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Title:

Gradual changes in range size accompany long-term trends in species richness

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Data accessibility statement: Code and aggregated data are available on the public GitHub repository: <https://github.com/rBatt/trawlDiversity>. All processed data and all raw data for which we have permission to share publicly are available on a second public GitHub repository: <https://github.com/rBatt/trawlData>. Each repository contains the source code of a documented R

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30 package by the same name. Upon acceptance of this article, we agree to create archives of these
31 repositories and associate each with a DOI.

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33 75 References, 4 Figures, 1 Tables, 0 Text Boxes

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35 **Words:** 149 Abstract, 5000 Main text

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37

38 **Abstract**

39 Species richness has long been used as an indicator of ecosystem functioning and health.
40 Global richness is declining, but it is unclear whether sub-global trends differ. Regional trends
41 are especially understudied, with most focused on island regions where richness is strongly
42 impacted by novel colonizations. We addressed this knowledge gap by testing for multi-decade
43 trends in species richness in nine open marine regions around North America (197 region-years)
44 while accounting for imperfect observations and grounding our findings in species-level range
45 dynamics. We found positive richness trends in eight of nine regions, four of which were
46 statistically significant. Species' range sizes generally contracted pre-extinction and expanded
47 post-colonization, but the ranges of transient species expanded over the long-term, slowly
48 increasing their regional retention and driving increasing richness. These results provide more
49 evidence that sub-global richness trends are stable or increasing, and highlight the utility of range
50 size for understanding richness dynamics.

51 **Introduction**

52 Biological diversity is a key determinant of ecosystem function and change. It affects
53 food web stability (Hooper *et al.* 2005; Loreau & de Mazancourt 2013), ecosystem productivity
54 (Tilman *et al.* 2001), and benefits human well being through ecosystem services and its social
55 and cultural value (Millennium Ecosystem Assessment 2005; Cardinale *et al.* 2012).
56 Anthropogenic forcings are causing rapid and long-term change in biodiversity (Newbold *et al.*
57 2015), but the magnitude of this change varies across the globe and is difficult to measure.
58 Species richness, for example, is a straightforward enumeration of distinct species, but precise
59 measurement is difficult because there are many species, most of them are rare, and observations
60 are imperfect (Darwin 1859; Gotelli & Colwell 2011). Despite this difficulty, estimates of

61 species richness and extinction rates make it clear that global species richness is currently
62 declining and will likely continue to do so over the next century (Pereira *et al.* 2010; Pimm *et al.*
63 2014). Biodiversity trends are therefore an important focus of current research and conservation
64 efforts.

65 Though declining globally, biodiversity is scale dependent, and processes like
66 colonization and extirpation only affect sub-global diversity, potentially decoupling trends at
67 different spatial scales (Sax & Gaines 2003). In fact, recent studies have found that, on average,
68 net changes and multi-year trends in local-scale diversity are approximately stable (Vellend *et al.*
69 2013; Dornelas *et al.* 2014). These results have sparked controversy about whether diversity
70 trends differ between local and global scales (Gonzalez *et al.* 2016; Vellend *et al.* 2016);
71 however, relatively few studies have quantified contemporary changes in biodiversity at regional
72 scales. Most studies of regional richness focus on islands, where richness has often increased
73 through human introduction of novel species (Sax *et al.* 2002; Sax & Gaines 2008; Vellend *et al.*
74 2017). Marine systems are particularly underrepresented (McGill *et al.* 2015), with the few
75 existing studies suggesting diversity has increased in some regions and decreased in others
76 (Hiddink & ter Hofstede 2008; ter Hofstede *et al.* 2010; Hiddink & Coleby 2012).

77 Conclusions of existing sub-global studies of diversity change have been criticized on
78 grounds of their geographic representativeness and statistical methods. First, sub-global studies
79 are not spatially comprehensive (Vellend *et al.* 2016) and are not representative of spatially
80 heterogeneous drivers of richness (Gonzalez *et al.* 2016) like geographic connectivity,
81 environmental change, and anthropogenic stressors (Hiddink & Coleby 2012; Burrows *et al.*
82 2014; Elahi *et al.* 2015). Other critiques have focused on statistical tests for richness trends and
83 the need for multi-decade time series (Gonzalez *et al.* 2016; Vellend *et al.* 2016), although
84 measurement error is another important statistical challenge affecting trends (Dornelas *et al.*
85 2013). Specifically, equipment and observation techniques often improve over time, potentially
86 improving detection of rare species and introducing a bias to long-term richness surveys (Tingley
87 & Beissinger 2013). Statistical methods that account for imperfect detection with community
88 datasets have been developed (Iknayan *et al.* 2014; Guillera-Aroita 2016), but are not
89 commonly used (Kellner & Swihart 2014). Overcoming statistical challenges and estimating
90 diversity trends for a wider representation of ecosystems will improve understanding of global
91 diversity change.

92 Species-level dynamics provide insight into the process of diversity change. Changes in
93 regional species richness are primarily driven by individual species shifting their ranges into
94 (colonization) or out of (extinction) a region. Range shifts – which can include changes in range
95 size or location – can be driven by changes in local habitat suitability (Cheung *et al.* 2009; Elahi
96 *et al.* 2015; Molinos *et al.* 2015) or human-facilitated changes in connectivity (Sax & Gaines
97 2008). Changes in range size (proportion of occupied sites within a region) often also reflect
98 changes in population size (Fretwell & Lucas 1969; Hanski 1982; MacCall 1990), and in turn
99 predict extinction probability, as small populations (or ranges) have short expected times to
100 extinction (MacArthur & Wilson 1967). However, changes in range size depend on both
101 abundance and density, and range can change rapidly after colonizations (van den Bosch *et al.*
102 1992; Hastings *et al.* 2004; Urban *et al.* 2008) or before extinctions (Wilcove & Terborgh 1984;
103 Lawton 1993). Range dynamics are further complicated when different processes govern the
104 dynamics of rare and common species (Hanski 1982; Gaston *et al.* 1997; Holt *et al.* 1997; Yenni
105 *et al.* 2012), and by the difficulty in modeling the distribution of rare species (Lomba *et al.*
106 2010). Thus, range size should provide insights into richness dynamics, but quantifying range
107 trends for rare species is challenging.

108 Nonetheless, time series of range size and its related measures have been used to
109 illustrate how changes in community structure arise from population processes. In the eastern
110 North Sea, species-level range size trends in fished *versus* unfished populations explained
111 increased local species richness over an eight year period (Hiddink & Coleby 2012). Similar
112 processes contributed to changes in local richness over a longer period in the Scotian Shelf
113 (Shackell & Frank 2003). In another part of the eastern North Sea, local species richness was
114 generally stable, but large compositional changes were observed in the form of assemblage
115 homogenization (Magurran *et al.* 2015), due either to range expansion or shifts in range location.
116 Conversely, local richness and beta diversity both increased over several decades on the Scotian
117 Shelf, likely as a consequence of fishing reducing the abundance of cod, an important predator in
118 the region (Ellingsen *et al.* 2015). Although range size and spatial community turnover are
119 inversely related, it is important to note that beta diversity depends on both range size and
120 location (Harrison *et al.* 1992). These studies emphasize how changes in range size and beta
121 diversity impact changes in local richness.

122 Less clear is how species-level range size affects richness at regional scales. Changes in
123 range sizes have the potential to increase regional richness via two separate processes:
124 colonization and retention. First, a species not present in a region may expand its range,
125 eventually colonizing; this process is important for increasing island richness (Sax & Gaines
126 2008; Byers *et al.* 2015). In this case, prior to the colonization, no within-region change in range
127 size would be observed. For the second process, retention, it is useful to distinguish between core
128 species that are widespread and always present, and transient species that are sometimes present
129 and geographically constrained (Hanski 1982; Magurran & Henderson 2003). Retention
130 increases richness by reducing species loss, and would be expected to increase as a result of
131 range expansions. Since they are rare, transient species have the greatest potential for increased
132 retention. Therefore, long-term trends in species richness could be reflected in range expansion,
133 but only if richness trends are not dominated by changes in colonization rates. There are few
134 tests of this idea at regional and decadal scales.

135 We tested for long-term changes in regional species richness and for contributions of
136 range size dynamics to these trends. We analyzed multi-decade time series of the occupancy and
137 geographic distribution of marine fishes and invertebrates in nine ecosystems around the North
138 American coastline. The large area of our study regions might suggest that their richness trends
139 should be similar to the negative global trend, but neutral or positive trends would match results
140 from previous regional studies (Sax & Gaines 2008; Hiddink & Coleby 2012), of which only a
141 few were in open or marine ecosystems. We hypothesized that a trend in richness should be, at
142 least in part, driven by changes in range size. Range size should influence richness trends if 1)
143 range size declines with increased proximity to extinction, 2) transient species have small ranges,
144 and 3) the range size of transient species exhibits a long-term trend. The first two conditions are
145 commonly met, but we tested for their applicability to our study systems and used them to
146 facilitate the interpretation of other results. If the third condition is also met, then changes in
147 richness were at least partly driven by changes in the persistence of rare species.

148

149 **Methods**

150 *Survey Data*

151 We used data on the presence and absence of marine species sampled by scientific
152 bottom trawl surveys from nine regions around the North American continental shelf. We

153 analyzed observations of 581 species, which principally included bottom-dwelling fishes and
154 invertebrates such as flatfishes and shellfish (Supporting Information). Sampled regions were
155 Eastern Bering Sea (1984-2014, n=31), Aleutian Islands (1983-2014, n=12), Gulf of Alaska
156 (1984-2013, n=13), West Coast U.S. (1977-2004, n=10), Gulf of Mexico (1984-2000, n=17),
157 Southeast U.S. (1990-2014, n=25), Northeast U.S. (1982-2013, n=32), Scotian Shelf (1970-2010,
158 n=41), and Newfoundland (1996-2011, n=16; Table S1, Fig. S1). Measurements of bottom water
159 temperature and bottom depth were taken for each trawl sample; these values were used as
160 covariates in models.

161 We restricted our analysis to samples from years and sites that had the most consistent
162 sampling methods. The fundamental sampling unit is the tow, a drag of the trawl net at a given
163 place and time. Data were restricted to tows with consistent gear, season, and site; tows within a
164 site and year were considered repeat samples of that site. Sites were defined by binning regular
165 intervals of longitude, latitude, and depth. We chose a spatial resolution (0.5° for longitude and
166 latitude) that yielded a large number of sites that were sampled at least once in most years. Sites
167 were then binned by 500 m or 100 m depth increments. In most regions we used 500 m depth
168 increments, which rarely subdivided the 0.5° bins but guarded against large within-site
169 differences in depth-related habitat suitability. However, sampling was relatively dense across
170 longitude and latitude in the Aleutian Islands and the West Coast U.S., allowing us to use 100 m
171 depth increments while still sampling the sites in most years. We only included sites in our
172 analysis that were sampled in at least 85% of years, except in Eastern Bering Sea and Gulf of
173 Alaska where sites had to be present in all years to avoid large interannual changes in the
174 extremes of longitude or latitude (Supporting Information: Excluding Years).

175 Analyses were restricted to taxa identified to species and that were not known to have
176 undergone large changes in identification accuracy. We used automated and manual procedures
177 to correct errors in taxonomy (Supporting Information: Taxonomic & Sampling Consistency).
178 After these corrections, we removed any species that were not observed in at least 10 tows over
179 the course of that region's time series.

180

181 *Species Richness*

182 We refer to the number of species in a sampled assemblage as the species richness of that
183 community. Note that because sampling methods differ somewhat among regions, definitions of
184 “community”, and therefore richness values, are not entirely comparable across regions.

185 Species richness is rarely ascertained accurately from raw survey data (Gotelli & Colwell
186 2001). We calculated a naïve measure of species richness (observed species counts) and
187 estimated true richness using a multispecies occupancy model (MSOM; (Dorazio & Royle
188 2005)). MSOMs accounted for imperfect detection of species, making estimates of richness more
189 robust to possible methodological improvements in survey methods that could bias naïve trends
190 (Iknayan *et al.* 2014).

191 MSOMs use a mixed modeling and state-space framework to separate true absences (1 -
192 occupancy probability) from false absences (1 - detection probability), and to estimate true
193 richness by accounting for those undetected species likely to be present at a site. Both
194 probabilities of occupancy and detection can each be modeled as a function of *a priori*
195 covariates. Covariate coefficients and intercepts are species-specific, but are drawn from
196 community-wide hyper-distributions, making the model hierarchical. Model hierarchy allows
197 observations of one species to inform parameter fits for other species, including the membership
198 and occupancy parameters of unobserved species (Supporting Information: Occupancy Model),
199 allowing estimated richness to exceed observed richness. This technique is known as data
200 augmentation, and has previously been used to estimate occupancy and species richness (Royle
201 *et al.* 2007; Kéry *et al.* 2009). We fit the MSOMs in a Bayesian framework using JAGS
202 (Plummer 2003), and fit 197 separate models, one for each year and region.

203

204 *Trends in Species Richness*

205 Species richness trends were quantified using Kendall’s τ_b , which measures the similarity
206 in rank-order for two variables, or in this case, whether richness tended to exhibit a monotonic
207 trend over time. We used Kendall’s τ_b because it is nonparametric and does not assume a linear
208 trend, which visual inspection indicated may not be the case for several time series. Our
209 calculation of Kendall’s τ_b uses the MSOM posterior samples of richness and accounts for serial
210 correlation (Supporting Information: Trends in Species Richness).

211

212 *Range Size*

213 Range size is the proportion of sites in a region occupied by a species in a year. To
214 account for variation in the number of tows per site, for each site we calculated the fraction of
215 tows that contained the species; range size was rarefied to a single tow by summing this fraction
216 across sites. This measure of range size was used to compare changes in range size prior to
217 extinction and after colonization, and to compare long-term changes in range size for transient
218 and core groups of species.

219 In addition to range size, we define a long-term species range index (SRI), and the cross-
220 species average of SRI, community range index (CRI). SRI is the long-term average of a species'
221 range size (excluding range sizes of 0). SRI is the typical range size of a species when it was
222 present. SRI was compared with the total number of a species' colonizations and extinctions in
223 order to relate range size to transience (transient species were expected to have a small SRI). CRI
224 was calculated annually as the average SRI of species present in that year. We used CRI as a test
225 for how community composition might change with richness; decreases in CRI are expected to
226 occur as the number of transient species increases (as a proportion of richness).

227
228 *Species Categories*

229 Colonizations and extinctions were defined according to observed changes in occupancy.
230 As a result, a species that was present but undetected would be recorded as absent since it was
231 not observed. Furthermore, extinctions were defined regionally, not globally; therefore, a species
232 could repeatedly colonize and go extinct.

233 All species were categorized as either core or transient in each region. Core species were
234 those that were present in a region in all years, and transient species were those that were absent
235 from a region in at least one year (but not all years). Each transient species was further
236 categorized according to its colonization and extinction history. *Colonizing* species colonized the
237 region but never went extinct, *leaving* species went extinct from the region but were never
238 observed to have colonized, and the remaining transient species, categorized as *both*,
239 experienced at least one colonization and extinction.

240

241 *Trends in Range Size*

242 We tested for pre-extinction contractions and post-colonization expansions of range size
243 for transient species. For any year in which the species was present, a variable *time to absence*
244 was defined as the number of years before an absence (*years before extinction*) or after an
245 absence (*years after colonization*). Each transient species' time series was separated into years
246 that were either post-colonization or pre-extinction, depending on which event type was most
247 proximal (ties were post-colonization). No analysis included range sizes of 0 because range size
248 is defined as 0 when *time to absence* is 0. We performed regressions separately for each region
249 using a linear mixed effects model with *range size* as the response variable and *time to absence*
250 as a covariate (we excluded stretches of fewer than three years); species identity was modeled as
251 a random effect that allowed the slope parameter associated with *time to absence* and the
252 intercept parameter to vary among species. This is the final model used for all regions, except the
253 Gulf of Mexico, for which we did not allow intercept to vary among species because this term
254 prevented the model from properly converging. Models that allowed slopes and intercepts to
255 change with phase *type* did not improve fit according to AIC, except for Scotian Shelf (intercept
256 \times *type* $p = 0.005$, Δ AIC = 0.228), though improvement was minor. Henceforth we present results
257 from the simpler models because the purpose here was to test the idea that range size changes in
258 proximity to colonization or extinction, and this outcome did not differ among model structures.

259 To test for long-term changes in range sizes of transient and core species, we used mixed
260 effects models with range size as the response variable. Predictors were year, species group
261 (*transient* or *core*; adjustment to intercept) and its interaction with year (adjustment to slope),
262 and species identity as a random factor that allowed the intercept parameter to vary among
263 species. Range sizes of 0 were excluded. Regressions were fit separately for each region.

264 All analyses aside from Bayesian model fitting were performed in R v3.3.0 (R Core
265 Team 2016). In calculating richness trends we used the `Kendall` function in the package
266 *Kendall* (McLeod 2011), and `auto.arima` in *forecast* v7.1 (Hyndman & Khandakar 2008).
267 The mixed effects regressions were performed using `lmer` in *lme4* (Bates *et al.* 2015).
268 Conditional and marginal R^2 values were calculated using `sem.model.fits` in *piecewiseSEM*
269 (Lefcheck 2016). Conditional R^2 indicates the variation explained by both fixed and random
270 effects; marginal R^2 indicates variation explained by fixed effects (Nakagawa & Schielzeth
271 2013).

272

273 **Results**

274 *Species Richness*

275 Estimated long-term trends (Kendall's τ_b) in both observed and estimated richness were
276 positive for most regions (Fig. 1, Table 1). Trends in MSOM estimates of species richness were
277 significant in four of the nine regions, and all significant trends were positive: Eastern Bering
278 Sea ($\tau_b = 0.42$), West Coast U.S. ($\tau_b = 0.61$), Scotian Shelf ($\tau_b = 0.45$), and Newfoundland ($\tau_b =$
279 0.73) (Table 1, Fig. 1). Any region with a significant MSOM trend also had a significant trend in
280 naïve richness; naïve richness was significant in three additional regions, including a negative
281 trend in the Southeast U.S. (Table S2). Although MSOM estimates of richness were greater than
282 naïve estimates, estimates from the two methods were correlated (Fig. S2). Henceforth, we report
283 species richness as MSOM estimates unless otherwise specified.

284

285 *Colonization and Extinction*

286 Across regions, most species were core species: with 536 out of 863 region-species
287 combinations being present in all years (Fig. S3). Core species were the most common group in
288 all regions except the Northeast U.S., where transient species that *both* colonized and went
289 extinct were the most common, followed by core species. Summed across regions, most transient
290 species were categorized as *both* (263 region-species), followed by *colonizing* (60) and *leaving*
291 (4). Aleutian Islands was the only region with more *colonizing* species than *both* species (Fig.
292 S3).

293 If richness increased and yet the number of *colonizing* species was less than the net
294 change in richness, then species that *both* colonized and went extinct (possibly multiple times)
295 from the region must also have contributed to the net change in richness. The net change in
296 richness was calculated as the difference between the last and first predicted values of a linear
297 trend fit to the time series of MSOM richness estimates. The number of *colonizing* species was
298 less than the net change in richness for all regions with a significant trend in richness (Table S3):
299 E. Bering Sea $\Delta = 12.5$, *colonizing* = 2; Newfoundland $\Delta = 12.7$, *colonizing* = 10; Scotian Shelf
300 $\Delta = 7.6$, *colonizing* = 1; West Coast US $\Delta = 18.8$, *colonizing* = 12, indicating that species that
301 had *both* entered and exited the region during the time series also contributed to increases in
302 richness.

303

304 *Trends in Range Size Near Colonizations and Extinctions*

305 Species' range sizes contracted in the years leading up to extinction (Fig. 2A), and
306 expanded in the years following colonization (Fig. 2B; *see* Fig. S5 for a version that is not
307 averaged). We fit separate mixed effects models for each region, and excluded points at $t=0$
308 years pre-extinction or post-colonization. As the number of years before extinction or after
309 colonization increased, range size also increased (across regions, $1.4 \leq \beta \leq 11.2$, average = 4.8
310 percent occupancy per decade, all corrected $p \leq 0.036$). Proximity to colonization or extinction
311 explained a modest amount of variation in range size ($0.06 \leq mR^2 \leq 0.19$). Among-species
312 differences in slopes and intercepts explained much more variance ($0.63 \leq cR^2 \leq 0.95$; Fig. S5).
313 Indeed, variation among species' slopes was similar to the average slope ($\bar{\sigma}_\beta = 6.5$ percent per
314 decade), indicating that some species exhibited very steep trends in range size. In general,
315 species were at their rarest just before extinction or just after colonization.

316

317 *Richness and Range Size*

318 The total number of colonizations and extinctions was greatest for species with small
319 SRIs, and many species (*both*) colonized and went extinct multiple times (Fig. S4). In mixed
320 effects models with intercepts varying among species and transient *versus* core as a categorical
321 predictor, transient species had range sizes that were 18 (% occupancy) smaller than the ranges
322 of core species (average intercept; all $p \leq 0.02$ after correcting for multiple tests). Furthermore,
323 species richness was negatively correlated with the community range index (CRI) in each region
324 (Fig. 3; separate linear regression for each region, for slope all corrected $p \leq 0.002$, $0.36 \leq R^2 \leq$
325 0.95 , average $R^2 = 0.79$). These results indicate that smaller long-term averages of range size
326 were characteristic of transient species, and richness was highest when more geographically
327 constrained (transient) species were present.

328 Richness was highest when more transient species were present, but why did transient
329 species accumulate in regions with positive trends in richness? Range size was negatively related
330 to the proximity of upcoming extinctions (Fig. 2, Fig. S4). We found that the range sizes of many
331 species, but particularly transient species, expanded over time in most regions (Fig. 4). We used
332 mixed effects models to predict range size from the main effects of survey year and the core-
333 transient category, their interaction, and an intercept that varied randomly among species. Range

334 sizes for core species decreased in Southeast U.S. ($\beta_Y = -1.8\%$ occupancy per decade),
335 Newfoundland ($\beta_Y = -1.7$), and Scotian Shelf ($\beta_Y = -0.36$), and increased in the six other regions (
336 $\bar{\beta}_Y = 1.6$; after correcting for multiple testing, all $p \leq 0.045$). However, the interaction term
337 indicated that the slopes of core and transient species were different in six of the regions ($p \leq$
338 0.004), including positive interactions in Newfoundland ($\beta_{Y \times T} = 4.8$) and Scotian Shelf ($\beta_{Y \times T}$
339 $= 2.1$), where the net trend ($\beta_Y + \beta_{Y \times T}$) for transient species was positive. In all regions except
340 Southeast U.S., the range sizes of transient species expanded over the course of the time series
341 (average = 2.6% occupancy per decade).

342

343 Discussion

344 We found that long-term trends in regional species richness tended to be positive.
345 Previous studies have found local trends to be stable (Dornelas *et al.* 2014; Magurran *et al.*
346 2015), and regional trends to increase (Sax & Gaines 2003, 2008; Hiddink & ter Hofstede 2008;
347 ter Hofstede *et al.* 2010; Hiddink & Coleby 2012). Although most of the regions studied were
348 islands, and only a few marine, our findings of positive trends in nine open marine ecosystems
349 lend more support to the conclusion that regional richness trends are generally positive around
350 the world and across ecosystems.

351 Trends in species richness require careful analysis and interpretation. First, changes in
352 richness can be context dependent, varying with space, time, and taxa (Sax & Gaines 2003; Elahi
353 *et al.* 2015; Gonzalez *et al.* 2016; Vellend *et al.* 2017). All datasets have limited taxonomic,
354 spatial, and temporal scope, but we analyzed many decades of observations from nine regions
355 that encompass a large fraction of coastal North America. Second, detection probability usually
356 increases with abundance and range size, causing the number of colonizations and extinctions to
357 be overestimated, and range sizes underestimated; for our purposes, these imperfections would
358 be most problematic if they were changing over time. However, our analysis of range size
359 detected both long-term trends and short-term rises and falls near absences, patterns unlikely to
360 be produced in nine regions by sampling artefacts alone. Furthermore, when estimating richness,
361 we accounted for possible temporal bias in detectability by using the MSOM (Tingley &
362 Beissinger 2013; Iknayan *et al.* 2014; Guillera-Arroita 2016). While MSOMs fit to many years
363 can infer colonization and extinction dynamics (Kéry *et al.* 2013), we fit models separately to
364 each year of data because we did not know how detectability would change over time. The

365 MSOM results had dampened trends compared to naïve results, suggesting that the MSOM
366 estimated more undetected-but-present species in early, low-richness years. These results
367 demonstrate how imperfect detection can exaggerate richness trends, and highlight a benefit of
368 using the MSOM.

369 A goal of our study was to gain insight into the process by which regional species
370 richness changes by decomposing these changes into colonizations and extinctions, which in turn
371 should be reflected in range size dynamics. We found pre-extinction range contractions and post-
372 colonization expansions, a pattern often reported in paleoecological, macroecological, and
373 metapopulation studies (Hanski 1982; Jablonski 1987; Harrison 1991; Gaston 2003). However,
374 these studies focused on select species with many consecutive years of presences, unlike the
375 numerous rare species in our analysis whose small ranges and short time series (average duration
376 of pre-extinction and post-colonization stretches = 4.2 years) made trend analysis challenging.
377 Nonlinear dynamics over long periods also obscure expected trends, such as for the green sea
378 urchin in the Aleutian Islands: originally at a range of < 1%, it increased to 66% over 11 years,
379 then declined to < 20% over 20 years before going extinct (Fig. S5, Fig. 2A). A linear trend
380 through this time series does not reflect the pre-extinction contraction. Therefore, it is
381 unsurprising that marginal R^2 values were low, and similar challenges likely apply to other
382 systems. Transient species are generally rare (Gaston 1994), and steep or nonlinear dynamics
383 frequently characterize both pre-extinction (Wilcove & Terborgh 1984; Simberloff & Gibbons
384 2004) and post-colonization (Lewis & Kareiva 1993; Hastings *et al.* 2004) dynamics. The
385 general rule of pre-extinction contractions and post-colonization extinctions encompasses a wide
386 variety of complex dynamics that are typically tested with select, well-observed species. Our
387 findings suggest that similar theory and analysis can be applied to a large number of rare and
388 intermittently present species whose occupancy dynamics define species richness.

389 Trends in the range size of transient species were essential for linking range size to
390 regional trends in richness. Richness was tightly correlated with CRI, which is readily explained
391 by a tendency for transient species – whose occupancy defines richness change – to have small
392 ranges (see above). These relationships, however, do not imply a trend in species richness, which
393 results from changes in colonization or extinction rates. We found that transient species had
394 positive, long-term trends in their range sizes, which implies decreased extinction rates. Thus,
395 increased retention allowed species to accumulate. However, our analysis may have excluded

396 some colonizing species that did not persist or were infrequently detected, and so may not be a
397 comprehensive test of the relative roles of increased colonization *versus* retention. Species
398 distribution models that cover multiple regions (Molinos *et al.* 2015) and include rare species
399 (Lomba *et al.* 2010) might be useful for testing this idea. Nonetheless, the role of increased
400 retention in these marine regions contrasts with past studies of regional richness on islands,
401 where increased connectivity and novel colonizations were important processes (Sax & Gaines
402 2003, 2008). Thus, marine regions and islands both experienced increased species richness, but
403 for different reasons.

404 Temperature and fishing are factors that could have contributed to the range expansion of
405 transient species. The geographic ranges and abundances of the more common species in these
406 data are known to be responsive to temperature changes (Mueter & Litzow 2008; Pinsky *et al.*
407 2013; Sunday *et al.* 2015; Morley *et al.* 2017), and temperature changes could increase the
408 prevalence of certain species. For example, there is a biogeographic break between the Northeast
409 U.S. and the warmer Southeast U.S., and the strength of the latitudinal diversity gradient
410 fluctuates with climate oscillations (Fisher *et al.* 2008). During warm years, southerly fish may
411 be introduced to the northern region, but retreat upon cooling. The Northeast U.S. has
412 experienced long-term warming trends (Pershing *et al.* 2015), possibly enhancing the range and
413 duration of the northern establishment of southern species. In addition, fishing resulted in the
414 collapse of cod in the 1990's, after which many invertebrates expanded (Shackell & Frank 2003;
415 Choi *et al.* 2004; Boudreau & Worm 2010; Ellingsen *et al.* 2015). The timing of perturbations
416 can determine whether positive trends indicate a recovery to a "normal" state or an increase
417 beyond baseline conditions. In this case, the effect of cod collapse did not explain differences in
418 richness trends among the Northeast U.S. (began before the collapse, no trend), Scotian Shelf
419 (began before, positive trend), and Newfoundland (began after, positive trend). However, we did
420 not specifically test for the drivers of richness change. Future work should consider which
421 drivers played a role in increased range sizes and richness, and how the timing of changes in
422 drivers might affect what are perceived as baseline conditions.

423 Long-term changes in species richness have been the subject of recent debate (Gonzalez
424 *et al.* 2016; Vellend *et al.* 2016): do global and sub-global time series have opposing trends? We
425 tested for multi-decade trends in regional marine species richness, an underrepresented
426 ecosystem and spatial scale (McGill *et al.* 2015). Our results supported the general conclusion

427 that regional trends are stable or increasing, and that this result is consistent across ecosystems
428 types. However, richness is a measure of community change that aggregates over the dynamics
429 of many species. By decomposing richness change into the range dynamics of individual species,
430 we also found that increases in regional richness were driven by the long-term tendency for
431 regionally rare species to expand their geographic ranges and become more common as more
432 sites became suitable for them, which contrasted with previous results emphasizing changes in
433 connectivity. Our results suggest that the spatial dynamics of individual species are closely tied
434 to richness dynamics, which might explain differences between local, regional, and global trends.
435 Continuing to improve our understanding of these trends and their drivers is critical to the
436 successful prediction and management of the biodiversity changes taking place around the globe.

437

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446

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691

692

693 **Tables**

694 **Table 1.** Trends in MSOM estimates of richness. Kendall's τ_b , which accounts for ties, was
695 calculated after removing serial correlation in each resampled time series of the posterior. P-
696 values were corrected for multiple comparisons in order to maintain a false discovery rate of
697 $\alpha = 0.05$ (Benjamini & Hochberg 1995). Significant trends and p-values are bolded.

Region	Kendall's τ	P-value (BH)
Aleutian Islands	0.23	0.37
E. Bering Sea	0.42	0.0030
Gulf of Mexico	0.098	0.61
Gulf of Alaska	0.24	0.36
Northeast US	0.19	0.22
Newfoundland	0.73	6.4E-4
Southeast US	-0.22	0.22
Scotian Shelf	0.45	4.4E-4
West Coast US	0.61	0.042

698

699

700 Figure Legends

701 **Fig. 1.** Time series of MSOM estimates of regional richness. Each point is the posterior mean of
702 regional richness in a year. Lines indicate long-term trends from fitted values of linear regression
703 models predicting richness from time. Solid lines indicate that τ_b was significant, dashed lines
704 insignificant (Table 1).

705

706 **Fig. 2.** Range size versus years before extinction (A) and years after colonization (B). The
707 horizontal axis is the number of years to the nearest absence, separated into either a pre-
708 extinction or post-colonization phase. A species might experience repeated pre-extinction and
709 post-colonization phases in the same time series. For visualization, range sizes within a region
710 were averaged across each species-phase combination for a given number of years to absence.
711 Statistics (see main text) use unaggregated data (see Fig. S5). By definition, range size is 0 when
712 years to event is 0, and we excluded points at (0,0) from all figures and analyses. Lines are trends
713 from linear regressions fit to aggregated range sizes.

714

715 **Fig. 3.** Regional species richness (estimated from MSOM) versus community range index (CRI).
716 CRI is the community average of each species' typical range size. There is one point per region
717 per year. Solid lines are linear regression fits. Colors represent different regions (Figs. 1,2).

718

719 **Fig 4.** Changes in range sizes (rarefied) for the transient (red) and core (blue) members of each
720 of the nine regional assemblages. The shading encompasses the middle 50% of the observations,
721 and thick lines are at the median. The black line represents CRI, which is the same metric
722 represented by the horizontal axis of Fig. 3. Range sizes of zero were excluded when calculating
723 all metrics.

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