Interconnections accelerate collapse in a socio-ecological metapopulation

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ABSTRACT

Resource over-exploitation can have profound effects on both ecosystems and the human populations residing in them. Models of population growth based on a depletable resources have been studied previously, but relatively few consider metapopulation effects. Here we analyze a socio-ecological metapopulation model where resources grow logistically on each patch. Each population harvests resources on its own patch to support population growth, but can also harvest resources from other patches when their own patch resources become scarce. We find that allowing populations to harvest from other patches significantly accelerates collapse and also increases the parameter regime for which collapse occurs, compared to a model where populations are not able to harvest resources from other patches. As the number of patches in the metapopulation increases, collapse is more sudden, more severe, and occurs sooner. These effects also persist under scenarios of asymmetry and inequality between patches. We conclude that metapopulation effects in socio-ecological systems can be both helpful and harmful and therefore require urgent study.

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1. Background

Simple population dynamic models have long been used in theoretical population biology, beginning with the logistic growth model developed by Verhulst [1]:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right),$$

where $N(t)$ is the population size at time t, r is the net growth rate, and K is the carrying capacity. This model represents resource-limited population growth reaching a carrying capacity K that is the largest population size that the resources of the environment can support. The logistic growth model and various extensions thereof are richly represented in the ecological literature and have been used as a framework to study population dynamics in a variety of species [2, 3, 4].

Other literature has extended single population models to study metapopulation dynamics. A metapopulation is a collection of spatially distributed populations all belonging to the same species [5]. Metapopulation models provide important insight into interactions of connected populations. Previous research on metapopulations has identified phenomena such as the rescue effect and extinction debt. In a rescue effect, the local extinction of a population is prevented due to immigration of a neighboring population residing in the same metapopulation [6]. In contrast, extinction debt refers to an effect whereby destruction of a natural habitat has not only immediate impacts on populations, but also creates a 'debt' effect whereby future extinctions will occur as well long after habitat destruction has ceased [7].

Although population growth models such as the logistic growth model have arguably found their fullest expression in ecology, Verhulst developed his model for application to human populations and he inferred the model's parameter values using population data from Belgium and other countries. This interest in human populations may have been due to the influence of Thomas Malthus and his work 'An Essay on the Principle of Population', which is well known for its hypothesis that famine and poverty are mathematically inevitable [8].

Malthus continues to influence our thought in a time of severe global over-consumption and resource depletion. Resource depletion has been conceptualized and quantified in various ways. For instance, recent literature identifies seven planetary boundaries that must not be transgressed if humans are able to live

24 sustainably on the planet, and finds that three of these boundaries have already been transgressed [9].

25 More recently, researchers have introduced frameworks to describe the process by which over-

26 consumption occurs. For instance, the red/green sustainability framework describes how populations

27 become increasingly disconnected from their impacts as they urbanize [10]. In a 'green' phase, popula-

28 tions are highly dependent on their local environment for their subsistence, and therefore feedback from

29 environmental implications of human activity are quick to down-regulate the human activity. However, as

30 populations develop and draw their resources from a global resource pool, their economic activities cause

31 environmental impacts that are no longer felt by them but rather by geographically distant populations,

32 weakening the short-term coupling between humans and their environment. This process is captured

33 by, for instance, the linkages between local deforestation and high pressure for international agricultural

34 exports [11], and the large dependence seafood markets in Japan, the United States, and the European

35 Union on foreign sources [12].

36 Although logistic growth models and its variations are most widely used in ecology, the application of

37 population growth models to resource-limited human populations has also received attention, perhaps on

38 account of our growing awareness of the possible ramifications of resource over-exploitation, especially in

39 the face of environmental change [13]. Mathematical models have been used to study phenomena such as

40 human population collapse in a model with resource dynamics [14] and conflict among metapopulations

41 arising over common resources [15, 16]. Models have also been used to study historical human population

42 collapses such as in the people of Easter Island [17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27], the Kayenta

43 Anasazi [28], and the Andean Tiwanaku civilization [29], as well as collapse of modern populations

44 [30, 31, 32, 33].

45 With some exceptions [15, 16, 27, 34], most previous research on resource-limited population growth

46 focuses on single populations and not on multi-population interactions. However, multi-population interac-

47 tions through trade and other mechanisms are an inescapable feature of the world's human metapopulation

48 dynamic, and can have significant impacts on ecosystems and resource levels [35]. The literature on

49 multi-population interactions has explored meta-population models involving migration of individuals

50 between patches [28], or competing populations conflicting and bargaining over a common resource

51 [15, 16]. A multi-patch model of human populations fitted to data from Easter Island has predicted

that coupling human populations together through exchange of resources, migration and technology can stabilize the entire metapopulation [27].

In this paper we build on a previous single population model [18] to create a metapopulation model of resource-limited growth that captures mechanisms similar to the red/green sustainability framework. Populations grow logistically by exploiting a depletable resource that obeys a resource dynamic. Local populations can take resources not only from their own patch but also from other patches, when resources in their own patch become scarce. Our research objective was to determine whether the metapopulation collapses faster or more often when patches are allowed to harvest resources from other patches. We describe the model in the next section, followed by Results and a Discussion section.

2. Model

We build on a previous single-population model analyzed by Basener and Ross [18] who formulated a model whereby the population grows logistically to a carrying capacity that is proportional to the resource level. A second equation describes the logistic growth of resources to a separate carrying capacity, minus harvesting. We develop both two-patch and ten-patch versions of our model.

Two-patch model

In the two-patch model, patch 1 has population size P_1 and resource level R_1, and patch 2 has population size P_2 and resource level R_2:

$$\frac{dP_1}{dt} = a_1 P_1 \left(1 - \frac{P_1}{R_1 + b_1 R_2} \right) \tag{1}$$

$$\frac{dR_1}{dt} = c_1 R_1 \left(1 - \frac{R_1}{K_1} \right) - h_1 P_1 - b_2 h_2 P_2 \tag{2}$$

$$\frac{dP_2}{dt} = a_2 P_2 \left(1 - \frac{P_2}{R_2 + b_2 R_1} \right) \tag{3}$$

$$\frac{dR_2}{dt} = c_2 R_2 \left(1 - \frac{R_2}{K_2} \right) - h_2 P_2 - b_1 h_1 P_1 \tag{4}$$

where $a_{1,2}$ is the growth rate of patch 1 (resp. 2); $c_{1,2}$ is the resource renewal rate in patch 1 (resp. 2); $K_{1,2}$ is the carrying capacity of the depletable resource in patch 1 (resp. 2); $h_{1,2}$ is the baseline harvesting rate at which patch 1 (resp. patch 2) harvests resources for its population's consumption; b_1 is the proportion

72 of resources that patch 1 takes from patch 2, and similarly for b_2. In this model, the carrying capacity of

73 the human populations is determined by how much resource is available to support them, either from their

74 own patch or taken from the other patch. When $b_1 = b_2 = 0$ we recover the original model by Basener

75 and Ross [18].

76 We set $b_1 = b_1(R_1, P_1)$ and assume that patch 1 will attempt to harvest more resources from patch

77 2 when the resources from patch 1 are not enough to support the patch 1 population. Similarly, $b_2 =$

78 $b_2(R_2, P_2)$. These functions take the form

$$
\begin{aligned}
b_1(R_1, P_1) &= \frac{1}{1 + e^{(\beta_1 - \gamma_1 P_1 / R_1)}} & (5) \\
b_2(R_2, P_2) &= \frac{1}{1 + e^{(\beta_2 - \gamma_2 P_2 / R_2)}} & (6)
\end{aligned}
$$

79 These are sigmoidal functions where the rate at which patch 1 harvests from patch 2 is higher when P_1/R_1

80 is higher, and *vice versa*, where $\beta_1 > 0$ controls the location of the mid-point of the sigmoid, and where

81 $\gamma_1 > 0$ controls how steep the curve is. Parameters β_2 and γ_2 are similarly defined.

Ten-patch model

83 We also analyzed a version of the model where ten patches are interconnected and can take resources from

84 one another. The dynamics of patch i in the ten-patch model are given by

$$
\begin{aligned}
\frac{dP_i}{dt} &= a_i P_i \left(1 - \frac{P_i}{R_i + \sum_{j=1, j \neq i}^{10} b_i R_j} \right) & (7) \\
\frac{dR_i}{dt} &= c_i R_i \left(1 - \frac{R_i}{K_i} \right) - h_i P_i - \sum_{j=1, j \neq i}^{10} b_j h_j P_j
\end{aligned}
$$

85 where parameter definitions are the same as in the two-patch case.

Baseline parameter values

87 The baseline values of our parameters appear in Table 1. The population growth rate $a_{1,2}$ was estimated

88 by historical world population growth rates [36]. The resource growth rate $c_{1,2}$ was taken as the average

89 increase in crop yield since 1961 [37]. The values of the harvesting efficiency $h_{1,2}$ and carrying capacity

Symbol	Definition	Value	Source
$a_{1,2}$	Population 1,2 net growth rate	0.0177/year	[36]
$c_{1,2}$	Resource growth rate in patch 1, 2	0.015/year	[37]
$h_{1,2}$	Harvesting efficiency of population 1, 2	0.008/year	calibrated
$K_{1,2}$	Carrying capacity of resources in patch 1, 2	1,000,000	calibrated
$\beta_{1,2}$	Controls location of the mid-point of the sigmoid for population 1, 2	3.5	calibrated
$\gamma_{1,2}$	Controls steepness of the sigmoid for population 1, 2	5	calibrated

Table 1. Baseline model parameter values.

of the resources $K_{1,2}$ were calibrated so that the populations would begin with enough resources to survive for several centuries regardless of their rates of resource use, and so their harvesting efficiency was high enough that there were consequences to over-exploitation but not high enough to make resource use incredibly costly. At these parameter values, the population size of a single patch grows to $650,000$ and then declines somewhat to an equilibrium population size of $480,000$ over a timescale of several hundred years.

The parameters controlling the midpoint and steepness of the sigmoid function (β and γ) were obtained through calibration by analyzing the effect they had on how much and when the populations would take from neighboring populations. To calibrate β, our intention was that the populations did not take much from neighbors when they were not in need. In contrast, they would take more when their resources began to dwindle and neighbour's resources were needed to survive. To calibrate γ we choose a value such that the switch between these two described states was relatively gradual. In particular, we required β_i and γ_i to satisfy the property that if $P_i/R_i = 1/2$ and thus resources were abundant, then b_i was roughly 25%, whereas if $P_i/R_i = 1$, indicating a situation where a shortage of resources was beginning to become worrisome, then b_i would be greater than 75%.

Initial conditions were $P_1(0) = 50,000$, $P_2(0) = 50,000$, $R_1(0) = 1,000,000$, and $R_2(0) = 1,000,000$. These initial conditions corresponded to two populations with relatively low starting population levels and with initially abundant resources at carrying capacity in their respective patches.

We solved the model equations numerically using the adaptive fourth-fifth order Runge Kutta method implemented via Matlab's ODE45 solver. The code can be found on Github [38]. We compared model dynamics for both interconnected and isolated versions of the two-patch and ten-patch models to determine

the impact of interconnectedness on the likelihood and timing of collapse.

We explored the sensitivity of model predictions to parameter variations away from the baseline parameter values. In this process we considered two different scenarios for parameter variations. In most figures, populations were always assumed symmetric and had identical parameter values, but some figures explore the case of asymmetric populations where the two populations differ in one parameter value.

3. Results

3.1. Baseline Scenario

The baseline scenario was simulated for both the interconnected ($b_1, b_2 > 0$) and isolated ($b_1 = b_2 = 0$) versions of the model. In the interconnected baseline scenario (Fig. 1), the populations begin a nearly exponential increase in their population growth (Fig. 1a) as they quickly reduce their local resources (Fig. 1b). This decrease in local resources causes the populations to begin taking resources from their neighboring patch to continue supporting their population (Fig. 1d). This results in greater resource availability (Fig. 1c) which stimulates further unsustainable population growth. Once the resources of both patches are strongly depleted, both populations collapse.

In contrast to the interconnected case, both populations achieve sustainability in the isolated case at baseline parameter values (Fig. 1). Much like the interconnected scenario, the population of both civilizations grow very quickly, reaching a peak and then beginning to decline (Fig. 1a). However, instead of complete extinction of the population, the population decline begins to slow as the system reaches a steady state in which the population and resources equilibrate at an intermediate level, achieving sustainability.

Dynamics in the 10-patch model amplify the trends in dynamics observed in the 2-patch model. The initial increase in population size is much more rapid, but the following collapse happens much sooner and is much more sudden than in the 2-patch model (Fig. 1a). Collapse occurs after 159 years in the 10-patch model compared to the 289 years in the 2-patch model. Resources are depleted much more rapidly in the 10-patch model (Fig. 1b-d).
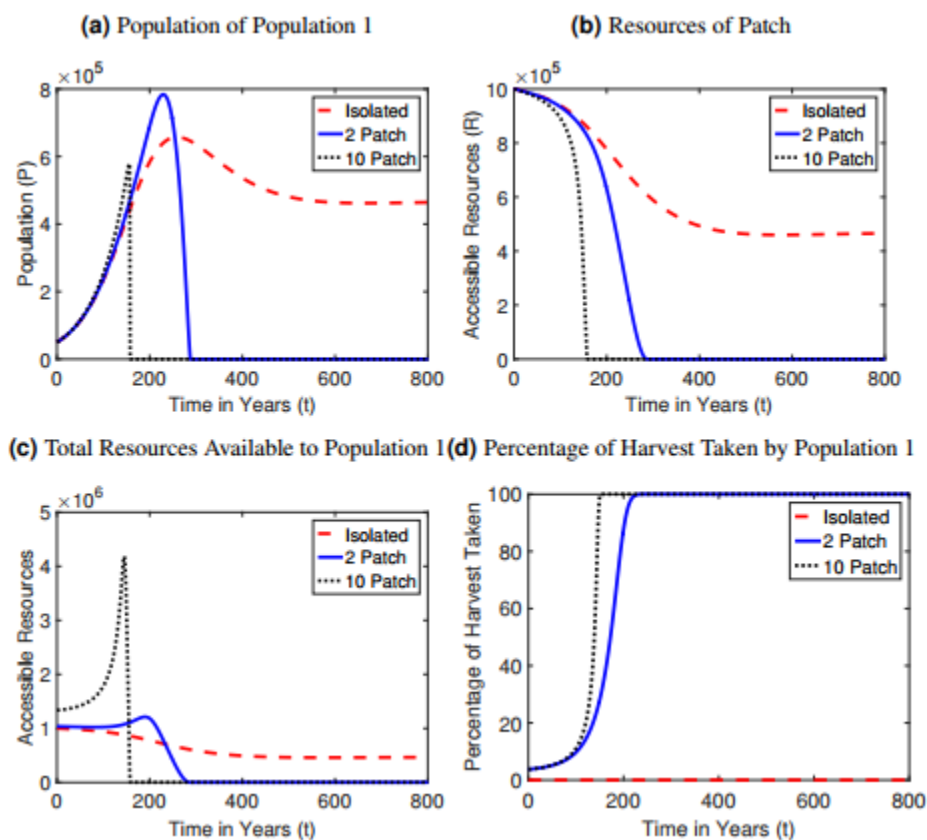
Figure 1. Model dynamics at baseline parameter values for the isolated, interconnected, and 10 population scenarios for (a) population size P_1 of patch 1, (b) resource availability R_1 in patch 1, (c) total resources available to population 1, and (d) percentage of harvest of patch 2 taken by population 1. Results for population 2 and patch 2 are symmetrical.

3.2. Time to collapse

We also studied how the time to collapse depends on parameter values for the isolated and interconnected

scenarios. Time to collapse was defined as the time elapsed until the populations of both patches reaches

zero ($P_{1,2} < 10^{-7}$). We generated plots showing the time to collapse versus a single parameter, with all

other parameter values held constant at their baseline values (Fig. 2,3). By doing so, we obtain an idea

of whether the more rapid collapse of interconnected systems compared to isolated systems is robust

to changes in model parameter values, and which parameter values are most influential in determining

collapse.

Across a broad range of parameter values, time to collapse in the interconnected case is much shorter,

demonstrating that the interconnection of the two populations is detrimental to the stability of the system

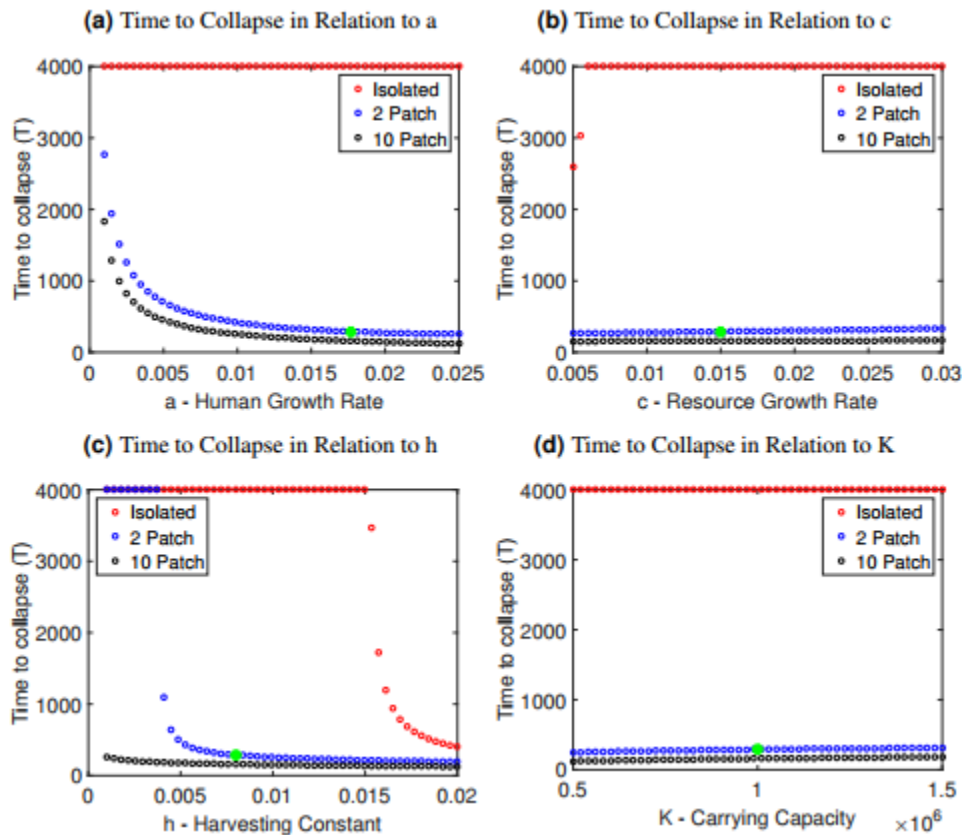(Fig. 2, 3). The isolated case is more resilient to collapse, as we see that the model often survives

Figure 2. Time to collapse for the isolated and interconnected cases as it depends on changes in (a) the human growth rate a, (b) the resource growth rate c, (c) the harvesting constant h and (d) the carrying capacity K. The parameter along the horizontal axes was changed for both patches, thus preserving symmetry. A green star has been included in each graph to indicate the value of the parameter in the baseline scenario.

147   indefinitely in all cases except when the harvesting constant or resource growth rate are changed drastically

148   relative to the baseline values (Fig. 2b, c). This is in contrast to the interconnected case, where nearly

149   all parameter choices for the human growth rate a, the resource growth rate c, the harvesting constant

150   h and the carrying capacity K lead to collapse. Collapse occurs more rapidly when the human growth

151   rate a or the harvesting constant h are increased, since both scenarios correspond to populations growing

152   unsustainably quickly (a) or exploiting their resources unsustainably quickly (h). Interestingly, it is

153   relatively independent of the carrying capacity K and the resource growth rate c. Therefore in this system,

154   increasing carrying capacity (K) by boosting yield by, or increasing the ability of the resource to replenish

155   itself (r) has relatively little effect in delaying the collapse.

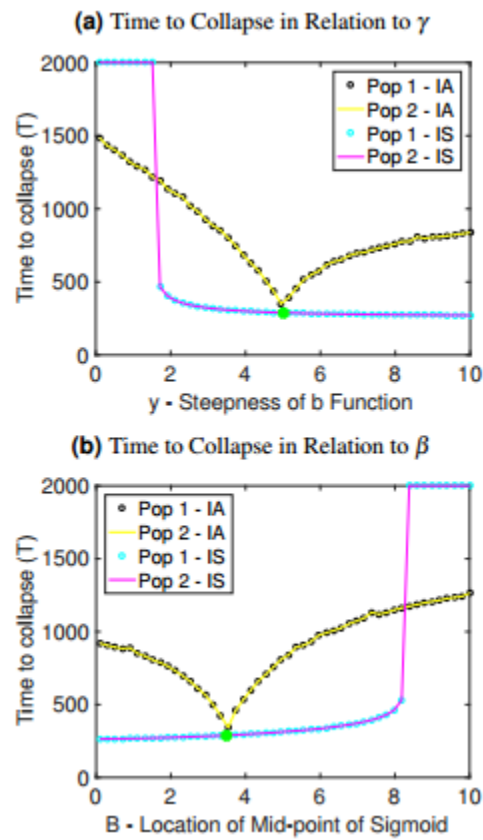   The more rapid collapse observed in the 10-patch model compared to the 2-patch model (Fig. 1) is

156

(a) Time to Collapse in Relation to γ

(b) Time to Collapse in Relation to β

Figure 3. Time to collapse for the isolated and interconnected cases as it depends on changes in (a) the steepness of sigmoidal function γ, (b) the midpoint of sigmoidal function β. A green and yellow star have been included in each graph to indicate the value of the parameter in the baseline scenario of the interconnected case and isolated case, respectively. IS denotes interconnected symmetric, wherein the parameter along the horizontal axes was changed for both patches, thus preserving symmetry, while IA denotes interconnected asymmetric, wherein the parameter values for population 1 was changed while the parameter values for population 2 was held constant at its baseline value.
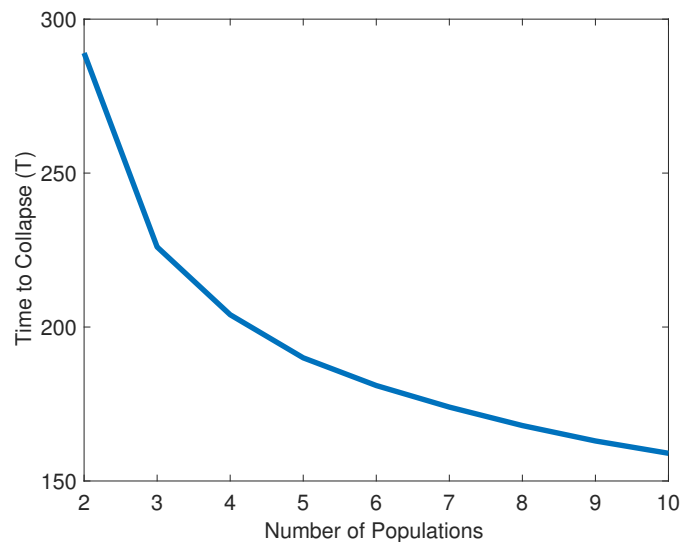
Figure 4. Time to collapse versus number of populations included in model. Baseline parameter values were used (Table 1).

157   also robust under these parameter variations (Fig. 2). As the number of populations increases from 2 to 10,

158   the time to collapse declines with the number of populations (Fig. 4).

159   The observed relationships between time to collapse and interconnectedness are also preserved under

160   variation in parameters controlling the rate at which one patch harvests resources from another patch:

161   β, which controls the midpoint location in the sigmoidal function, and γ, which controls the steepness

162   of the sigmoidal function (Fig. 3). When γ is increased, the switch to harvesting from other patches

163   happens more quickly, causing more rapid collapse (Fig. 3a). Interestingly, if γ is sufficiently low

164   (meaning the sigmoidal function transitions smoothly), then collapse does not occur. Hence, if populations

165   transition more gradually to harvesting from other patches, collapse can be avoided. When β is decreased,

166   populations begin harvesting from other patches earlier and more intensely, causing more rapid collapse

167   (Fig. 3b).

168   The case of asymmetric parameter variation is also considered in Fig. 3 to provide a contrast with our

169   baseline assumption of symmetric parameter values. As the value of γ is increased for only one of the

170   populations while the value of γ for the other population is held constant, the time to collapse decreases

171   for both populations until it reaches a minimum at the baseline value, and then starts to increase again

172   (Fig. 3a). Similarly, if β is increased for only one of the populations, time to collapse decreases until

173   it reaches the baseline value but then increases again (Fig. 3b). This suggests that heterogeneity in the

metapopulation may stave off collapse.

3.3. Parameter planes

By varying two parameters at one time and holding all others constant at their baseline values, we can understand parameter combinations that lead to collapse or survival under the isolated and interconnected scenarios. It is evident from these parameter planes that the isolated case of the model is far less prone to collapse over the same ranges of parameter values. Collapse occurs for a much wider part of the parameter plane under the interconnected symmetric case than under the isolated case (electronic supplementary material, Figure S1). In contrast to the baseline parameter values, we observe parameter regimes in the interconnected symmetric case where increasing the resource growth rate c can move the populations into a region of sustainability. Introducing asymmetry to the parameter plans, such that the two parameter values for one population are varied while the parameter values for the other population are held at baseline values, we observe that sustainability is a more frequent outcome than in the symmetric case, but occurs less frequently than in the isolated case (electronic supplementary material, Figure S1).

3.4. Impact of Inequality

To observe the effect of inequality on system dynamics, we created an additional scenario involving two unequal populations. Population 1 has a higher starting population size, population growth rate, resource growth rate and harvesting efficiency, but a lower carrying capacity than population 2, which has more resources but a lower starting population size and growth rate. Population 1 is also more prone to take resources from population 2 than *vice versa*. The inequality scenario was simulated with and without interconnections. Parameter values can be found in electronic supplementary material, Table S1 and the initial conditions were $P_1(0)$=50,000, $P_2(0)$=25,000, $R_1(0)$ = 250,000, $R_2(0)$=1,000,000.

In the interconnected case (electronic supplementary material, Figure S2), population 1 grows relatively quickly (Fig. S2a), reaching their maximum population size nearly 100 years before population 2. In the process, they exhaust all of their resources early in the simulation (Fig. S2b). However, this causes very little disturbance to population 1 since there is only a small, nearly non-existent, decrease in population size at the time of resource depletion. This is due to their early dependence on population 2's resources (Fig. S2g) dampening the effect that over-exploitation has on their own population. After this point, both

201 populations continue to consume population 2's resources (Fig. S2d) until the inevitable depletion, causing

202 both populations to collapse.

203   In the corresponding isolated but unequal case (electronic supplementary material, Figure S3), the

204 outcomes are very different. Population 2 begins a similar population increase as in the interconnected

205 case, but the population avoids complete collapse and instead recovers to a stable state (Figure S3c).

206 However, population 1 grows unsustainably, over-depletes their resource, and collapses (Fig. S3a,b).

207 Hence, for these parameter values, we observe that the dichotomy between outcomes in the isolated and

208 interconnected scenario persists when the two populations are unequal.

4. Discussion

210 In this paper we extended a simple population model where a population harvests a depletable resource to

211 a metapopulation setting where a population patch can also harvest resources from other patches when

212 their own resources run low. We showed how the populations collapse faster and for a broader range of

213 parameter values when patches are allowed to harvest resources from other patches. As the number of

214 patches increases, the effect is amplified.

215   Interconnections accelerate collapse in this model because the ability to harvest resources from other

216 patches enables populations to access a larger resource pool. Consequently, the populations are able to

217 grow at a very rapid rate, compared to the case where patches are isolated from one another. Each patch

218 population size grows beyond what is sustainable using only the resources in a single patch, and this causes

219 rapid collapse as the resources disappear and all patches are left with unsustainably high populations. This

220 mechanism operates even when the net resource growth rate $c_{1,2}$ parameter exceeds the net population

221 growth rate parameter $a_{1,2}$. Collapse remains possible in the isolated scenario, but the smaller available

222 resource pools tend to prevent it.

223   This effect was robust under a wide range of parameter variation. We also found that asymmetry in

224 parameter values between the two patches does not change the qualitative results, but does tend to stave

225 off collapse. We speculate that models with greater heterogeneity (such that each patch has a unique set of

226 parameter values) might replicate this feature, but we leave this for future work. We furthermore found

227 that collapse can occur in a scenario of inequality between the two patches, although we did not test the

robustness of this finding to parameter variation.

In some respects, our model embodies some of the ideas of "red and green loop" dynamics as introduced by Cumming et al [10]. Populations in our model can depend on resources harvested non-locally, such that the population is buffered from the implications of their harvesting activities in the short term. Thus, in the interconnected case, populations are in a red loop regime. As the population transitions to relying on the resources of other patches as its own resources are depleted, the red loop progresses to a red trap corresponding to collapse of both populations in the interconnected scenario. In comparison, in the isolated case, populations are much more dependent on their local resources and feel the impacts of their harvesting choices immediately: a green loop regime.

Our model makes simplifying assumptions that may influence its predictions. For instance, due to the structure of our sigmoidal function governing cross-patch harvesting and in particular the assumed dependence of cross-patch harvesting on P_i/R_i, patches tend to collapse simultaneously when R_i becomes small. Moreover, patches cannot prevent cross-patch harvesting. In reality, effective institutions (where they exist) would be able to prevent cross-patch harvesting through legislation and this might have the effect of preventing collapse from spreading to all patches. Future work could study the effects of retaining a portion of local resources for the native patch's exclusive use. Similarly, allowing migration of individuals as well as cross-patch harvesting could influence dynamics, perhaps even to the point of preventing collapse [27]. Non-human species migrate when local resources are depleted; humans migrate but technology now allows them to import the resources they need without migrating. Allowing cross-patch harvesting while preventing migration could therefore be particularly dangerous.

Similarly, we assumed a Malthusean world where more resources are always converted into more offspring. However, it is observed that most populations go through a demographic transition to lower fertility when they become sufficiently industrialized [39]. Incorporating this effect into the model may help prevent unsustainable growth, although the strength of the effect depends on whether increases in per capita resource consumption outstrip the benefits of slowed population growth.

Another possible extension of the model is to include dynamically changing parameters. At the moment, all parameters in the model are static. However, technological improvements mean that parameters like the harvesting efficiency h and cross-patch harvesting should change over the course of the simulation. In this

vein, work by Reuveny and Decker [25] explores how technological advancement affects a human-resource population model. Similarly modifications to our model could be implemented, and their effects studied.

In our multi-population socio-ecological model where populations grow by harvesting a depletable resource, the ability of one patch to support its population growth by harvesting resources from other patches increases population growth in the short run, but causes population collapse in all patches in the long run. This effect is robust to parameter variation, and is accelerated significantly by the inclusion of more patches. Given the ubiquity of cross-patch harvesting in real populations, socio-ecological models of human growth and resource consumption should consider the role of metapopulation effects.

Competing Interests

The authors declare no competing interests.

Author Contributions

M.A. and C.T.B. conceived the study; Z.D. analyzed the model and generated figures; all authors wrote and reviewed the manuscript.

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