

Passing the quadrat: investigator effects and biodiversity change on a rocky shore over three to nine decades

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Abstract

Long-term ecological monitoring inevitably requires a ‘passing of the quadrat’ from one investigator to another. Here we present the challenge and opportunity of interpreting biodiversity change across investigators using a rocky intertidal case study. The intertidal transect was surveyed initially by Willis Hewatt in 1931-1933, then resurveyed in detail by Rafe Sagarin, Sarah Gilman, and their mentors in 1993 and 1996. In total, the transect has been resurveyed 17 times over the past three decades, and we divided the survey efforts into six investigator eras. Taxonomic uniqueness within eras ranged from 8 to 41%, with total species turnover ranging from 24 to 68% between consecutive time points. Apart from the largest turnover observed from 1933 to 1993, the transition between investigators did not coincide with peaks of species turnover. However, one era (1999-2015) exhibited consistently low species turnover, and coincided with relatively low species abundances. We hypothesize that variation in sampling effort contributed to highly variable trends in richness over time, but we highlight reductions in the biodiversity of common species (Hill-Shannon) and dominant species (Hill-Simpson) over time, particularly for mobile taxa. These declines were associated with the rise of a few numerically dominant species and a trend of increasing spatial similarity. The magnitude and direction of trends in temporal similarity depended on the baseline (1933 or 1993), with a stronger trend of declining similarity since 1993. Relative to the historical baseline, we identify several ‘winners’ and ‘losers’ but emphasize that such designations can be complicated by non-linear population trajectories.

Introduction

Observational field studies are the foundation of ecology by providing the inspiration and context for experiments, theoretical models, and management. Long-term field studies are disproportionately valuable to ecology and policy (Hughes et al., 2017) and critical to the assessment of biodiversity change in a climate of anthropogenic forcing (Magurran et al., 2010). Most long-term quantitative studies are on the order of several decades (Vellend et al., 2013; Dornelas et al., 2014; Elahi et al., 2015; Kaplanis, 2023), with notable exceptions rooted in the century-long tradition of Western European natural history (Southward, Hawkins & Burrows, 1995; Richardson et al., 2006; Silvertown et al., 2006). Despite their importance, funding for long-term monitoring has declined (Hughes et al., 2017) and thus the maintenance of these studies is a challenge. Besides funding, the transfer of knowledge, methods, and data between sequential investigators is critical to extend long-term datasets beyond a few decades, the typical length of an academic career.

Here we examine the study of a rocky intertidal shore initiated in 1931 and repeated thereafter by five different lead investigators or groups (Micheli et al., 2020). In contrast to recent rocky shore monitoring studies (Murray, Ambrose & Dethier, 2006; Kaplanis, 2023), our 90 year historical study trades what are now considered fundamental aspects of study design (e.g., randomization, replication) for the detailed enumeration of the complete macroscopic animal community along a single continuous transect. The 90-year duration is accompanied necessarily by two key investigator-dependent challenges, particularly species identification and variation in sampling effort. We highlight the strengths and limitations of the dataset to assess temporal change in biodiversity (*sensu* Magurran, 2021) relative to the historical baseline (1931-1933) and the past thirty years (1993-2023).

Methods

History of the intertidal survey

We start with a brief history of the intertidal survey methods and the lead investigators that conducted the study on the rocky shore at Hopkins Marine Station. We divided the survey efforts into six investigator eras, because we hypothesized that differences in species identification and sampling effort could affect inferences of biodiversity change over the ninety years of sampling.

This study was initiated in 1931 and completed in 1933 by Willis Hewatt, a graduate student at Stanford (Hewatt, 1934). Hewatt surveyed 108 consecutive square yards along a transect perpendicular to shore at Hopkins Marine Station (HMS). A primary focus of Hewatt's work was the spatial distribution of animals along the shore; the abundances of 90 species in each quadrat were presented in his Table 10 (Hewatt, 1937). Nineteen of these 90 species were not counted but instead categorized qualitatively as "abundant", "common", "occasional", or "rare." After the surveys had been completed for the 108 quadrats, four "typical squares" were selected as representative of intertidal zones; these four quadrats were resurveyed intermittently during changing seasons. A complete list of species ($n = 170$) was also provided (Section VII; Hewatt, 1937); Hewatt acknowledged assistance with the identification of crustaceans, gastropods (including nudibranchs), and fishes.

Bruce Provin was the first to resurvey Hewatt's transect as part of a student project at Hopkins Marine Station (Provin, 1949). Provin relocated (using permanent markers and maps) and resurveyed four of Hewatt's "typical squares" (quadrats 12, 24, 35, 90). All macroscopic organisms were counted and presented in the manuscript; those that couldn't be counted exactly were rated as "abundant", "common", "occasional", or "rare." Species were identified using *Between Pacific Tides* (Ricketts & Calvin, 1948), *A Laboratory and Field Textbook of Invertebrate Zoology* (Light, 1941), and various monographs and papers; help was also obtained from the course instructors and other students.

Between 1993 and 1996, Hewatt's transect was again resurveyed by undergraduate students (Rafe Sagarin, Sara Gilman) and their mentors (Charles Baxter, Jim Barry); hereafter referred to as SBGB (Sagarin et al., 1999). Sagarin and Gilman relocated and resurveyed 57 plots between spring 1993 and summer 1995. During summer 1996 SBGB resurveyed the first 19 plots surveyed in spring 1993; this included quadrats 27-38 and 62-68 (these 19 quadrats are hereafter referred to as 'core' quadrats). With few exceptions, all individuals within a plot were counted, including those on or under marine plants or other species. Several species were ignored deliberately. Species that could not be readily and nondestructively identified were not counted; only species that could be identified with the unaided eye were counted (Sagarin et al., 1999). Regional guides were used for species identification (Smith & Carlton, 1975; Morris, Abbott & Haderlie, 1980).

To continue the long-term monitoring effort between 1999 and 2015, Sagarin returned to HMS intermittently to resurvey the core quadrats. These resurveys occurred in 1999, 2002, 2005, 2009, 2014, 2015. No description of methods is available; we assume that the methods were similar to

the methods described by SBGB for the years 1993 and 1996. Field notes indicated that within a given year, quadrats were occasionally sampled in different seasons.

After Sagarin's death in 2015, Fiorenza Micheli and James Watanabe continued surveying the core quadrats on an annual basis. Surveys were conducted between May and July; the sampling effort often included students from an undergraduate spring course at HMS. The sampling methods described by SBGB (Sagarin et al., 1999) were maintained. Regional guides were used for species identification (Morris, Abbott & Haderlie, 1980; Carlton, 2007).

Robin Elahi began leading the survey effort in 2019, with transfer of knowledge from Watanabe and Micheli. In addition to the core quadrats, Elahi began surveying quadrats 12, 16, 20, and 24 (hereafter referred to as 'extra' quadrats) to address biodiversity change in the upper intertidal. In addition to the annual late spring sampling, a subset of quadrats was also sampled during winter months. The sampling methods remained the same, with a few exceptions (details in supplement). Regional guides were used for species identification (Morris, Abbott & Haderlie, 1980; Carlton, 2007).

Additional details on sampling methods are provided in supplementary information (Appendix S1).

Quantifying taxonomic overlap

The quantitative and qualitative data for core and extra quadrats across all investigator eras were assembled into a database. For species listed in our database, we tabulated the scientific names used by Hewatt (1937) and Sagarin et al. (1999), reconciling them with current names provided in the World Register of Marine Species (WoRMS Editorial Board, 2023) (Appendix S2, Table S1). For example, the whelk *Acanthinucella punctulata* was recorded as *Acanthina punctulata* and *Acanthina lapilloides* by Sagarin et al. (1999) and Hewatt (1937), respectively.

Once we synonymized the species names in the database, we next tabulated the overlap in species presence across investigator eras (Appendix S2, Table S2). We omitted amphipods (*Ampithoe*, *Atylopsis*, *Melita*) and spirorbid tubeworms (*Spirorbis*) from this overlap analysis because these species are small, inconspicuous, and the monitoring records suggested inconsistencies in surveying effort for these taxa. We also omitted animals recorded at taxonomic levels above genus, which started in 2020. We then removed animals that were recorded as genera, when there was also a species recorded within that genus. In cases where a species (or genus) was recorded in 1993 or after, but the abundance was not quantified by Hewatt, we checked to see whether Hewatt had recorded the species in the complete list (Appendix X in Hewatt, 1934). If it was not on the list, we recorded it as absent from Hewatt's study; if it was on the list, then we recorded it as present in Hewatt's study. In total, 196 animals at the genus or species level were identified across the 90 years of the study (Appendix S2, Table S1). We visualized species overlap for three investigator eras (1931-1933, 1993-1996, and 2020-2023). We then repeated the visualization, but using species for which quantitative abundances were available. We also visualized turnover between consecutive time points at the species and genus level (hereafter referred to as 'species turnover') for the quantitative subset of data. We calculated total turnover as $\frac{\text{Species gained} + \text{Species lost}}{\text{Total species observed in both time points}}$; in addition we partitioned

turnover into appearances (species gains) and disappearances (species losses) (Hallett et al., 2016).

Estimating temporal trends in biodiversity

We investigated temporal trends in biodiversity using quantitative abundance data in the historical database. We included years from the five (of six) investigator eras when all nineteen core quadrats were sampled, omitting the 1947 era because Provin (1949) sampled only three of these core quadrats. As described above, we omitted amphipods (*Ampithoe*, *Atylopsis*, *Melita*) and spirorbid tubeworms (*Spirorbis*). We removed hermit crabs (*Pagurus*), and limpet epibionts (*Lottia asmi*, *Lottia* spp.) on trochid snails (*Tegula*) because they were not sampled quantitatively by Hewatt. Lastly, we removed taxa above genus; all filtering steps are summarized in Table S3 (Appendix S2). Next, we had to reconcile potential ambiguities in species identification across investigator eras. For each taxon listed in Table S1 (Appendix S2), we identified the taxonomic level at which we felt comfortable inferring patterns of biodiversity change, and summarized the abundances to that level.

Temporal patterns at the quadrat scale (0.84m²) were examined for richness (i.e., species density; Gotelli & Colwell, 2001), Hill-Shannon diversity, and Hill-Simpson diversity; these three diversity indices are also known as Hill numbers of orders $q = 0$, 1, and 2, respectively (Hill, 1973). Hill numbers can be interpreted as the effective number of species for all species ($q = 0$; richness), common species ($q = 1$; Hill-Shannon), and dominant species ($q = 2$; Hill-Simpson) (Chao et al., 2014). For the quadrat scale, diversity indices were averaged across all quadrats ($n = 19$) and visualized with 95% confidence intervals (assuming a normal distribution). Although the same 19 quadrats were sampled in each of the 18 years, the number of individuals within quadrats was highly variable and could confound interpretations of changes in diversity per se (Gotelli & Colwell, 2001). Therefore, we also evaluated temporal patterns in diversity at the site level using coverage-based estimators (Hsieh, Ma & Chao, 2016; Roswell, Dushoff & Winfree, 2021). Hereafter, we will refer to the number of taxa (at quadrat and site scales) as ‘richness’, and Hill-Shannon and Hill-Simpson indices as ‘diversity’.

In addition to examining temporal variation in alpha diversity metrics, we investigated temporal trends in beta diversity using the same quantitative database that was used for richness and diversity. First, we tested the hypothesis that taxonomic homogenization has occurred over the past three to nine decades years, by quantifying temporal patterns in spatial beta diversity (Olden & Rooney, 2006). For each year, we calculated the median pair-wise Jaccard distance (based on species presence-absence) between each quadrat and every other quadrat and then averaged these quadrat medians to obtain an estimate of similarity at the site scale; in this framework a positive temporal trend in community similarity indicates biotic homogenization. Second, we tested whether the rate and direction of community turnover (i.e., temporal beta diversity) depended on the baseline chosen for comparison. For each year, we calculated Jaccard similarity between a baseline year (1933 or 1993) and subsequent years; presence and absence across all quadrats was used to represent the community at the site scale at each time point. In this framework, a positive trend indicates that the community is becoming more similar to the baseline over time.

We used Spearman rank tests to assess the significance of temporal correlations of alpha diversity metrics and spatial beta diversity over the entire course of the study (1933-2023). We used rank correlation tests because the historical data, collected by Hewatt in 1931-1933, preceded the remainder of the data by 60 years and thus could potentially exert considerable leverage in a linear regression. Moreover, the time-series did not all exhibit linear trends, as assumed in ordinary least squares (OLS) regression. However, we did use OLS regression to test for temporal trends of alpha diversity and beta diversity over the final 30 years of the study (1993-2023) when visual inspection of data suggested the assumption of linearity was met. We did not incorporate temporal autocorrelation into our linear models because the residuals did not exhibit evidence of a time lag for any of the diversity metrics. Residuals of the linear models did not display patterns of heteroscedasticity.

Summarizing changes in abundance of genera

To summarize changes in the composition of animal taxa on the Hewatt transect, we compared each of the recent years of sampling (1993-2023) to the baseline (1931-1933). First, the total abundance of each genus (across 19 quadrats) was calculated for each year. Then the log change in abundance was calculated for each of the recent years, relative to the baseline year ($\log change = \ln[(n_{year} + 1) / (n_{baseline} + 1)]$). The average log change and 95% confidence interval (CI) summarized the recent years relative to the baseline; we considered the change in abundance to be significant when the 95% CI did not overlap zero.

We relied on the ‘tidyverse’ (Wickham et al., 2019), ‘iNext’ (Hsieh, Ma & Chao, 2016), ‘vegan’ (Oksanen et al., 2011), ‘codyn’ (Hallett et al., 2016), ‘eulerr’ (Larsson et al., 2016), and ‘patchwork’ (Pedersen, 2024) packages in R 4.3 (R Development Core Team, 2023) for data processing, visualization, and analysis. All data and code are (will be made) available in a permanent repository (<https://sdr.stanford.edu/>).

Results

The taxa recorded on the resurveyed permanent quadrats on the Hewatt transect during each of the six investigator eras varied considerably (Appendix S2, Table S1). For example, only 24% of the taxa (genera and species) was shared by three eras (1931-1933, 1993-1996, 2020-2023) for the qualitative (i.e., complete) set of animal taxa (Fig. 1A), and the quantitative subset of animal taxa (Fig. 1B). The most recent era (2020-2023) shared 36-44% of taxa with 1993-1996, and 32-29% of taxa with 1931-1933. Taxonomic uniqueness within these three eras ranged from 6 to 32% for the quantitative subset of data; this variability is a consequence of variation in repeated annual sampling (Appendix S2, Table S5). Considering only the core quadrats during the annual spring sampling, total species turnover between consecutive time points ranged from 24% (1999) to 68% (1993) (Fig. 2). Total species turnover was generally lower during sampling between 1999-2015, due to a combination of lower species appearances and disappearances (Fig. 2).

In all, 365,914 invertebrates were counted and identified. After removing amphipods, *Spirorbis*, limpet epibionts on *Tegula* spp., *Pagurus* spp., and taxa above genus, 347,543 records remained (95%). Initially, the database contained 232 unique taxa (180 species-level taxa, 28 genus-level taxa, 24 higher level clades). After lumping species to higher taxonomic levels for the purposes of quantitative analysis, the wrangled database contained 157 taxa (119 species-level taxa, 38 genus-level taxa); this database was used for all temporal analyses of biodiversity change using alpha and beta diversity indices. The wrangled database contained 144 unique animal genera, and a subset of these genera were used to visualize changes underlying the aggregate metrics of alpha and beta diversity. That is, we focused on the genera that comprised 99% of the individuals counted on the Hewatt transect over the nine decades; this threshold removed 108 genera that made up <1% of the individuals.

At quadrat scales, Hill-Shannon and Hill-Simpson indices of diversity (but not richness) declined over the 90-year period (Fig. 3; Appendix S2, Table S6). Richness at quadrat scales exhibited a marked decline between 1999 and 2015, one of the predefined investigator eras. During this era, fewer individuals were counted and the species-accumulation curves saturated at relatively low values of site-scale richness (< 50 taxa; Appendix S2, Fig. S2). When analyzed at the site scale with a coverage-based estimator, there was no correlation over 90 years ($\rho = 0.25$, $p = 0.32$) or non-linearity between richness and year over the recent 30 years (Fig. 3D). At the site scale over 90 years, estimated Hill-Shannon diversity was correlated negatively with year ($\rho = -0.50$, $p = 0.04$); Hill-Simpson diversity was weakly correlated with year ($\rho = -0.42$, $p = 0.08$). Over 30 years, Hill diversity exhibited significant linear declines over time (Appendix S2, Table S5) at both quadrat and site scales (Fig. 3; Appendix S2, Table S7). At quadrat scales, diversity was comparable between 1931-1933 and 1993-1996 (Fig. 3B, C), but at site scales diversity was higher in 1931-1933 relative to 1993-2023 (Fig. 3E, F).

Trends in spatial beta diversity (Fig. 4A) indicated an increase in community similarity over nine decades ($\rho = 0.82$, $p < 0.001$), and a linear increase over three decades ($t = 5.6$, $r^2 = 0.68$, $p < 0.001$). Temporal similarity (i.e., temporal beta diversity) increased from 1993 to 2023 ($t = 3.2$, $r^2 = 0.40$, $p = 0.006$) when compared to 1931-1933, but decreased ($t = -5.8$, $r^2 = 0.71$, $p < 0.001$) from 1996 to 2023 when compared to 1993 (Fig. 4B, C). The magnitude of the trend in temporal similarity (i.e., the absolute value of the estimated slope) was three-fold higher when the baseline

was 1993 (slope = 0.003 ± 0.002 ; mean \pm 95% CI), than when the baseline was 1931-1933 (slope = -0.009 ± 0.004).

A significant change in abundance, relative to the original survey by Hewatt in 1931-1933, was observed in 35 of 36 genera at the 95% level, and 33 genera at the 99% level (Fig. 5). Changes in the snail *Littorina* were not significant, and changes in the ascidian *Eudistoma* and isopod *Cirolana* were significant only at the 95% level. On average, barnacles (*Chthamalus*, *Balanus*, *Tetraclita*) and anemones (*Anthopleura*, *Corynactis*) have been more abundant, and mussels (*Mytilus*) and the social ascidian *Clavelina* less abundant over the past 30 years. Gastropod mollusks exhibited a variety of trends. For example, limpets (*Lottia*, *Acmaea*, *Fissurella*) and columbellid gastropods (*Alia*, *Amphissa*) have declined in abundance, whereas whelks (*Paciocinebrina*, *Acanthinucella*) have increased in abundance. Crabs (*Pachycheles*, *Pachygrapsus*, *Petrolisthes*, *Pugettia*), annelid worms (*Halosydna*, *Phascolosoma*), and echinoderms (*Amphipholis*, *Leptasterias*, *Strongylocentrotus*) have declined since the 1930s. Despite these average changes in abundance, many of these taxa exhibited non-linear trends over the recent thirty years. For example, mussels (*Mytilus*) and urchins (*Strongylocentrotus*) have recently recovered to or exceeded historical abundances. In contrast, the strawberry anemone (*Corynactis*) declined abruptly to zero in the last decade (Fig. 6).

Discussion

There are several key messages from our intertidal sampling program that are relevant to inferences about biodiversity change from long-term ecological monitoring studies. First, it is critical to have an ‘open’ species list due to species turnover, especially in the context of climate change and species range shifts. Second, consistency in the number of samples (e.g., quadrats) does not guarantee consistency in species abundances, which we interpret as variation in sampling effort. Therefore, inferences about trends in species turnover and species richness are sensitive to investigator effects because of the inherent difficulty in observing rare or cryptic species. Finally, inferences about ecological ‘winners’ and ‘losers’ can be complicated by non-linear population trajectories.

One of the unique strengths of our intertidal sampling program, initiated by Hewatt (Hewatt, 1937) and restarted in earnest by Sagarin and Gilman (Barry et al., 1995; Sagarin et al., 1999), is the enumeration of all macroscopic invertebrates in our quadrats. This feature permits the estimation of diversity metrics (e.g., richness, diversity), which rely on (i) quantifying abundance, and (ii) maintaining an ‘open’ species list. Given the high density of intertidal invertebrates on the rocky shore, and the taxonomic expertise required to identify taxa, it is imperative to examine whether inferences on biodiversity change are sensitive to observer (e.g., investigator) effects. In the context of sampling small and numerous rocky shore invertebrates, investigators may vary in their taxonomic ability, eyesight, time constraints, attention to detail; these aspects can also change over time for the same investigator. Our analyses suggest that these kinds of investigator effects are particularly relevant for species density (number of species observed in a quadrat or sample) and species turnover between time points. This makes sense, because these metrics hinge on the relative abundance of species and the identification of rare, cryptic and/or potentially new species. Species density is well known to be subject to biases related to sampling effort (Gotelli & Colwell, 2001). Estimated species richness (at the site scale), however, displayed no trend over time, consistent with syntheses (Vellend et al., 2013; Dornelas et al., 2014; Elahi et al., 2015) and theory suggesting a net balance between species colonizations and extinctions (Brown et al., 2001). The latter depends on having an ‘open’ species list and is critical in the context of geographic range shifts (Sagarin et al., 1999).

In contrast to species density, the use of diversity metrics (i.e., Hill-Shannon and Hill-Simpson) that reduce the leverage of rare species (Roswell, Dushoff & Winfree, 2021) was robust to investigator effects in our study. Across quadrat and site spatial scales, the diversity of common (Hill-Shannon) and dominant (Hill-Simpson) species has declined over the past three decades and to a lesser extent since the 1930s. Temporal declines in these Hill indices were accompanied increases in spatial similarity. That is, the quadrats across the transect became more similar to each other over time, indicating biotic homogenization (Olden & Rooney, 2006; Blowes et al., 2024). The rate of turnover (temporal similarity) depended on the baseline chosen for comparison; animal composition in 2023 became more similar to 1933 over the past three decades, but has become less similar to 1993 over the same period. Moreover, the rate of change relative to 1993 is three-fold higher than when compared to 1933. Despite their long history of study (Ricketts & Calvin, 1948; Connell, 1961; Paine, 1966; Underwood, 1978), rocky intertidal shores do not feature prominently in recent syntheses of biodiversity change; for example, 0 out of 471 coastal time series (Elahi et al., 2015) and 3 of 152 marine time series (Dornelas et al., 2018)

included time series data from the rocky intertidal zone. This may be because species richness as a response variable has often been deemphasized in favor of the cover, biomass, or abundance of dominant foundation species such as mussels, barnacles, or seaweeds (Dayton, 1971; Miner et al., 2021; Whalen et al., 2023). As such, our case study represents a useful comparison to generalizations from recent syntheses of biodiversity change which tend to highlight considerable variability in biodiversity trends (Vellend et al., 2013; Dornelas et al., 2014; Elahi et al., 2015; Blowes et al., 2024).

There were some clear ‘winners’ and ‘losers’ underlying changes in alpha and beta diversity. Here we define winners and losers as those genera with consistently higher and lower densities, respectively, in the recent 30 years relative to the 1930s. Winners included certain snails (*Tegula*), anemones (*Anthopleura*), chitons (*Nuttalina*), barnacles (e.g., *Chthamalus*, *Tetraclita*), and whelks (e.g., *Acanthinucella*, *Paciocinebrina*). Losers included other snails (*Alia*), limpets (*Lottia*, *Acmaea*), crabs (*Pugettia*, *Pachygrapsus*), and brittle stars (*Amphipholis*). However, many of the apparent winners and losers displayed non-linear trajectories over the past thirty years. In particular, mussels (*Mytilus*) and urchins (*Strongylocentrotus*) recovered to or exceeded historic levels after prolonged declines; urchin recruits were particularly abundant in the dense mussel beds towards the wave exposed portion of the transect. An increase in the deposition of mussel shells and sand, associated with intense winter storms in 2022 and 2023 may have facilitated the recovery of cryptic species that occupy interstitial and mussel shell habitats (*Pachycheles*, *Phascolosoma*, *Petrolisthes*, *Cirolana*, *Halosydna* and other polychaete worms); distinguishing between a population rebound associated with an increase in favorable habitat versus investigator effort remains a challenge for these cryptic and less common species. More generally, the assignment of labels such as winners and losers based on two time points is problematic in the context of dynamic population trajectories, and again highlights the value of long-term monitoring efforts (Hughes et al., 2017).

Despite the prevalence of nonlinear trends, there were several unambiguous changes to the community relative to the 1930s. First, the intertidal green anemones with southern affinity (*Anthopleura sola*) are well-established on the transect. Second, the smaller *Chthamalus* and southern volcano barnacle (*Tetraclita rubescens*) have replaced the formerly more abundant *Balanus glandula*. Associated with these barnacle increases, whelks have increased; *Acanthinucella punctulata* is another species with southern affinity. Lastly, *Tegula* snails have replaced *Lottia* limpets as the dominant grazer along the transect. It is beyond the scope of our study to ascribe mechanisms to the many changes in biodiversity and species composition, but we hypothesize that the conspicuous patterns are consistent with predictions related to climate warming. That is, we expected to see increases in the abundance of species with southern affinity (Sagarin et al., 1999; Sanford et al., 2019; Micheli et al., 2020) and increases in the prevalence of smaller-bodied species and individuals (Forster, Hirst & Atkinson, 2012; Ohlberger, 2013; Elahi, Miller & Litvin, 2020). We speculate that the shift from limpet to snail grazers is related to their morphology. Given their large foot and inability to retract within their shell, the body temperatures of limpets are more likely to match surrounding rock temperature which may influence survival during periods of thermal stress (Denny & Harley, 2006; Miller & Denny, 2011). Despite these hypothesized long-term consequences of warming, we did not observe a short-term effect of the 2014-2016 heat wave, but this appears to be consistent with a broader pattern of recent stability of intertidal rocky shores in central California (Miner et al., 2021).

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380 We view these observations not as the end goal, but rather as starting points for detailed studies
381 on the underlying organismal attributes and ecological processes underpinning stasis or change.
382 Despite the primary limitation of this historical study, namely that it is a single continuous
383 transect across one rocky shore, we view this as a worthwhile tradeoff with the level of
384 taxonomic detail; such trade-offs in design and implementation are common in other long-term
385 rocky shore studies (Kaplanis, 2023). As a stark contrast to our study, a spatially extensive, well-
386 replicated, and coordinated effort across the west coast of North America must, out of necessity,
387 limit surveys to a pre-selected group of focal species; more thorough taxonomic surveys can only
388 be completed on a less regular basis when funding permits (Multi-Agency Rocky Intertidal
389 Network; Gilbane et al., 2022). Beyond the utility of this long-term ecological monitoring effort
390 to track detailed biodiversity change at a single rocky shore, the integration of the long-term
391 survey into teaching at Hopkins Marine Station is another important reason to continue the
392 legacy. Collaborative field courses have a disproportionate impact on students' sense of
393 belonging to science in general and ecology in particular (Race, Beltran & Zavaleta, 2021), and
394 feedback from recent students highlights the value of being in the field and contributing to a
395 ninety-year ecological study.

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397

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399 the long-term monitoring effort on the historical transect at Hopkins Marine Station.

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Figure Legends

Figure 1. Area-proportional Euler diagrams showing the overlap in the complete set of animal taxa ($n=171$; A) and the quantitative subset of taxa ($n=130$; B) observed on the Hewatt transect during three investigator eras (1931-1933; 1993,1996; 2020-2023).

Figure 2. Species turnover in the animal community on the Hewatt transect; gray boxes represent the 95% confidence interval for turnover ($n = 17$). For each time point, turnover was calculated relative to the previous time point; e.g., turnover calculated in 1993 was relative to 1931-33. Total turnover is the sum of appearances (species gains) and disappearances (species losses) divided by the total number of species observed in both pairs of time points.

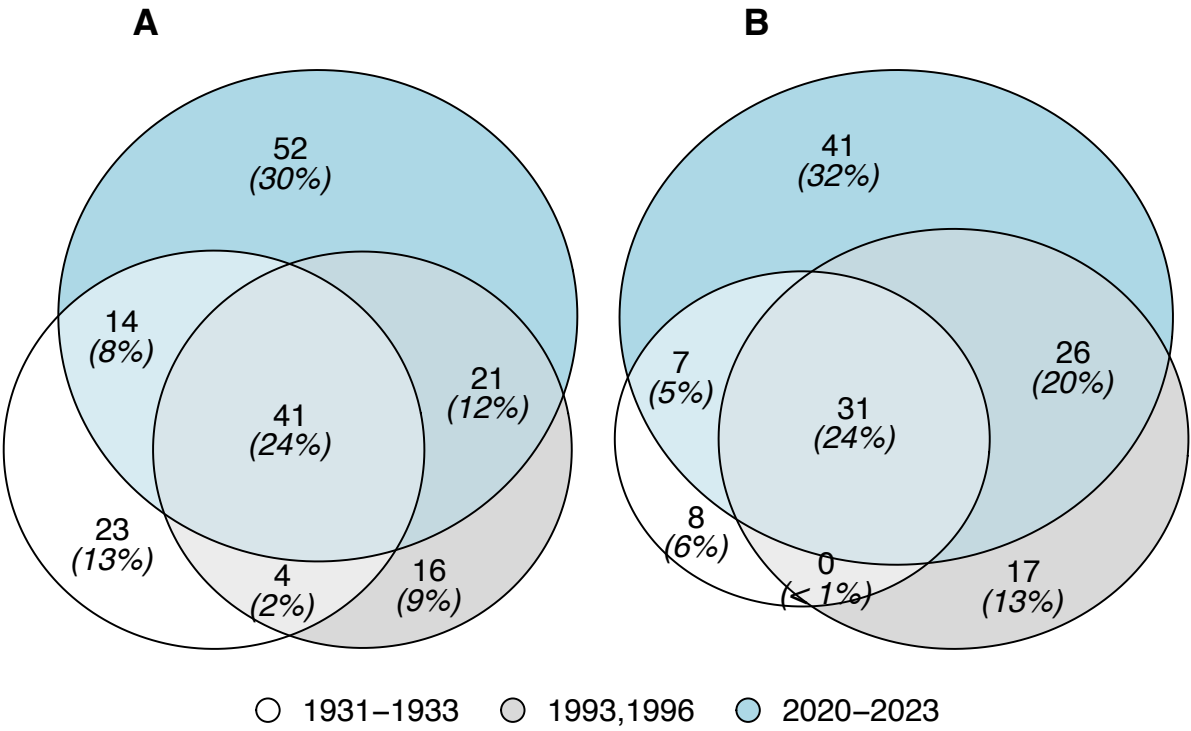
Figure 3. The animal community on the Hewatt transect has declined linearly in diversity (Hill-Shannon and Hill-Simpson indices) over the past three and nine decades, but no linear trends in species richness were observed. At quadrat scales (A-C), diversity metrics are summarized across quadrats ($n = 19$; mean \pm 95% CI). At the site scale (D-F), diversity metrics are estimated using a coverage-based estimator (estimate \pm 95% CI). Linear fits with 95% confidence intervals are visualized for 1993-2023 when the assumption of linearity was met (B-F) and the trend was significant (B,C,E,F).

Figure 4. The animal community on the Hewatt transect has become more homogeneous over the past three and nine decades (A). Over the three recent decades (B), the community has become more similar to the community sampled originally in 1931-1933. In contrast, when compared to 1993, the community has diverged at a faster pace over nearly three decades (C). Similarity was measured using the Jaccard index, where 0 and 1 represent completely different and exactly identical communities, respectively. Linear fits with 95% confidence intervals are visualized for 1993-2023.

Figure 5. Changes in abundance (mean \pm 95% CI; $n = 17$) of animal genera on the Hewatt transect over the past 30 years (1993-2023) relative to the initial survey in 1931-1933. Change in abundance (the total abundance for each genus in year i , where i ranges from 1993 to 2023) is expressed as the natural log of a ratio [$\ln(\text{abundance} + 1 \text{ in year } i / \text{abundance} + 1 \text{ in the original survey})$]. The size of points corresponds to the log mean density, averaged across all 18 years of sampling (1931-1933, 1993-2023). These 36 genera comprise 99% of the individuals counted on the transect over the 90-year duration of the study.

Figure 6. Temporal variation (1993-2023) in the log change in abundance of animal genera on the Hewatt transect, relative to the historical baseline in 1931-1933. Change in abundance (the total abundance for each genus in year i , where i ranges from 2020 to 2023) is expressed as the natural log of a ratio [$\ln(\text{abundance} + 1 \text{ in year } i / \text{abundance} + 1 \text{ in the baseline year})$] where 1931-1933 was the first sampling event. The size of points corresponds to the log total count. These 36 genera comprise 99% of the individuals counted on the transect over the 90-year duration of the study. Squares and circles represent sessile and mobile genera, respectively. Smoothed curves represent generalized additive models.

578 **Figures**
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583 Figure 1.
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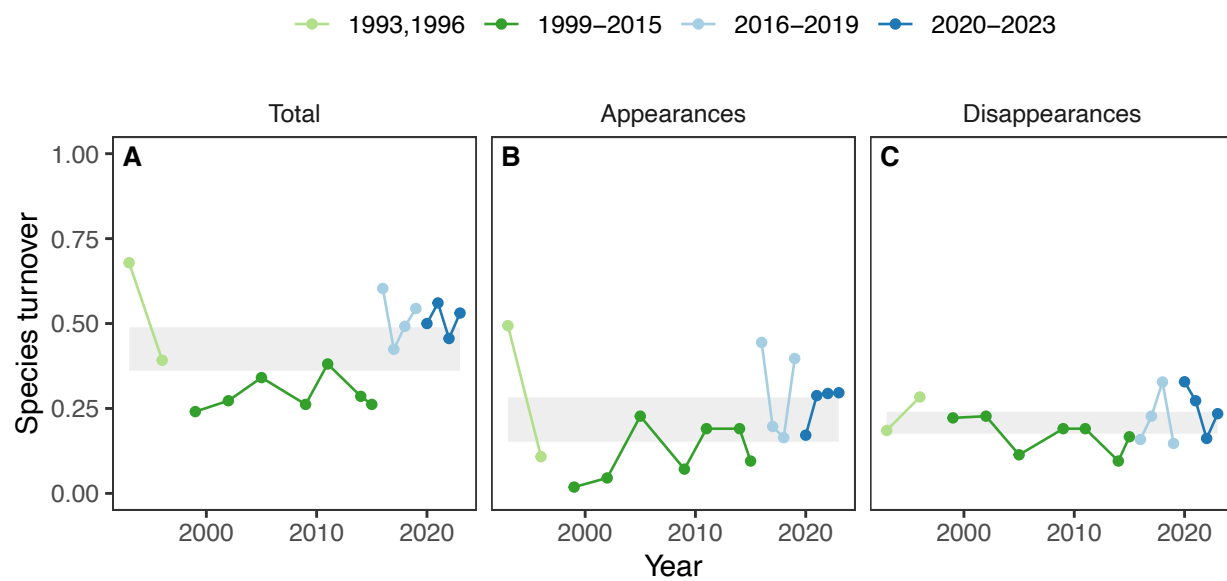
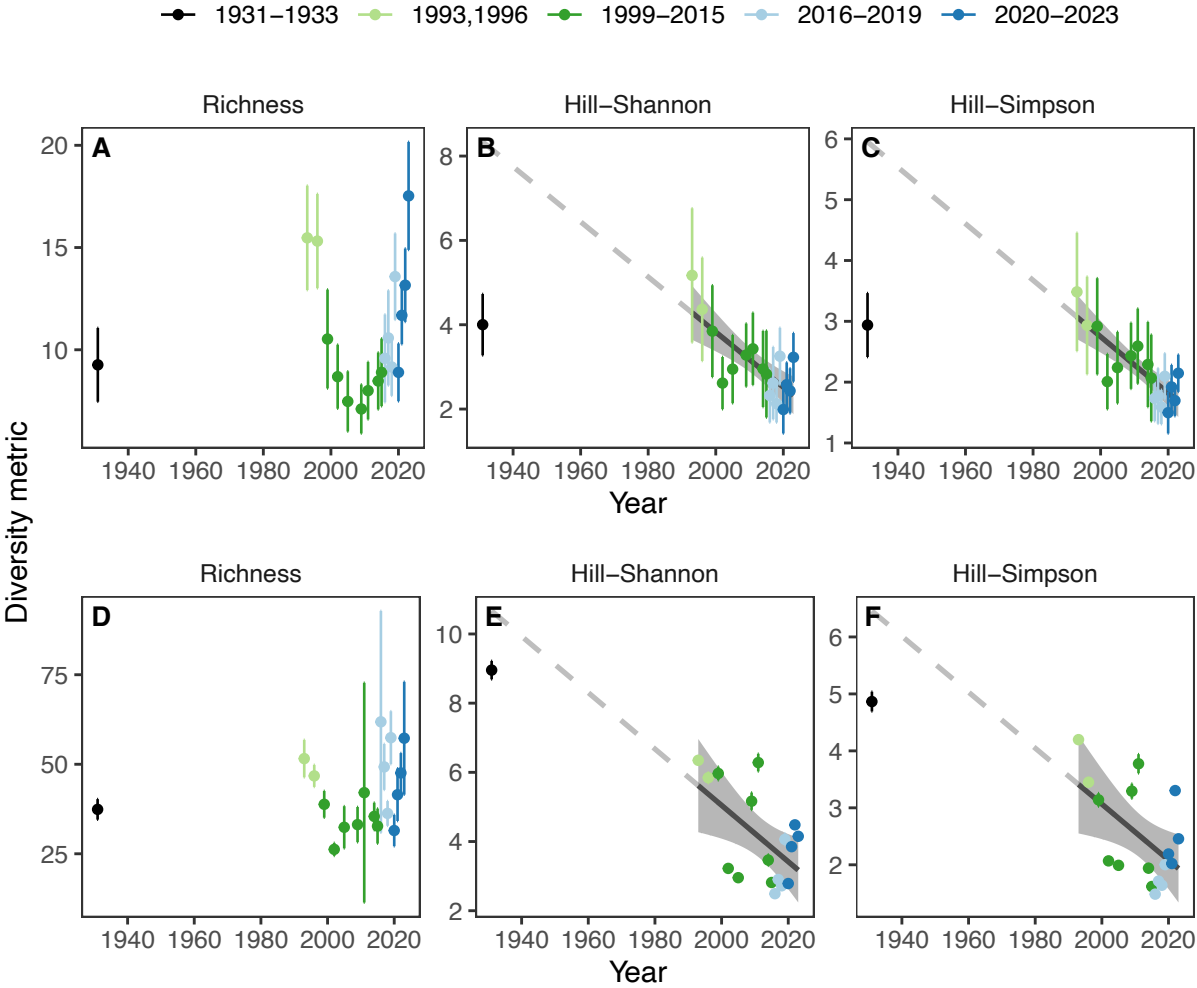
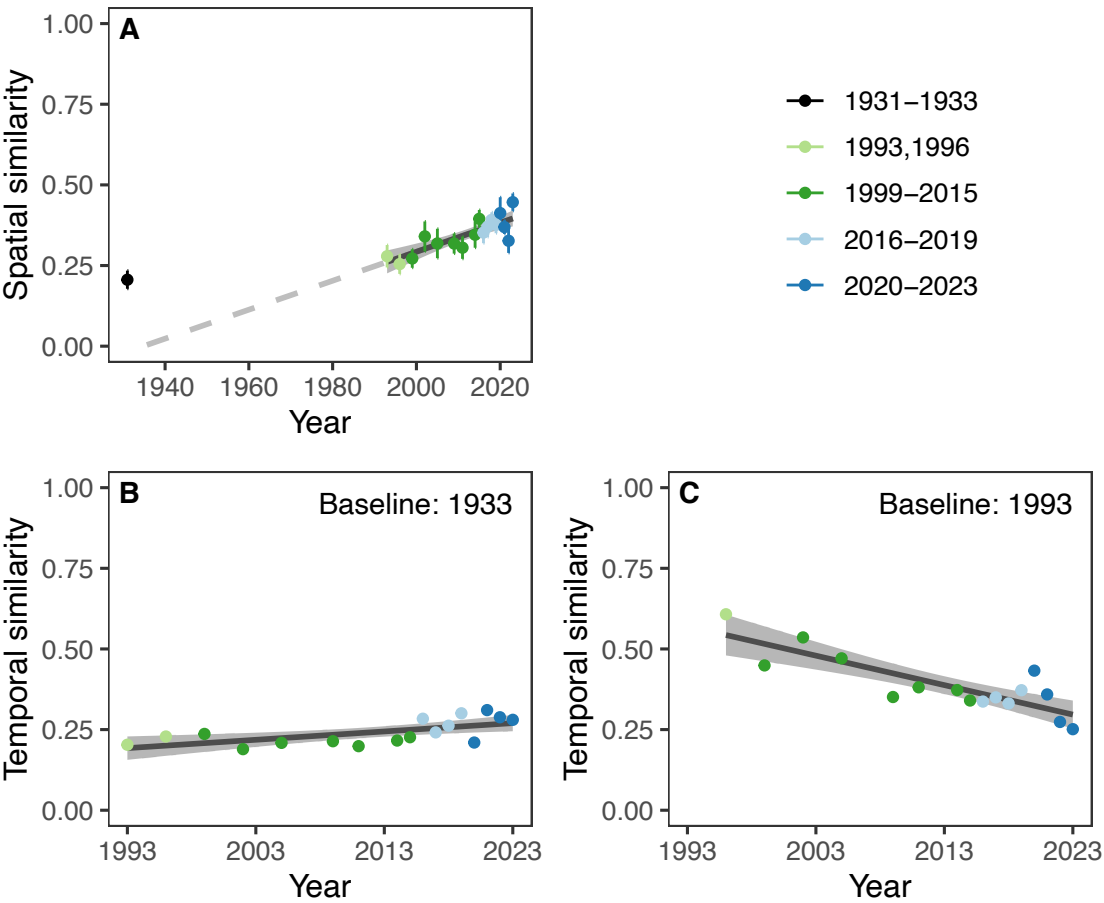


Figure 2.



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Figure 4.

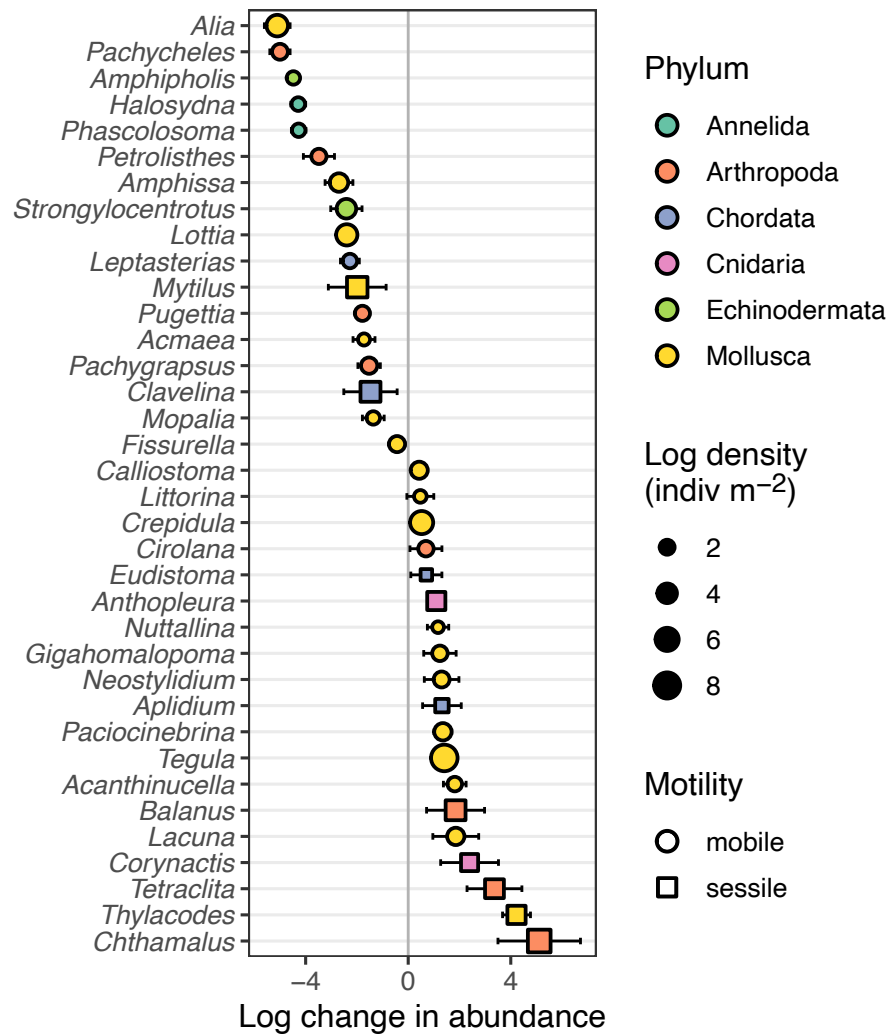


Figure 5.

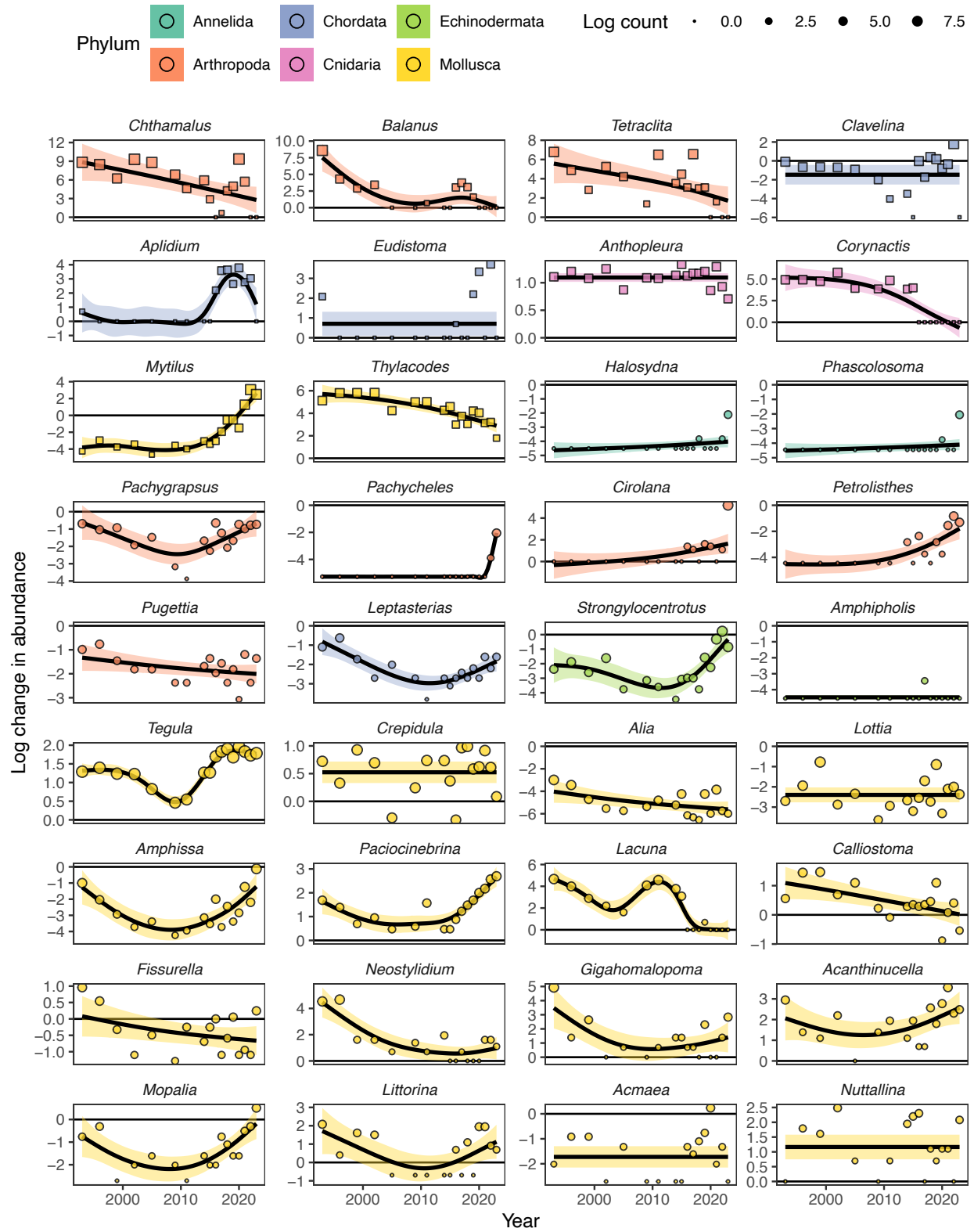


Figure 6.