A long-term conservation benefit of protected areas in stochastic population dynamics

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Abstract

Terrestrial and marine protected areas have been essential tools to mitigate anthropogenic impacts and promote population persistence and resource sustainability. Adequately implemented protected areas promote a long-term conservation benefit. Stochasticity affects its long-term performance, and necessary to understand the general influence. Here, we investigate a long-term conservation benefit via stochastic models that encompass demographic or environmental stochasticity. We quantify a long-term conservation benefit by the coefficient of variation (CV) of population size in protected areas, where a low CV indicates high robustness against stochasticity. We demonstrate that adequately implemented protected areas promote a long-term conservation benefit under stochasticity and decrease otherwise. However, demographic and environmental stochasticity induce rather different consequences, although the former is suppressed with the population size. Multiple parameters in our framework determine the quality of protected areas, and systematic investigations for various scenarios facilitate an effective management decision.

Keywords: Ecosystem management, marine protected areas, population fluctuation, protected areas, stochastic models

1 Introduction

Terrestrial and marine protected areas have been expanding worldwide in response to increasing concern of species loss. These have been essential tools to mitigate anthropogenic impacts and promote population persistence, and resource sustainability [17,27,37]. Strategic site selection is often favored to fulfill a long-term conservation benefit [21, 26, 36]. Therefore, adequate evaluation of a long-term benefit of protected areas (PAs) is critical to ensure efficient and effective implementations.

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Discussions based on equilibrium status are straightforward to discuss a long-term benefit of PAs (e.g., [13, 24, 31]) that assumes populations approach to an equilibrium state after a long period of time since the implementation of PAs. This usefulness is evident as this characterizes an expected performance, and the concept is common in conservation practice and ecosystem management (e.g., [4, 14]). Alternatively, discussions based on temporal variation of PAs have been proven its utility [23]. In practice, population undergoes various stochasticity due to demographic and/or environmental noise [18, 25], and ecological status variates from an expected value. Consequently, PAs' performance fluctuates over time (Fig. 1a). The long-term PAs performance can be discussed by taking this effect into account (Fig. 1b).

In practice, long-term field observation is highly costly and, hence, there are limited time-series data available [11]. Instead, modeling is powerful machinery to effectively explore such a long-term effect. Most of modeling frameworks integrating stochastic effect on PAs performance are from the context of marine protected areas (MPAs) (e.g., [2, 15]) that is often associated with fisheries management with a focus on optimal harvesting strategy [5], tradeoffs between conservation benefit vs. fisheries profit [7,20], population persistence [2,39], and resilience [1, 3, 38]. Previous numerical studies suggest MPAs can reduce stochastic variations. Barnett and Baskett [3] demonstrated that by assuming stochastic recruitments in predatory fish species, the coefficient of variation in the catch is reduced in fisheries management with MPAs. With a case study of metapopulation dynamics in Great Barrier Reef Marine Park, Hopf et al. [15] demonstrated marine reserves could promote stability of population and fisheries yields regardless of fishing intensity. However, more variant outcomes may also occur if disturbed reefs are protected rather than protecting undisturbed sites.

Here, we intend to develop general insights into a long-term performance of PAs; hence we do not restrict our discussions to fisheries management either to the marine environment, unlike existing studies. Especially, the following questions have not sufficiently investigated but essential to further improve our insights: (i) when do PAs provide persistent conservation benefit; (ii) does the effectiveness of PAs affect performance; and (iii) do demographic and environmental stochasticity affect differently? We also intend to develop analytical understanding that are of extra benefits and is currently largely limited.

In the paper, we address these questions using a spatially-explicit stochastic population model where we begin with individual processes described by a master equation. We measure the time variations of PA performance via the coefficient of variations (CV) where a smaller value indicates robust and persistent performance against stochasticity, and *vice versa*. In the model, the focal region has two categories; PAs and non-PAs. Immigrations to PAs and emigrations from PAs of individuals connect these areas. The sizes and site preferences affect the likelihood of individual migration. Inhomogeneous mortality rates and sizes in the two regions induce different growth rates and carrying capacities (Fig. 2), which characterizes the "goodness" of PAs. Our master equation approach allows us to derive a concrete analytical insight when population size remains fixed. We then discuss a more general situation where demographic stochasticity occurs in birth, death, and migration events. We also

made explicit the connection to existing deterministic models, and, using this, we introduce stochastic differential equations with environmental stochasticity.

This approach enables us to discuss a long-term conservation benefit of PAs under stochasticity. Multiple parameters determine the quality of PAs, and we can examine various biological and management scenarios. Our approach offers us an opportunity to discuss effective PAs implementations under stochastic population dynamics.

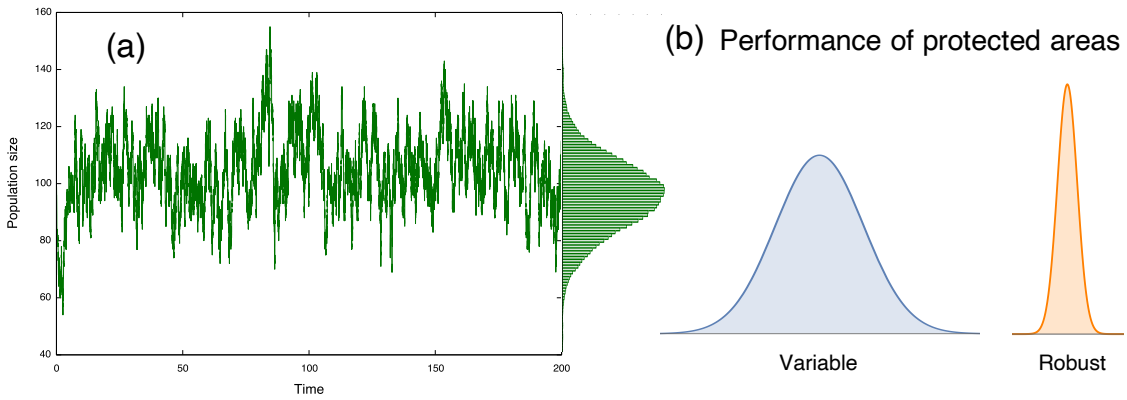

Figure 1: (a) Population size in protected areas show variations over time; and (b) such variations characterizes a long-term performance of protected areas. A large variation indicates the performance is variable over time, while a small variation provides a persistent performance.

2 Methods

We outline the general model scheme in Figure 2. In the model, the density-independent mortality rates in PA and non-PAs distinguish the two areas, and this causes different growth rates r_i and carrying capacities K_i in the two areas. When PAs have a higher growth rate than non-PAs, it is possible to swap the definition of the two areas. That is, one can regard the area having a lower growth rate as PAs, and discuss the effect of "poorly implemented" PAs. In the following, we will provide results in both PAs and non-PAs, and the discussion of "good" PAs encompasses "poor" PAs.

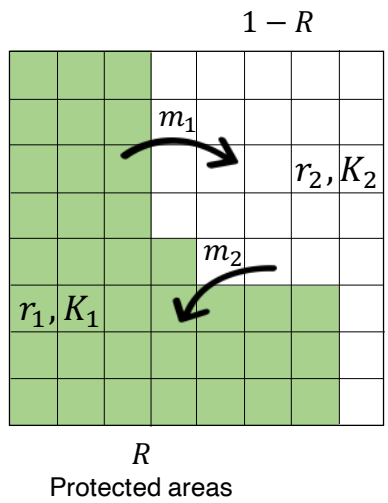

Figure 2: The region has two categories: protected area (fraction R; green) and non-protected area (fraction 1-R; white). The emigration from protected area (at rate m_1) and the immigration (at rate m_2) to protected areas exchange individuals between the areas. Each area is characterized intrinsic growth rate r_i and the carrying capacity K_i ($i = 1, 2$), and site preference affects the likelihood of individual migration (see the main text).

2.1 Population dynamics with fixed population size

We begin with a simple situation where the population dynamics of a focal species are driven by immigration to PAs and emigration from PAs of individuals, and not birth and death events occur. Each area has a site preference, and it affects the realized migration rate. Detailed technical discussions are found in Appendix A.1.

The number of individuals remains fixed to N, and we write the population sizes in PAs and non-PAs as n and $N - n$, respectively. Let $p(n, t)$ be the probability of n individuals located in PAs at time t. Then the population dynamics can be described by a simple gain–loss process (Appendix A.1)

$$\frac{dp(n,t)}{dt} = g_{n-1}p(n-1,t) + l_{n+1}p(n+1,t) - (g_n + l_n)p(n,t), \tag{1}$$

where, g_n and l_n are the gain and loss rates corresponding to one individual gain and loss in PAs, respectively. Let N_s and n_s be the number of total sites, and sites with a category of "protected area", respectively, and $R = n_s/N_s$ be the PAs fraction in the concerned region (Fig. 2). Only immigrations and emigrations of individuals drive population changes in PAs, and the gain and loss terms become

$$g_n = m_2(N-n)R^\alpha, \tag{2a}$$

$$l_n = m_1 n \left(1 - R^\alpha\right), \tag{2b}$$

where, m_1 and m_2 are the emigration and immigration rates, respectively. The parameter α controls the preference of PAs, accounting for preferred/non-preferred/neutral site by the species (Fig. A.1). Neutral preference ($\alpha = 1$) means that the destination of an individual on the move is determined randomly with weights of the sizes of PAs and noon-PAs. When PAs are preferred ($\alpha < 1$) or non-preferred ($\alpha > 1$) region by the species, the probability of choosing the PAs is higher or lower than the neutral choice, respectively.

2.2 Population dynamics under demographic stochasticity

When birth and death occur in the population, the total population number N is no longer constant, and it is the sum of the population sizes in PAs n_1 and non-PAs n_2: $N = n_1 + n_2$. PAs and non-PAs cause a density-independent mortality at rate d_1 and d_2, respectively. When the population size dynamically changes due to birth, death, and migrations, Eq. (1) becomes, with a concise description (Appendix A.2)

$$\frac{dP(\mathbf{n},t)}{dt} = \sum_{\mathbf{r}} W(\mathbf{n} \mid \mathbf{n}-\mathbf{r})P(\mathbf{n}-\mathbf{r},t) - \sum_{\mathbf{r}} W(\mathbf{n}-\mathbf{r} \mid \mathbf{n})P(\mathbf{n},t) \tag{3}$$

where $W(\mathbf{n} \mid \mathbf{m})$ is the transition rate from state $\mathbf{m}$ to state $\mathbf{n}$, and these are

$$W(n_1+1, n_2 \mid n_1, n_2) = bn_1, \tag{4a}$$
$$W(n_1, n_2+1 \mid n_1, n_2) = bn_2, \tag{4b}$$
$$W(n_1-1, n_2 \mid n_1, n_2) = d_1 n_1 + \frac{d}{R} n_1^2, \tag{4c}$$
$$W(n_1, n_2-1 \mid n_1, n_2) = d_2 n_2 + \frac{d}{1-R} n_2^2, \tag{4d}$$
$$W(n_1-1, n_2+1 \mid n_1, n_2) = m_1 n_1 \left(1 - R^{\alpha}\right), \tag{4e}$$
$$W(n_1+1, n_2-1 \mid n_1, n_2) = m_2 n_2 R^{\alpha}, \tag{4f}$$

where, the factors R and $1-R$ in Eqs. (4c) and (4d), respectively, account for the size of PAs and non-PAs with the density-dependent mortality rate d. This induces a larger density-dependent mortality in a smaller region.

We observe connections to existing deterministic models, by deriving a deterministic representation of Eq. (3). With multiplying by n_1 both sides and summing over all probabilities, we recover a deterministic two-patch dynamics (Appendix A.2) discussed, for example, in [32, 33] with some arrangements.

2.3 Population dynamics under environmental stochasticity

We next introduce a stochastic model incorporating environmental stochasticity. This can be obtained from the representation of stochastic differential equations (SDEs) [18,35]. Provided by the deterministic dynamics of Eq. (3) (Appendix A.2) and continuous variables X_i

representing the population size in PAs ($i = 1$) and non-PAs ($i = 2$), we can write the SDEs [10]:

$$\begin{aligned} dX_1 &= M_1(X_1, X_2)dt + \sigma_e X_1 dW(t), \\ dX_2 &= M_2(X_1, X_2)dt + \sigma_e X_2 dW(t) \end{aligned} \tag{5}$$

where M_i corresponds to the deterministic part of the population dynamics in region i (Eq. A.19), and σ_e is the intensity of environmental stochasticity.

3 Results

3.1 Long-term PAs performance with a fixed population size

When population changes in PAs are sorely due to migrations between PAs and non-PAs, we can obtain analytical insights that are not possible for more general situations discussed below. Later, we show that analytical insights from this simple situation can applied to more general situations.

In the model, we can derive explicit forms of the mean and the CV in PAs as follows (Appendix A.1)

$$\mathrm{E}[n] = \frac{N m_2}{m_1 \left(\left(\frac{n_s}{N_s} \right)^{-\alpha} - 1 \right) + m_2}, \tag{6a}$$

$$\mathrm{CV} = \sqrt{\frac{(1 - R^\alpha)\, m_1}{N R^\alpha m_2}}. \tag{6b}$$

The parameter dependence on the CV in PAs is analyzed by differentiating Eq. (6b) with respect to a parameter of interest. For example, we have $\partial \mathrm{CV}/\partial m_2 < 0$ and $\partial \mathrm{CV}/\partial \alpha > 0$, and these mean that an increase the values in the immigration rate to PAs m_2 and the site preference of PAs α, decreases and increases the CV, respectively. In addition, we conclude that an increase of the PA fraction always decreases the CV in PAs due to $\partial \mathrm{CV}/\partial R < 0$. Fig. 3 represents the relationship of Eqs. (6), and this confirms the discussions above.

We see that the CV in PAs can be described only by the population size in PAs, n, and the total population size, N (Appendix A.1). This indicates that the larger population size in PAs gets, the smaller its CV results. Hence, we conclude here that any parameters improving the population size in PAs reduce its CV.

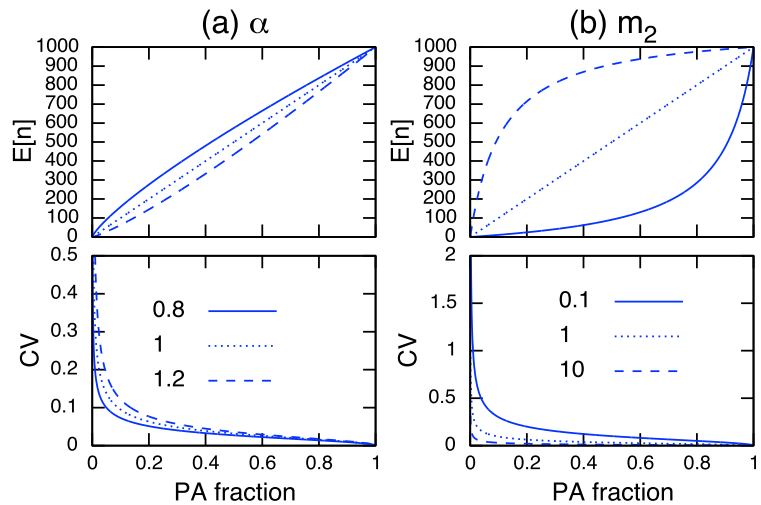

Figure 3: Parameter dependence on E[n] (top) and the CV in protected areas (bottom) of site preference α (left) and; of immigration rate to protected areas m_2 (right). Other parameter values used are $N = 1000$, $m_1 = 1$ (left) and $\alpha = 1$ (right).

3.2 Long-term PAs performance under demographic stochasticity

When birth and death events occur in addition to migrations, the total population size dynamically changes. Although this situation is not amenable to mathematical analysis due to nonlinearlity in the demographic rate terms, numerical simulations imply that we can still discuss in a similar line with the analytical discussions above. For instance, Fig. 4a and b show that the parameter dependence of the site preference α, the immigration rate to PAs m_2, and the PA fraction on the CV in PAs are qualitatively similar to that of the fixed-population scenario (Fig. 3).

For the dependence of demographic parameters, we can use the rules of thumb obtained in the preceding analysis. That is, changes of parameter values to increase the population size in PAs reduces its CV (Fig. 4, c,d). This can be heuristically seen by using the result in the preceding analysis (Appendix A.1) where a larger population size in PAs, n_1, leads to a smaller CV in PAs, while the magnitude of the population size in non-PAs, n_2, scales the CV:

$$\mathrm{CV} \propto \sqrt{\frac{n_2}{n_1 N}}. \tag{7}$$

Generally speaking, expanding PAs increases the population size in PAs and decreases that in non-PAs. If a conservation benefit of PAs is sufficient, it also improves the total population size N. These lead to a smaller value in the CV in PAs with the PA fraction (Fig. 4).

Fig. A.2 shows the results in non-PAs and the whole region concerned, and we observe an opposite trend from that in PAs: increasing the PA fraction increases the CV in non-PAs,

associated with a population decline in the region. Also, the total population size determines the CV in the whole region.

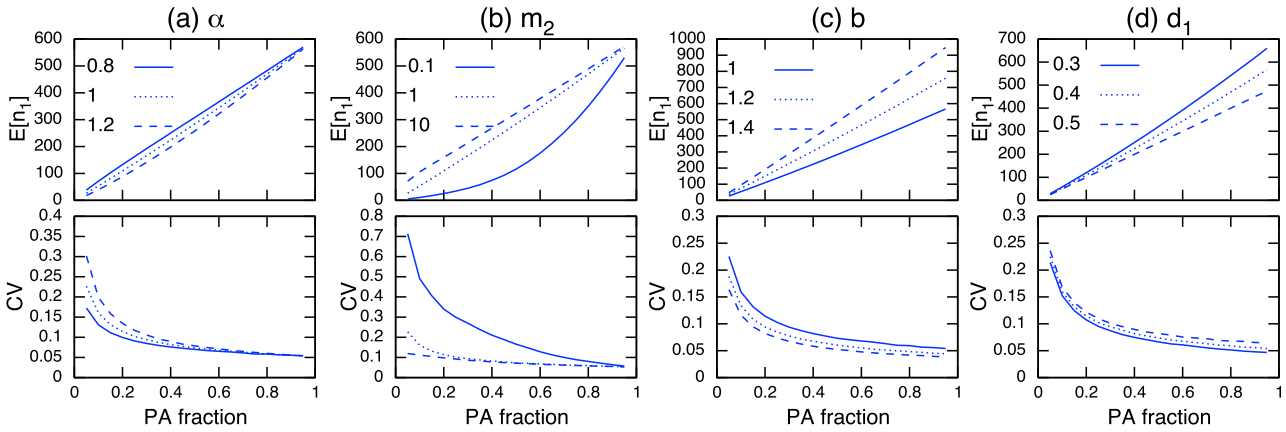

Figure 4: Parameter dependence on E[n_1] (top) and CV in protected areas (bottom) under demographic stochasticity. A parameter examined is specified on the top of each column. Other parameter values used (unless specified) are $b = 1$, $d = 0.001$, $d_1 = 0.4$, $d_2 = 0.5$, $m_1 = 1$, $m_2 = 1$, and $\alpha = 1$.

3.3 Long-term PAs performance under environmental stochasticity

Environmental stochasticity affects the whole population and the influence does not vanish even with large population size, unlike demographic stochasticity. Under environmental stochasticity, the rules of thumbs discussed above are no longer useful, and interpretations of results become intricate. For example, increasing the PA fraction and population size in PAs do not guarantee the reduction of its coefficient of variation, but it can increase (Fig. 5b; m_2=0.1 and 10). However, it has an effect to reduce the CV when $m_2 = 1.0$. Similarly, the site preference α also shows complex responses in the effect on the CV in PAs (Fig. 5a), and PAs with a higher preference may increase the CV with the PA fraction (Fig. 5a; $\alpha = 0.8$ and the PA fraction $R < 0.2$).

An establishment of PAs is likely to decrease the CV in PAs if a conservation benefit of PAs is increased by reducing the density-independent mortality rate in PAs, d_1 (Fig. 5d). Increasing the birth rate, b (a focal species has a high fecundity rate) shows a similar effect and it tends to decrease the CV regardless of the PA fraction (Fig. 5c). However, a larger birth rate decreases the conservation effects of PAs (e.g., the relative difference of the net growth rate of PA and non-PAs $(b - d_1)/(b - d_2)$ is decreased with b increased), and the effect of reducing the CV in PAs becomes smaller.

These numerical observation can be verified analytically when the immigration and emigration rates are sufficiently large ($m_1, m_2 \gg 1$). In this condition, the CV in PAs is described as (Appendix A.3)

$$\mathrm{CV} = \left(1 - \frac{\sigma_e^2}{2\hat{r}}\right)^{-\frac{1}{2}}. \tag{8}$$

where $\hat{r}$ can be interpreted as an average population growth rate in the whole region concerned weighted by the site preference (α). From Eq. (8), we conclude that an increase the PAs fraction decreases the CV in PAs if the growth rate in PAs is larger than that in non-PAs ($b - d_1 > b - d_2$), and *vice versa*. We also found that a small PA size has a large effect of reducing the CV when the site preference of PAs is higher than non-PAs ($\alpha < 1$), and *vice versa* (Appendix A.3).

Results in non-PAs and the whole region concerned are also provided in Fig. A.3, but trends in the CVs in these cases are not largely distinctive from PAs. This highlights the difference from the situations under demographic stochasticity (Figs. 4 and A.2; bottom) where trends of population sizes and CVs are opposite between the two areas. This may be because environmental stochasticity affects all individuals regardless of the population size, and the stochastic influence tends to be consistent across the whole region. Also, the CV in the whole area is more likely to be reduced with the total population size (Fig. A.3). However, it is not the case when the immigration rate is large (Fig. A.3f; $m_2 = 10$).

When PAs provide a higher conservation benefit $d_1 = 0.1$, the trend to increase the CV in PAs would be mitigated (Fig. A.4b; $m = 0.1$, 10), or reversed (Fig. A.4a; $\alpha = 0.8$). We also examined a situation with a higher environmental stochasticity $\sigma_e^2 = 0.3$ and confirmed qualitatively similar results (Fig. A.5).

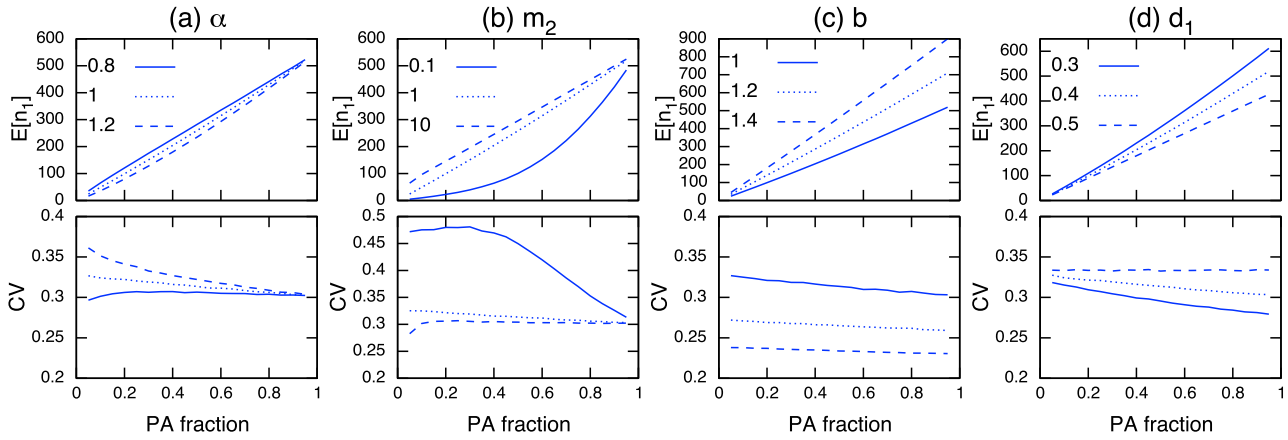

Figure 5: Parameter dependence on E[n_1] (top) and CV in protected areas (bottom) under environmental stochasticity. A parameter examined is specified on the top of each column. Other parameter values used (unless specified) are $b = 1$, $d = 0.001$, $d_1 = 0.4$, $d_2 = 0.5$, $m_1 = 1$, $m_2 = 1$, $\alpha = 1$, and $\sigma_e^2 = 0.1$.

4 Discussion

A multitude of indices can characterize the performance of PAs [19]. Here, we discuss a long-term conservation benefit of PAs under stochasticity that is beyond an equilibrium discussion. We measured a long-term PAs performance via the coefficient of variation (CV) of the population size where PAs with a small CV offers less variant; hence, persistent conservation benefit. Loosely speaking, we find the CV in PAs is suppressed by increasing its area if PAs provide sufficient conservation benefit. Hence, the implementation of effective PAs promotes a long-term conservation benefit. This general finding agrees with previous studies focused on the marine environment [3, 15, 23].

The demographic stochasticity is suppressed with a large population size [18]. Therefore, if PAs increase the population size by, for example, expanding its size or increasing the immigration probability (Figs. 3, 4a, b), or reducing the mortality rate (Fig. 4d), population fluctuations are suppressed; mechanisms for achieving persistent conservation benefit. Moreover, if PAs increase the total population size in the focal region, fluctuations in the population are also suppressed by the same mechanism (Fig. A.2e-h). Our master equation approach allows us to derive a concrete analytical insight when population size remains fixed; an assumption that a target species has a low growth rate compared to a timescale of a conservation program. In fact, many conservation practices concern with a much shorter timescale than ecological time scales [9, 40].

Instead, environmental stochasticity affects all individuals, and the population size plays a minor role in determining a long-term conservation benefit (Fig. 5a, b, and d). However, if

the conservation effect of PAs is high (e.g., mortality is sufficiently reduced in PAs), expanding PAs tends to reduce the CV. Equivalently, the CV in PAs is increased by introducing ineffective PAs (e.g., mortality is not sufficiently reduced or increased in PAs). In addition, if PAs increase the total population size in the whole region concerned, it tends to reduce the CV in the whole region (Fig. A.3) except for the situations with a high immigration rate where the opposite trend is observed (e.g., Fig. A.3f; $m_2 = 10$).

We identify different mechanisms to enhance the population size in PAs such as those to improve demographic rate (i.e., birth b and death d_1), and those to promote the probability of staying in PAs (i.e., site preference α, emigration m_1, and immigration m_2 rates). In practice, if PAs adequately regulate anthropogenic activities and is monitored (e.g., strict nature reserve [17]), it may improve the demographic rate in PAs and, hence, provide a long-term conservation benefit under demographic/environmental stochasticity. However, ineffective PAs managements are often associated with failure to reduce human activities [6, 29], which may amplify population fluctuation. The immigration and emigration rates are not purely biological parameters but can be controlled by the configuration of PAs [32]. Protecting favored sites by a target species is desirable to increase conservation benefit in PAs [16]. However, when MPAs are used for a sustainable fisheries management tool, a moderate spillover effect is necessary to promote fishing yields [22,30]. Under environmental stochasticity, these can lead to the reduced long-term benefit of PAs, and careful assessment is necessary.

MPAs can improve the resilience of populations under existing multiple stable states [1,3,34]. Our findings further complement this insight. Namely, while a catastrophic shift of population is incurred by population perturbation [28], adequately established PA tends to suppress population fluctuations (i.e., the population is more robust against perturbation). Therefore, the population with PAs is more likely to stay in the basin of attraction of a current stable state. A more explicit discussion addressing the relationships between the CV of the population dynamics, the strength of perturbations, and the basin of attraction will further improve our understanding.

Likewise, there are multiple directions for further extending our analysis. For example, here, we assumed that environmental stochasticity affects PAs and non-PAs equally. While this is reasonable when the concerned region is small, and the environment is not different between the areas, two areas may undergo other environmental fluctuations otherwise [12]. In fact, the size of an MPA sometimes becomes significant [8], and our model needs to incorporate heterogeneous environmental stochasticities. Age and metapopulation structures have been used in the context of fisheries management [15], and these investigations are also worthy in our context. However, one should be noted that applying complex models come with a large cost to reduce generality and analytical intractability. With this care in mind, our approach will guide developing a general framework to discuss a long-term conservation benefit of PAs.

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Electronic supplementary material:

A long-term conservation benefit of protected areas in stochastic population dynamics by Nao Takashina

Appendix Figures

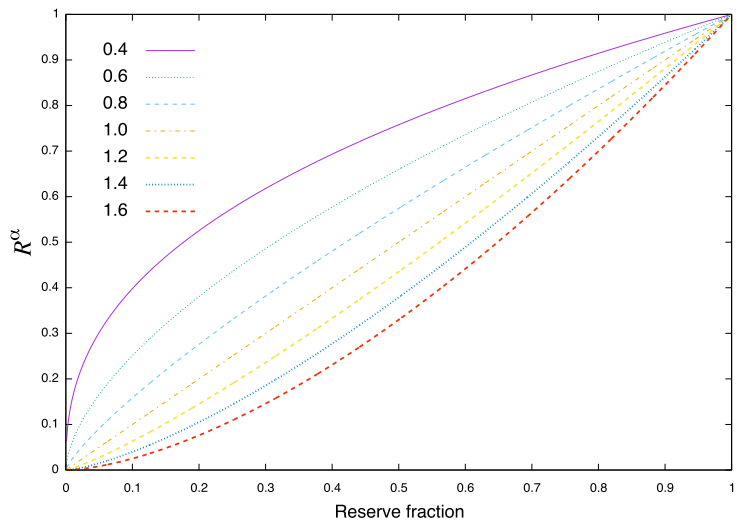

Figure A.1: Effect of the site preference α on the probability of the immigration to protected areas given the fraction of protected areas R. When $\alpha = 1$, the migration occurs at random.

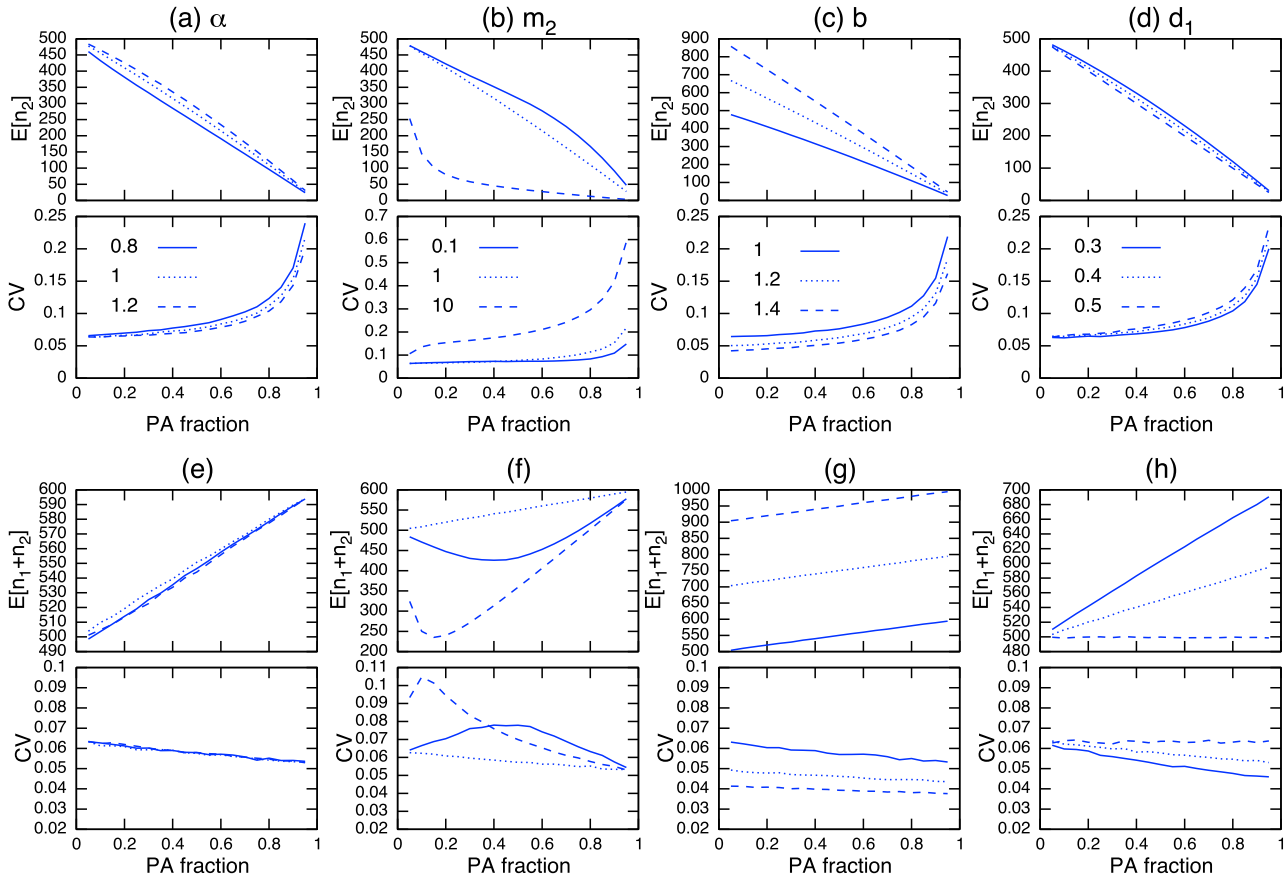

Figure A.2: Parameter dependence on E$[n_2]$ and CV of n_2 (a-d); and E$[n_1 + n_2]$ and CV of $n_1 + n_2$ (e-h) under demographic stochasticity. A parameter examined is specified on the top of each column. Other parameter values used (unless specified) are $b = 1$, $d = 0.001$, $d_1 = 0.4$, $d_2 = 0.5$, $m_1 = 1$, $m_2 = 1$, and $\alpha = 1$.

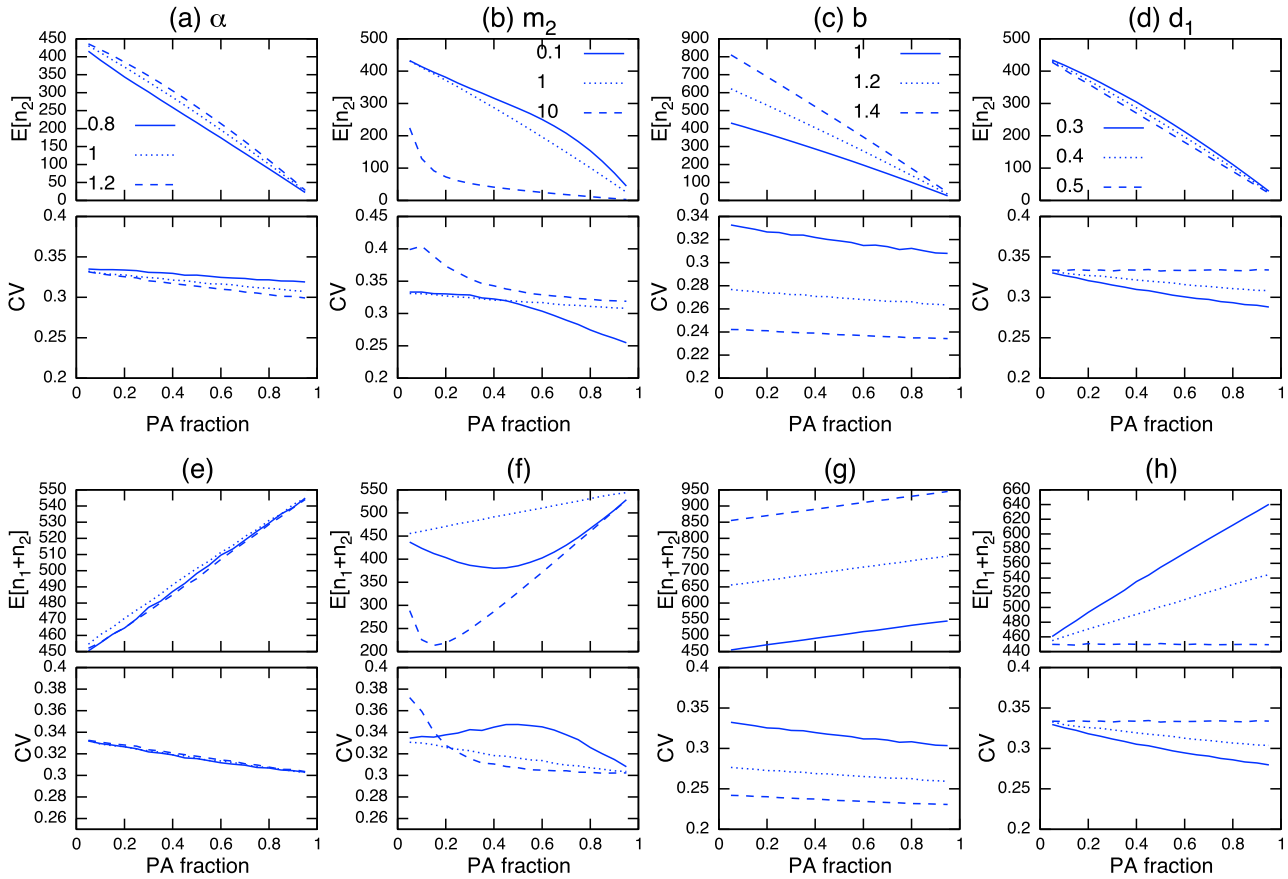

Figure A.3: Parameter dependence on E$[n_2]$ and CV of n_2 (a-d); and E$[n_1 + n_2]$ and CV of $n_1 + n_2$ (e-h) under environmental stochasticity with the intensity $\sigma_e^2 = 0.1$. A parameter examined is specified on the top of each column. Other parameter values used (unless specified) are $b = 1$, $d = 0.001$, $d_1 = 0.4$, $d_2 = 0.5$, $m_1 = 1$, $m_2 = 1$, and $\alpha = 1$.

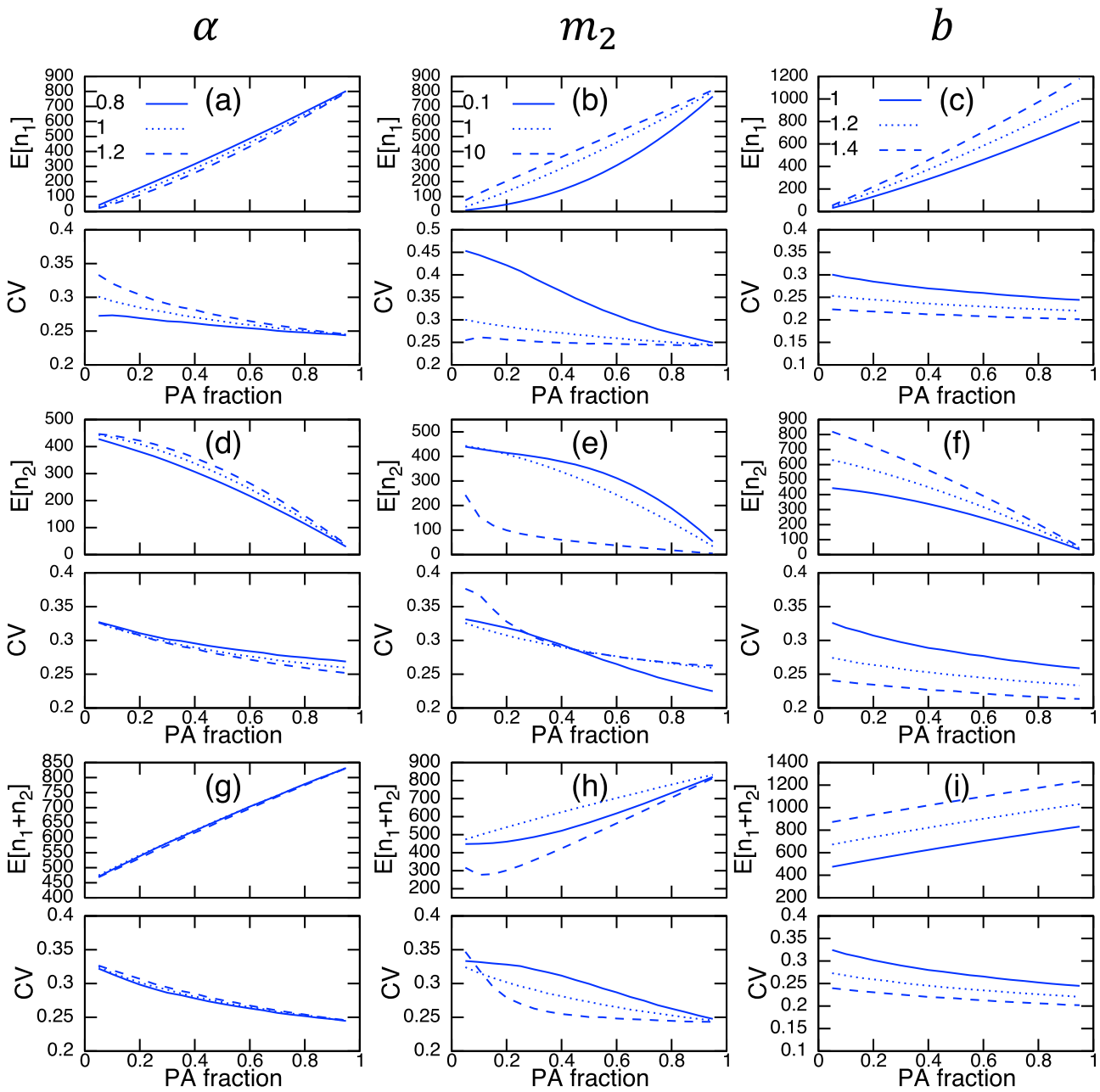

Figure A.4: Parameter dependence on E$[n_1]$ and CV of n_1 (a-c); E$[n_2]$ and CV of n_2 (d-f); and E$[n_1 + n_2]$ and CV of $n_1 + n_2$ (g-i) under environmental stochasticity with the intensity $\sigma_e^2 = 0.1$. A parameter examined is specified on the top of each column. Other parameter values used (unless specified) are $b = 1$, $d = 0.001$, $d_1 = 0.1$, $d_2 = 0.5$, $m_1 = 1$, $m_2 = 1$, and $\alpha = 1$.

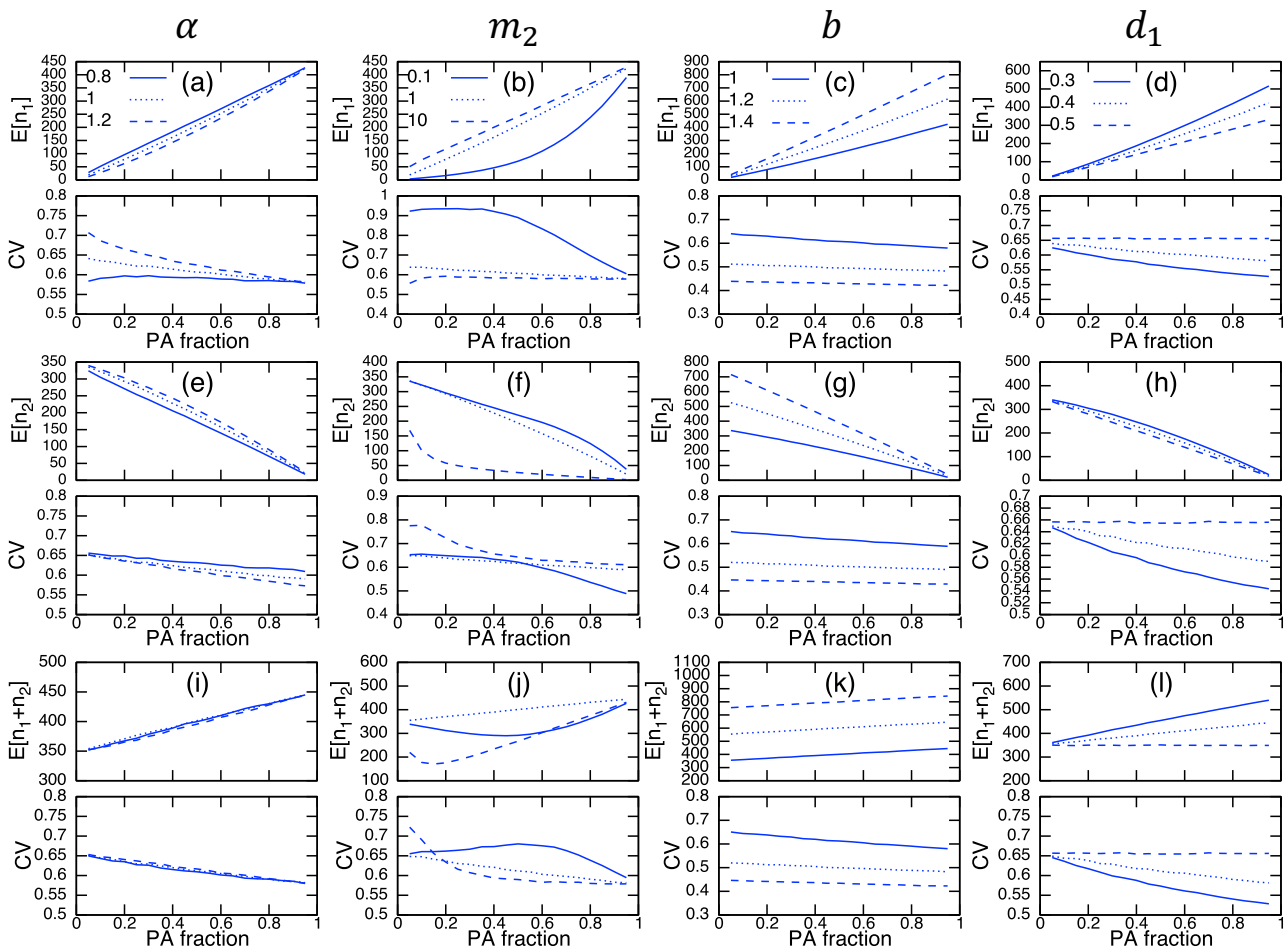

Figure A.5: Parameter dependence on E[n_1] and CV of n_1 (a-d); E[n_2] and CV of n_2 (e-h); and E[$n_1 + n_2$] and CV of $n_1 + n_2$ (i-l) under environmental stochasticity with the intensity $\sigma_e^2 = 0.3$. A parameter examined is specified on the top of each column. Other parameter values used (unless specified) are $b = 1$, $d = 0.001$, $d_1 = 0.4$, $d_2 = 0.5$, $m_1 = 1$, $m_2 = 1$, and $\alpha = 1$.

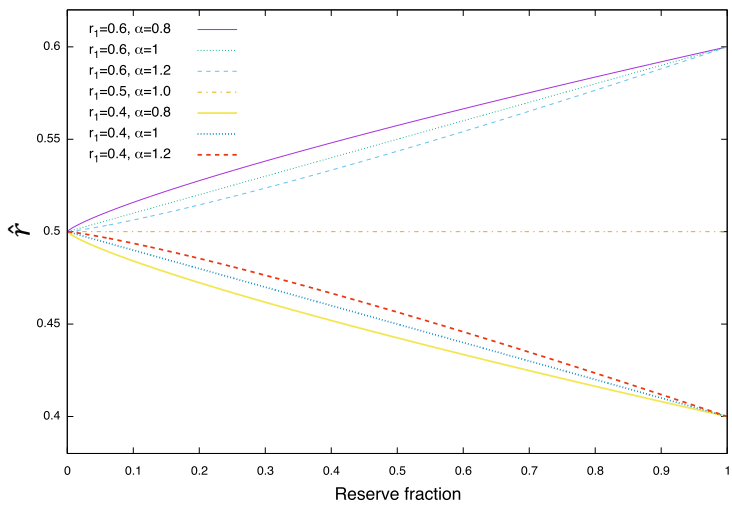

Figure A.6: Parameter dependence on $\hat{r}$ (Eq. A.23a). We set $r_2 = 0.5$.

Appendix

A.1 Population dynamics with fixed population size

We begin with a simple situation where the population dynamics of a focal species are driven by immigration to protected areas (PAs) and emigration from PAs of individuals, and not by birth and death events. Each area has a site preference, and it affects the realized migration rate between the two areas. Let $p(n,t)$ be the probability of n individuals located in PAs at time t. Then the population change is described by the following relationship:

$$p(n, t+\Delta t) = \Delta t g_{n-1} p(n-1,t) + \Delta t l_{n+1} p(n+1,t) + (1 - \Delta t(g_n + l_n))p(n,t), \tag{A.1}$$

where, g_n and l_n are the gain and loss probability corresponding to a gain and a loss of an individual in PAs. Eq. (A.1) leads to the following gain–loss process

$$\frac{dp(n,t)}{dt} = g_{n-1}p(n-1,t) + l_{n+1}p(n+1,t) - (g_n + l_n)p(n,t). \tag{A.2}$$

Let N_s and n_s be the total sites and PA sites, respectively, and define the PA fraction as $R = n_s/N_s$. Then an individual gain and loss are due to immigrations and emigrations, and the gain and loss terms become

$$g_n = m_2(N-n)R^{\alpha}, \tag{A.3a}$$
$$l_n = m_1 n\left(1 - R^{\alpha}\right), \tag{A.3b}$$

where, m_1 and m_2 are the emigration and immigration rates, respectively. The parameter α controls the preference of PAs. From Eq. (A.3b), we see $l_0 = 0$. By setting $dp/dt = 0$ in Eq.

(A.2), we get a stationary state

$$l_{n+1}p_s(n+1) - g_n p_s(n) = l_n p_s(n) - g_{n-1}p_s(n-1), \tag{A.4}$$

where it satisfies with all $n = 0, 1, \cdots$. By setting $n = 0$, we get

$$\begin{aligned} &l_1 p_s(1) - g_0 p_s(0) = l_0 p_s(0) - g_{-1}p_s(-1), \\ &\Rightarrow p_s(1) = \frac{g_0}{l_1} p_s(0). \end{aligned} \tag{A.5}$$

Therefore, we have

$$p_s(n) = \frac{g_0 g_1 \cdots g_{n-1}}{l_1 l_2 \cdots l_n} p_s(0). \tag{A.6}$$

The probability should be normalized to 1, and $p(0)$ here is the normalizing factor. This is calculated as

$$\begin{aligned} 1 &= \sum_{n=0}^{N} p_s(n) = p_s(0) + \sum_{n=1}^{N} p_s(n), \\ \Rightarrow p_s(0)^{-1} &= 1 + \sum_{n=1}^{N} \frac{g_0 g_1 \cdots g_{n-1}}{l_1 l_2 \cdots l_n}, \end{aligned} \tag{A.7}$$

where, with Eqs. (A.3), the last expression becomes

$$p_s(0)^{-1} = \frac{m_2 R^\alpha N}{(m_1 (1 - R^\alpha))} + \frac{(m_2 R^\alpha)^2 N(N-1)}{(m_1 (1 - R^\alpha))^2 2!} + \cdots, \tag{A.8}$$

and its nth term is described as

$$\frac{(m_2 R^\alpha)^n N(N-1)\cdots(N-n+1)}{(m_1 (1 - R^\alpha))^n n!}. \tag{A.9}$$

This expression leads to

$$\begin{aligned} p_s(0)^{-1} &= \sum_{n=0}^{N} \left(\frac{m_2}{m_1} \frac{R^\alpha}{1 - R^\alpha} \right)^n \binom{N}{n} \\ &= \left(1 + \frac{m_2}{m_1} \frac{R^\alpha}{1 - R^\alpha} \right)^N. \end{aligned} \tag{A.10}$$

Hence, by substituting this into Eq. (A.6), we obtain the stationary probability

$$p_s(n) = \binom{N}{n} \left(1 + \frac{m_2}{m_1} \frac{R^\alpha}{1 - R^\alpha} \right)^{-N} \left(\frac{m_2}{m_1} \frac{R^\alpha}{1 - R^\alpha} \right)^n. \tag{A.11}$$

The mean, variance, and coefficient of variation (CV) are calculated from Eq. (A.11) as

$$\mathrm{E}[n] = \frac{Nm_2}{m_1\left(R^{-\alpha}-1\right)+m_2}, \tag{A.12a}$$

$$\mathrm{Var}[n] = \frac{N\left(1-R^{\alpha}\right)R^{\alpha}m_1m_2}{((1-R^{\alpha})m_1+R^{\alpha}m_2)^2}, \tag{A.12b}$$

$$\mathrm{CV} = \sqrt{\frac{\left(1-R^{\alpha}\right)m_1}{NR^{\alpha}m_2}}. \tag{A.12c}$$

We can see the parameter dependence on the CV, by differentiating Eq. (A.12c) with respective to a parameter of interest,

$$\frac{\partial}{\partial m_1}\mathrm{CV} > 0, \tag{A.13a}$$

$$\frac{\partial}{\partial m_2}\mathrm{CV} < 0, \tag{A.13b}$$

$$\frac{\partial}{\partial \alpha}\mathrm{CV} > 0, \tag{A.13c}$$

$$\frac{\partial}{\partial R}\mathrm{CV} < 0. \tag{A.13d}$$

Furthermore, by setting $\mathrm{E}[n] = n$ in Eq. (A.12a), solving about an arbitrary parameter in the equation, and plugging this into Eq. (A.12c), we have the following relationship:

$$\mathrm{CV} = \sqrt{\frac{1}{n}-\frac{1}{N}}. \tag{A.14}$$

Hence, the CV is a function of n and N only, and parameters in the model affect the PA performance by changing the population size in PAs, n.

A.2 Population dynamics under demographic stochasticity

Here, we extend the gain–loss process Eq. (A.2) to incorporate population changes due to birth and death events. Let n_1 and n_2 be the population size in PAs and non-PAs, respectively, and d_1 and d_2 be the density-independent mortality rate in PAs and non-PAs, respectively. When the total population size N dynamically changes, the gain–loss process

Eq. (A.2) becomes

$$\begin{aligned}\frac{dp(n_1,n_2,t)}{dt} =& W(n_1,n_2 \mid n_1-1,n_2)p(n_1-1,n_2,t)\\ &+W(n_1,n_2 \mid n_1,n_2-1)p(n_1,n_2-1,t)\\ &+W(n_1,n_2 \mid n_1+1,n_2)p(n_1+1,n_2,t)\\ &+W(n_1,n_2 \mid n_1,n_2+1)p(n_1,n_2+1,t)\\ &+W(n_1,n_2 \mid n_1+1,n_2-1)p(n_1+1,n_2-1,t)\\ &+W(n_1,n_2 \mid n_1-1,n_2+1)p(n_1-1,n_2+1,t)\\ &-[W(n_1+1,n_2 \mid n_1,n_2)+W(n_1,n_2+1 \mid n_1,n_2)\\ &+W(n_1-1,n_2 \mid n_1,n_2)+W(n_1,n_2-1 \mid n_1,n_2)\\ &+W(n_1+1,n_2-1 \mid n_1,n_2)+W(n_1-1,n_2+1 \mid n_1,n_2)]p(n_1,n_2,t)\end{aligned} \tag{A.15}$$

where $W(n_1',n_2' \mid n_1,n_2)$ is the transition probability from a state (n_1,n_2) to (n_1',n_2'), and these are

$$W(n_1+1,n_2 \mid n_1,n_2) = bn_1, \tag{A.16a}$$
$$W(n_1,n_2+1 \mid n_1,n_2) = bn_2, \tag{A.16b}$$
$$W(n_1-1,n_2 \mid n_1,n_2) = d_1n_1 + \frac{d}{R}n_1^2, \tag{A.16c}$$
$$W(n_1,n_2-1 \mid n_1,n_2) = d_2n_2 + \frac{d}{1-R}n_2^2, \tag{A.16d}$$
$$W(n_1-1,n_2+1 \mid n_1,n_2) = m_1n_1\left(1-R^\alpha\right), \tag{A.16e}$$
$$W(n_1+1,n_2-1 \mid n_1,n_2) = m_2n_2R^\alpha, \tag{A.16f}$$

where, R and $1-R$ in Eqs. (A.16c), (A.16d), respectively, account for the size of the PAs and non-PAs in the density-dependent mortality rate d, so as to induce a larger density-dependent mortality in a smaller region.

This model is not amenable to analytical approaches due to nonlinearity in the transition probabilities. Hence, we need to rely on numerical simulations. However, we heuristically found the CV in PAs is scaled by the relationship in Eq. (A.14), but the total population size N is also a random variable in this situation:

$$\mathrm{CV} \propto \sqrt{\frac{n_2}{n_1N}}. \tag{A.17}$$

The deterministic dynamics of n_1 from Eq. (A.19) is derived by multiplying by n_1 on both sides and summing over all possible probabilities, we get

$$\begin{aligned}\frac{dE[n_1]}{dt} =& E[W(n_1+1,n_2 \mid n_1,n_2)] - E[W(n_1-1,n_2 \mid n_1,n_2)]\\ &+E[W(n_1+1,n_2-1 \mid n_1,n_2)] - E[W(n_1-1,n_2+1 \mid n_1,n_2)],\\ =& bE[n_1] - \left(d_1E[n_1] + \frac{d}{R}E[n_1^2]\right) + m_2E[n_2]R^\alpha - m_1E[n_1]\left(1-R^\alpha\right).\end{aligned} \tag{A.18}$$

With the decoupling approximation $E[n_1^2] = E[n_1]^2$ and together with the dynamics of $E[n_2]$, we have

$$\frac{dE[n_1]}{dt} = r_1 E[n_1]\left(1 - \frac{E[n_1]}{RK_1}\right) + m_2 E[n_2]R^\alpha - m_1 E[n_1](1 - R^\alpha), \tag{A.19a}$$

$$\frac{dE[n_2]}{dt} = r_2 E[n_2]\left(1 - \frac{E[n_2]}{(1-R)K_2}\right) + m_1 E[n_1](1 - R^\alpha) - m_2 E[n_2]R^\alpha, \tag{A.19b}$$

where $r_i = b - d_i$ and $K_i = r_i/d$ are the growth rate and carrying capacity in area i.

A.3 Aggregated model and its stochastic dynamics

When the emigration and immigration rates are large ($m_1, m_2 \gg 1$), we can aggregate the deterministic dynamics Eq. (A.19). Let x_1 and x_2 be population size denoted by continuous variables in PAs and non-PAs, respectively, and $X = x_1 + x_2$ be the total population size. Then, we write the aggregate dynamics [1,2]

$$\frac{dX}{dt} = \hat{r}X\left(1 - \frac{X}{\hat{K}}\right), \tag{A.20}$$

where at equilibrium we have

$$x_1^* = AX^*, \tag{A.21a}$$

$$x_2^* = (1 - A)X^*, \tag{A.21b}$$

where $X^* = \hat{K}$ and $A = m_2 R^\alpha/(m_1(1 - R^\alpha) + m_2 R^\alpha)$. The aggregated parameters $\hat{r}$ and $\hat{K}$ are defined as

$$\hat{r} = r_1 A + r_2(1 - A), \tag{A.22a}$$

$$\hat{K} = \frac{K_1 K_2 R(1-R)(r_1 A + r_2(1-A))}{r_1 K_2 A^2(1-R) + r_2 K_1(1-A)^2 R} = \frac{R(1-R)(K_1 A + K_2(1-A))}{A^2(1-R) + (1-A)^2 R}, \tag{A.22b}$$

where $r_i = b_i - d_i$ and $K_i = (b_i - d_i)/d$ are the growth rate and carrying capacity in area i. At the limit $m_1, m_2 \to \infty$ we have $\lim_{m_1,m_2\to\infty} A = R^\alpha$, and Eqs. (A.22) becomes

$$\hat{r} = r_1 R^\alpha + r_2(1 - R^\alpha), \tag{A.23a}$$

$$\hat{K} = \frac{(1-R)(K_1 R^\alpha + K_2(1 - R^\alpha))}{1 - 2R^\alpha + R^{2\alpha-1}}. \tag{A.23b}$$

Alternatively, by putting $m_2 = Bm_1$ and taking the limit $m_1 \to \infty$, we have

$$\lim_{m_1\to\infty} A = \frac{BR^\alpha}{1 + (B-1)R^\alpha} = A', \tag{A.24}$$

where the coefficient B represents the ratio of m_1 and m_2, and $B = 1$ realizes $A = R^\alpha$. Plugging this expression into Eqs. (A.22) enables us to examine asymmetric migrations between PAs and non-PAs.

One can describe the stochastic differential equation with the notation of Eq. (A.20):

$$dX = \hat{r}X\left(1 - \frac{X}{\hat{K}}\right)dt + \sigma_e X dW(t), \tag{A.25}$$

where X is now a random variable. In the Itô's interpretation, this is equivalent to the following Fokker-Planck equation [3]

$$\frac{\partial p(x,t)}{\partial t} = -\frac{\partial}{\partial x}\left[\hat{r}x\left(1 - \frac{x}{\hat{K}}\right)p(x,t)\right] + \frac{1}{2}\frac{\partial^2}{\partial x^2}[\sigma_e^2 x^2 p(x,t)], \tag{A.26}$$

that has a quasi stationary distribution of the form of a Gaussian distribution

$$p_s(x) = c_0 \frac{x^{-2+\frac{2\hat{r}}{\sigma_e^2}}}{\sigma_e^2} \exp\left(-\frac{2\hat{r}x}{\hat{K}\sigma_e^2}\right), \tag{A.27}$$

where c_0 is a normalization constant. This expression gives the mean, variance, and CV of x as follows:

$$\mathrm{E}[x] = \hat{K}\left(1 - \frac{\sigma_e^2}{2\hat{r}}\right), \tag{A.28a}$$

$$\mathrm{Var}[x] = \hat{K}^2\left(1 - \frac{\sigma_e^2}{2\hat{r}}\right), \tag{A.28b}$$

$$\mathrm{CV} = \left(1 - \frac{\sigma_e^2}{2\hat{r}}\right)^{-\frac{1}{2}}. \tag{A.28c}$$

By taking the derivative of the CV (Eq. A.28c) with respective to $\hat{r}$ with the positivity requirement $\hat{r} > \sigma_e^2/2$, we have

$$\frac{\partial}{\partial \hat{r}}\mathrm{CV} < 0. \tag{A.29}$$

This means that an increment of $\hat{r}$ reduces the CV. From Eq. (A.22a), we see that the value $\hat{r}$ becomes large by increasing the PA fraction, R, when $r_1 > r_2$. That is, if PAs have a larger intrinsic growth rate than non-PAs, introducing such "good" PAs reduce the CV. The parameter α controls the sensitivity of this effect; if $\alpha < 1$ the largest rate of reduction of the CV is achieved (i.e., curve with diminishing return) when R is small. While the opposite trend is realized if $\alpha > 1$. These are depicted in Fig. A.6.

Note Eq. (A.27) is the probability in the whole region concerned, but the carrying capacity $\hat{K}$ is cancelled in the expression of the CV (Eq. A.28c). It also suggests that the subregions (i.e., PAs and non-PAs) of the concerned region have the same CV in the large limit of m_1 and m_2 as expected.

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