

1 **Transient demographic approaches can drastically expand the toolbox of** 2 **coral reef science**

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24 **Abstract**

25 Coral communities are threatened by an increasing plethora of abiotic and biotic disturbances.
26 Preventing the ensuing loss of coral coverage and diversity calls for a mechanistic
27 understanding of resilience across coral species and populations that is currently lacking in
28 coral reef science. Assessments into the dynamics of coral populations typically focus on their
29 long-term (*i.e. asymptotic*) characteristics, tacitly assuming stable environments in which
30 populations can attain their long-term characteristics. Instead, we argue that greater focus is
31 needed on investigating the *transient* (*i.e. short-term*) dynamics of coral populations to describe
32 and predict their characteristics and trajectories within unstable environments. Applying
33 transient demographic approaches to the evaluation and forecasting of the responses of coral
34 populations to disturbance holds promise for expediting our capacity to predict and manage the
35 resilience of coral populations, species, and communities.

36

37 **Keywords:**

38 Asymptotic dynamics, Population dynamics, Reef Conservation, Resilience, Short-term
39 characteristics.

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46 **Introduction**

47 Coral populations are sensitive to a range of biotic and abiotic pressures (Riegl 2020), many of
48 which will be exacerbated by future climatic change and human exploitation (Wolff et al. 2018;
49 Riegl and Glynn 2020). The future resilience of coral populations subsequently comprises their
50 capacity for enduring, and recovering from, this increased disturbance (Holling 1973).
51 Accordingly, a resilience-orientated focus is becoming commonplace in reef management
52 (McLeod et al. 2019; McLeod et al. 2021), although this requires the ability for anticipating the
53 responses of coral populations to varying biotic and abiotic regimes (Lam et al. 2020).
54 Appropriately, state-structured demographic models are being increasingly utilised for
55 quantifying the mechanisms supporting or preventing the persistence and revival of disturbed
56 coral communities (e.g. Kayal et al. 2018; Cant et al. 2021). Indeed, understanding how
57 patterns in the survival, size, and reproduction of individual colonies influences population-
58 level characteristics is paramount for effectively managing conservation resources (Riegl et al.
59 2018; Pisapia et al. 2020). However, the contemporary application of state-structured
60 demographic approaches to ascertain the viability of coral populations does not reflect our need
61 to evaluate their resilience.

62 Structured population approaches examine how variation at the level of individuals
63 translates to population-level attributes (Caswell 2001). The state of individuals (typically their
64 size, age, or developmental stage [Caswell 2001]) arbitrates their survival and reproduction,
65 which in turn shape the responses of their population to local biotic and abiotic conditions
66 (Benton et al. 2006). Within natural populations, the diversity of individual-level
67 characteristics can be expressed through the state-structured vital rates of survival, progression
68 (growth & development), retrogression (shrinkage [Salguero-Gómez and Casper 2010] &
69 rejuvenation [Salguero-Gómez et al. 2013]), and reproduction (Metcalf and Pavard 2007).
70 Patterns across these vital rates, and their response to changing population structures,

71 subsequently underpin the characteristics of populations and define their capacity for tolerating
72 various environments (Boyce et al. 2006; Ehrlén et al. 2016). Equally, combined with an
73 explicit consideration for the interaction between multiple populations, structured population
74 analyses also facilitate the exploration of community recovery (Kayal et al. 2018) and
75 coexistence (Adler et al. 2010). Evaluating the vital rates and structure of numerous
76 populations, and their association with abiotic regimes, has thus proven instrumental in
77 calculating the extinction risk of highly threatened populations (Mace et al. 2008), and the
78 management, and conservation of natural communities (Morris and Doak 2002; Jongejans et
79 al. 2008).

80 With many coral communities facing imminent reassembly and population collapse,
81 the demand for an improved understanding of coral population dynamics has never been greater
82 (Edmunds and Riegl 2020). Although limited, the application of demographic theory within
83 coral research is not a novel concept (Edmunds et al. 2014). Veritably, there is a growing
84 appreciation for how the size structure of coral populations influences their dynamics and
85 endurance, with recent appeals for demographic approaches to be concentrated towards
86 gauging the resilience of coral communities (Dietzel et al. 2020; Pisapia et al. 2020; Cant et al.
87 2021; Lachs et al. 2021). However, prevailing knowledge of coral population dynamics centres
88 around isolated patterns in colony survival, changes in size, or recruitment, and long-term
89 (*asymptotic*) population characteristics. Quantifying the asymptotic characteristics of various
90 populations presents a valuable comparative tool for exploring abiotic tolerances (Beissinger
91 and Westphal 1998). Yet, to achieve their asymptotic dynamics, populations typically require
92 stable conditions, which seldom occur naturally, and are becoming increasingly unlikely given
93 current climate projections (Hastings et al. 2018; Francis et al. 2021). Consequently, a focus
94 towards exploring the asymptotic characteristics of populations limits our appreciation of their

95 dynamics within natural environments (Ezard et al. 2010), and will inhibit our capacity to
96 accurately predict the future condition of global coral assemblages.

97 Cyclic abiotic and biotic disturbances (e.g. seasonality in temperature or resource
98 availability) ensure that natural environments rarely exist at a stable equilibrium (Williams et
99 al. 2011). The perpetual instability generated by regular disturbances ensures that natural
100 populations rarely attain their asymptotic trajectories (Hastings 2001; Hastings et al. 2018).
101 Instead, the short-term or *transient* characteristics of populations, which reflect their dynamics
102 within non-equilibrate environments, play a fundamental role in the assembly of biological
103 communities (Hastings 2004). With the transient dynamics of populations defining their
104 performance following disturbance, these characteristics also represent quantifiable measures
105 of population resilience (Capdevila et al. 2020). Globally, coral communities are being exposed
106 to increasingly recurrent disturbance events (Hughes et al. 2018), with various species shifting
107 their distributions poleward or establishing populations within marginal habitats (Beger et al.
108 2014; Camp et al. 2018; Vergés et al. 2019). Here, we discuss why enhancing our capacity for
109 anticipating the future resilience of coral communities requires an understanding of the
110 transient dynamics in their constituent populations.

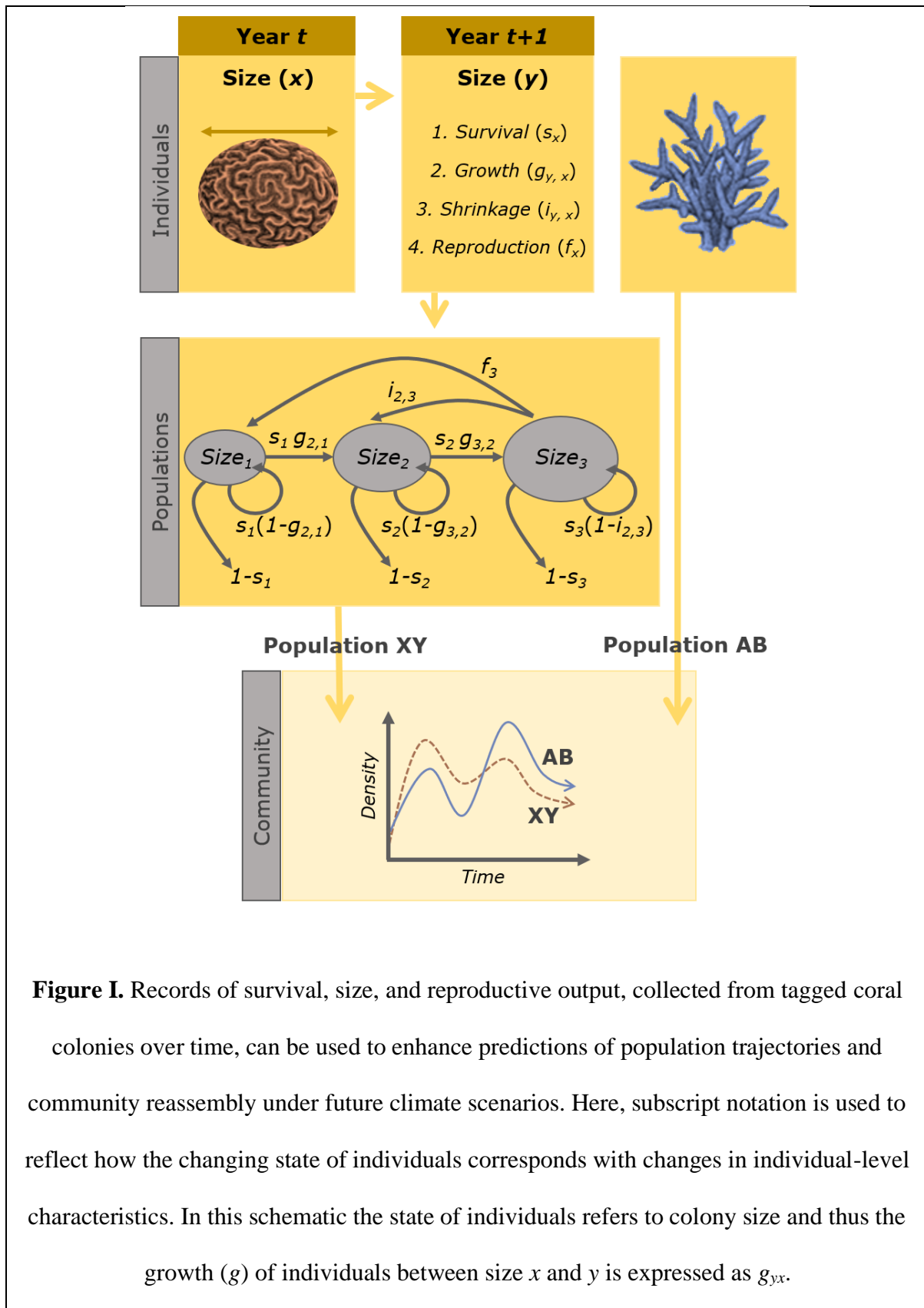
111 **Transient *versus* asymptotic population dynamics**

112 Population dynamics characterise and define the trajectories of populations according to the
113 individual-level allocation of resources towards survival, changes in size (or the state of
114 interest), and reproduction (Box 1). Any population can be structured according to the
115 distribution of its individuals across some state variable, be that age, size, developmental stage,
116 or a combination. The transition of individuals across state classes is, in turn, mediated by
117 selection gradients that emerge from the state-specific patterns of survival and reproduction
118 (Groenendael et al. 1988; van Tienderen 2000). In state-structured demography, patterns across

Box 1: Scaling from individuals to communities.

Following individual corals over time facilitates the calculation of vital rate patterns relating to colony survival, size, and reproduction, and how they govern the characteristics of populations and their wider community interactions (Fig. I). As corals mature and grow, they experience changes in their resource demands, with the capacity of corals for continually meeting these changing demands subsequently influencing their ability to maintain their somatic condition and tolerate local biotic and abiotic stressors (Hughes 1984). The repeated survey of individual colonies allows for documenting how the size of individuals regulates their survival, development, and reproductive contribution over time, and how this is shaped by changing environmental conditions. Condensing these temporal observations from across multiple tagged colonies then allows population ecologists to explore how individual-level vital rates underpin the dynamics of populations.

Crucially, state-structured demographic approaches enable the quantification of the relationship between abiotic conditions and population-level characteristics. Such an understanding is necessary if ecologists are to accurately predict the impact of recurrent disturbances and simulate populations under varying climate scenarios. Similarly, by understanding interactions across the dynamics of various co-occurring populations, and their differential responses to changing conditions, ecologists can better understand the mechanisms driving coexistence (Adler et al. 2010), and predict the transition of coral communities amidst changing climatic conditions (Hughes 1996; Kayal et al. 2018; Cant et al. 2021). Indeed, although more time consuming, demographic approaches transcend the correlative techniques previously used for evaluating the viability of coral populations and communities, and for predicting their resilience to future climatic stressors (Edmunds et al. 2014; Edmunds and Riegl 2020).



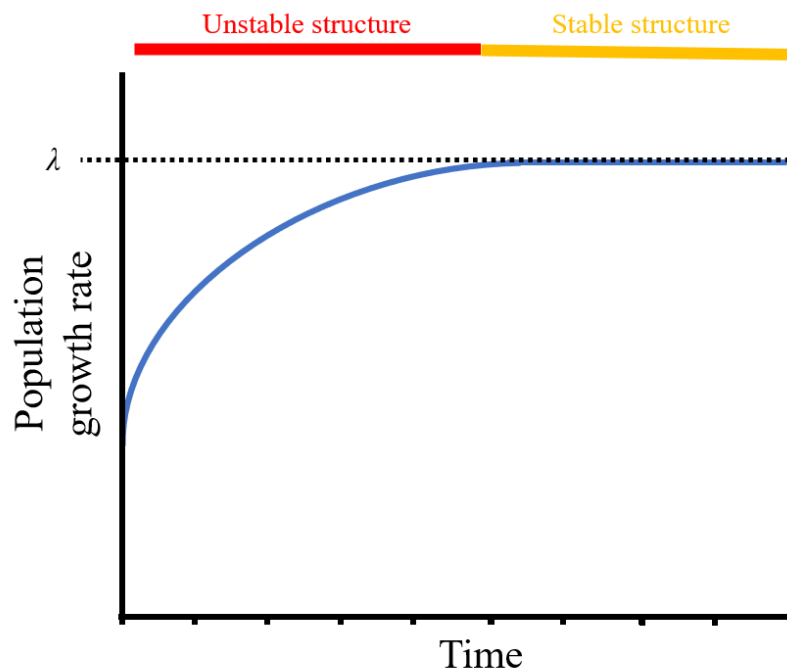
120 these multiple vital rates can subsequently be condensed into a population projection matrix
121 (\mathbf{A}), with each matrix element (a_{ij}) expressing the expected transition of individuals into state
122 class i from state class j during the time interval t to $t+I$, or the per-capita a/sexual contributions
123 of state j individuals into state class i during that same interval (Caswell 2001). This population
124 matrix can then be used to project the size of a population (N , number of individuals) over time,
125 using the change in its state structure (\mathbf{n}):

$$126 \quad N_{t+1} = \sum \mathbf{n}_{t+1} = \sum \mathbf{A} \mathbf{n}_t. \quad (1)$$

127 Within a stable environment, the state structure of a population is expected to converge towards
128 an equilibrium state (Caswell 2001). At equilibrium, the size of a population is then expected
129 to change at a constant rate over time, termed its asymptotic population growth rate (λ , Caswell
130 2001). The value of λ , for any state-structured population, is equal to the dominant eigenvalue
131 of its corresponding population matrix \mathbf{A} . Estimates of λ represent the proportional change in
132 the size of populations over time, and exist on a non-negative scale reflecting population
133 growth ($\lambda > 1$), decline ($\lambda < 1$), or stasis ($\lambda = 1$).

134 Crucially, though, with populations rarely exposed to stable conditions or equilibria,
135 deterministic estimates of λ are unlikely to represent a true reflection of a population's
136 trajectory (Boyce 1992; Beissinger and Westphal 1998). To achieve their asymptotic growth
137 rate populations require a stable population structure, at which their vital rate patterns will
138 maintain a consistent distribution of individuals across state classes over time (Caswell 2001).
139 Yet, for their stable structure to manifest, populations typically require time in a constant
140 environment to allow the state distribution of individuals to convergence towards equilibrium,
141 without displacement by local disturbances (Fig 1; Bierzychudek 1999). Additionally, the vital
142 rate patterns used in constructing population projection matrices are themselves not consistent,
143 and contingent on the environmental conditions in which they are observed (Benton and Grant

144 1996; Boyce et al. 2006). Equally, as populations change in size their dynamics are subject to
145 density–dependant processes that regulate their trajectories within shared environments (Engen
146 et al. 1998; Lande et al. 2003). Thus the dynamics of populations can be expected to vary over
147 time as environmental conditions change (Tuljapurkar and Orzack 1980; Tuljapurkar 1989).



148 **Figure 1.** At stationary equilibrium, populations are expected to change size at a constant
149 rate, termed their asymptotic growth rate (λ). However, to display asymptotic characteristics,
150 populations need a stable state structure and so require time at equilibrium to enable the
151 development of this stable structure. In the absence of a stable state structure, populations
152 will display varying growth rates as they converge towards asymptotic expectations, even
153 within equilibrate environments. Note that, although in this schematic the populations growth
154 rate is increasing towards its asymptotic trajectory, estimates of λ can also reflect asymptotic
155 decline.

156

157 Recurrent perturbations prevent populations from acquiring, or preserving, a stable
158 state structure (Bierzychudek 1999; Williams et al. 2011). Instead, environments persist within

159 a non-equilibrate condition maintaining populations within a transient state during which their
160 trajectories can radically differ from asymptotic expectations (Stott et al. 2010, 2011; Hastings
161 et al. 2018). Accordingly, anticipating the future condition and endurance of populations
162 requires an awareness for their transient characteristics (Box 2; Ezard et al. 2010). Moreover,
163 with the transient characteristics of populations reflecting their response to disturbance and
164 instability, they represent quantifiable measures of population resilience (Capdevila et al.
165 2020). Transient shifts in the state structure of populations can elevate (*amplification*) or
166 diminish (*attenuation*) their growth rates relative to asymptotic projections (Townley et al.
167 2007). Equally, for populations existing in a transient state, there is a natural tendency for their
168 state structure to converge towards a stable structure (Caswell 2001). Intuitively, with
169 population resilience comprised of the attributes of *resistance* (the ability to withstand
170 disturbances), *compensation* (the ability to benefit from disturbances) and *recovery* (the speed
171 and ability to reattain stability), the transient characteristics of populations resemble these
172 features of resilience (Hodgson et al. 2015; Capdevila et al. 2020).

Box 2: Measuring transient population characteristics.

Within natural environments, abiotic and biotic perturbations generate constant shifts within the state structure of populations ensuring they persist within a transient state, rather than converging towards equilibrium (Hastings et al. 2018). Within this transient state, the growth rate of populations can differ dramatically from their asymptotic trajectories, with populations undergoing *amplification* (increases in growth rate) or *attenuation* (declines in growth rate), which can subsequently influence the viability of a population in the longer-term (Fig. II). Accordingly, it is necessary to explore the transient characteristics of populations to gain insights into their responses to disturbance, and therefore better

understand their resilience (Ezard et al. 2010; Capdevila et al. 2020). Evaluating the transient dynamics of populations is made possible through the calculation of transient indices from population projection matrices (Stott et al. 2011). These measures include population reactivity ($\bar{\rho}$) and first-timestep attenuation ($\underline{\rho}$) which describe the increase or decline in a population's growth rate within one time interval of a perturbation, relative to λ (Stott et al. 2011). Equally, the measures of maximal amplification ($\bar{\rho}_{max}$) and maximal attenuation ($\underline{\rho}_{max}$) can be used to evaluate the maximum amplification or attenuation expected in the growth rate of populations, relative to λ (Townley et al. 2007; Townley and Hodgson 2008).

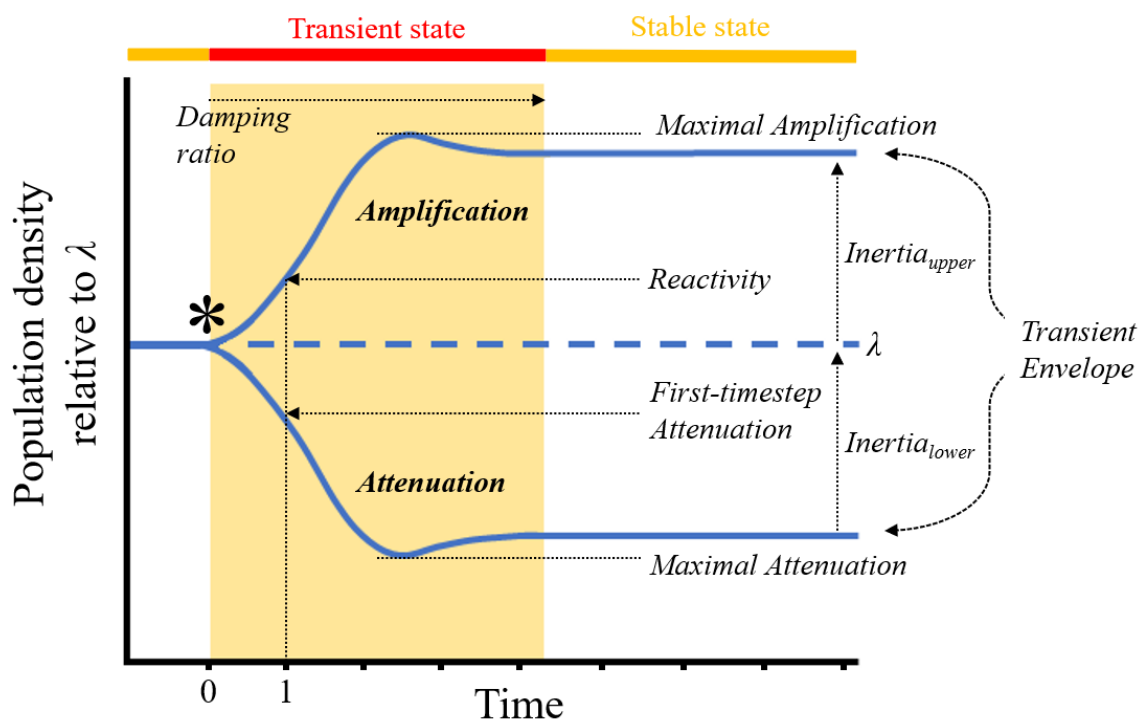


Figure II. Various measures exist for quantifying the transient characteristics of populations, and how the short-term responses of populations following a disturbance (*) will modify their trajectories relative to asymptotic expectations.

The *damping ratio* (ρ) of a population defines the rate at which a population will converge back to a stable equilibrium following a perturbation to its stable structure (Caswell 2001). Finally, *upper & lower population inertia* ($Inertia_{upper}$ & $Inertia_{lower}$ respectively) can be used to explore the extent to which the transient characteristics of populations influence their long-term trajectories, also known as a population's *transient envelope* (TE) (Koons et al. 2005; Stott et al. 2011).

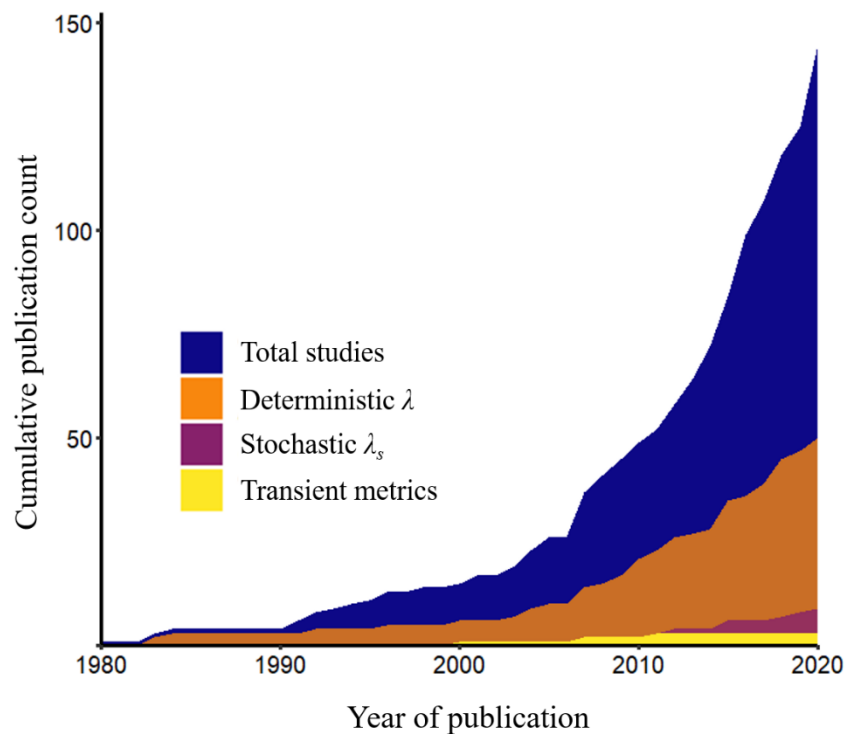
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174 Evaluating the transient characteristics of populations, and therefore their demographic
175 resilience, is possible through the calculation of transient measures readily accessible from
176 population projection matrices (Box 2; see Stott et al. [2011] for a detailed review). Briefly,
177 measures of *reactivity* ($\bar{\rho}$) and *first-timestep attenuation* ($\underline{\rho}$) reflect the initial behaviour in a
178 population's growth rate following a perturbation, with the *damping ratio* (ρ) describing the
179 rate at which a population is expected to reacquire a stable state structure (Caswell 2001; Stott
180 et al. 2011). Alternatively, estimates of *maximal amplification* ($\bar{\rho}_{max}$), *maximal attenuation*
181 ($\underline{\rho}_{max}$), and *population inertia* ($Inertia_x$) illustrate the magnitude by which the growth rate of
182 a population can be expected to fluctuate, and the influence of this short-term variation on the
183 population's long-term trajectory (Koons et al. 2005; Townley et al. 2007; Stott et al. 2011).
184 Furthermore, with population projection matrices providing a link between each transient
185 characteristic and a population's vital rates, sensitivity analyses can be applied to evaluate the
186 mechanistic drivers underlying the short-term characteristics of populations (Stott 2016;
187 Caswell 2019). Overall, transient demographic approaches present an effective tool for
188 explicitly evaluating the resilience of natural populations (Capdevila et al. 2020), and have
189 proven instrumental in our understanding of the establishment of populations within new and
190 variable environments (Iles et al. 2016; McDonald et al. 2016, 2017; Jelbert et al. 2019).

191 **Coral population dynamics: Current knowledge**

192 To examine the advancement of state-structured population approaches within coral research,
193 we conducted a review of the relevant ecological literature. Specifically, we searched for the
194 term coral* AND demograph* across the titles, abstracts, and keywords of research literature
195 within the SCOPUS database. We applied our search across all indexed peer-reviewed journals
196 published between 1960 and 2020, inclusive. This search initially returned 781 studies, from
197 which we retained all studies that explicitly measured or quantified state-structured patterns in
198 the survival, size transitions (including shrinkage via partial mortality or fission), and/or
199 reproduction (e.g. fecundity) of coral colonies. We also retained studies measuring larval
200 settlement rates, as the recruitment of early life stage individuals is a key demographic aspect
201 within coral communities (Adjerdou et al. 2017). Following this refinement, we retained a total
202 of 145 studies (~19% of our original search), which we then categorised according to whether
203 they involved the presentation of (i) asymptotic dynamics/simulations, (ii) transient
204 characteristics, or (iii) an assessment of vital rate patterns only.

205 Following the seminal work of Hughes and Jackson (1980), the application of state-
206 structured demographic assessments has increased within coral research, with a particularly
207 rapid growth in popularity since 2007 (Fig. 2). However, much of this research (97%) has
208 focused on either exploring the asymptotic dynamics of coral populations (34%; 50 studies) or
209 solely evaluating patterns across one or more of the vital rates of survival, changes in size, or
210 reproduction (63%; 91 studies). Presently, the majority of knowledge regarding the dynamics
211 of coral populations centres around their long-term trajectories. Thus, our current
212 understanding regarding the dynamics of coral populations assumes that these populations will
213 experience the stable environments necessary for achieving optimum population structures.



214 **Figure 2.** The cumulative number of studies that explicitly explore the state-structured
215 demographics of coral populations as identified by our search for the term coral* AND
216 demograph* across the peer-reviewed literature within the SCOPUS database. The colour
217 scale differentiates between studies that focus on only investigating patterns in colony
218 survival, growth, and/or reproduction, and those that utilised estimates of either deterministic
219 population growth (λ), stochastic asymptotic characteristics (λ_s), or transient population
220 characteristics, to evaluate the dynamics of coral populations.

221

222 A limited amount of previous research has considered the unpredictable nature of
223 natural environments when evaluating the future trajectories of coral populations. Our search
224 identified nine studies that either included estimates of stochastic population growth (λ_s ;
225 Lewontin and Cohen 1969) or explicitly parameterised the density-dependant regulation of
226 vital rates within their population models (Fig. 2; see Linares et al. 2007; Linares and Doak

227 2010; Hernandez-Pacheco et al. 2011; Vardi et al. 2012; Bramanti et al. 2015; Mercado-Molina
228 et al. 2015; Kayal et al. 2018; Montero-Serra et al. 2019). Estimates of λ_s describe the average
229 periodic change in the size of a population over a series of successive time intervals (Engen
230 and Saether 1998). As such, this metric of population performance provides a more accurate
231 consideration of vital rate and environmental variation when evaluating future population
232 trajectories, compared to deterministic λ . However, with estimates of λ_s often derived using a
233 series of population sizes estimated over numerous time intervals or with initial inconsistent
234 estimates of population size omitted, λ_s is still fundamentally a long-term measure of population
235 viability (Ellner and Rees 2007). Consequently, this measure still neglects the short-term
236 characteristics of populations, and thus our capacity to fully anticipate the future dynamics of
237 coral populations remains restricted.

238 Whilst state-structured demographic approaches are being adopted within coral
239 research, our review of the literature demonstrates how prominently the assumption of stable
240 equilibria dominates our understanding of coral population dynamics. Subsequently, we lack
241 the understanding necessary for accurately projecting the future reassembly and persistence of
242 coral communities under increasingly recurrent disturbance regimes. Only three of the 145
243 studies in our literature search calculated measures of the transient characteristics of coral
244 populations (Fig. 2; see Hughes and Tanner 2000; Linares et al. 2007; Bruno et al. 2011).
245 Alongside asymptotic population characteristics, these studies estimated population damping
246 ratios to outline the rate at which their focal populations would converge back to a stable state
247 structure following a perturbation. Yet, the damping ratio represents a dimensionless,
248 mathematical property of population projection matrices, and alone is of limited use to
249 population managers seeking to predict the short term responses of populations to disturbance
250 (Stott et al. 2011). Forecasting the resilience of coral populations is essential for the future
251 conservation of various reef communities (Roche et al. 2018; Lam et al. 2020). We have

252 illustrated here, however, that current approaches used in coral population ecology to evaluate
253 population growth rates do not constitute measures of population resilience. Our understanding
254 of coral population dynamics needs to be further expanded in order to meet our need for
255 quantifying the resilience, and responses, of coral communities to increasingly frequent
256 disturbances.

257 **Transient dynamics and the resilience of coral communities**

258 Exploring the transient characteristics of coral populations will enhance our understanding
259 regarding the future diversity, condition, and resilience, of coral communities. The frequency
260 of widespread thermal stress events is increasing across global coral communities, and soon
261 expected to exceed the recovery time required by most coral species (Hughes et al. 2018; Sully
262 et al. 2019). Presently, considerable value is placed on classifying coral species according to
263 their morphological and functional traits, with the subsequent categorisation of coral taxa
264 offering proxies for the vulnerability of various coral communities to said recurrent stress
265 events (Darling et al. 2012, 2019). Quantifying the relative affinities of different coral
266 populations for demographic recovery presents the opportunity for justifying these
267 assumptions; helping to distinguish the species and populations most vulnerable and or resilient
268 to projected recurrent disturbance regimes.

269 Intuitively, the amplification and attenuation characteristics of populations
270 simultaneously reflect their stability following a disturbance. However, recognising the
271 differential attributes of compensation and resistance in different populations is important for
272 managing the future condition of biological communities (Capdevila et al. 2020). Assessments
273 of coral communities following repeated disturbances have demonstrated divergent shifts in
274 species compositions (Adjeroud et al. 2009; Pratchett et al. 2011, 2020). With knowledge of
275 the capacity for various coral populations to undergo demographic amplification or for

276 avoiding demographic attenuation, we can begin to forecast and anticipate the reassembly of
277 coral communities, thereby improving the effectiveness of adaptive reef management.
278 Alternatively, a disturbance does not necessarily imply a negative impact, merely a change to
279 a system (Pickett and White 1985). Disturbances to the structure of populations can be brought
280 about by the cessation of a continuous pressure, changes in resource availability, or
281 establishment within a novel environment. The transient characteristics of populations offer
282 insights into their invasive potential (Iles et al. 2016), with the ability of natural populations
283 for undergoing demographic compensation underpinning their capacity for exploiting changes
284 within their local environments (Jelbert et al. 2019). Accordingly, comprehending and
285 quantifying demographic compensation within coral populations will aid predicting the
286 winners and losers in reef communities targeted by conservation initiatives, restoration
287 strategies, or climate induced range shifts. Assessing coral reef community resilience within
288 such a framework requires an increased focus on the temporal nature of resilience, a view that
289 would transcend current approaches of conducting single reef assessments to determine
290 resilience (Maynard et al. 2015; McLeod et al. 2021).

291 Complexities in the modelling approaches used to explore the dynamics of natural
292 populations have resulted in these techniques remaining largely overlooked within coral
293 research (Edmunds et al. 2014). Indeed, parametrising the demographic models needed to
294 quantify population characteristics requires considerable amounts of data (Ellner et al. 2002).
295 Although, despite the data demanding nature of state-structured demographic models, the
296 collection of the necessary data regarding the survival, transitions in size, fragmentation, and
297 recruitment, of individual coral colonies is possible alongside current reef monitoring efforts
298 (Edmunds and Riegl 2020). Furthermore, new techniques for analysing the demographic
299 characteristics of populations structured by a continuous state variable like size (Integral
300 Projection Models [IPMs; Easterling et al. 2000]) have reduced the data demands of

301 demographic assessments (Ramula et al. 2009). As a result, IPM frameworks are growing in
302 popularity throughout coral research (e.g. Bruno et al. 2011; Madin et al. 2012; Zychaluk et al.
303 2012; Elahi et al. 2016; Kayal et al. 2018; Precoda et al. 2018; Scavo Lord et al. 2020; Cant et
304 al. 2021; Carlot et al. 2021). Finally, studying the dynamics, particularly the transient
305 characteristics, of coral populations is made increasingly accessible by the development of
306 demographic analysis packages such as *popdemo* (Stott et al. 2012).

307 It is not our intention to dismiss previous efforts to evaluate the dynamics of coral
308 populations using asymptotic characteristics. Changes in individual vital rates can of course
309 have critical repercussions on the dynamics of populations (e.g. Bellier et al. 2018), and
310 asymptotic characteristics provide valuable insights for the management of threatened
311 populations (e.g. Johnson et al. 2010). However, as we have illustrated here, the asymptotic
312 characteristics of populations do not represent indicators of population resilience. Here, we
313 advocate for a greater commitment towards investigating the transient dynamics of coral
314 populations that more accurately reflect their dynamics within natural environments (Ezard et
315 al. 2010; Stott et al. 2011; Capdevila et al. 2020). With changing climatic regimes and increased
316 anthropogenic interference exposing global reef ecosystems to increasingly frequent
317 disturbances (Hoegh-Guldberg et al. 2017), evaluating the transient dynamics of coral
318 populations, and their mechanistic drivers, will provide a new effective lens on coral reef
319 resilience.

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