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Research

Transient amplification enhances the persistence of tropicalising coral assemblages in marginal high-latitude environments

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Predicting the viability of species exposed to increasing climatic stress requires an appreciation for the mechanisms underpinning the success or failure of marginal populations. Rather than traditional metrics of long-term population performance, here we illustrate that short-term (i.e. transient) demographic characteristics, including measures of resistance, recovery and compensation, are fundamental in the poleward range expansion of hard corals, facilitating the establishment of coral populations at higher latitudes. Through the annual census of subtropical and temperate *Acropora* spp. colonies in Japan between 2017 and 2019, we show how enhanced transient amplification (i.e. short-term increases in population growth following disturbance) supports the persistence of coral assemblages within more variable high-latitude environments. The transient dynamics of both the subtropical and temperate assemblages were strongly influenced by their corresponding recruitment patterns. However, we demonstrate that variation in colony survival and fragmentation patterns between the two assemblages determines their relative capacities for transient amplification. This latitudinal variation in the transient dynamics of *Acropora* spp. assemblages emphasizes that coral populations can possess the demographic plasticity necessary for exploiting more variable, marginal conditions.

Keywords: *Acropora* spp., amplification, integral projection model (IPM), Kitagawa and Keyfitz decomposition, subtropical, transient life table response experiment

Introduction

The latitudinal diversity gradient, or poleward decline in biodiversity (von Humboldt 1808), is a fundamental macroecological pattern evident across all major taxa (Hillebrand 2004, Fine 2015). This pattern emerges partly due to increased climatic variation at

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higher latitudes (Willig et al. 2003, Archibald et al. 2010, Mannion et al. 2014). Increased environmental variation exerts a strong filter on the assembly of biological communities, selecting for species with broader ecological niches (Janzen 1967). Yet, corresponding with the changing global climate, many ecosystems face imminent reassembly as species distributions shift to track favourable conditions (Pecl et al. 2017, Williams and Blois 2018). Along shifting distributional boundaries, the endurance of populations depends on their ability to withstand abiotic fluctuations (Valladares et al. 2014). Across a given species' range, its populations are exposed to a series of environmental pressures giving rise to contrasting abilities between core and peripheral populations for tolerating abiotic variation (Angert 2009, Purves 2009). However, whilst the extent to which marginal populations can embrace environmental variation underpins the continued viability of numerous species, it is poorly understood how variation in the attributes that define the life cycles of species, such as longevity and age at reproduction, influences the persistence of populations along range boundaries (Valladares et al. 2014, Paniw et al. 2018, Healy et al. 2019).

Transient dynamics describe the characteristics of populations following their displacement from a stable equilibrium (Hastings 2001, Stott et al. 2011). Population viability assessments typically explore long-term asymptotic dynamics, such as estimates of population growth rate (λ; Beissinger and Westphal 1998, Crone et al. 2011, Selwood et al. 2015). However, this approach assumes that natural populations are able to maintain a stable structural composition, whereby the proportion of individuals across state classes (i.e. age, developmental class and/or size) remains consistent. Instead, evaluating the transient, or short-term, dynamics of natural populations is as important, if not more so, for anticipating the persistence of various species (Hastings 2004, McDonald et al. 2016, Hastings et al. 2018). With the inherent instability of natural environments ensuring that populations are unable to persist at their stable equilibrium (Hastings 2001), transient population dynamics describe how a population's trajectory is expected to change in the short term relative to its asymptotic growth rate (Stott et al. 2011; Fig. 1). Transient dynamics therefore provide a convenient means for quantifying population resilience, specifically, the ability of populations to resist and recover after disturbances (Capdevila et al. 2020). Following a disturbance, transient dynamics can provoke the increase (*amplification*) or decline (*attenuation*) of a population, relative to its long-term characteristics. With these transient dynamics underpinning population viability within variable environments (McDonald et al. 2016), and the ability for species to colonise new environments (Jelbert et al. 2019), understanding and predicting transient population dynamics is a priority for ecosystem management and conservation (Ezard et al. 2010, Hodgson et al. 2015, Capdevila et al. 2020).

Global warming and strengthening poleward boundary currents are driving the rapid tropicalisation of marine communities along tropical to temperate transition zones (Vergés et al. 2014, Kumagai et al. 2018). Consequently,

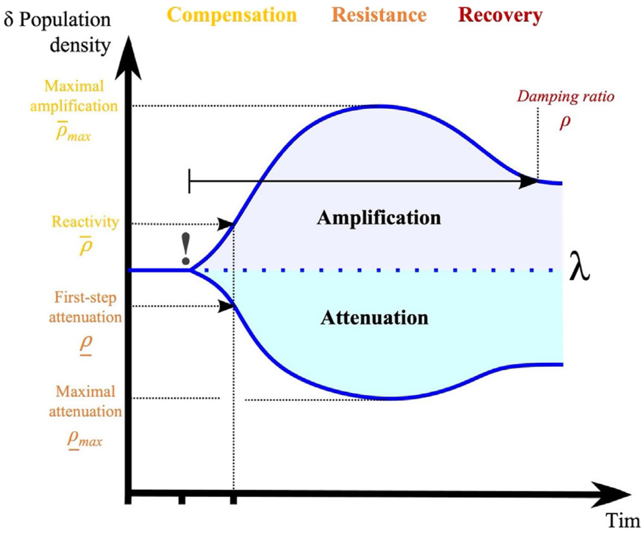

Figure 1. Disturbances disrupt the structural composition of natural populations, causing their trajectories to deviate from long-term expectations. At a stable equilibrium populations are expected to change in size at a constant rate (λ, dashed line). However, following disturbance (!) populations can experience a transient phase during which their trajectories are determined by their propensity for amplification (increases in population growth) and attenuation (declines in population growth). By revealing the potential for populations to grow (*compensation*), persist (*resistance*) and *recover* following disturbance, relative to their long-term trajectories, estimates of transient population characteristics represent key measures of population resilience. Specifically, the measures of reactivity ($\bar{\rho}$) and maximal amplification ($\bar{\rho}_{max}$) describe the initial growth, and maximum increase, in population growth rate expected during transient conditions. Meanwhile, first-step attenuation ($\underline{\rho}$) and maximal attenuation ($\underline{\rho}_{max}$) describe the initial decline, and minimum rate of population growth expected during transient conditions. Finally, damping ratio (ρ) estimates reflect the rate at which a population is expected to reobtain a stable equilibrium post-disturbance. Note, for consistency, changes in population size are displayed here relative to long-term population growth rate; in reality, population growth can reflect both increases and declines in population size.

tropical taxa, including many zooxanthellate hard coral species, are becoming increasingly prevalent in higher-latitude subtropical and temperate environments (Denis et al. 2013, Vergés et al. 2019). This establishment of tropical coral populations along higher-latitude coastlines has many similarities to the dynamics of invasive populations following their relocation, which, economic and ecological costs aside, represent the growth of small populations within novel environments (Iles et al. 2016). Particularly relevant in this context is evidence that the transient dynamics of plant populations are effective predictors of invasive potential (Iles et al. 2016). Indeed, populations possessing the capacity for rapid amplification following a perturbation (reflected here by the introduction of a novel environment) are more capable of exploiting new habitats (Jelbert et al. 2019). It can be expected, therefore, that the capacity of coral populations for establishing at higher latitudes may be dictated by their transient dynamics, rather than asymptotic population trajectories. Nevertheless, the transient dynamics of coral populations remain unexplored (Cant et al. 2021a).

Here, we explore if and how variation in the transient dynamics of coral assemblages is consistent with their exposure to abiotic variability. Specifically, we compare the relative stability (attenuation and amplification; Fig. 1) and recovery attributes of subtropical and temperate *Acropora* spp. assemblages in southern Japan (Fig. 2), a region considered an epicentre of tropicalisation (Vergés et al. 2014, Kumagai et al. 2018). Transient dynamics are thought to buffer the effects of environmental variability and are therefore accentuated in populations exposed to more frequent disturbances (Ellis and Crone 2013). Accordingly, we investigate whether coral assemblages at higher latitudes exhibit more pronounced transient dynamics than their tropical counterparts. Equally, the reproductive isolation associated with high-latitude coral assemblages ensures that they are typically supported

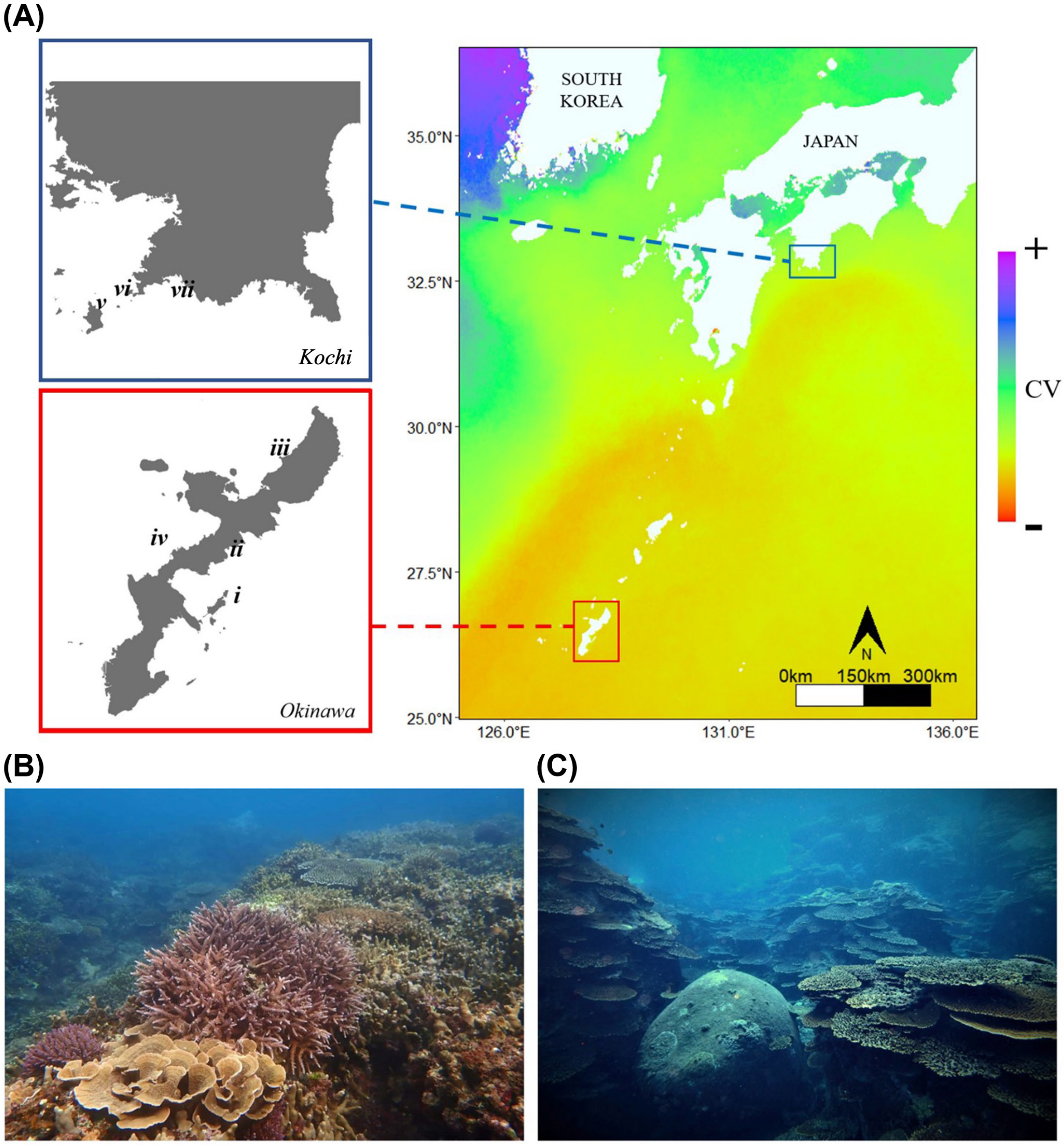

Figure 2. The locations of the surveyed subtropical and temperate *Acropora* spp. assemblages in Japan, separated by a distance of 990 km. (A) Mediated by the Kuroshio Current, the coastline of southern Japan aligns with a distinct gradient in environmental variability (coefficient of variation, CV) in monthly sea surface temperatures (SSTs) recorded during our annual sampling between 2017 and 2019. We tagged individual *Acropora* spp. colonies at four locations within the subtropical reef communities of Okinawa (Red): (i) Miyagi Channel, (ii) Oura Bay, (iii) Hentona and (iv) Onna (only visited for deploying settlement tiles used to quantify recruitment patterns), and at three locations within the temperate coral communities of Kochi (Blue): (v) Okinoshima, (vi) Kashiwajima and (vii) Nishidomari. Representative photographs of surveyed subtropical and temperate coral assemblages at (B) Hentona, Okinawa, and (C) Kashiwajima, Kochi. Photograph credits: K. Cook.

by sporadic recruitment from up-current reef communities, with their endurance instead reliant on the dynamics of existing colonies (Cant et al. 2021b). Subsequently, we also conduct a transient life table response experiment (transient LTRE) (Koons et al. 2016) decomposing variation in the transient dynamics of subtropical versus temperate *Acropora* spp. assemblages, to test whether the transient dynamics of coral populations at higher latitudes are indeed sustained by the dynamics of existing colonies.

Material and methods

Model parameterisation

To explore the influence of environmental variability on the transient dynamics of coral populations, we utilised an integral projection model (IPM) framework (Easterling et al. 2000) to quantify the respective dynamics of *Acropora* spp. assemblages from a subtropical and a temperate environment. An IPM describes how size-specific vital rates (e.g. survival, recruitment) determine the transition of individuals from size z at time t, to size z' at time $t + 1$, and how these individual-level patterns translate into population characteristics (Eq. 1):

$$n\left(z',t+1\right)=\int_{L}^{U}\left[P\left(z',z\right)+F\left(z',z\right)\right]n\left(z,t\right)\Delta z \qquad (1)$$

The size (in this case colony surface area, cm^2) structure, $n(z', t+1)$, of a population at time $t + 1$ is a function of its structure at time t, $n(z, t)$, and the demographic patterns estimated across a size range (Δz) outlined in the sub-kernels P and F. Here, Δz ranges between 10% above and below the maximum (U) and minimum (L) observed sizes to avoid accidental eviction (Williams et al. 2012). P describes size-specific patterns relating to colony survival probability (σ), transitions in size (γ; growth, stasis and shrinkage), the probability of fragmentation (κ) and the number and size of fragments produced (κ_n and κ_0, respectively) (Eq. 2):

$$P\left(z',z\right)=\left[1-\kappa\left(z\right)\right]\sigma\left(z\right)\gamma\left(z',z\right)+\kappa\left(z\right)\kappa_n\left(z\right)\kappa_0\left(z'\right) \qquad (2)$$

F describes the recruitment of new, sexually produced individuals (C_0), which are the outcome of larval production per colony (colony fecundity, f_n). Crucially, we also included measures of larval settlement probability (ψ), and post-settlement survival probability (Ŧ), within our parameterisation of F (Eq. 3):

$$F\left(z',z\right)=\psi f_n\left(z\right)\text{Ŧ}\,C_0\left(z'\right) \qquad (3)$$

Incorporating larval settlement and post-settlement survival ensured that, with *Acropora* spp. assemblages influenced more by larval dispersal than by local colony fecundity patterns (Hughes et al. 2000), recruitment within our models was determined by empirical settlement observations and not colony fecundity. The inclusion of fecundity instead enabled us to close the loop between adult and recruit colony dynamics, necessary for quantifying transient population characteristics (Caswell 2001).

We empirically parameterised our IPMs through the annual census of subtropical and temperate *Acropora* spp. assemblages in southern Japan (Fig. 2). The in situ identification of *Acropora* colonies to species level is complicated by the widespread occurrence of morphologically cryptic subspecies and species hybridisation (Richards and Hobbs 2015, Richards et al. 2016). Thus, working at the genus level we pooled data from across repeated surveys of tagged colonies in September 2017, August 2018 and August 2019, to quantify the regional dynamics of subtropical and temperate *Acropora* spp. assemblages. Although restricted, the temporal extent of our demographic assessment here corresponds with timelines applied across previous work evaluating the performance characteristics of coral populations (Precoda et al. 2018, Shlesinger and van Woesik 2021), ensuring comparability between our findings and those of past research.

During our surveys we recorded region- and size-specific patterns in colony survival (σ), transitions in size (γ) and fragmentation (κ; Supporting information). Colony survival represented the continued presence of tagged colonies over time and was modelled as a function of colony size at time t. Alternatively, transitions in colony size reflected the difference between colony surface areas recorded during successive annual surveys. In this context, transitions in colony size reflected both growth due to colony extension, and shrinkage following partial mortality (Madin et al. 2020), and was calculated using the relationship between colony size at time t and at time $t + 1$. Next, using data pooled from both the subtropical and temperate assemblages, we modelled the probability of colony fragmentation as a function of colony size at time t. This approach was necessary due to the low frequency of annual fragmentation events (number of events reported, n_i^{κ}) observed within our subtropical assemblage, although we weighted fragmentation probabilities according to the relative proportion of annual events recorded across the subtropical and temperate assemblages ($n_i^{\kappa} / n_{\text{total}}^{\kappa}$; see Supporting information for further details). We acknowledge that, irrespective of the approach used, the likelihood of fragments dispersing away from our plots means that our estimates of fragmentation patterns are likely to be underestimates. Finally, we estimated patterns in fragment production (κ_n) and fragment size (κ_0) as a function of initial colony size, using the number and recorded size of all observed colony fragments.

In our IPMs, recruitment encompassed patterns in colony fecundity (f_n), and the probabilities of larval settlement (ψ) and post-settlement survival (henceforth recruit survival probability [Ŧ]). Although we did not directly measure colony fecundity, owing to the logistical challenges involved (Gilmour et al. 2016), we estimated annual larval output (volume of larvae produced, cm^3) as a function of colony size using a relationship reported for *Acropora* spp. on the Great Barrier Reef (Hall and Hughes 1996; Supporting information). Additionally, we determined the probabilities of larval settlement and recruit survival, using larval counts made during prior subtropical (2011–2013; Nakamura et al. 2015) and temperate (2016–2018; Nakamura, unpubl.) settlement tile surveys in southern Japan (see Supporting information for further details). Combining the larval counts per unit area from these earlier surveys with our regional estimates of larval output and observed recruit densities enabled us to estimate ratios translating colony larval output from a measure of larval volume into expected counts of settling larvae (ψ; sensu Bramanti et al. 2015) and to define a series of post-settlement survival probabilities reflecting temporal trends in the survival of coral larvae between settlement and the point of observation within both a subtropical and a temperate setting (Ŧ; Supporting information). Finally, consistent with evidence that larval settlement and survival are coordinated by interactions between local biotic and abiotic drivers (Vermeij et al. 2009, Doropoulos et al. 2016), we modelled the size distribution (C_0) of tropical and subtropical recruits independently of parent colony size.

Quantifying transient dynamics

We used our IPMs to test our hypothesis of variation in the transient dynamics of coral assemblages at increasingly higher latitudes. We focused on transient measures depicting the demographic resilience attributes of recovery (damping ratio [ρ]), resistance (first-step attenuation [$\underline{\rho}$] and maximal attenuation [$\underline{\rho}_{\max}$]), and compensation (reactivity [$\bar{\rho}$] and maximal amplification [$\bar{\rho}_{\max}$]; Fig. 1). To obtain estimates of variance in these transient metrics, we generated 1000 variants of our subtropical and temperate IPMs using jack-knife resampling, each time omitting 5% of our data without replacement whilst allowing the modelled probabilities of larval settlement (ψ) and recruit survival (Ŧ) to vary within observed limits. Next, we integrated the kernel of each model variant into a high-dimension matrix (200 × 200 cells) using the 'midpoint rule' (Ellner and Rees 2006, Zuidema et al. 2010), with the probability of individuals transitioning from one cell to the next estimated at the cell midpoint and multiplied by the cell width. In our case the cell width corresponded with colony size increments of 0.716 cm^2 on the log-scale. Following this discretisation, we calculated the distribution (mean and variance) of each transient metric for the subtropical and temperate assemblages using the R package *popdemo* (Stott et al. 2012).

We calculated the amplification and attenuation characteristics of the subtropical and temperate assemblages as population structure-specific measures. Population structure-specific transient measures provide the predicted transient dynamics of a population given its current state distribution, as opposed to transient bounds which reflect the potential dynamics of a population irrespective of its state distribution (Stott et al. 2011). For these calculations, we derived the state distributions of both the subtropical and temperate *Acropora* spp. assemblages using the size distributions of tagged colonies recorded during our 2019 census. Across our jack-knife model variants, some combinations of resampled vital rate schedules lacked the capacity for eliciting either amplification or attenuation in their corresponding population relative to asymptotic growth rates. We therefore present the percentage of model variants from which predictions of amplification and attenuation could be obtained as an additional indication of the relative transient potential of the two *Acropora* spp. assemblages. Finally, to contextualise our estimates of transient dynamics against the long-term trends of each population, we calculated mean and variance estimates of their asymptotic growth rates (λ), with $\lambda < 1$ or > 1 reflecting negative or positive population growth (Caswell 2001).

Model decomposition

We tested our hypothesis that the transient dynamics of temperate coral assemblages are sustained by the survival, transitions in size and fragmentation patterns of existing colonies, rather than by patterns in recruitment, using a transient LTRE (Koons et al. 2016). The amplification characteristics of populations define their capacity to exploit and thrive within novel, variable environments (McDonald et al. 2016, Jelbert et al. 2019). Thus, we decomposed the vital rate influences of the relative maximal amplification characteristics ($\bar{\rho}_{\max}$) of the subtropical versus temperate *Acropora* spp. assemblages. The transient dynamics of our focal coral assemblages (ξ) are contingent on three components: the size-specific vital rate patterns of established colonies (Θ), and the probabilities of larval settlement (ψ) and recruit survival (Ŧ). Variation in these components between the tropical and subtropical assemblages consequently drives any variation between their characteristics (Eq. 4 and 5):

$$\xi^{(\text{subtropical})} = \xi\left[\Theta^{(1)}, \psi^{(1)}, \text{Ŧ}^{(1)}\right] \tag{4}$$

$$\xi^{(\text{temperate})} = \xi\left[\Theta^{(2)}, \psi^{(2)}, \text{Ŧ}^{(2)}\right]. \tag{5}$$

Within coral populations, rates of larval settlement and survival oscillate considerably over time (Davidson et al. 2019). Thus, we incorporated this variability into our IPMs by allowing the probabilities of larval settlement and recruit survival to fluctuate within observed boundaries, therefore introducing an element of within-assemblage variability to our models. Using the transient LTRE approach detailed below, we combined a traditional LTRE with a Kitagawa and Keyfitz decomposition (Kitagawa 1955, Keyfitz 1968, Caswell 2019). Briefly, this decomposition approach allowed us to account for within-assemblage variability when evaluating the vital rate mechanisms underlying the differences between the transient dynamics of the two assemblages (Maldonado-Chaparro et al. 2018, Layton-Matthews et al. 2021).

We first paired up subtropical and temperate model variants to evaluate the overall contributions (C) of the vital rate patterns of established colonies (Θ), larval settlement (ψ) and recruit survival (Ŧ), towards variation in $\bar{\rho}_{\max}$ using a Kitagawa and Keyfitz decomposition. The overall contribution of each component was obtained by averaging the effect on $\bar{\rho}_{\max}$ of substituting the subtropical and temperate form of the selected component against a fixed background of the other components (Caswell 2019) (Eq. 6):

$$
\begin{aligned}
C\left(\Theta\right) \approx \frac{1}{4}\Big(& \bar{\rho}_{\max}\left[\Theta^{(1)}, \psi^{(1)}, \text{Ŧ}^{(1)}\right] - \bar{\rho}_{\max}\left[\Theta^{(2)}, \psi^{(1)}, \text{Ŧ}^{(1)}\right] \\
& + \bar{\rho}_{\max}\left[\Theta^{(1)}, \psi^{(2)}, \text{Ŧ}^{(2)}\right] - \bar{\rho}_{\max}\left[\Theta^{(2)}, \psi^{(2)}, \text{Ŧ}^{(2)}\right] \\
& + \bar{\rho}_{\max}\left[\Theta^{(1)}, \psi^{(1)}, \text{Ŧ}^{(2)}\right] - \bar{\rho}_{\max}\left[\Theta^{(2)}, \psi^{(1)}, \text{Ŧ}^{(2)}\right] \\
& + \bar{\rho}_{\max}\left[\Theta^{(1)}, \psi^{(2)}, \text{Ŧ}^{(1)}\right] - \bar{\rho}_{\max}\left[\Theta^{(2)}, \psi^{(2)}, \text{Ŧ}^{(1)}\right]\Big)
\end{aligned}
\tag{6}
$$

Across all decomposition analyses, we defined the subtropical assemblage as our control model. Subsequently, positive contributions reflect greater influence towards the dynamics of the subtropical assemblage, whereas negative contributions imply a greater importance towards the temperate assemblage.

Next, we decomposed the separate contributions of the vital rates of survival, changes in size and fragmentation, observed in established colonies, towards variation in $\bar{\rho}_{\max}$. The contribution of each vital rate ($C[\theta_i]$) corresponds with the change in that vital rate between paired subtropical and temperate models combined with the environmental-specific elasticity matrices of $\bar{\rho}_{\max}$ (Caswell 2019) (Eq. 7):

$$
C\left(\theta_i\right) \approx \frac{1}{2}\left[\begin{aligned} & \left(\left.\frac{\partial\bar{\rho}_{\max}\left[\bar{\Theta}, \psi^{(1)}, \text{Ŧ}^{(1)}\right]}{\partial\theta}\right|_{u=i}\right)\left(\theta_i^{(1)} - \theta_i^{(2)}\right) + \\ & \left(\left.\frac{\partial\bar{\rho}_{\max}\left[\bar{\Theta}, \psi^{(2)}, \text{Ŧ}^{(2)}\right]}{\partial\theta}\right|_{u=i}\right)\left(\theta_i^{(1)} - \theta_i^{(2)}\right) \end{aligned}\right]. \tag{7}
$$

Here, the subtropical- and temperate-specific elasticity matrices of $\bar{\rho}_{\max}$ ($\frac{\partial\bar{\rho}_{\max}[\bar{\Theta}, \psi^{i}, \text{Ŧ}^{i}]}{\partial\theta}$) were composed of the proportional sensitivities (e_{ij}) of $\bar{\rho}_{\max}$ towards the matrix elements (a_{ij}) of a discretised IPM kernel parameterised using the mean vital rates across our subtropical and temperate assemblages ($\bar{\rho}$) (Eq. 8):

$$
e_{ij} = \frac{a_{ij}}{x}\frac{\partial x}{\partial a_{ij}} = \frac{a_{ij}}{x}\frac{\left(x^{\text{Perturbed}} - \mathrm{x}^{\text{Original}}\right)}{\left(a_{ij}^{\text{Perturbed}} - a_{ij}^{\text{Original}}\right)} \text{ where } x = \bar{\rho}_{\max}. \tag{8}
$$

Results

Trends in transient dynamics: subtropical versus temperate

Considering the prevalence of uncertainties within coral taxonomy (Fukami et al. 2004), there is a precedent for assessments into the characteristics of coral populations to operate at higher taxonomic levels (Darling et al. 2019, Edmunds 2020). Thus, we present here a demographic assessment of *Acropora* spp. assemblages focused at the genus level. The subsequent interpretation of our results therefore assumes a consistency in species configurations across the subtropical and temperate assemblages. Species records from both Okinawa and Kochi (Nishihira and Veron 1995, Veron et al. 2016) indicate a considerable overlap in the composition of these subtropical and temperate *Acropora* spp. assemblages (Supporting information). Equally, there is minimal variation in the morphological and functional traits of acroporid species associated with the coastal communities of Okinawa and Kochi (Supporting information), reinforcing our interpretations of the observed demographic variation between the two assemblages described below.

The transient characteristics of the temperate *Acropora* spp. assemblage were more pronounced than those of its subtropical counterpart (Fig. 3). Of the two assemblages, the subtropical *Acropora* spp. assemblage displayed the highest asymptotic growth rate (λ: subtropical = 0.916 [95% CI: 0.914, 0.918]; temperate = 0.655 [0.654, 0.655]). However, despite exhibiting a higher long-term population growth rate, following perturbation the subtropical assemblage is predisposed to experience attenuation ($\underline{\rho}$), resulting in a post-disturbance decline in its growth rate ($\underline{\rho}$: 0.985 [0.983, 0.986]). Alternatively, the temperate assemblage is expected to exhibit a reactive ($\bar{\rho}$) transient response to perturbation, experiencing an increase in its growth rate relative to its asymptotic trajectory ($\bar{\rho}$: 1.033 [1.027, 1.039]). However, across all jack-knifed model variants, the temperate variants presented more heterogenous responses to perturbation than the subtropical variants (Fig. 3A).

Notably, in comparison with the subtropical assemblage, the transient dynamics of the temperate assemblage demonstrated a superior capacity for maintaining elevated growth within unstable environments (Fig. 3B). Amplification was observed in 84.5% of temperate model variants as opposed to in just 23.1% of subtropical variants. Indeed, expected maximal amplification ($\bar{\rho}_{\max}$) was also highest within the temperate assemblage, and reflected a potential ~22% increase in population growth rate following a disturbance relative to asymptotic expectations ($\bar{\rho}_{\max}$; subtropical = 1.019 [1.012, 1.026]; temperate = 1.228 [1.215, 1.241]). The subtropical assemblage did, however, display a higher damping ratio (ρ) than the temperate assemblage (ρ; subtropical = 1.638 [1.634, 1.641]; temperate = 1.429 [1.424, 1.433]), indicating a faster convergence rate to an equilibrium state. Yet, in this context, this disparity in convergence rate corresponds with the more prominent transient displacement

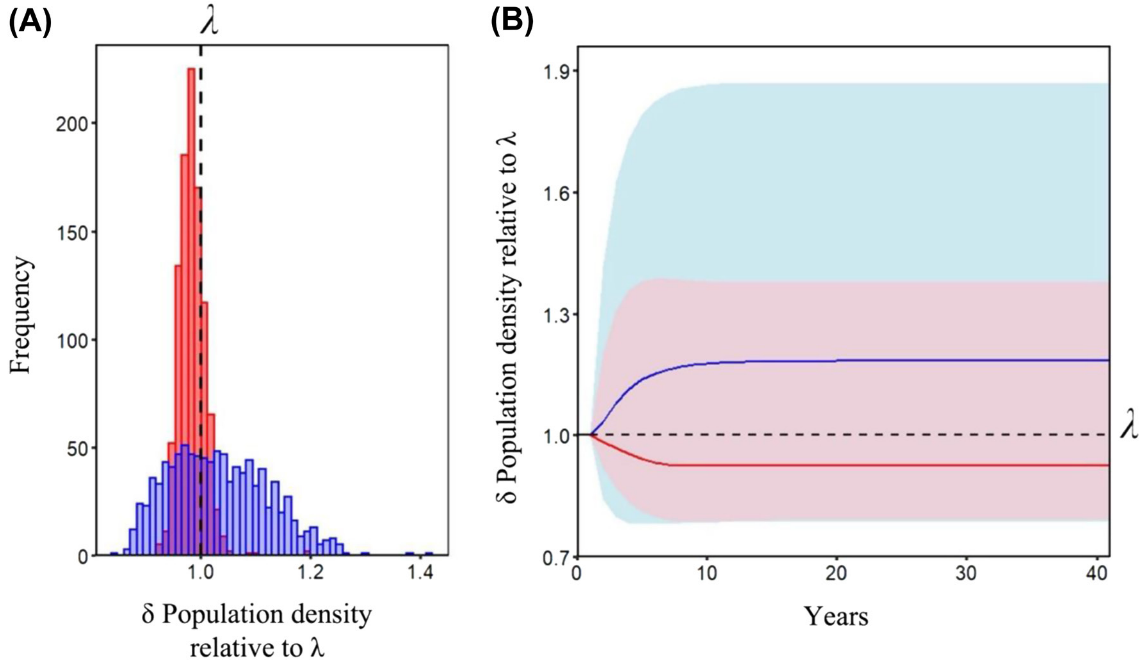

Figure 3. The temperate *Acropora* spp. assemblage displays an enhanced capacity for demographic amplification compared to its subtropical counterpart. We estimated measures of transient (short-term) dynamics describing the dynamics of the subtropical (red) and temperate (blue) *Acropora* spp. assemblages following disturbance across a series of jack-knifed model variants. (A) Variation in the transient responses observed across jack-knifed model variants within one time-step of a perturbation. (B) Illustrates how the transient dynamics observed across model variants manifest over 40 years post-disturbance to modify population trajectories relative to original asymptotic expectations. Solid lines represent the mean population trends with shaded areas reflecting the range of observed transient patterns for each population. Across both panels transient responses (TR) are displayed in their standardised form (i.e. TR/λ) such that all changes in population size (δ) are displayed relative to corresponding asymptotic growth rate estimates (λ, dashed line).

observed in the temperate model variants relative to their asymptotic characteristics (Fig. 3B). Conversely, maximal attenuation ($\underline{\rho}_{max}$) estimates for the subtropical and temperate assemblages suggest that, whilst attenuation was more readily observed within subtropical model variants (observed in 96% and 40.3% of subtropical and temperate variants, respectively), both assemblages are only expected to experience a < 10% reduction in their growth rates relative to asymptotic expectations should attenuation occur ($\underline{\rho}_{max}$; subtropical = 0.919 [0.916, 0.923]; temperate = 0.940 [0.935, 0.946]).

Transient LTRE decomposition

Despite evidence that recruitment patterns impact upon the transient dynamics of the subtropical and temperate *Acropora* spp. assemblages, the differential vital rate schedules of existing colonies are responsible for shaping the variation observed between the amplification capacities of the two assemblages (Fig. 4). Patterns in larval settlement (ψ), recruit survival (Ϯ) and the vital rates of existing colonies (Θ) varied significantly in their contributions towards variation in the maximal amplification ($\bar{\rho}_{max}$) (ANOVA: $F_{2,2997} = 29557$, $p < 0.001$; Tukey: $\psi > \Theta >$ Ϯ). Overall, larval settlement (ψ) and recruit survival (Ϯ) exerted the greatest influence on estimates of $\bar{\rho}_{max}$; however, these two properties had contrasting impacts across the subtropical and temperate assemblages (Fig. 4A). Amplification in the subtropical *Acropora* spp. assemblage appears enhanced by higher rates of larval settlement, whilst higher post-settlement larval survival elevates amplification in the temperate assemblage (see Supporting information for details on the recruitment patterns observed across each assemblage). Combining these contrasting patterns, and their relative augmentation of the amplification characteristics of each assemblage, results in a net zero contribution and, ultimately, nullifies the proportional contribution of recruitment dynamics towards variation in $\bar{\rho}_{max}$ between the subtropical and temperate assemblages.

Consequently, the cumulative contribution of the vital rate patterns of existing subtropical and temperate colonies, specifically their survival and fragmentation characteristics, underpins the contrasting amplification capacities of the two assemblages (Fig. 4B). Inter-assemblage variation in the survival patterns of smaller colonies (< 4 cm^2 on the log scale) benefitted the amplification characteristics of the subtropical assemblage, whilst variation in the survival patterns of larger colonies (4–7 cm^2 on the log scale) enhanced the amplification characteristics of the temperate assemblage (Fig. 4B). Broadly, however, the relative contribution of colony survival towards $\bar{\rho}_{max}$ decreased with increasing colony size (Fig. 4B). Alternatively, the contribution of colony fragmentation towards $\bar{\rho}_{max}$ increased with colony size; and although

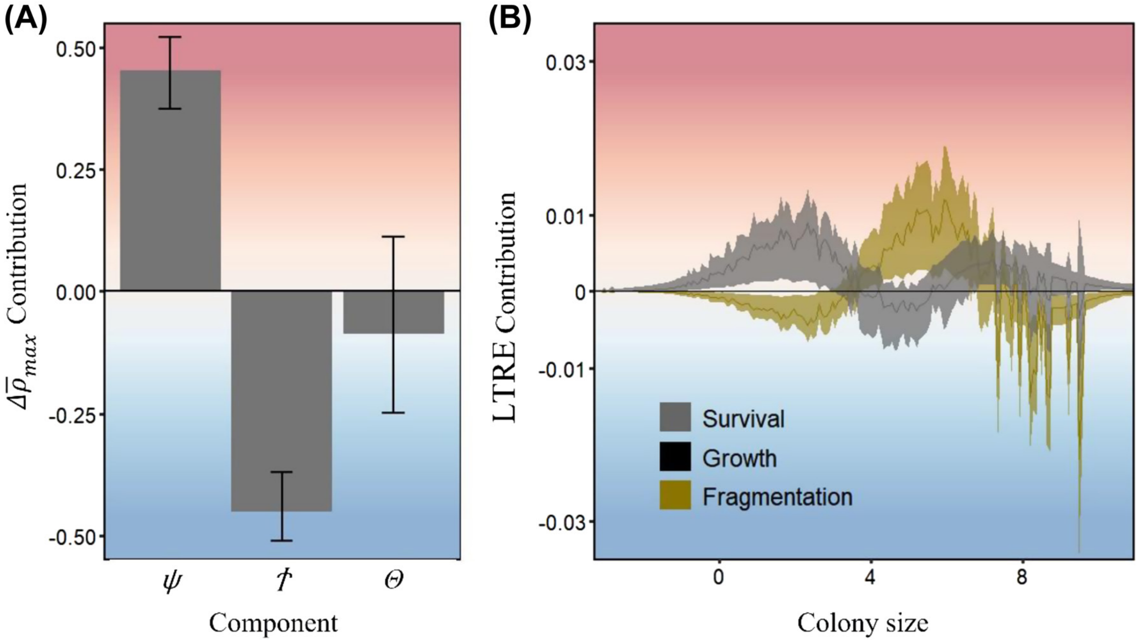

Figure 4. Size-specific patterns in colony survival and fragmentation underpin the varying amplification characteristics of the subtropical and temperate *Acropora* spp. assemblages. We used a transient life table response experiment (LTRE) to explore the vital rate contributions underpinning variation between the transient dynamics of subtropical and temperate *Acropora* spp. assemblages. (A) The proportional contribution of patterns in larval settlement (ψ), recruit survival ($\dagger$) and the vital rate schedules of existing colonies (Θ) towards differences in the maximal amplification characteristics between the two assemblages ($\Delta\bar{\rho}_{max}$). (B) The relative size-specific contributions of the vital rates of survival, growth and fragmentation towards the maximal amplification characteristics of the temperate *Acropora* spp. assemblage compared with its subtropical counterpart as a baseline. Solid lines represent mean contribution patterns. Across both panels, positive contributions reflect greater influence of a given vital rate towards enhancing maximal amplification in the subtropical assemblage (red), whilst negative values reflect greater influence towards enhanced amplification in the temperate assemblage (blue). All error displayed represents the full range of observations observed across tropical and subtropical model variants.

variation in the fragmentation patterns of larger colonies (> 4 cm^2 on the log scale) does benefit amplification in the subtropical assemblage, the fragmentation dynamics of very large colonies (> 7 cm^2 on the log scale) enhances the amplification capacity of the temperate assemblage (Fig. 4B). Meanwhile, the influence of colony growth characteristics on the transient amplification potential of either assemblage was negligible (Fig. 4B). Consequently, the enhanced amplification capacity of the temperate coral assemblage appears associated with the survival and fragmentation characteristics of larger colonies.

Discussion

Global climatic change is reassembling coral reef communities worldwide (Hughes et al. 2017, 2018). Accordingly, understanding the mechanisms underpinning the establishment and persistence of range-shifting coral species in subtropical and temperate locations is imperative for anticipating the future success or failure of global coral assemblages, and their continued provision of essential ecosystem services (Hoegh-Guldberg et al. 2017, Camp et al. 2018, Sommer et al. 2018). Comparing between the dynamics of subtropical and temperate *Acropora* spp. assemblages we reveal a decrease in asymptotic growth rate with increasing latitude. However, we illustrate that the expansion and endurance of a coral assemblage within a highly variable – and comparatively stressful – temperate environment corresponds with its superior capacity for amplified growth following disturbance compared to an up-current subtropical assemblage (Fig. 3). We also highlight how the transient dynamics of a temperate *Acropora* spp. assemblage are contingent on the survival and fragmentation dynamics of existing colonies, highlighting key drivers underpinning the fitness of coral populations at increasingly higher latitudes. Recruitment had the largest overall effect on the dynamics of both the subtropical and temperate *Acropora* spp. assemblages. Nevertheless, divergent larval settlement and recruit survival probabilities between the two assemblages ensure that the dynamics of existing colonies underpin the relative differences between their transient dynamics (Fig. 4).

Overall, our findings here are consistent with insights from invasive populations whose transient demographic characteristics facilitate the persistence of a small number of individuals following their introduction within non-native environments (Iles et al. 2016, Jelbert et al. 2019). Thus, we present evidence for the mechanisms helping to shape the ability for coral species to shift their distributions into subtropical and temperate environments.

Transient versus asymptotic dynamics

Understanding within-species demographic variation across climatic gradients is essential for forecasting the success of populations at tracking favourable conditions and establishing themselves within novel environments (Merow et al. 2017). Our findings display an emergent latitudinal trade-off between the long-term viability and short-term exploitation potential of *Acropora* spp. assemblages in southern Japan. Similar divergent latitudinal patterns in stability and variability have been observed across various biological scales (Hillebrand et al. 2018, Antão et al. 2020), and are thought to underpin the vulnerability of lower-latitude populations to future climatic change (Barlow et al. 2018). Across subtropical and temperate *Acropora* spp. assemblages, asymptotic population growth was higher at lower latitudes, aligning with traditional expectations that population growth rates will decline towards species range boundaries as populations encounter increasingly demanding environments (Vucetich and Waite 2003). However, the strength and universal nature of this expectation is widely refuted (Sagarin and Gaines 2002, Sexton et al. 2009, Villellas et al. 2013). Instead, peripheral populations have been demonstrated to exhibit greater temporal variability in population growth rates (Villellas et al. 2013). Indeed, maximising transient amplification potential is considered a more beneficial strategy than prioritising long-term population growth for enhancing population persistence within unstable, marginal, environments (McDonald et al. 2016). Thus, whilst the subtropical *Acropora* spp. assemblage appears more viable under stable conditions, the temperate assemblage displays demographic strategies associated with the enhanced exploitation of more variable environments.

Peripheral populations inhabiting suboptimal or more varied environments compared to core populations are becoming increasingly crucial for species persistence under climate change (Valladares et al. 2014). The mechanisms behind the long-term viability of coral populations at higher latitudes have long been disputed (Beger et al. 2014). At higher latitudes, coral populations are susceptible to bioerosion (Nozawa et al. 2008), thermal stress (Kim et al. 2019, Cant et al. 2021b), and reproductive and genetic isolation (Thomas et al. 2017, Precoda et al. 2018, Nakabayashi et al. 2019), and are exposed to cooler, highly seasonal abiotic regimes and reduced irradiance (Yamano et al. 2012, Muir et al. 2015, Sommer et al. 2017). However, legacies of exposure to variable environments affords populations with greater adaptive capacity, as abiotic variability cultivates and filters the traits necessary for the tolerance of further disturbances (Kroeker et al. 2020). In higher-latitude subtropical and temperate coral communities, the maintenance of diverse gene pools largely relies on connectivity with up-current tropical reefs, a characteristic that is restricted in many of these systems (Noreen et al. 2009, Beger et al. 2014). However, sporadic larval supply into higher-latitude coral communities may benefit their adaptation to abiotic variability, preventing genetic swamping from lower-latitude communities that experience radically different selection pressures (Galipaud and Kokko 2020). However, as marginal populations become increasingly fragmented or isolated, their diminished genetic diversity may inhibit their durability within variable environments (Pearson et al. 2009). Thus, whilst we have demonstrated that coral populations could display the necessary demographic plasticity for exploiting more variable regimes, the continued success of high-latitude coral populations is likely to be contingent on continued support from core populations (Cant et al. 2021b).

The different strategies exhibited by corals at higher latitudes, compared to their tropical counterparts, could be explained by either inherent plasticity within the dynamics of coral populations, adaptation in response to selective processes or biological interactions. Without detailed genomic assessments, however, we are unable to evaluate whether adaptive processes are at play. We also must acknowledge here the omission of spatial measures within our modelling approach. The demographic traits of coral populations are closely tied to their morphological characteristics (Álvarez-Noriega et al. 2016). Considering the gradient in diversity and density that exists between tropical, subtropical and temperate coral communities (Harriott et al. 1994, Harriott and Banks 2002, Sommer et al. 2014), it is therefore logical that an increased availability of space may reveal traits in higher-latitude coral assemblages that would otherwise remain inhibited by intense competitive interaction.

In sessile communities, the spatial arrangement of hetero- and con-specific individuals influences the performance of coexisting populations (Buss and Jackson 1979, Hart and Marshall 2009, McWilliam et al. 2018). For instance, the spatial aggregation of species can inhibit the growth of more dominant individuals and facilitate the persistence of more inferior competitors (Idjadi and Karlson 2007, Álvarez-Noriega et al. 2020). Indeed, the spatial arrangement of reef communities does influence their resilience to coral–algal phase shifts (Brito-Millán et al. 2019). However, even within tropical reef assemblages, it is debated whether spatial aggregation occurs naturally at sufficient intensities for inhibiting competitive dominance (Alvarez-Noriega et al. 2018). Equally, previous spatially implicit assessments into the dynamics of reef systems following disturbance (Sandin and McNamara 2012, Brito-Millán et al. 2019) have focused at the functional group level, thereby masking the changing implications of competition and coexistence across the size spectrum of co-occurring individuals. Accordingly, whilst there is a clear and worthwhile need for implementing spatially implicit size-structured assessments of coral communities (Adler et al. 2010), our work here represents an important advancement in understanding coral population dynamics.

Decomposing latitudinal contrasts within vital rate patterns

The size structure of coral populations has considerable repercussions on their dynamics and interactions within their wider reef communities (Dietzel et al. 2020, Pisapia et al. 2020). The heightened amplification characteristics we observed in the temperate *Acropora* spp. assemblage were primarily supported by the survival and fragmentation patterns of larger individuals (Fig. 4). This pattern reflects our expectation that, with these temperate coral populations reliant on sporadic recruitment events, their endurance is conditional on the vital rates of existing colonies. Colony fragmentation is commonly observed within disturbed environments (Pisapia et al. 2019), and is a common trait amongst acroporid species, enabling the rapid colonisation of available substrate (Roth et al. 2013). Indeed, the growth of colony remnants following fragmentation has been shown to support faster rates of recovery in coral cover than the growth of recruits and younger colonies of equal size (Connell 1997). Along tropicalising coastlines, colonisation through individual fragmentation could prove particularly effective, with rising temperatures and grazing tropical migrants reducing macroalgal competition (Vergés et al. 2016, Kumagai et al. 2018), and limited accretion reducing the density of existing coral communities (Kleypas et al. 1999). However, increased fragmentation can imply the accumulation of smaller-sized colonies, to which has been attributed the diminishing capacity for coral populations to persist during recurrent climatic disturbances (Riegl et al. 2012, Riegl and Purkis 2015, Pisapia et al. 2019). Equally, investments into the process of fragmentation, and how it is utilised for growth and reproduction, differ across coral species (Kayal et al. 2015). Accordingly, variation in how coral taxa utilise fragmentation may represent a key determinant in delineating gradients in species composition across tropical–temperate transition zones.

It is not unusual for the dynamics of coral communities to revolve around the vital rates of the largest colonies (Dietzel et al. 2020), yet the reliance of the temperate *Acropora* spp. assemblage on the dynamics of larger individuals could render it sensitive to future climate shifts. In Japan, the frequency of severe typhoon storms is increasing (Hoshino et al. 2016). These storms are known to disproportionally impact upon the largest individuals within coral communities, particularly those with delicate tabular and branching structures such as *Acropora* spp. (Bries et al. 2004, Madin and Connolly 2006). During September 2018, Typhoon Jebi, possessing wind speeds upwards of 158 km h^{-1}, made landfall along the southern coastline of Shikoku Island (Mori et al. 2019). This storm caused considerable structural damage within the temperate coral communities of Kochi (Cant et al. unpubl.), and is deemed responsible for the decline in mean colony size we observed within the temperate *Acropora* spp. assemblage during 2019 (Supporting information). The dominance of larger-sized colonies in this temperate assemblage (Supporting information) suggests that this assemblage has successfully navigated past typhoon storms. However, with the intensity of future storms increasing (Hoshino et al. 2016), destructive events on the scale of Typhoon Jebi will become more frequent, possibly undermining the success of coral populations overly reliant on the characteristics of larger individuals.

Overall, differences between the transient dynamics of the subtropical and temperate *Acropora* spp. assemblages were underpinned by variation in the vital rate patterns of existing colonies. However, recruitment is a fundamental component in the dynamics and resilience of coral communities (Adjeroud et al. 2017). Accordingly, we observed that recruitment patterns actually exerted the largest absolute influence on the transient dynamics of the two assemblages, although this influence was masked by contrasting patterns in larval settlement and recruit survival (Fig. 4A). We observed that the settlement of *Acropora* spp. larvae was lower in the temperate region compared with the subtropics. With abiotic barriers limiting the dispersal and survival of coral larvae at higher latitudes this pattern is to be expected (Nakabayashi et al. 2019), despite the conflicting evidence of recent warming-induced increases in the densities of settling larvae at higher latitudes (Price et al. 2019). Intriguingly, though, we report that the survival of coral larvae following successful settlement appeared highest in the temperate region. Whilst consistent with expected density-dependent patterns in the survival of newly settled larvae (Cameron and Harrison 2020), our finding disagrees with previous reports of extremely high annual post-settlement larval mortality within higher- latitude environments (Wilson and Harrison 2005). Seawater temperatures at the time of settlement influence the survival of coral larvae (Randall and Szmant 2009). Equally, acroporid corals are known to be highly sensitive to cold shock (short-term exposure to cold temperatures; Roth et al. 2012). Therefore, with our assessment of recruitment patterns reliant on settlement plates and plot surveys occurring during boreal summer months, we acknowledge that our estimates of temperate recruit survival may represent overestimates arising from the inclusion of individuals yet to experience the selective pressures of cooler temperate seasons.

Conclusions

It is necessary to understand both the extent to which marginal populations can embrace environmental variation, and the mechanisms that underpin the success or failure of populations along range boundaries, if we are to anticipate the continued viability of crucial species, communities and ecosystems (Valladares et al. 2014, Merow et al. 2017). Equally, distinguishing how vital rate characteristics manifest under differing environmental regimes will help resolve the climate envelopes of different species and ecosystems, allowing for more accurate predictions of population persistence or collapse (Trisos et al. 2020). Climatic warming is facilitating the poleward expansion of coral populations into subtropical and temperate coastal ecosystems (Beger et al. 2014, Vergés et al. 2019). The dynamics of coral populations establishing within tropicalising environments offer valuable insights into the ability of coral communities for persisting within suboptimal habitats and adapting to future, more variable, climates (Camp et al. 2018). However, our lack of an appreciation for the demographic characteristics of coral populations and their abiotic drivers (Edmunds et al. 2014, Edmunds and Riegl 2020) inhibits our capacity for exploring these insights.

The transient dynamics of populations define their responses to disturbance, and ultimately their dynamics within variable environments (Hastings 2004, Stott et al. 2011, McDonald et al. 2016, Hastings et al. 2018). Transient demographic theory has advanced our understanding of invasive potential, allowing us to forecast the ability of species to establish populations outside their core range (Iles et al. 2016, Merow et al. 2017, Jelbert et al. 2019). We have illustrated here how the transient dynamics of coral populations coordinate their establishment at increasingly higher latitudes, mediating their response to enhanced seasonal variation. Equally, *Acropora* spp. assemblages in southern Japan display the demographic plasticity necessary for the continued exploitation of higher-latitude environments. However, with this work we have only begun to gather evidence of the mechanisms supporting the redistribution of coral populations. It is crucial we continue evaluating how patterns in the transient dynamics of coral populations translate across various species, and over broader spatial scales. Without improving current knowledge regarding the dynamics of coral populations we will be unable to predict the persistence and future reassembly of coral communities and their associated reef taxa (Edmunds and Riegl 2020, Pisapia et al. 2020, Cant et al. 2021a).

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Data availability statement

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.d7wm37q43> (Cant et al. 2022).

Supporting information

The Supporting information associated with this article is available with the online version.

References

Adjeroud, M. et al. 2017. Importance of recruitment processes in the dynamics and resilience of coral reef assemblages. – In: Rossi, S. et al. (eds), Marine animal forests: the ecology of benthic biodiversity hotspots. Springer International Publishing, pp. 549–569.

Adler, P. B. et al. 2010. Coexistence of perennial plants: an embarrassment of niches. – Ecol. Lett. 13: 1019–1029.

Álvarez-Noriega, M. et al. 2016. Fecundity and the demographic strategies of coral morphologies. – Ecol. Soc. Am. 97: 3485–3493.

Alvarez-Noriega, M. et al. 2018. Negligible effect of competition on coral colony growth. – Ecology 99: 1347–1356.

Álvarez-Noriega, M. et al. 2020. Disturbance-induced changes in size-structure promote coral biodiversity. – bioRxiv doi: 10.1101/2020.05.21.094797.

Angert, A. L. 2009. The niche, limits to species' distributions and spatiotemporal variation in demography across the elevation ranges of two monkeyflowers. – Proc. Natl Acad. Sci. USA 106: 19693–19698.

Antão, L. H. et al. 2020. Contrasting latitudinal patterns in diversity and stability in a high-latitude species-rich moth community. – Global Ecol. Biogeogr. 29: 896–907.

Archibald, S. B. et al. 2010. Seasonality, the latitudinal gradient of diversity and Eocene insects. – Paleobiology 36: 374–398.

Barlow, J. et al. 2018. The future of hyperdiverse tropical ecosystems. – Nature 559: 517–526.

Beger, M. et al. 2014. Conserving potential coral reef refuges at high latitudes. – Divers. Distrib. 20: 1–13.

Beissinger, S. R. and Westphal, M. I. 1998. On the use of demographic models of population viability in endangered species management. – J. Wildl. Manage. 62: 821–841.

Bramanti, L. et al. 2015. Using demographic models to project the effects of climate change on scleractinian corals: *Pocillopora damicornis* as a case study. – Coral Reefs 34: 505–515.

Bries, J. M. et al. 2004. Damage to the leeward reefs of Curaçao and Bonaire, Netherlands Antilles from a rare storm event: Hurricane Lenny, November 1999. – Coral Reefs 23: 297–307.

Brito-Millán, M. et al. 2019. Influence of aggregation on benthic coral reef spatio-temporal dynamics. – R. Soc. Open Sci. 6: 1–14.

Buss, L. W. and Jackson, J. B. C. 1979. Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. – Am. Nat. 113: 223–234.

Cameron, K. A. and Harrison, P. L. 2020. Density of coral larvae can influence settlement, post-settlement colony abundance and coral cover in larval restoration. – Sci. Rep. 10: 5488.

Camp, E. F. et al. 2018. The future of coral reefs subject to rapid climate change: lessons from natural extreme environments. – Front. Mar. Sci. 5: 1–21.

Cant, J. et al. 2021a. Transient demographic approaches can drastically expand the toolbox of coral reef science. – Coral Reefs 41: 885–896.

Cant, J. et al. 2021b. The projected degradation of subtropical coral assemblages by recurrent thermal stress. – J. Anim. Ecol. 90: 233–247.

Cant, J. et al. 2022. Data from: Transient amplification enhances the persistence of tropicalising coral assemblages in marginal high-latitude environments. – Dryad Digital Repository, <https://doi.org/10.5061/dryad.d7wm37q43>.

Capdevila, P. et al. 2020. Towards a comparative framework of demographic resilience. – Trends Ecol. Evol. 35: 776–786.

Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. – Oxford Univ. Press.

Caswell, H. 2019. Sensitivity analysis: matrix methods in demography and ecology. – Springer.

Connell, J. H. 1997. Disturbance and recovery of coral assemblages. – Coral Reefs 16: 101–113.

Crone, E. E. et al. 2011. How do plant ecologists use matrix population models? – Ecol. Lett. 14: 1–8.

Darling, E. S. et al. 2019. Social–environmental drivers inform strategic management of coral reefs in the Anthropocene. – Nat. Ecol. Evol. 3: 1341–1350.

Davidson, J. et al. 2019. High spatio-temporal variability in *Acroporidae* settlement to inshore reefs of the Great Barrier Reef. – PLoS One 14: e0209771.

Denis, V. et al. 2013. Coverage, diversity and functionality of a high-latitude coral community (Tatsukushi, Shikoku Island, Japan). – PLoS One 8: e54330.

Dietzel, A. et al. 2020. Long-term shifts in the colony size structure of coral populations along the Great Barrier Reef. – Proc. R. Soc. B 287: 20201432.

Doropoulos, C. et al. 2016. Characterizing the ecological trade-offs throughout the early ontogeny of coral recruitment. – Ecol. Monogr. 86: 20–44.

Easterling, M. R. et al. 2000. Size-specific sensitivity: applying a new structured population model. – Ecology 81: 694–708.

Edmunds, P. J. 2020. Vital rates of small reef corals are associated with variation in climate. – Limnol. Oceanogr. 66: 901–913.

Edmunds, P. J. and Riegl, B. 2020. Urgent need for coral demography in a world where corals are disappearing. – Mar. Ecol. Prog. Ser. 635: 233–242.

Edmunds, P. J. et al. 2014. Evaluating the causal basis of ecological success within the Scleractinia: an integral projection model approach. – Mar. Biol. 161: 2719–2734.

Ellis, M. M. and Crone, E. E. 2013. The role of transient dynamics in stochastic population growth for nine perennial plants. – Ecology 94: 1681–1686.

Ellner, S. P. and Rees, M. 2006. Integral projection models for species with complex demography. – Am. Nat. 167: 410–428.

Ezard, T. H. G. et al. 2010. Matrix models for a changeable world: the importance of transient dynamics in population management. – J. Appl. Ecol. 47: 515–523.

Fine, P. V. A. 2015. Ecological and evolutionary drivers of geographic variation in species diversity. – Annu. Rev. Ecol. Evol. Syst. 46: 369–392.

Fukami, H. et al. 2004. Conventional taxonomy obscures deep divergence between Pacific and Atlantic corals. – Nature 427: 829–832.

Galipaud, M. and Kokko, H. 2020. Adaptation and plasticity in life-history theory: how to derive predictions. – Evol. Hum. Behav. 41: 493–501.

Gilmour, J. et al. 2016. Coral reproduction in Western Australia. – PeerJ 4: e2010.

Hall, V. R. and Hughes, T. P. 1996. Reproductive strategies of modular organisms: comparative studies of reef-building corals. – Ecology 77: 950–963.

Harriott, V. J. and Banks, S. A. 2002. Latitudinal variation in coral communities in eastern Australia: a qualitative biophysical model of factors regulating coral reefs. – Coral Reefs 21: 83–94.

Harriott, V. J. et al. 1994. Patterns of coral community structure of subtropical reefs in the Solitary Islands. – Mar. Ecol. Prog. Ser. 109: 67–76.

Hart, S. P. and Marshall, D. J. 2009. Spatial arrangement affects population dynamics and competition independent of community composition. – Ecology 90: 1485–1491.

Hastings, A. 2001. Transient dynamics and persistence of ecological systems. – Ecol. Lett. 4: 215–220.

Hastings, A. 2004. Transients: the key to long-term ecological understanding? – Trends Ecol. Evol. 19: 39–45.

Hastings, A. et al. 2018. Transient phenomena in ecology. – Science 361: 990.

Healy, K. et al. 2019. Animal life history is shaped by the pace of life and the distribution of age-specific mortality and reproduction. – Nat. Ecol. Evol. 3: 1217–1224.

Hillebrand, H. 2004. On the generality of the latitudinal diversity gradient. – Am. Nat. 163: 192–211.

Hillebrand, H. et al. 2018. Biodiversity change is uncoupled from species richness trends: consequences for conservation and monitoring. – J. Appl. Ecol. 55: 169–184.

Hodgson, D. et al. 2015. What do you mean, 'resilient'? – Trends Ecol. Evol. 30: 503–506.

Hoegh-Guldberg, O. et al. 2017. Coral reef ecosystems under climate change and ocean acidification. – Front. Mar. Sci. 4: 158.

Hoshino, S. et al. 2016. Estimation of increase in storm surge damage due to climate change and sea level rise in the Greater Tokyo area. – Nat. Hazards 80: 539–565.

Hughes, T. P. et al. 2000. Supply-side ecology works both ways: the link between benthic adults, fecundity and larval recruits. – Ecology 81: 2241–2249.

Hughes, T. P. et al. 2017. Coral reefs in the Anthropocene. – Nature 546: 82–90.

Hughes, T. P. et al. 2018. Global warming transforms coral reef assemblages. – Nature 556: 492–496.

Idjadi, J. A. and Karlson, R. H. 2007. Spatial arrangement of competitors influences coexistence of reef-building corals. – Ecology 88: 2449–2454.

Iles, D. T. et al. 2016. Linking transient dynamics and life history to biological invasion success. – J. Ecol. 104: 399–408.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. – Am. Nat. 101: 233–249.

Jelbert, K. et al. 2019. Demographic amplification is a predictor of invasiveness among plants. – Nat. Commun. 10: 1–6.

Kayal, M. et al. 2015. Searching for the best bet in life-strategy: a quantitative approach to individual performance and population dynamics in reef-building corals. – Ecol. Complex. 23: 73–84.

Keyfitz, N. 1968. Introduction to the mathematics of population. – Addison-Wesley Publishing Co.

Kim, W. S. et al. 2019. Refugia under threat: mass bleaching of coral assemblages in high-latitude eastern Australia. – Global Change Biol. 25: 3918–3931.

Kitagawa, E. M. 1955. Components of a difference between two rates. – J. Am. Stat. Assoc. 50: 1168–1194.

Kleypas, J. A. et al. 1999. Environmental limits to coral reef development: where do we draw the line? – Am. Zool. 39: 146–15.

Koons, D. N. et al. 2016. A life-history perspective on the demographic drivers of structured population dynamics in changing environments. – Ecol. Lett. 19: 1023–1031.

Kroeker, K. E. et al. 2020. Ecological change in dynamic environments: accounting for temporal environmental variability in studies of ocean change biology. – Global Change Biol. 26: 54–67.

Kumagai, N. H. et al. 2018. Ocean currents and herbivory drive macroalgae-to-coral community shift under climate warming. – Proc. Natl Acad. Sci. USA 115: 8990–8995.

Layton-Matthews, K. et al. 2021. Environmental change reduces body condition, but not population growth, in a high-arctic herbivore. – Ecol. Lett. 24: 227–238.

Madin, J. S. and Connolly, S. R. 2006. Ecological consequences of major hydrodynamic disturbances on coral reefs. – Nature 444: 477–480.

Madin, J. S. et al. 2020. Partitioning colony size variation into growth and partial mortality. – Biol. Lett. 16: 1–5.

Maldonado-Chaparro, A. A. et al. 2018. Transient LTRE analysis reveals the demographic and trait-mediated processes that buffer population growth. – Ecol. Lett. 21: 1693–1703.

Mannion, P. D. et al. 2014. The latitudinal biodiversity gradient through deep time. – Trends Ecol. Evol. 29: 42–50.

McDonald, J. L. et al. 2016. Transients drive the demographic dynamics of plant populations in variable environments. – J. Ecol. 104: 306–314.

McWilliam, M. et al. 2018. Neighbor diversity regulates the productivity of coral assemblages. – Curr. Biol. 28: 3634–3639.

Merow, C. et al. 2017. Climate change both facilitates and inhibits invasive plant ranges in New England. – Proc. Natl Acad. Sci. USA 114: 1–9.

Mori, N. et al. 2019. 2018 Typhoon Jebi post-event survey of coastal damage in the Kansai region, Japan. – Coastal Eng. J. 61: 278–294.

Muir, P. et al. 2015. Limited scope for latitudinal extension of reef corals. – Science 348: 1135–1138.

Nakabayashi, A. et al. 2019. The potential role of temperate Japanese regions as refugia for the coral *Acropora hyacinthus* in the face of climate change. – Sci. Rep. 9: 1–12.

Nakamura, M. et al. 2015. Spatial variability in recruitment of acroporid corals and predatory starfish along the Onna coast, Okinawa, Japan. – Mar. Ecol. Prog. Ser. 540: 1–12.

Nishihira, M. and Veron, J. E. N. 1995. Hermatypic corals of Japan. – Kaiyusha, Tokyo. p. 439.

Noreen, A. M. E. et al. 2009. Genetic diversity and connectivity in a brooding reef coral at the limit of its distribution. – Proc. R. Soc. B 276: 3927–3935.

Nozawa, Y. et al. 2008. Structure and dynamics of a high-latitude scleractinian coral community in Amakusa, southwestern Japan. – Mar. Ecol. Prog. Ser. 358: 151–160.

Paniw, M. et al. 2018. Interactive life-history traits predict sensitivity of plants and animals to temporal autocorrelation. – Ecol. Lett. 21: 275–286.

Pearson, G. A. et al. 2009. Frayed at the edges: selective pressure and adaptive response to abiotic stressors are mismatched in low diversity edge populations. – J. Ecol. 97: 450–462.

Pecl, G. et al. 2017. Biodiversity redistribution under climate change: impacts on ecosystems and human well-being publication details. – Science 355: 1–9.

Pisapia, C. et al. 2019. Changes in the population and community structure of corals during recent disturbances (February 2016–October 2017) on Maldivian coral reefs. – Sci. Rep. 9: 8402.

Pisapia, C. et al. 2020. Projected shifts in coral size structure in the Anthropocene. – In: Riegl, B. M. (ed.), Advances in marine biology. Academic Press, pp. 31–60.

Precoda, K. et al. 2018. How does a widespread reef coral maintain a population in an isolated environment? – Mar. Ecol. Prog. Ser. 594: 85–94.

Price, N. N. et al. 2019. Global biogeography of coral recruitment: tropical decline and subtropical increase. – Mar. Ecol. Prog. Ser. 621: 1–17.

Purves, D. W. 2009. The demography of range boundaries versus range cores in eastern US tree species. – Proc. R. Soc. B 276: 1477–1484.

Randall, C. J. and Szmant, A. M. 2009. Elevated temperature reduces survivorship and settlement of the larvae of the Caribbean scleractinian coral, *Favia fragum* (Esper). – Coral Reefs 28: 537–545.

Richards, Z. T. and Hobbs, J. P. A. 2015. Hybridisation on coral reefs and the conservation of evolutionary novelty. – Curr. Zool. 61: 132–145.

Richards, Z. T. et al. 2016. Cryptic genetic divergence within threatened species of Acropora coral from the Indian and Pacific Oceans. – Conserv. Genet. 17: 577–591.

Riegl, B. and Purkis, S. 2015. Coral population dynamics across consecutive mass mortality events. – Global Change Biol. 21: 3995–4005.

Riegl, B. M. et al. 2012. Red Sea coral reef trajectories over 2 decades suggest increasing community homogenization and decline in coral size. – PLoS One 7: e38396.

Roth, L. et al. 2013. Tracking *Acropora* fragmentation and population structure through thermal-stress events. – Ecol. Model. 263: 223–232.

Roth, M. S. et al. 2012. Cold induces acute stress but heat is ultimately more deleterious for the reef-building coral *Acropora yongei*. – Sci. Rep. 2: 240.

Sagarin, R. D. and Gaines, S. D. 2002. The 'abundant centre' distribution: to what extent is it a biogeographical rule? – Ecol. Lett. 5: 137–147.

Sandin, S. A. and McNamara, D. E. 2012. Spatial dynamics of benthic competition on coral reefs. – Oecologia 168: 1079–1090.

Selwood, K. E. et al. 2015. The effects of climate change and land-use change on demographic rates and population viability. – Biol. Rev. 90: 837–853.

Sexton, J. P. et al. 2009. Evolution and ecology of species range limits. – Annu. Rev. Ecol. Evol. Syst. 40: 415–436.

Shlesinger, T. and van Woesik, R. 2021. Different population trajectories of two reef-building corals with similar life-history traits. – J. Anim. Ecol. 90: 1379–1389.

Sommer, B. et al. 2014. Trait-mediated environmental filtering drives assembly at biogeographic transition zones. – Ecology 95: 1000–1009.

Sommer, B. et al. 2017. Local and regional controls of phylogenetic structure at the high- latitude range limits of corals. – Proc. R. Soc. B 284: 20170915.

Sommer, B. et al. 2018. Differential response to abiotic stress controls species distributions at biogeographic transition zones. – Ecography 41: 478–490.

Stott, I. et al. 2011. A framework for studying transient dynamics of population projection matrix models. – Ecol. Lett. 14: 959–970.

Stott, I. et al. 2012. popdemo: an R package for population demography using projection matrix analysis. – Methods Ecol. Evol. 3: 797–802.

Thomas, L. et al. 2017. Restricted gene flow and local adaptation highlight the vulnerability of high-latitude reefs to rapid environmental change. – Global Change Biol. 23: 2197–2205.

Trisos, C. H. et al. 2020. The projected timing of abrupt ecological disruption from climate change. – Nature 580: 496–501.

Valladares, F. et al. 2014. The effects of phenotypic plasticity and local adaptation on forecasts of species range shifts under climate change. – Ecol. Lett. 17: 1351–1364.

Vergés, A. et al. 2014. The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. – Proc. R. Soc. B 281: 20140846.

Vergés, A. et al. 2016. Long-term empirical evidence of ocean warming leading to tropicalization of fish communities, increased herbivory and loss of kelp. – Proc. Natl Acad. Sci. USA 113: 13791–13796.

Vergés, A. et al. 2019. Tropicalisation of temperate reefs: implications for ecosystem functions and management actions. – Funct. Ecol. 33: 1000–1013.

Vermeij, M. J. A. et al. 2009. Survival and settlement success of coral planulae: independent and synergistic effects of macroalgae and microbes. – Oecologia 159: 325–336.

Veron, J. E. N. et al. 2016. Corals of the World. – <http://www.coralsoftheworld.org/page/home/>, accessed 12 Nov 2019.

Villellas, J. et al. 2013. Variation in stochastic demography between and within central and peripheral regions in a widespread short-lived herb. – Ecology 94: 1378–1388.

von Humboldt, A. 1808. Ansichten der Natur: mit wissenschaftlichen Erläuterungen. – J. G. Cotta.

Vucetich, J. A. and Waite, T. A. 2003. Spatial patterns of demography and genetic processes across the species' range: null hypotheses for landscape conservation genetics. – Conserv. Genet. 4: 639–645.

Williams, J. E. and Blois, J. L. 2018. Range shifts in response to past and future climate change: can climate velocities and species' dispersal capabilities explain variation in mammalian range shifts? – J. Biogeogr. 45: 2175–2189.

Williams, J. L. et al. 2012. Avoiding unintentional eviction from integral projection models. – Ecology 93: 2008–2014.

Willig, M. R. et al. 2003. Latitudinal gradients of biodiversity: pattern, process, scale and synthesis. – Annu. Rev. Ecol. Evol. Syst. 34: 273–309.

Wilson, J. and Harrison, P. 2005. Post-settlement mortality and growth of newly settled reef corals in a subtropical environment. – Coral Reefs 24: 418–421.

Yamano, H. et al. 2012. Coral reefs at 34°N, Japan: exploring the end of environmental gradients. – Geology 40: 835–838.

Zuidema, P. A. et al. 2010. Integral projection models for trees: a new parameterization method and a validation of model output. – J. Ecol. 98: 345–355.