

# 1 Coral assemblages at higher latitudes favour short-term potential over 2 long-term performance

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30 dynamics.

31 **Abstract**

32 The current exposure of species assemblages to high environmental variability may grant them  
33 resilience to future increases in climatic variability. In globally threatened coral reef  
34 ecosystems, management seeks to protect resilient reefs within variable environments. Yet, our  
35 lack of understanding for the determinants of coral population performance within variable  
36 environments hinders forecasting the future reassembly of coral communities. Here, using  
37 Integral Projection Models, we compare the short- (*i.e.*, transient) and long-term (*i.e.*,  
38 asymptotic) demographic characteristics of tropical and subtropical coral assemblages to  
39 evaluate how thermal variability influences the structural composition of coral communities  
40 over time. Exploring spatial variation across the dynamics of functionally different  
41 competitive, stress-tolerant, and weedy coral assemblages in Australia and Japan, we show that  
42 coral assemblages trade-off long-term performance for transient potential in response to  
43 thermal variability. We illustrate how coral assemblages can reduce their susceptibility towards  
44 environmental variation by exploiting volatile short-term demographic strategies, thus  
45 enhancing their persistence within variable environments. However, we also reveal  
46 considerable variation across the vulnerability of competitive, stress-tolerant, and weedy coral  
47 assemblages towards future increases in thermal variability. In particular, stress-tolerant and  
48 weedy corals possess an enhanced capacity for elevating their transient potential in response to  
49 environmental variability. Accordingly, despite their current exposure to high thermal  
50 variability, future climatic shifts threaten the structural complexity of coral assemblages,  
51 derived mostly from competitive coral taxa within highly variable subtropical environments,  
52 emulating the degradation expected across global coral communities.

53

54

## 55 **Introduction**

56 Coral reefs worldwide are threatened by unprecedented climatic and anthropogenic disruption  
57 (1, 2), with their conservation now reliant on enhancing the resilience of coral communities,  
58 specifically their capacity to resist and recover from increased climatic variability (3, 4).  
59 Changes in environmental regimes provoke spatial shifts in the performance and distribution  
60 of populations, which ultimately upscale to the compositional reassembly of biological  
61 communities (5, 6). Exposure to increased environmental variability is, however, expected to  
62 indirectly augment the capacity for populations to resist and recover from repeated disturbances  
63 (7, 8). Yet, nuanced relationships between population characteristics and biophysical  
64 conditions ensure inconsistent responses towards climate shifts, even across populations within  
65 the same region (9, 10). For instance, differential population sensitivities to habitat change can  
66 accelerate or reverse expected poleward range shifts in response to climate warming (10). Thus,  
67 anticipating the future resilience of natural communities requires understanding the collective  
68 vulnerabilities of their constituent populations (11) and the determinants underpinning their  
69 resilience to increasingly recurrent disturbances (12, 13). However, regional variations in the  
70 response of coral assemblages to climatic disturbances have generated misconceptions in our  
71 interpretation of the status of coral communities worldwide, with global population sizes of  
72 many species perhaps larger than previously anticipated (14). Only by linking the mechanisms  
73 underpinning heterospecific variation across the responses of populations to environmental  
74 variability can one predict the resilience of biological communities to increased climatic  
75 variability (11, 15, 16). Evidently, to accurately forecast the ongoing reassembly of global coral  
76 communities we must improve our understanding for how environmental variability shapes  
77 coral population performance across community- and regional-scales (7).

78 To explore the performance of populations exposed to recurrent disturbances within  
79 variable environments, their transient (*i.e.*, short-term) dynamics must be considered (17–20).

80 Yet, asymptotic (*i.e.*, long-term) population growth rate ( $\lambda$ ), a metric that describes temporal  
81 changes in population size at stationary equilibrium (21), is the predominant metric used to  
82 quantify population performance (21, 22). In reality, though, natural populations are exposed  
83 to repeated disturbances that favour the persistence of transient conditions, preventing the  
84 emergence of stationary equilibria (17, 20, 23). Within variable environments, repeated  
85 disturbances impose short-term changes upon the structure of populations that can elevate  
86 (*amplify*) or diminish (*attenuate*) their growth rates, resulting in population performance  
87 characteristics deviating from long-term expectations (18, 24). Quantifying how transient  
88 population performance deviates from long-term expectations (henceforth *transient potential*)  
89 is therefore crucial for predicting the success or failure of natural populations (25); an approach  
90 that remains neglected within coral research (19).

91 Located at the intersection of tropical and temperate ecoregions, subtropical coral  
92 communities provide an opportunity for evaluating the abiotic determinants of coral population  
93 performance (26–28). Over recent decades, subtropical coral communities have undergone  
94 transformation with various coral taxa undergoing poleward range expansions in response to  
95 shifting thermal regimes (29–33). However, at higher latitudes, coral communities are exposed  
96 to enhanced seasonality and cooler winter temperatures, and thus experience greater abiotic  
97 variability relative to their tropical reef counterparts (34). Over time, the persistence of  
98 populations within stable environments diminishes their capacity for tolerating novel  
99 environmental states, thus reducing their resilience towards future climatic shifts (8).  
100 Consequently, the endurance of subtropical coral communities within variable high-latitude  
101 environments is expected to enhance their abiotic resilience (7). Indeed, as seen across other  
102 communities (e.g., plants; 35), enhanced transient potential can elevate the performance of  
103 acroporid coral populations within variable subtropical environments (36). Yet, without  
104 knowledge for how differing coral assemblages utilise demographic strategies to mediate their

105 performance in response to environmental variability, we will be unable to forecast the impacts  
106 of increasing climatic variability on the condition of global coral reef ecosystems.

107 In species rich communities, evaluating ecological dynamics requires a trait-based  
108 approach to condense vast quantities of demographic detail (37). Given the diversity of coral  
109 reef ecosystems, exploring patterns across the demographic characteristics of co-occurring  
110 coral species presents a logistical challenge (38). Yet, this is a challenge that can be navigated  
111 by pooling individuals based on shared trait characteristics. Morphological, physiological and  
112 phenological functional traits influence the fitness of individuals and thus determine the  
113 demographic characteristics of their populations (39), their responses to disturbances (40), and  
114 subsequently the assembly of biological communities (41–43). Indeed, functional trait  
115 characteristics impact upon the demographic properties of coral populations (e.g., colony  
116 growth and reproduction; 44, 45), mediating their ability to respond to local abiotic patterns  
117 (46). Given such strong links between coral traits and demographic performance, the  
118 categorisation of coral taxa into competitive, stress tolerant, generalist and weedy life history  
119 assemblages (*sensu* 47) is used to evaluate broadscale patterns in coral community reassembly  
120 (48–50). The trait-based assessment of coral community assembly also offers greater insight  
121 into the wider implications of ongoing community shifts than taxonomic-based assessments,  
122 thereby aiding the management of coral reef ecosystems (50).

123 Here, we investigate how the performance characteristics of tropical and subtropical  
124 coral populations map onto patterns of thermal variability across assemblages of competitive,  
125 stress-tolerant, and weedy coral taxa. Using Integral Projection Models (IPMs; 51), we quantify  
126 the association between different dimensions of thermal variability (monthly mean sea surface  
127 temperature [SST], monthly SST variance, and monthly SST frequency spectrum) and the  
128 transient potential and long-term performance characteristics of tropical and subtropical coral  
129 assemblages in southern Japan and eastern Australia (Fig. 1). Specifically, we anticipate that,

130 in accordance with their exposure to elevated thermal variability, subtropical coral assemblages  
131 will possess greater transient potential in comparison to tropical assemblages. We expect that  
132 this pattern will persist irrespective of functional strategy, corresponding with the need for  
133 subtropical coral populations to exploit periodically disturbed environments.

## 134 **Results and Discussion**

135 Our analyses reveal a trade-off between long-term performance and transient potential across  
136 the examined coral assemblages. We find that this trade-off corresponds with the exposure of  
137 coral populations to thermal variability along a gradient from warmer, more stable  
138 environments to cooler, more variable conditions (Fig. 2). Using partial least squares  
139 regression, we evaluated how patterns in the long-term performance, demographic recovery,  
140 and transient potential, of coral populations conform with their exposure to abiotic variability.  
141 We obtained estimates of long-term population performance (asymptotic population growth  
142 rate,  $\lambda$ ), demographic recovery (damping ratio  $[\rho]$ , *i.e.*, a relative measure of the time needed  
143 for a population to converge to a stable equilibrium; 21), and transient potential (transient  
144 envelope  $[TE]$ , *i.e.*, the difference between maximum and minimum population size following  
145 disturbance; 24, 52) from IPMs depicting the dynamics of tropical and subtropical assemblages  
146 of competitive, stress-tolerant, and weedy coral taxa in Japan and Australia (Fig. 1;  
147 Supplementary S1 & S2). Furthermore, we quantified the exposure of these assemblages to  
148 thermal variability using three measures of local SST regimes: monthly mean SST ( $\bar{x}_{sst}$ ),  
149 monthly SST variance ( $cv_{sst}$ ), and monthly SST frequency spectrum ( $\beta_{sst}$ ; Supplementary S3).

150 Notably, the coral assemblages exposed to more variable thermal conditions display  
151 enhanced transient potential. Our partial least squares regression explains 92.17% of the  
152 variance in the three measures of thermal exposure ( $\bar{x}_{sst}$ ,  $cv_{sst}$ , and  $\beta_{sst}$ ), whilst also capturing  
153 37.43% of the variance in long-term performance ( $\lambda$ ), demographic recovery ( $\rho$ ), and transient

154 potential ( $TE$ ; Fig. 2,  $r_{[y]}^2$ ). The first partial least squares regression component reflects a  
155 gradient in SST variability, capturing 60.97% of the variance in thermal conditions experienced  
156 by our examined coral assemblages. It is along this component that divergent patterns within  
157 estimates of  $\lambda$  and  $TE$  are most pronounced. Subsequently, estimates of  $TE$  are positively  
158 correlated with the measures of thermal variability ( $cv_{sst}$ ) and frequency spectrum ( $\beta_{sst}$ ), whilst  
159 higher  $\lambda$  estimates associate with warmer mean monthly SSTs ( $\bar{x}_{sst}$ ; Fig. 2). Meanwhile,  
160 damping ratio ( $\rho$ ) estimates are aligned with the second partial least squares regression  
161 component describing secondary patterns in the mean SST ( $\bar{x}_{sst}$ ) and frequency ( $\beta_{sst}$ ) variables.  
162 Enhanced transient potential is thought to buffer the performance of populations in response to  
163 elevated abiotic variability, thereby underpinning their capacity to exploit more variable  
164 environments (35, 53). However, variation in transient potential across the assemblages of  
165 differing coral taxa, in response to increased thermal variability (Fig. 3), suggests that exposure  
166 to abiotic variability alone does not assure resilience towards future climatic variability.

167         The trade-off between long-term performance and transient potential does not manifest  
168 consistently across the examined tropical and subtropical coral assemblages (Fig. 3A & Table  
169 1), with inter-specific variation mediated instead by characteristics of population turnover (Fig.  
170 3B & C). We explore inter-assemblage variation across estimates of long-term performance  
171 and transient population growth potential. Again, we quantified long-term performance using  
172  $\lambda$ , whilst the *demographic stability index* ( $DSI$ ) calculated from our IPMs provided a measure  
173 of transient growth potential. A three-way ANOVA reveals significant interactions between  
174 the three factors of assemblage classification (competitive, stress-Tolerant or weedy),  
175 ecoregion (tropical vs. subtropical), and country (Australia vs. Japan; ANOVA $_{\lambda}$ :  $F_{2,11562} =$   
176  $5698.47$ ,  $p < 0.001$ ; ANOVA $_{DSI}$ :  $F_{2,11581} = 589.8$ ,  $p < 0.001$ ). Despite this, the tropical  
177 assemblages routinely possess higher estimates of  $\lambda$  relative to their corresponding subtropical  
178 counterparts (Tukey:  $p < 0.001$  in all cases; Table 1). The one exception were weedy corals in

179 Japan, where  $\lambda$  is highest in the subtropics ( $\lambda_{[t]} = 0.760$  [95% CI: 0.750, 0.770],  $\lambda_{[s]} = 0.807$   
180 [0.802, 0.812];  $p < 0.001$ ). Alternatively, the subtropical coral assemblages typically possess a  
181 greater capacity for amplifying population growth following a disturbance than the tropical  
182 assemblages (Fig. 3A). However, this pattern is not consistent across life history strategies,  
183 with competitive assemblages exhibiting the opposite trend in Australia ( $p < 0.001$ ), and no  
184 variation in Japan ( $p = 0.999$ ).

185 The long-term performance and transient potential of the coral assemblages  
186 corresponds with patterns in their generation time (Fig. 3B & C). To further evaluate the drivers  
187 mediating coral population performance within variable environments we used Type 2 linear  
188 regression (54) to explore the relationship between estimates of generation time ( $T$ , *i.e.*, the  
189 time needed for individuals of a population to be replaced; 55), long-term performance ( $\lambda$ ), and  
190 transient potential ( $TE$ ) calculated from our IPMs. Generation time is a strong predictor of long-  
191 term population growth rate ( $r^2 = 0.704$ ), with long-term performance increasing with  
192 generation time (Fig. 3B). Conversely, longer generation times are associated with reduced  
193 transient potential (Fig. 3C;  $r^2 = 0.409$ ). Hence, our observed trade-off between long-term  
194 performance and transient potential, in response to thermal variability, manifests inconsistently  
195 across our examined tropical and subtropical coral assemblages, due to variation in their  
196 characteristics of temporal population turnover.

### 197 *Transient buffering in variable environments*

198 Principally, a trade-off between long-term performance and transient potential implies that  
199 long-term performance does not predict the capacity for populations to endure repeated  
200 disturbances. Simultaneously, however, it also suggests that whilst enhanced transient potential  
201 may enable natural populations to persist within variable environments, it comes at a cost to  
202 their long-term performance. Historically, variability in population growth rate was thought to



203 diminish individual fitness (56), thus hindering the persistence of populations (57). This  
204 understanding formed the basis of the demographic buffering hypothesis, whereby populations  
205 can minimise the influence of environmental variability on their long-term performance by  
206 limiting temporal variability in crucial vital rates (e.g., survival, development and reproduction;  
207 58). Thus, variable environments were assumed to select for populations with the ability to  
208 buffer key vital rates, thereby reducing temporal variation in performance characteristics (56,  
209 58, 59). More recently, however, enhanced transient potential has been presented as an adaptive  
210 mechanism that allows populations to exploit regions with high environmental variability (35).  
211 Indeed, Ellis & Crone (53) demonstrated how increased transient potential can buffer the  
212 effects of stochastic conditions on population growth rates, an effect that was increasingly  
213 evident in populations possessing lower  $\lambda$  estimates. Thus, it is not unexpected, that coral  
214 assemblages established within variable environments, would possess enhanced transient  
215 potential (Fig. 2). Yet, if the vital rate schedules of these assemblages have indeed evolved  
216 specifically to maximise their short-term performance, this would likely carry an energetic cost  
217 to their long-term performance characteristics.

218         Our finding that transient potential is greatest in coral assemblages displaying reduced  
219 long-term performance contrasts with previous work on mammals and plants showing a  
220 positive association between population growth rates and transient potential (e.g., 60, 61).  
221 Faster population growth rates are assumed of populations characterised by faster individual  
222 development and high fecundity (62), with these populations also expected to exhibit greater  
223 variability in size following disturbances (61). Whilst it is concerning that each of our surveyed  
224 assemblages are in, or close to, a state of long-term decline ( $\lambda < 1$ ; Table 1), projected long-  
225 term performance is greatest in the tropical assemblages which also typically display lower  
226 transient amplification in population growth (Fig. 3A). These findings agree with evidence that  
227 transient potential is mediated by population turnover. Populations exhibiting longer

228 generation times typically display reduced temporal variability in size corresponding with the  
229 fact that higher individual survival reduces the need to counteract disturbances (60); a pattern  
230 that we show to be evident in our examined coral assemblages (Fig. 3C). Accordingly, our  
231 observation that long-term performance is positively correlated with generation time in coral  
232 populations (Fig. 3B), perhaps presents a more intriguing result. Although, with the long- and  
233 short-term performance characteristics of coral assemblages corresponding with their relative  
234 exposure to thermal variability (Fig. 2), this finding further implies that trading off long-term  
235 performance for transient potential is an adaptive characteristic in coral populations.

### 236 *Forecasting community reassembly*

237 Here we show that stress-tolerant and weedy coral taxa possess more pronounced transient  
238 amplification, highlighting a potential mechanism supporting their persistence at higher  
239 latitudes. Using a subset of the dataset presented here, Cant *et al.* (36) recently demonstrated  
240 how short-term increases in population growth following disturbance could support the  
241 establishment of a subtropical coral assemblage of competitive *Acropora* spp. in southern  
242 Japan. However, subtropical-tropical variation in the amplification capacity of competitive  
243 coral assemblages appears minimal in comparison to the variation we observe across the stress-  
244 tolerant and weedy assemblages in both Australia and Japan (Fig. 3A). Weedy corals comprise  
245 species that exhibit small colony sizes, fast growth rates, and internal fertilisation, producing  
246 larvae that settle quickly after release (47, 63). Together, these strategies support faster  
247 population turnover, enabling weedy coral species to proliferate within highly disturbed  
248 environments (64). Conversely, stress-tolerant corals display slower growth rates, longer life  
249 expectancies, high fecundity, and broadcast spawning strategies (47, 65). The larger, more  
250 robust, morphologies associated with stress-tolerant coral taxa maximise energy storage,  
251 promoting their persistence within challenging environments (66). Meanwhile, longer lifespans  
252 and elevated fecundity allow stress-tolerant corals to endure abiotic variation by taking

253 advantage of sporadic improvements in local conditions (47). Consequently, our findings  
254 support existing projections that weedy and stress-tolerant coral taxa are likely to become  
255 increasingly prevalent throughout disturbed coral communities (67, 68). However, these  
256 projections herald the future loss of the structural complexity considered essential to the  
257 functioning of reef ecosystems (69).

258         Crucially, our findings do not reflect the current reality for many coral assemblages  
259 within regions of high environmental variability, suggesting that the composition of coral  
260 communities is not solely mediated by the interplay between transient dynamics and abiotic  
261 variability. Despite the lower amplificatory capacity we report for subtropical competitive  
262 corals compared to the subtropical weedy and stress-tolerant assemblages, competitive coral  
263 taxa dominate many subtropical coral assemblages (70–72). Utilising fast growth strategies,  
264 colonies of competitive coral taxa are capable of rapidly colonising available substrate, quickly  
265 outcompeting heterospecific colonies for both space and light (47). Whilst this competitive  
266 nature perhaps explains the enhanced amplificatory capacity of the tropical competitive  
267 assemblages relative to the tropical stress-tolerant and weedy assemblages (Fig. 3A), the  
268 sensitivity of many competitive coral taxa to environmental change means that these  
269 assemblages are often regarded as early successional, dominating only within optimal  
270 environments and receding as reef ecosystems approach climax states (73, 74). Within  
271 subtropical environments, however, coral community composition is mediated by  
272 environmental pressures and dispersal barriers that filter the occurrence of species according  
273 to their trait characteristics (46, 75). As a result, subtropical coral assemblages typically consist  
274 of a subset of tropical species found on tropical coral reefs (46), as well as subtropical  
275 specialists and endemics. The dominance of competitive coral taxa within subtropical coral  
276 assemblages, despite their reduced transient performance relative to other coral taxa, therefore,  
277 implies that competitive interactions profoundly influence the performance of coral

278 populations (76, 77). Certainly, further investigation into the influence of competitive  
279 interactions on the transient dynamics of coral populations is needed to disentangle how the  
280 dynamics of coexistence between coral populations facilitate their persistence within variable  
281 environments.

## 282 *Conclusions*

283 Limitations in our understanding for the abiotic determinants driving the dynamics of coral  
284 assemblages inhibits our capacity to forecast their future performance and, therefore, manage  
285 global coral community reassembly (78–80). Here, we demonstrate how coral assemblages  
286 within regions of high environmental variability exhibit demographic strategies associated with  
287 enhanced transient potential, but at a cost to their long-term performance (Fig. 2). Climatic  
288 change is exposing coral communities worldwide to increased abiotic variability. Crucially,  
289 our findings here emphasize that whilst coral assemblages can adopt demographic strategies to  
290 enhance their viability when exposed to abiotic variability, the winners and losers within future,  
291 more variable environments cannot be predicted from existing measures of long-term  
292 performance. However, the relationship that we observed between transient potential and  
293 thermal variability was not universal across coral taxa, nor did it manifest identically across  
294 hemispheres. Subtle patterns in the association between population dynamics and their climate  
295 drivers hinder predictions of the consequences of environmental change within biological  
296 communities (81). Nevertheless, relative to competitive coral taxa, weedy and stress-tolerant  
297 corals appear to possess a greater capacity for enduring within environments characterised by  
298 repeated abiotic disturbances. Yet, competitive coral taxa are often associated with more  
299 complex morphologies and therefore support the structural complexity critical to the wider  
300 functioning of coral associated ecosystems (69). Accordingly, future increases in abiotic  
301 variability threaten the viability of coral associated ecosystems.

## 302 **Methods**

### 303 *Modelling population dynamics*

304 Integral Projection Models (IPMs) capture the influences of the state composition of  
305 individuals on the performance of populations over discrete time periods ( $t$  to  $t+1$ ; 51). Here,  
306 to quantify the long-term performance characteristics and transient (*i.e.*, short-term) potential  
307 of coral populations, we used IPMs describing patterns in colony survival ( $\sigma$ ), transitions in  
308 size (growth and shrinkage,  $\gamma$ ), fragmentation probability ( $\kappa$ ), fecundity ( $\varphi$ ), and recruitment  
309 ( $\phi$ ), each as a function of colony size ( $z$ ; visible horizontal surface area,  $\text{cm}^2$ ). Specifically, our  
310 IPMs took the form

$$311 \quad n[z', t + 1] = \int_L^U (P_{z'z} + F_{z'z} n[z, t]) \delta z \quad (1)$$

$$312 \quad P_{z'z} = (1 - \kappa_z) \sigma_z \gamma_{z'z} + (\kappa_z \kappa_b z \kappa_z^0) \quad (2)$$

$$313 \quad F_{z'z} = \varphi_z \phi C_0 \quad (3)$$

314 with  $[L, U]$  representing the range of possible colony sizes; calculated as 10% above and below  
315 observed maximum and minimum colony sizes to avoid accidental exclusion (82).  
316 Accordingly, the structure of a population at time  $t+1$  ( $n[z', t+1]$ ) is a product of its structure  
317 at time  $t$  ( $n[z, t]$ ) subject to the survival ( $\sigma_z$ ) and transition of individual colonies from size  $z$   
318 to size  $z'$  ( $\gamma_{z'z}$ ); the probability of colony fragmentation ( $\kappa_z$ ) and the number ( $\kappa_b z$ ) and size  
319 distribution of any colony remnants produced ( $\kappa_z^0$ ); and colony fecundity ( $\varphi_z$ ) combined with  
320 the probability of successful recruitment ( $\phi$ ) and the size distribution of surviving recruits ( $C_0$ ).

### 321 *Data Collection*

322 We parameterised our IPMs using data collected during repeated annual surveys of 3171 tagged  
323 colonies within tropical and subtropical coral communities in southern Japan and eastern  
324 Australia, conducted between 2016 and 2019 (Fig. 1; Supplementary S1). We tagged individual

325 colonies using permanent plots arranged haphazardly throughout four focal coral communities  
326 (Australian subtropics [AS], Australian tropics [AT], Japanese subtropics [JS], Japanese  
327 tropics [JT]) and demarcated with numbered tags (36, 68). All tagged colonies were identified  
328 *in situ* to the lowest possible taxonomic level (either genus or species). No samples were taken  
329 from tagged colonies, as although this would have allowed us to resolve species identity, we  
330 wanted to avoid any lasting interference with the processes of colony survival, growth, and  
331 fragmentation.

332 To facilitate comparing population characteristics observed across spatially distinct  
333 regions in Australia and Japan with varying degrees of species overlap (83), we grouped tagged  
334 colonies across each region according to shared life-history-strategies (*sensu* 47–49), primarily  
335 delineated based on their morphology, growth rate and reproductive mode (47). Specifically,  
336 we categorised colonies as ‘competitive’, ‘weedy’, ‘stress-tolerant’ or ‘generalist’ following  
337 the genera classifications of Darling *et al.* (47), with minor adaptations made based on local  
338 expertise (see supplementary S2 for a detailed list). In the event that genera represented species  
339 classified across different categories (19 cases), we randomly assigned individuals across the  
340 relevant categories in proportion with the number of species within each category known to  
341 occur in the area (*sensu* 49). Following the pooling of colonies according to their life-history-  
342 strategies, we omitted all individuals defined as generalists from subsequent analyses due to  
343 their limited representation across our regional samples ( $n$ : AS = 22 colonies; AT = 31; JS =  
344 17; JT = 65). Consequently, we constructed IPMs concerning the dynamics of 12 coral  
345 assemblages corresponding with competitive, stress-tolerant, and weedy coral taxa across four  
346 geographical locations (Fig. 1).

347 Photographs capturing the visible horizontal extent of tagged colonies were used to  
348 follow individuals over successive surveys and obtain longitudinal records of colony surface  
349 area ( $\text{cm}^2$ ; transformed to a  $\log_{10}$  scale) over time. Using generalised linear mixed models

350 (GLMMs), we estimated size-specific patterns in colony survival ( $\sigma$ ), transitions in size ( $\gamma$ ),  
351 and fragmentation probability ( $\kappa$ ) for each population (Supplementary S1). In each case, our  
352 GLMMs included random effects (colony identity and survey location) to account for any  
353 autocorrelation between observations and within-subject variability associated with our  
354 pooling of data recorded from individuals followed across multiple years, and at different sites.  
355 Colony survival ( $\sigma$ ) reflected the continued presence of tagged individuals across survey  
356 intervals ( $t$  to  $t+1$ ) and was modelled as a logistic function of colony surface area at time  $t$ .  
357 Colony size transitions ( $\gamma$ ), representing both growth through colony extension, and shrinkage  
358 through partial mortality (84), were modelled using the polynomial relationship between initial  
359 colony surface area at time  $t$  and subsequent surface area at time  $t+1$ . Colony fragmentation  
360 probability ( $\kappa$ ) was then modelled as a polynomial logistic function of colony size at time  $t$ .  
361 During our surveys, we recorded fragmentation in the event of observed colony breakage,  
362 recording the size (surface area,  $\text{cm}^2$ ) of all remnants produced in each case. Subsequently, we  
363 also modelled the number ( $\kappa b_z$ ) and size ( $\kappa_z^0$ ) of remnant colonies produced during  
364 fragmentation as a function of colony size at time  $t$ , using Poisson and polynomial GLMMs,  
365 respectively.

366         Alongside our surveys of tagged individual colonies, we also monitored colony  
367 recruitment within our permanent coral plots. During each annual survey, we recorded the  
368 number and size of new colonies appearing within each plot. These recruitment counts enabled  
369 us to quantify annual and regional variability in recruit densities (Table S2), as well as estimate  
370 population-specific recruit size distributions ( $C_0$ ; Supplementary S1). However, prior to  
371 parameterising recruitment dynamics within our IPMs, we determined patterns in colony  
372 fecundity ( $\varphi$ ). This approach was necessary because evaluating population performance  
373 requires an explicit consideration of fecundity to link the dynamics of existing individuals with  
374 the introduction of new, genetically distinct individuals (21). Using data relating colony size

375 and larval output (larval density,  $\text{cm}^3$ ) extracted from the Coral Trait Database (85, 86), we  
376 calculated colony fecundity ( $\phi$ ) as the polynomial relationship between colony size at  $t$  and  
377 expected larval output (Supplementary S1). Next, to ensure our modelled recruitment dynamics  
378 accurately reflected our empirical observations we parameterised a recruit survival function ( $\phi$ )  
379 within our IPMs. Here, recruit survival ( $\phi$ ) serves as a probability function converting expected  
380 larval output into a proportional contribution of observed recruit counts as a function of colony  
381 size, which we calculated by dividing total expected larval output in any given year by the  
382 corresponding annual recruitment count (Supplementary S1, *sensu* 68, 87).

### 383 *Quantifying population characteristics*

384 From our IPMs, we obtained estimates of long-term performance (asymptotic population  
385 growth,  $\lambda$ ), generation time ( $T$ ), and transient potential (damping ratio [ $\rho$ ], maximal  
386 amplification [ $\bar{\rho}_{max}$ ] & transient envelope [ $TE$ ]) for each tropical and subtropical coral  
387 assemblage (21, 24, 52, 55, 88). Estimates of  $\lambda$  are typically used as a measure of long-term  
388 population viability (22), and reflect whether a population is expected to grow ( $\lambda > 1$ ) or decline  
389 ( $\lambda < 1$ ) when at stationary equilibrium (21). Generation time is a measure of population  
390 turnover, describing the time needed for individuals of a population to be replaced (55).  
391 Alternatively, the measures of transient potential describe the expected characteristics of  
392 populations following their displacement from stationary equilibrium due to disturbances. The  
393 damping ratio constitutes a measure of demographic recovery (52, 89), describing the rate at  
394 which a population perturbed from its stationary equilibrium converges back to its asymptotic  
395 growth trajectory (21). Meanwhile, maximal amplification quantifies the greatest increase in  
396 population size following a disturbance, relative to its asymptotic growth trajectory (24, 88).  
397 Finally, the transient envelope quantifies the magnitude by which the transient dynamics of a  
398 population deviates from its long-term trajectory (52).



399 To calculate the aforementioned demographic characteristics, we discretised our IPMs  
400 into large matrices. We attained these matrices by applying the ‘midpoint rule’ to integrate  
401 each IPM into a high-dimension matrix (200×200 cells), with the probability of transitioning  
402 from one cell to the next approximated at the cell midpoint and multiplied by the cell width as  
403 per (90). Estimates of  $\lambda$  were then identified as the dominant eigenvalue of each discretised  
404 matrix, whilst we estimated damping ratios as the ratio between the subdominant and dominant  
405 eigenvalues. With the *R* package *Rage* (91) we then calculated generation time using estimates  
406 of net reproductive rate ( $R_0$ ) and  $\lambda$  obtained from each matrix,

$$407 \quad T = \log(R_0) - \log(\lambda). \quad (4)$$

408 Next, we determined the transient envelope of each assemblage using their associated Kreiss  
409 bounds of amplification ( $\overline{K}_\lambda^*$ ) and attenuation ( $\underline{K}_\lambda^*$ ),

$$410 \quad TE = \overline{K}_\lambda^* - \underline{K}_\lambda^*. \quad (5)$$

411 Respectively, the Kreiss bounds of amplification and attenuation reflect the largest and smallest  
412 expected long-term density of a population following the dissipation of transient conditions,  
413 relative to its asymptotic growth trajectory (92–94). We acknowledge here that this definition  
414 is more commonly applied to measures of population inertia (24), which are more typically  
415 used in estimating transient envelopes (52). However, Kreiss bound estimates have been  
416 demonstrated to align with corresponding estimates of population inertia and, unlike estimates  
417 of population inertia, are not sensitive to imprimitive population models (*i.e.*, non-negative  
418 models permitting transitions between all state classes, but with transitions between certain  
419 stages occurring only at periodic intervals; 21, 24); hence their selection here. We derived these  
420 Kreiss bounds, alongside estimates of maximal amplification, using their corresponding  
421 functions in the *R* package *popdemo* (95).

422 Across each demographic measure, we determined the variance in our assemblage-  
423 specific estimates through Jack-knife resampling. During resampling, we generated 1,000 IPM  
424 variants for each assemblage, each time using 95% of our original data sample without  
425 replacement, whilst permitting recruit survival probabilities ( $\phi$ ) to vary within observed limits.  
426 Finally, prior to their inclusion in further analyses, the jack-knifed distributions of the  $\lambda$ ,  
427 generation time, transient envelope, and maximal amplification variables required  
428 transforming to ensure approximate normality. We omitted 26 variants for which  $\lambda > 2$ , as these  
429 presented unrealistic illustrations of population performance (*i.e.*, more than doubling  
430 population size every year), before applying a log transformation to the generation time  
431 variable and a power transformation ( $y^x$ ) across the damping ratio ( $y^{-2.0}$ ), transient envelope ( $y^{-$   
432  $0.1$ ) and maximal amplification variables ( $y^{-0.5}$ ).

#### 433 *Evaluating spatial trends in population characteristics*

434 To test for patterns in the spatial variation of long-term performance and transient potential  
435 across tropical and subtropical coral assemblages, we utilised partial least squares regression,  
436 ANOVA, and Type 2 linear regression. Initially, we applied a partial least squares regression  
437 to test whether trade-offs between the long-term performance characteristics and transient  
438 potential of coral assemblages align with their exposure to abiotic variability. Partial least  
439 squares regression quantifies the association between multiple predictor variables and one or  
440 more dependant variables (96). Subsequently, using this technique we simultaneously  
441 evaluated the relationships between mean estimates of  $\lambda$ , damping ratio, and transient envelope  
442 obtained for each assemblage, and their correlation with patterns in thermal conditions to  
443 provide an insight into the demographic trade-offs of coral assemblages and their mechanistic  
444 drivers.

445 To evaluate how abiotic variability mediates the trade-off between the short- and long-  
446 term performance characteristics of coral assemblages, within our partial least squares  
447 regression we quantified the abiotic conditions experienced by each coral assemblage using  
448 three measures of local sea surface temperature (SST) regimes: mean monthly SST ( $\bar{x}_{sst}$ ),  
449 monthly SST variance ( $cv_{sst}$ ), and monthly SST frequency spectrum ( $\beta_{sst}$ ; Supplementary S3).  
450 Focusing on the four geographical regions in which our focal coral assemblages were surveyed  
451 (GPS: AS = -30.3°, 153.1°; AT = -23.4°, 151.9°; JS = 32.8°, 132.6°; JT = 26.5°, 128.1°; Fig.  
452 1), we extracted high resolution monthly SST readings (°C; overlaid on a 1° latitude-longitude  
453 grid) taken between January 1950 and December 2019, inclusive, from the HadISST dataset  
454 (97). Arranging these SST records into 69-year timeseries for each location, we then calculated  
455 the mean ( $\bar{x}_{sst}$ ) and coefficient of variance ( $cv_{sst}$ ) for each timeseries. Next, we estimated the  
456 frequency spectrum of each time series. Spectral analysis is used to quantify the periodicity of  
457 recurrent variability within a timeseries, with higher frequencies associated with shorter-term  
458 fluctuations (98). The frequency spectrum of a time series is represented by its spectral  
459 exponent ( $\beta$ ) and equal to the negative slope between its log spectral density and log frequency  
460 (99), which we calculated using the package *stats* (100). After testing these abiotic predictor  
461 variables for collinearity (Supplementary S3), we performed our partial least square regression  
462 analyses using the *R* package *plsdepot* (101).

463 Next, we assessed how patterns in the long-term performance, and capacity for coral  
464 assemblages to benefit from recurrent disturbance vary between tropical and subtropical  
465 regions, and how this variation manifests across coral taxa. Using a three-way ANOVA, we  
466 separately investigated variation in estimates of  $\lambda$  and maximal amplification across the three  
467 factors of country (Australia vs. Japan), ecoregion (tropical vs. subtropical), and assemblage  
468 classification (competitive, stress-tolerant or weedy). With maximal amplification estimates  
469 inverted during transformation, larger values subsequently reflect reduced amplification

470 potential. For the purposes of clarity in this analysis, we will henceforth refer to this reversed  
471 scale as a *demographic stability index (DSI)*, with lower values corresponding with enhanced  
472 amplification. Finally, we evaluated drivers of long- and short-term performance, by using  
473 Type 2 linear regression to separately evaluate the relationship between generation time ( $T$ )  
474 and estimates of  $\lambda$  and transient envelope ( $TE$ ). Type 2 linear regression is an approach for  
475 quantifying the relationship between two non-independent variables, such that both variables  
476 include an element of error (54). Here, due to differences in the magnitude of the variance ( $\sigma^2$ )  
477 across our variables of generation time,  $\lambda$ , and transient envelope ( $\sigma^2$ :  $T = 1.139$ ;  $\lambda = 0.009$ ;  $TE$   
478  $= 0.016$ ) we performed a Ranged Major Axis regression using the *R* package *lmodel2* (102).

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## 746 **Tables and Figures**

747 **Figure 1. Using repeated annual surveys of tagged individual colonies, conducted between**  
748 **2016 and 2019, we quantified the influence of environmental variability on the long-term**  
749 **performance and transient potential of tropical and subtropical coral populations in**  
750 **southern Japan and eastern Australia. (A)** As climate shifts induce range expansions in  
751 many coral species worldwide, their populations are increasingly exposed to a gradient in  
752 thermal regimes, illustrated here by mean monthly sea surface temperatures ( $\bar{x}_{sst}$ ; °C) recorded  
753 between 1950 and 2019 (97). **(B)** To explore spatial patterns in the long-term performance and  
754 transient (short-term) potential of coral populations exposed to varying thermal regimes, we  
755 constructed Integral Projection Models (IPMs) describing the dynamics of tropical and  
756 subtropical assemblages of competitive, stress-tolerant, and weedy coral taxa. To parameterise



757 these models, between 2016 and 2019 we documented the survival, growth, fragmentation, and  
758 recruitment patterns of 3171 tagged individual colonies within the tropical reef communities  
759 (▲) of Okinawa (Japan) and Heron Island (Australia), and within the subtropical coral  
760 communities (●) of Kochi (Japan) and the Solitary Islands Marine Park (Australia).

761

762 **Figure 2. A trade-off exists between long-term performance and transient potential across**  
763 **our examined coral populations, corresponding with their relative exposure to thermal**  
764 **variability.** Partial least squares regression score plot illustrating the association between  
765 thermal conditions, and the long-term performance ( $\lambda$ ) and transient potential (transient  
766 envelope [TE] & damping ratio [ $\rho$ ]) of tropical (▲) and subtropical (●) populations of  
767 competitive (blue), stress-tolerant (yellow), and weedy (red) coral taxa. To quantify the thermal  
768 conditions experienced by each coral population, we used sea surface temperatures (SST)  
769 recorded between 1950 and 2019 to calculate regional estimates of mean monthly SST ( $\bar{x}_{sst}$ ),  
770 monthly SST variance ( $cv_{sst}$ ), and monthly SST frequency spectrum ( $\beta_{sst}$ ). Component scores  
771 illustrate the relative degree of variance explained in the thermal predictor variables, whilst  $r^2_{[y]}$   
772 reflects the cumulative variance explained across the demographic characteristics. The shaded  
773 polygons reflect the clustering of tropical and subtropical populations, whilst the dotted lines  
774 delineate regions of association to facilitate the visualisation of patterns in correlation between  
775 the abiotic and demographic variables.

776 **Figure 3. Inter-specific variation within the trade-off observed between long-term**  
777 **performance and transient potential across tropical and subtropical correlates with**  
778 **patterns in population turnover rate (A)** Interaction plot showcasing how estimates of  
779 demographic stability index (DSI) vary between associated tropical (▲) and subtropical (●)  
780 populations of competitive (blue), stress-tolerant (yellow), and weedy (red) coral taxa in

781 Australia and Japan. We present DSI, as an inverse measure of maximal amplification ( $\bar{\rho}_{max}$ ),  
782 describing the ability for populations to undergo elevated growth following disturbance. Thus,  
783 lower DSI estimates correspond with enhanced amplification capacity. We also applied Type  
784 2 linear regression to separately explore the association of population turnover characteristics  
785 with **(B)** long-term performance (asymptotic population growth rate;  $\lambda$ ), and **(C)** transient  
786 potential (transient envelope, *TE*) across tropical and subtropical populations of competitive,  
787 stress-tolerant, and weedy coral taxa in Australia and Japan. We note here that transient  
788 envelope estimates were reversed during transformation to achieve normality, thus higher  
789 values reflected diminished transient potential. We have therefore displayed transient potential  
790 on a reversed scale to facilitate comparisons with patterns in long-term performance ( $\lambda$ ). We  
791 used generation time (displayed here on the log scale) as a measure of population turnover rate,  
792 with higher estimates reflecting slower rates of population turnover. Across panels B and C  $r^2$   
793 values are provided as measure of model fit. Across all panels error is displayed using 95% CI.

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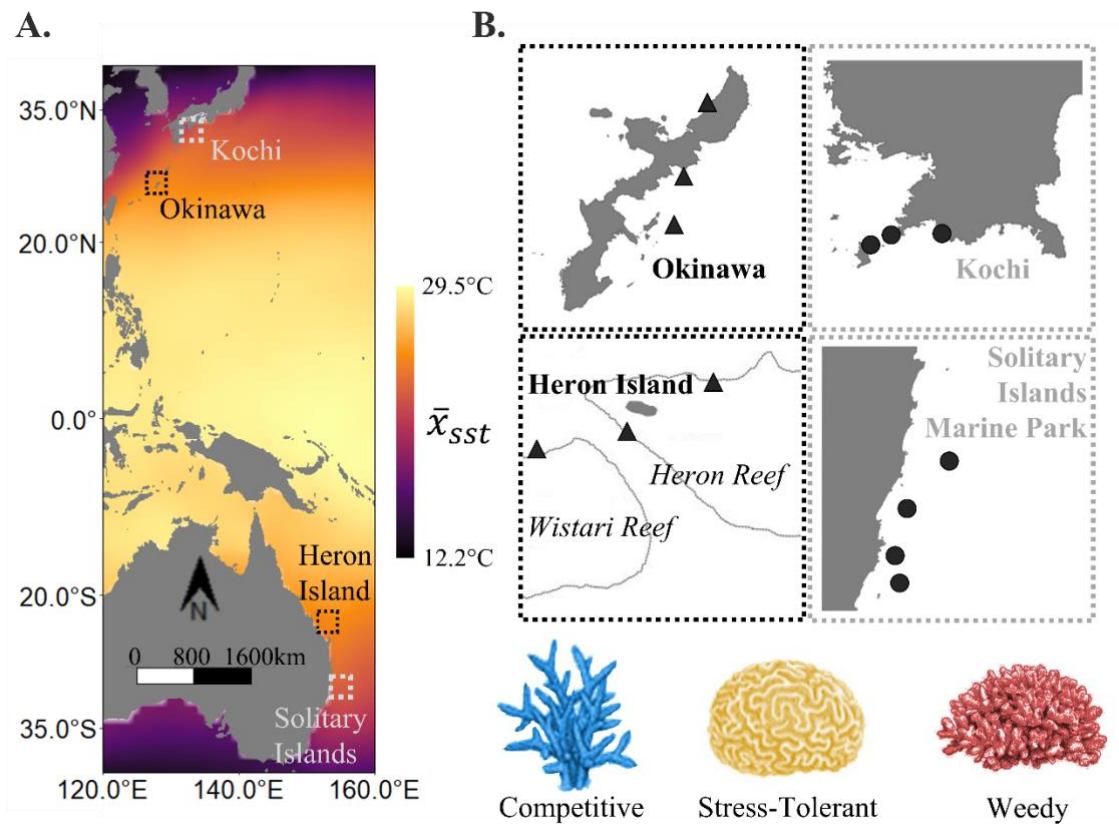
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803 **Figure 1**



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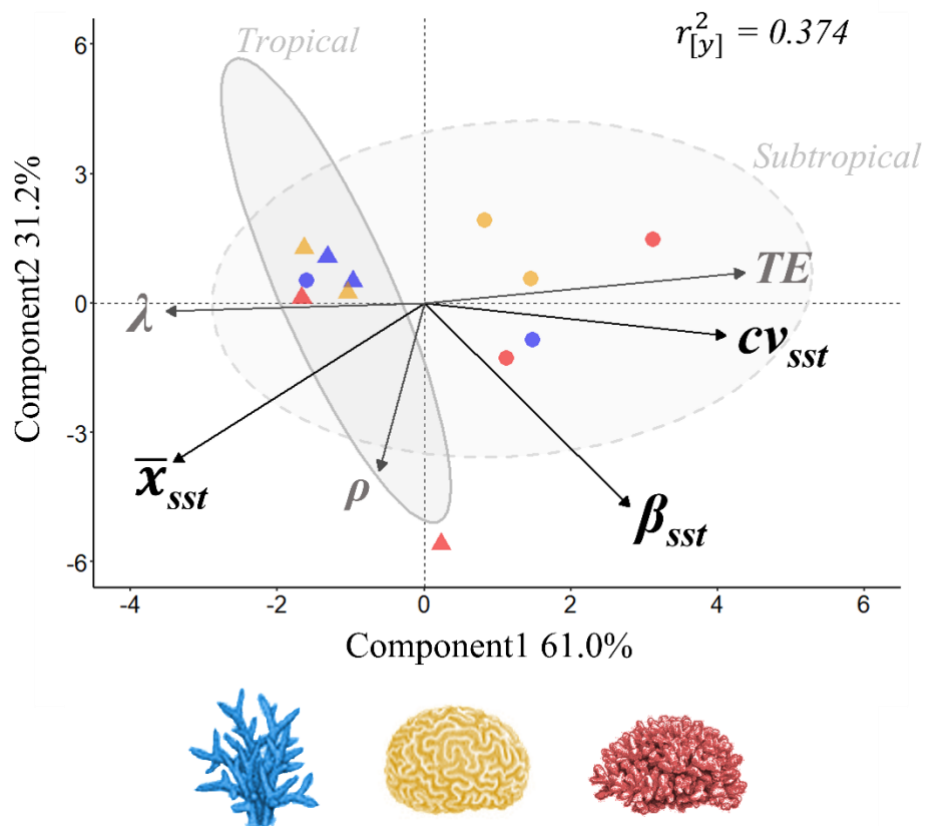
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813 **Figure 2**



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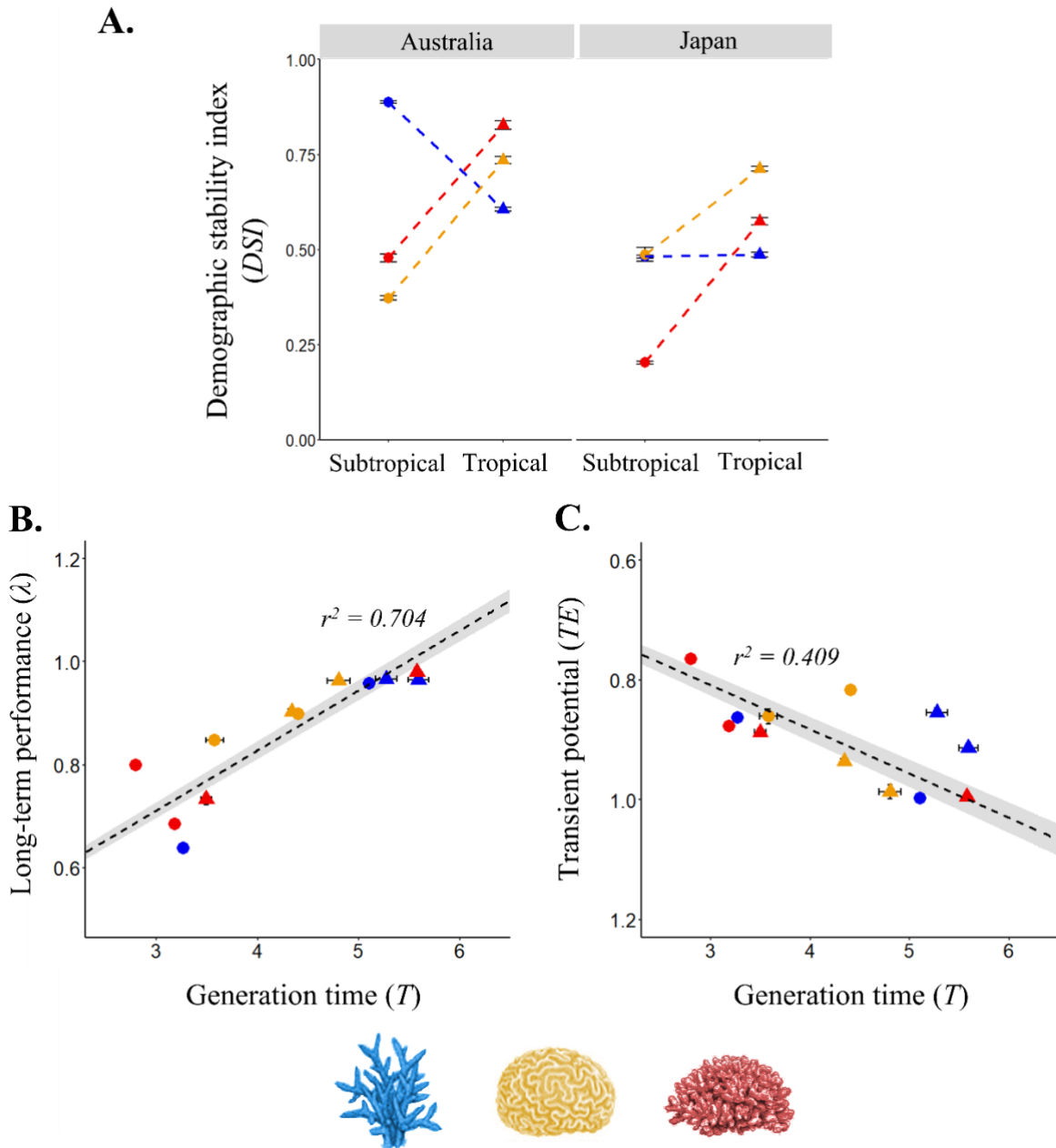
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824 **Figure 3**



830 **Table 1.** Population growth rates ( $\lambda$ ) obtained from corresponding tropical and subtropical  
831 populations of competitive, stress-tolerant, and weedy coral taxa in Australia and Japan.  
832 Shading used to highlight the highest estimate of population growth across each tropical-  
833 subtropical pairing. Error displayed using 95% CI.

834

Country	Life-history group	Tropical	Subtropical
Australia	Competitive	0.983 [0.981, 0.984]	0.958 [0.957, 0.959]
	Stress-tolerant	0.983 [0.980, 0.985]	0.899 [0.898, 0.899]
	Weedy	0.981 [0.980, 0.982]	0.686 [0.684, 0.687]
Japan	Competitive	1.001 [0.999, 1.004]	0.640 [0.639, 0.641]
	Stress-tolerant	0.913 [0.909, 0.917]	0.885 [0.877, 0.894]
	Weedy	0.760 [0.750, 0.770]	0.807 [0.802, 0.812]

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