa taylori*	Native	Y	N

*White *Bugula* individuals observed on our plates were identified as *B. stolonifera* as discussed in Fofonoff et al. (2018) and references therein

Response variables

To quantify the effects of diversity on establishment by exotic species, we calculated the change in exotic richness (ΔS) over each of the 2 week intervals as:

$$\Delta S = \mathrm{S}_{\mathrm{t}+1} - \mathrm{S}_{\mathrm{t}} \tag{1}$$

where S_t represents the richness of exotic species at a given observation, and $\mathrm{S}_{\mathrm{t}+1}$ represents the exotic richness present in the community at the subsequent observation.

We also calculated proportional changes in abundance between observations as:

$$\Delta A = \frac{\mathrm{A}_{\mathrm{t}+1} - \mathrm{A}_{\mathrm{t}}}{\mathrm{A}_{\mathrm{t}}} \tag{2}$$

where A_t represents the summed proportional abundance of exotic species (i.e., the total proportion of all exotic species out of 900 points) at a given observation, and $\mathrm{A}_{\mathrm{t}+1}$ represents proportional cover of exotic species at the subsequent observation. For instances in which no cover was observed at A_t but was present in $\mathrm{A}_{\mathrm{t}+1}$ (i.e., periods in which species [re]established in the community and for which change in abundance would be undefined), we assigned an initial value of 0.001 (equivalent to coverage of a single point out of our total 900 points). We compared initial values ranging from 0.0001 to 0.001 and found that our choice of value did not affect our conclusions (R. Beshai, unpubl. data).

Finally, we calculated exotic dominance using the ratio of total exotic cover to total native cover at a given observation:

$$\mathrm{E{:}N} = \frac{\mathrm{A}_\mathrm{E}}{\mathrm{A}_\mathrm{E} + \mathrm{A}_\mathrm{N}} \tag{3}$$

where A_E is the summed proportional cover of all exotic species and A_N is the summed proportional cover of native species. This index allowed us to compare how greatly exotic species contribute to the total cover of species with known origins between time points. Unresolved species accounted for $3.86 \pm 0.36\%$ cover across all plates and time points, with a maximum of 34.67% on one plate at one time point in Huntington, and were not included in these calculations.

Statistical analysis

We examined the influence of community diversity metrics (total or exotic richness) on changes in exotic richness using a model averaging approach. We defined a global linear mixed model (LMM) that included explanatory variables of richness (total or exotic, which were assessed separately), available space, site (Huntington or Newport), experimental day (the number of days the community had been assembling), and all two-way interactions between richness, available space, and experimental day; plate was included in the model as a random effect to account for repeated measures. To most accurately estimate both main effects and interactions (Grueber et al. 2011; Harrison et al. 2018) as well as alleviate potential issues arising from multicollinearity (Iacobucci et al. 2016), we centered and standardized our variables. We assessed multicollinearity using variance inflation factors, and found that $\mathrm{VIF} < 5.5$ for all global models, which falls within the previously-established standard threshold of 10 (Quinn and Keough 2002; Harrison et al. 2018). We then employed an all-subsets model selection approach on our global model to determine the best supported combination of explanatory variables, ensuring that all candidate models retained the random effect of plate to account for our repeated experimental design. Individual candidate model fits were evaluated using the conditional Akaike information criterion (AICc), and models with $\Delta\mathrm{AICc} < 6$ (Symonds and Moussalli 2011; Harrison et al. 2018) were incorporated into a best model set along with the best model; candidate models with $\Delta\mathrm{AICc} < 6$ that did not converge were excluded from the best model set. We then averaged our best model set and report the results according to the zero method (Grueber et al. 2011), where zero is substituted for a variable estimate in models where the parameter is absent.

To assess the relationship between richness metrics and changes in exotic abundance, we again applied our model averaging approach. However, because our change in abundance response had a lower bound of −1 (equal to a 100% loss of exotic cover) but no upper bound, we transformed our abundance response by adding 1.001 to all data points and instead fit a generalized linear mixed model (GLMM) with a gamma distribution and log link. This model structure was appropriate because our response variable was non-negative, positively skewed, and continuous following the transformation. Our global GLMM was then defined with an explanatory variable structure of richness, available space, site, experimental day, and the two-way interactions between richness, space availability, and experimental day; we again included a random effect of plate.

To determine the effects of time and exotic richness on exotic dominance, we applied a LMM to our calculated E:N ratio values with experimental day, exotic richness, the interaction between day and exotic richness, and site as fixed effects and plate as a random effect. We did not include available space in our model because we were predominantly interested in testing the relationship between exotic dominance and time and how it was influenced by exotic richness. All VIF for this model were < 3.

Due to the heavy influence of a rainfall event toward the end of the assembly period, all analyses presented here in the main text use data from prior to the rainfall event (for comparisons of analyses run with the full data set, see Supplementary Appendix Tables 1–5). Figures presenting trendlines in the main text do not include data following the rainfall event. Finally, to ensure that the length of the assembly period did not influence our results, we conducted a second analysis using only the first 28 days of our observations (see Supplementary Appendix Tables 6–10). All analyses were conducted in R (R Core Team 2020) using the *lme4* package (Bates et al. 2015) v. 1.1–27 to fit the global models, *MuMIn* v. 1.43.17 (Bartoń 2020) for the model selection and averaging process, and *ggplot2* (Wickham 2016) v. 3.3.5 for data visualization.

Results

Community structure and dynamics

We observed a total of 29 species across all plates and sites, with 27 species in Huntington and 22 species in Newport (Table 1). We identified 20 species as exotic in southern California, 7 as native, and 2 as unresolved or cryptogenic. Of the 27 species that recruited in Huntington, 19 (70%) were exotic, 6 were native (22%), and 2 (7%) were unresolved or cryptogenic. Biogeographic groups were similarly represented in Newport, with 14 (63%) exotic species, 6 (27%) native species, and 2 (9%) unresolved or cryptogenic species recruiting over the assembly period. Across both sites, the majority of exotic cover was the chordates *Botrylloides diegensis*, *Botryllus schlosseri*, *Ciona robusta*, *Ciona savignyi*, *Diplosoma listerianum*, and *Molgula manhattensis* as well as the bryozoans *Tricellaria inopinata* and *Watersipora* spp., while native cover was driven by the bryozoans *Diaperoecia californica* and *Thalamoporella californica* as well as the bivalve *Ostrea lurida*. The total cover from all other native and exotic species averaged $< 3\%$ across all time points and both sites.

Patterns of community assembly differed slightly between sites. In Huntington, community richness, both total and exotic, increased over time but decreased following a large rainfall event (Fig. 1a, Supplementary Figures and Tables Fig. S1a). A similar pattern was observed in Newport, but soft-bodied chordates comprised a greater proportion of the community and there was a greater reduction in richness following the rainfall event (Fig. 1b, Fig. S1b). In Huntington, exotic cover increased rapidly in the early stages of assembly, primarily driven by recruitment by the early-successional species *D. listerianum* (Edwards and Stachowicz 2010), and declined concomitant with *D. listerianum* die-offs (Fig. 1c, Fig. S1a). The total abundance of exotic species then underwent a second rapid increase following the disappearance of *D. listerianum*, driven by the growth of competitively-dominant chordates (Edwards and Stachowicz 2010), including *B. schlosseri* and *C. savignyi*. Native cover remained relatively stable at low levels throughout the assembly period. In Newport, assembly was similarly characterized by a rapid establishment and spread of exotic species, particularly *B. schlosseri* and *D. listerianum*, but the peak abundance of exotic species occurred approx. 50 days later than in Huntington communities (Fig. 1d, Fig. S1b). Native cover exhibited much greater increases over time in Newport than in Huntington, primarily as a result of greater oyster (*O. lurida*) growth (Fig. 1d; Fig. S1c, d).

Impacts of richness on exotic species

We found that changes in exotic richness were consistently driven by the main effects of richness (at the previous time point) and site over the course of the experiment (Tables S1, S2). Specifically, exotic

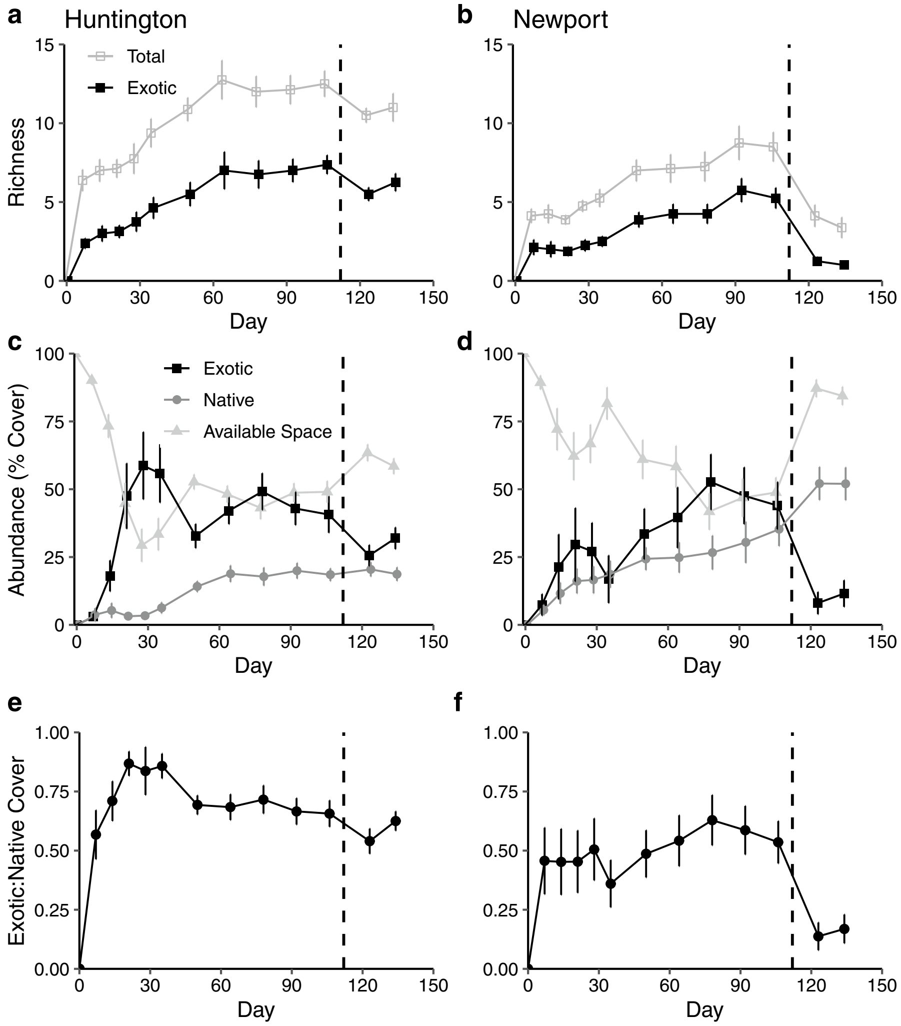

Fig. 1 Mean (±SE) richness (**a**, **b**), abundance (**c**, **d**) and ratios of exotic:native cover (i.e., exotic dominance) (**e**, **f**) observed in fouling communities assembling from August-December 2018 in Huntington (**a**, **c**, **e**) and Newport (**b**, **d**, **f**) Harbors, California, USA. Available space is calculated as the sum of bare primary space, biofilm, and oyster (*O. lurida*) cover. Values are averages from n = 8 plates. Assembling communities were impacted by a heavy rainfall event (indicated by a dashed vertical line) that occurred on Day 112 of the experiment

species established less often or were lost from the communities as richness increased; this pattern was evident considering the value at the previous time point of both total richness (Fig. 2a; $\beta = -1.28$, $p < 0.001$) and exotic richness (Fig. 2b; $\beta = -1.27$, $p < 0.001$). Additionally, significance of the site parameter in both total richness ($\beta = -1.38$, $p < 0.001$) and exotic richness ($\beta = -1.06$, $p = 0.003$) models revealed that exotic establishment differed between Newport and Huntington, but that greater richness was always associated with decreased exotic establishment. Importantly, the saturation of exotic species (the proportion of exotic species observed on a plate out of the site total) typically remained below 50% (Fig. S2). Space availability did not directly influence exotic establishment in models considering either total richness (Fig. 3a; $\beta = 0.467$, $p = 0.06$) or exotic richness ($\beta = 0.341$, $p = 0.14$).

Changes in the abundance of exotic species, on the other hand, were influenced by the main effects of space availability and day, as well as the richness × day and space × day interactions (Tables S3, S4). Regardless of whether our model was accounting for total richness ($\beta = 0.578$, $p < 0.001$) or exotic richness ($\beta = 0.582$, $p < 0.001$), exotic species exhibited greater growth in communities with ample space than in space-limited communities, where they generally experienced reduced growth or declines in abundance (Fig. 3b). Available space fluctuated throughout the assembly period, however, and we observed space × day interactions in both model sets (Tables S3, S4), where changes in

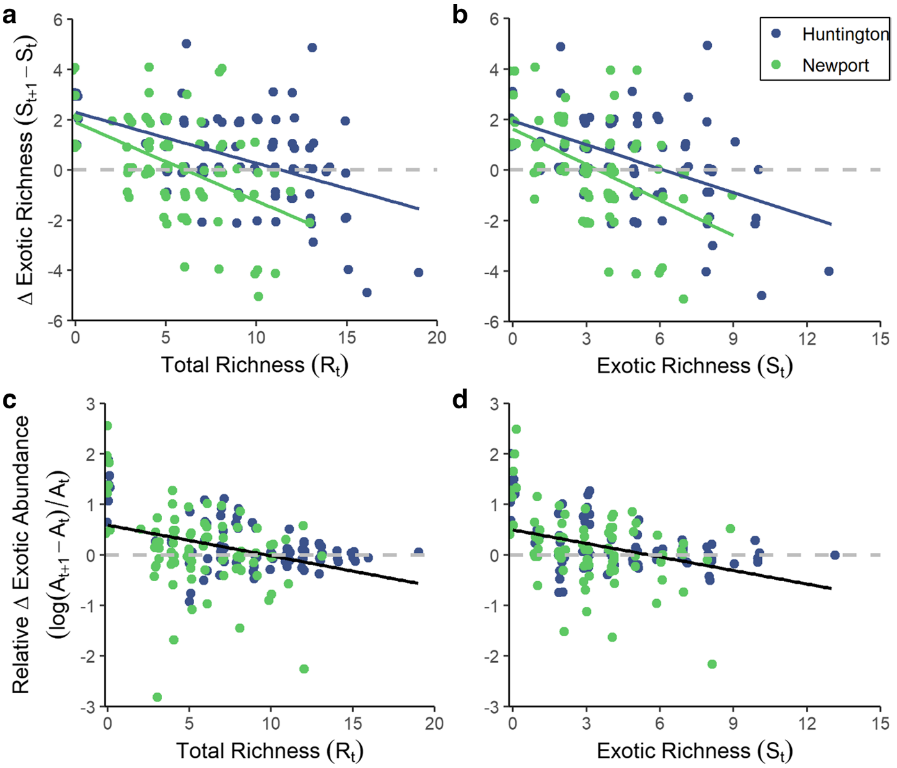

Fig. 2 The relationships between the total richness (**a**, **c**) and exotic richness (**b**, **d**) of a community at a given time point and changes in exotic richness (**a**, **b**) or exotic abundance (**c**, **d**) at the following time point in assembling fouling communities in Huntington and Newport Harbors, California, USA. In both sites, (**a**) fewer exotic species established as total richness increased ($\beta = -1.28$, $p < 0.001$) and (**c**) changes in total abundance of exotic species decreased via a richness × day interaction ($\beta = 0.468$, $p < 0.001$). A similar influence of exotic richness was observed when modelling both (**b**) changes in exotic richness ($\beta = -1.27$, $p < 0.001$) and (**d**) changes in exotic abundance ($\beta = 0.522$, $p < 0.001$). Points represent values from eight individual plates at two sites (Huntington in blue, Newport in green) across 7 time intervals ($n = 112$ total points, all of which were used in our statistical models after exclusion of post-rainfall data). Points below $y = 0$ indicate either losses in richness (**a**, **b**) or decreases in abundance (**c**, **d**). Data are slightly jittered to increase visibility. The data are presented unstandardized but were standardized for analysis. Black trendlines indicate significant relationships that do not vary by site, while colored trendlines indicate significant site-specific relationships

abundance were greatest early in assembly when space was freely available, and decreased over time as space became more limiting (Fig. S3). We did not find a main effect of richness on changes in abundance in either the total richness ($p = 0.62$) or exotic richness ($p = 0.67$) model. We did, however, detect a richness × day interaction in both total richness (Fig. 2c; $\beta = 0.486$, $p < 0.001$) and exotic richness (Fig. 2d; $\beta = 0.522$, $p < 0.001$) models, where changes in abundance were large and positive early in assembly when richness is low and then decreased in magnitude over time as community richness increased, eventually resulting in abundance decreases.

Exotic species were typically dominant over native species, though exotic patterns did vary by site. Exotic dominance generally increased with exotic richness (Table S5, $\beta = 0.110$, $p = 0.002$) but did not increase over time ($\beta = 0.008$, $p = 0.81$). Rather, in both Huntington and Newport, peak values of exotic dominance occurred synchronous with rapid proliferation of *D. listerianum* and *B. schlosseri* or *Watersipora* spp. (Fig. 1e,f; Fig. S1a,b), resulting in a significant day × exotic richness interaction (Fig. S4; $\beta = -0.156$, $p < 0.001$). Exotic dominance patterns differed between Huntington and Newport (Fig. 1e,f; Table S5), with greater exotic dominance in Huntington than in Newport throughout the assembly period

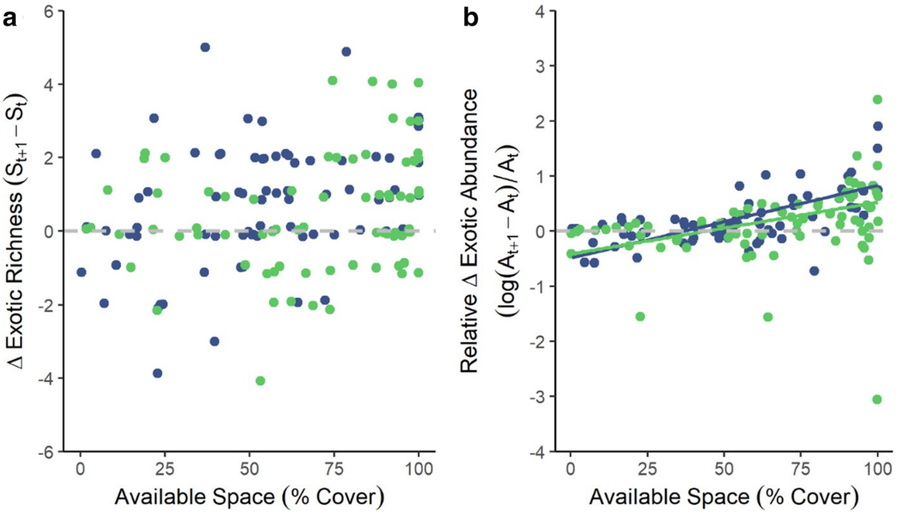

Fig. 3 The relationships between available space at a given time point and changes in (**a**) exotic richness and (**b**) proportional exotic abundance at the following time point during fouling community assembly in Huntington and Newport Harbors, California, USA. Available space was positively correlated with changes in exotic abundance but uncorrelated with changes in exotic, regardless of the richness metric used in the statistical model (Tables S1-S4). Points represent values from eight individual plates across two sites (Huntington in blue, Newport in green) and all 7 time intervals (n = 112 total points, all of which were used in our statistical models after exclusion of post-rainfall data). The data are presented unstandardized but were standardized for analysis. Data are slightly jittered to increase visibility. Colored trendlines indicate significant differences between sites, and plots without trendlines are nonsignificant

($\beta = -0.122$, $p = 0.009$). This pattern was primarily driven (1) the later dominance of colonial chordates in Newport (2), the generally lower abundance of exotic *Watersipora* spp. in Newport, and (3) the generally greater abundance of *O. lurida* in Newport. Removal of oyster cover from our exotic dominance index resulted in a non-significant difference between sites (Table S6). Though not included in our statistical models, we observed that exotic dominance was impacted by the Day 112 rainfall event at both sites. Generally, soft-bodied chordates declined leading to declines in overall exotic dominance, and in Newport, *D. listerianum* die-offs coincided with a period of dominance by native species.

Discussion

Our results suggest that biotic resistance may be more important in structuring communities like this sessile epibenthic community during the assembly period than invasional meltdown. Increased richness, measured by both total richness and that of exotic species only, was associated with reduced establishment success and population growth of later-arriving exotic species (Fig. 2a–d) and did not appear alter community assembly in a way that favored exotic species. Critically, this effect is potentially not driven strictly by increasing representation of the exotic species pool on our plates, as exotic saturation remained below 50% throughout the assembly period (Fig. S2). Our results are consistent with findings in established and/or manipulated (rather than assembling) communities that suggest that greater community richness reduces invasibility (Stachowicz et al. 1999, 2002; Stachowicz and Byrnes 2006). Our results also provide additional evidence that exotic species contribute to biotic resistance (Collin and Johnson 2014; Marraffini and Geller 2015) and that interactions between multiple exotic species may not be net positive or synergistic (Jackson 2015). Since it is possible that the process of manipulating epibenthic communities may undermine mechanisms that generate invasion patterns (Dunstan and Johnson 2004), consistency between our results and those of previous studies suggest that the effect of richness on invasibility is relatively robust in epibenthic systems. Finally, when taken together, the overall finding that greater richness was associated with reduced establishment success suggests that the combined effect of all interactions between exotic species may be more negative than positive.

Mechanistically, classical theory suggests that that invasibility is heavily determined by resource availability and fluctuations in limiting resources (Elton 1958; Davis et al. 2000; Davis and Pelsor 2001). In epibenthic communities, space is known to be a highly limiting resource, and a more consistent occupation of space has been suggested as a strong deterrent to invasions (Stachowicz et al. 1999, 2002; Stachowicz and Byrnes 2006; Marraffini and Geller 2015). Interestingly, our study found mixed evidence for this, as changes in exotic richness were unrelated to the amount of available space but available space significantly interacted with time to modulate changes in abundance. Epibenthic communities are notably stochastic (Sutherland and Karlson 1977), so it is possible that changes in richness were unrelated to resource availability because the space vacated by transient exotic species was rapidly filled through the arrival of secondary exotic species (Dunstan and Johnson 2004) or because high cover may limit, but not entirely prevent, establishment if exotic species are able to settle on other species (Lord 2017). The latter appears particularly likely in our system, as we observed that while taxa such as colonial chordates could not successfully establish on *Watersipora* spp., other taxa, such as solitary chordates, could. In contrast, changes in exotic abundance are limited by overgrowth and space occupation by neighboring species (Sebens 1987; Lord and Whitlatch 2015; Lord 2017). The greatest increases in exotic abundance occurred in Huntington as a result of rapid growth by *D. listerianum*. At this point in development, few other exotic species were present in the communities and space was freely available, so all growth by *D. listerianum* contributed to the area covered by exotic species. In comparison, the later spread of *D. listerianum* in Newport contributed less to the total abundance of exotic species, as *D. listerianum* began to compete with and overgrow other exotic species. In other words, growth of *D. listerianum* had disproportionate impacts on exotic cover early in assembly because the majority of new growth covered previously unoccupied space whereas in Newport, *D. listerianum* overgrew other exotic species, resulting in less total change in area covered by exotics. Thus, while the total abundance of exotic species generally increased over time, relative increases diminished.

Despite the influence of community richness and limiting resources, our results suggest that biotic resistance may not always influence ultimate exotic dominance. Instead, we found that exotic dominance was generally high over the course of our experiment. High exotic dominance is likely driven by several interacting factors. First, exotic species tend to display life-history characteristics that allow for rapid growth, maturation, and the production of large numbers of offspring, allowing them to efficiently establish and spread among recipient communities (Sakai et al. 2001; Theoharides and Dukes 2007). Thus, as exotic species establish, they may be able to consume even scarce resources and preempt native species. Second, a sampling effect might allow one or two most impactful exotic species to disproportionately influence community structure during community assembly. The greatest fluctuations in exotic dominance occurred during boom-bust periods of the chordates *D. listerianum* and *B. schlosseri*. Such dominance by a few exotic species may be particularly apparent in frequently-disturbed or newly-assembling communities due to the combined release or creation of resources (Davis et al. 2000; Strayer et al. 2017) and the "pioneering" characteristics of exotic species (Sakai et al. 2001). Notably, we observed that in Huntington, high exotic dominance was maintained following *D. listerianum*'s "bust" phase via the proliferation of later-successional exotic species (e.g., *B. schlosseri*) (Edwards and Stachowicz 2010), indicative of "over-invasion" (i.e., the replacement of an established exotic species by a second, later-arriving exotic; sensu Russell et al. 2014) limiting the establishment or recovery of native species (Strayer et al. 2017). Third, increased propagule pressure is known to drive invasion success (Lockwood et al. 2005; Simkanin et al. 2017; Cassey et al. 2018), and high exotic abundance in Huntington may be sustained by high regional propagule pressure from within and between adjacent ports. Several studies have connected high shipping intensity with increased rates of exotic establishment (Lord and Whitlatch 2015; Lacoursière-Roussel et al. 2016), and, when strong enough, propagule pressure may allow species to bypass biotic resistances

(Hollebone and Hay 2007). Huntington lies < 20 km from the Ports of Los Angeles and Long Beach, two of the busiest ports in the United States (Hu et al. 2021), and is likely receiving high regional propagule dispersal, whereas with a separation of > 30 km, it is possible that Newport experiences lower regional propagule pressure. Both sites, however, receive high local traffic from recreational vessels, which is also known to contribute significantly to the movement of exotic fouling species (Lambert and Lambert 1998, 2003; Davenport and Davenport 2006). Additionally, both sites are exposed to high internal propagule pressure from established communities on adjacent pilings and docks.

Despite the potential for biotic resistance to be greater in established communities, our study provides evidence for biotic resistance in assembling communities, which may influence ultimate community structure. Previous research has shown that in epibenthic communities, larger organisms are competitively dominant over smaller organisms (Buss 1979), and that more consistent utilization of available space—a product of greater diversity—reduces invasibility (Stachowicz et al. 2002). Together, these suggest that biotic resistance would be more likely to occur in older, more diverse communities containing larger organisms than in early-assembly communities that are relatively low-diversity and where species are likely to be initially similar in size. However, our study demonstrates the possibility for negative interactions to limit increases in exotic abundance during the assembly period, largely through space competition. The existence of competitive interactions is of particular importance during assembly, as priority effects from early-arrivals can influence ultimate community composition (Sutherland 1974; Connell and Slatyer 1977; Vieira et al. 2018a) and invasibility (Gerla and Mooij 2014). For example, Viera et al. (2018b) found that assemblages founded by encrusting bryozoans or colonial chordates, such as *D. listerianum* in this study, were typically low-diversity and dominated by species that occupy disproportionate amounts of available space later in development, whereas communities founded by arborescent bryozoans tended to become more diverse later in assembly. It is possible that rapid establishment of *D. listerianum* may have set our communities on a trajectory that led to reduced diversity of all species, including exotics.

There are several potential explanations for why we did not observe invasional meltdown occurring in our experiment. First, published examples of invasional meltdown typically document exotic species ameliorating conditions in recipient habitats to make them less hostile to subsequent exotic establishment or acting as disturbances in the recipient communities that free up resources (Simberloff and Von Holle 1999; Simberloff 2006). For example, *Watersipora* spp., which was abundant in Huntington, has been implicated in invasional meltdown elsewhere because it increases habitat availability (Stachowicz and Byrnes 2006; Scott and terHorst 2020) or acts as a settlement refuge in toxic environments (Floerl et al. 2004), thereby potentially promoting exotic species richness (Floerl et al. 2004; Scott and terHorst 2019; but see Scott and terHorst 2020). However, facilitation among sessile organisms, such as the production of secondary space, may influence both exotic and native species equally, not inherently favoring settlement by exotic species over natives. In our study, this is best illustrated by the settlement of both native (*T. californica*) and exotic (*B. schlosseri*) species on oyster valves. As a result, the presence of foundation species may be more important for increasing overall diversity of a system (Scott and terHorst 2020) rather than specifically facilitating exotic settlement and diversity. The presence of foundation species such as *Watersipora* spp. may also be more important for increasing the diversity of mobile species, which were not quantified in our study, than sessile species (Sellheim et al. 2010; Gavira-O'Neill et al. 2018; Scott and terHorst 2020). Second, though a foundation species may provide additional settlement space or structural complexity, it is possible that such habitat modifications may not fully compensate for the resources it consumes. For example, the lack of settlement we observed on *Watersipora* spp. by colonial chordates may be due to activity of feeding zooids, which could inhibit the settlement and/or growth of secondary sessile settlers (Scott and terHorst 2020) compared to smooth oyster valves which more readily mimic primary space. In this way, *Watersipora* spp. may reduce, rather than increase, the likelihood of establishment for later-arriving sessile species, despite creating additional or more structurally-complex habitat. Third, some tunicates secrete chemicals that inhibit settlement by other species (Davis 1991; Mayzel et al. 2014); thus, overgrowth competition and chemical-mediated settlement inhibition, which allow exotics to occupy primary space but not actively displace adjacent organisms, might act as the primary antagonistic interactions between epibenthic exotics (and natives). This limits the potential for exotic species to alleviate space restrictions for subsequently-arriving exotic species by acting as disturbances (and freeing up resources) and instead serves to increase competitive interactions between exotic species. Finally, several of the exotic species present in our study (e.g., *B. schlosseri*, *C. robusta* [previously identified as *C. intestinalis*], and *S. plicata*) are believed to have been introduced in the early 1900s (Lambert and Lambert 1998) and have become established, forming self-sustaining populations alongside native species throughout southern California. Therefore, it is possible that these species are now "behaving like the natives" during assembly (Pearson et al. 2018), where a lack of "novel" biotic interactions between natives and exotics allows assembly patterns to be primarily determined by species' intrinsic traits such as recruitment patterns, relative competitive abilities, and life history trade-offs (Edwards and Stachowicz 2010, 2012) rather than provenance-mediated biotic interactions, resulting in a negligible influence provenance itself on the outcome of assembly or reassembly, in the case of highly-disturbed communities.

Biotic and abiotic factors not examined here are known to influence epibenthic community structure and composition. While studies have demonstrated that predation may have strong impacts on epibenthic community composition (Vieira et al. 2012; Oricchio et al. 2016; Freestone et al. 2021), its role in modulating exotic establishment is debated. In epibenthic communities, predation might serve to limit the establishment (Dumont et al. 2011; Collin and Johnson 2014; Rogers et al. 2016; Kremer and da Rocha 2016; Leclerc et al. 2020) or dominance of exotic organisms, as predators tend to target poorly-defended, soft-bodied chordates (Kremer and da Rocha 2016), which were characteristics of the species that we found to be primary drivers of changes in exotic abundance and dominance. Thus, predation could alter the succession sequence by suppressing rapidly growing initial colonizers (Nydam and Stachowicz 2007), which could allow for greater initial growth of native species, though this effect (which we did not observe) is not consistently documented (e.g., Freeman et al. 2016). Epibenthic communities are also known to be sensitive to changes in abiotic conditions, which may have differed between our two study locations, such as temperature (Lord 2017), nutrient availability and flow patterns (Palardy and Witman 2014), water quality (Lenz et al. 2011) and fluctuating salinity (Chang et al. 2018). Here, we observed rapid declines in the abundance of chordates at both harbors following a heavy rainfall event, and these effects were particularly pronounced in Newport (Fig. 1c,d), where chordates constituted a relatively greater proportion of the overall community (Fig. S1). Similar effects have been observed in the past, where large, rainfall-driven fluctuations in salinity have been associated with dramatic changes in chordate populations (MacGinitie 1939; Lambert and Lambert 2003; Nydam and Stachowicz 2007). While still exhibiting a dramatic change in the total abundance of invasive species, the decline in exotic abundance in Huntington was less dramatic due to the presence of the bryozoan *Watersipora* spp., which is known to be widely tolerant to both temperature and salinity fluctuations (Afonso et al. 2020). The heavy impacts of environmental disturbance on epibenthic community structure, combined with naturally high turnover rates (Sutherland and Karlson 1977) and the creation of new habitat structures, mean that natural succession patterns in epibenthic community [re] assembly are frequently reset and suggest that it is particularly important to understand processes influencing the establishment and dominance of exotic species during these [re]assembly periods.

It is critical to recognize that the conclusions drawn from this study are also intertwined with seasonal recruitment patterns for both native and exotic species, as we measured the impacts of diversity on establishment during the fall; different patterns could have emerged had this study been conducted in the spring. Recruitment in many epibenthic communities varies throughout the year (e.g., Sutherland and Karlson 1977; Stachowicz and Byrnes 2006; Sorte and Stachowicz 2011; Tracy and Reyns 2014), and seasonal recruitment patterns can produce different communities depending on when growth panels are deployed (Cifuentes et al. 2010). It is important to keep this in mind when interpreting the results our study for two reasons. First, it is possible that we observed decreased exotic recruitment across the experiment due to the natural decline in recruitment towards the end of the observational period. However, many of the exotics we identified tend to continue recruiting into the late fall or early winter, albeit at lower recruitment intensities (Lambert and Lambert 2003; Tracy and Reyns 2014; Culver et al. 2021). Thus, it is possible that the reduced establishment we observed could be influenced by a combination of seasonally-reduced propagule pressure and resistance to establishment by the incumbent exotic species. Second, it is possible that primarily spring-recruiting species might respond differently to the diversity of established species. This could be particularly important to consider if native species recruit more heavily in the spring than the fall. However, our results align with previous research in southern California finding that exotic colonial chordates (such as *B. schlosseri* or *D. listerianum*) tend to be the initial colonizers (Tracy and Reyns 2014) and that exotic species tend to be numerically dominant (Tracy and Reyns 2014; Obaza and Williams 2018).

Finally, there are several limitations to this study that must be considered when drawing conclusions about the roles of invasional meltdown or biotic resistance in this system. First, this study is observational rather than manipulative. Such a design is beneficial in that it allows us to generally assess the natural trajectory of community development and compare with our hypothesized outcomes of biotic resistance and invasional meltdown. The drawback, however, is that it reduces our ability to disentangle mechanisms by fully quantifying individual interspecific interactions that promote or inhibit exotic species establishments throughout community assembly. Second, this study had a relatively small sample size and geographic extent (n = 16 plates across 2 sites in southern California). Though our within-site replication is on par with previous studies in the epibenthos (e.g., Tracy and Reyns 2014; Scott and terHorst 2019), more research is required to generalize about the relative strength of invasion dynamics in distant communities. Finally, this study did not test the impact of predation on community assembly, though our experimental plates were uncovered and exposed to potential predators, such as fish or crabs (Gestoso et al. 2018). Interestingly, recent research has suggested that facilitation between exotic species may be most apparent when communities are exposed to predators (Gestoso et al. 2018), so while we cannot explicitly identify the effect of predation with our study design, it may be another contributing factor to the patterns we observed, including generally high degree of exotic cover and dominance.

In conclusion, our results suggest that biotic resistance plays a role in limiting the establishment and spread of exotic species during community assembly in these subtidal epibenthic communities. In heavily-invaded systems such as those studied here, resistance may not reduce the ultimate dominance of exotic species, but does not necessarily lead to meltdown. However, as noted above, seasonality, which was not addressed in this study, plays an important role in determining community composition, and community-level properties such as biotic resistance are known to have scale and context-dependent strengths (Fridley et al. 2007; Kimbro et al. 2013). Therefore, future research should examine whether the patterns observed in this study are consistent if communities begin assembling at different times of the year and whether resistance is able to limit exotic dominance along broader scales and environmental gradients.

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Author contributions DAT, AKH, and CJBS designed the assembly experiment. DAT collected the data. RAB and CJBS generated the hypotheses. RAB, AKH, and CJBS designed the analyses. RAB conducted the statistical analysis and wrote the manuscript. All authors revised drafts and approved the final manuscript.

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Data availability The dataset analyzed during the current study will available in the Dryad repository or from RAB upon publication of this manuscript.

Code availability Code will be uploaded to Dryad or available from RAB upon publication of this manuscript.

Declarations

Conflict of interest The authors declare no conflicts of interest.

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