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# Long-term transients help explain regime shifts in consumer-renewable resource systems

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As planetary boundaries loom, there is an urgent need to develop sustainable equilibriums between societies and the resources they consume, thereby avoiding regime shifts to undesired states. Transient system trajectories to a stable state may differ substantially, posing significant challenges to distinguishing sustainable from unsustainable trajectories. We use stylized models to show how feedbacks between anthropogenic harvest regimes and resource availability drive transient dynamics. We show how substantial time lags may occur between interventions and social-ecological outcomes, and that sudden system collapses need not be linked to recent environmental changes. Historical reconstructions of island state populations show a variety of transient dynamics that closely corresponds to model expectations based on island differences in productivity and harvesting regime. We conclude that vulnerable social-ecological systems may persist when the population:resource ratio remains within a viable range of intermediate (rather than small) values, which implies that averting environmental crises may require counter-intuitive measures.

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Despite modern technological advances, understanding the conditions under which a human population can develop a sustainable equilibrium with the natural resources it consumes remains a key challenge for the natural and social sciences[1–4]. Current rates of human appropriation of natural resources are surpassing regional and planetary carrying capacities, and curtailing natural resource use requires interventions[5–7]. Stylized theoretical models provide an effective way to study the interactions between human activities and renewable resources[8–11]. Specifically, such models provide a means to study feedbacks between social and ecological processes in an analytically tractable way[11–14]. Analytical stylized model analyses may then also aid subsequent studies of more complex social-ecological models that need to rely on numerical simulation[15].

Human populations can control the relative extraction of resources through technology (e.g., ref. [16]), and the introduction of rules and regulations (e.g., ref. [17]). The latter may emerge through self-organization of communities or through top-down management[18]. The use of stylized theoretical models requires specific assumptions about how consumers' extraction behavior responds to changing resource stocks[14,18,19]. When assuming that a renewable resource can be accessed by multiple independent users who act out of self-interest and do not actively promote its growth, it can be assumed that per capita extraction rates are relatively constant[20,21]. Stylized models developed under these assumptions allow for the formulation of hypotheses of emerging social-ecological dynamics in unorganized resource systems accessible to all.

Besides an assumption on resource extraction behavior, the use of stylized theoretical models requires a clear demarcation of system boundaries. As social-ecological systems are typically open, it may be challenging to identify their boundaries[18]. One way to circumvent this is to study social-ecological interactions within past societies that developed in relatively isolated or confined locations such as oceanic islands[22–25]. These case studies have interested a variety of research disciplines, partly because elements of them can provide analogs for current social-ecological systems and their resource management challenges[26–28]. Within this context, several dynamical models of consumer-renewable resource systems have been proposed, linked to specific case studies reconstructed from archeological, paleo-environmental, and anthropological data (e.g., refs. [8–10,29]).

Renewable natural resources, by definition, regenerate at timescales relevant to the rate of human extraction[30], but their transient regeneration dynamics can be complex[27,31]. Within social-ecological systems, it is important to consider how resource regeneration dynamics may be impacted by human harvesting activities[32]. For certain biotic resources, the regeneration rate slows down at low resource density, an effect referred to as depensation[27,33–35]. Examples include recruitment limitation in overharvested fish populations[36], and increased susceptibility to erosion of soils with reduced tree cover[37,38]. Owing to depensation, overexploited states with no or little resource availability and system states with relatively high resource availability may be alternative stable equilibria[39,40]. For systems with such characteristics, the critical transition toward the degraded state has been described as the "depensation catastrophe"[41], and may occur when a system has passed a tipping point (e.g., ref. [42]). After a transition or regime shift has occurred, restoration efforts may no longer be successful in reestablishing the renewable resource supply[43]. It is, therefore, of considerable interest to explore ways to change the course of systems that are on such a trajectory toward a regime shift to an alternative, degraded state[44,45].

The framework of tipping points between alternate stable states has provided important tools to analyze transitions resulting from gradual changes in environmental conditions or exploitation pressure[39,41,42]. Recently, a theory of long transients has been proposed as a counterpart to this framework[46,47]. Transients are persistent dynamical regimes that are not truly stable states of a system, meaning these regimes will not persist on the (very) long term[46]. Transients provide an alternative explanation for regime shifts resulting from passing a tipping point, because they do not result from recent changes in environmental conditions or exploitation pressure[46]. While previous studies have discussed the role of long transients in ecological systems[46–48], the mechanisms involved in creating these transients may be relevant for social-ecological systems as well. Specifically, long transient dynamics would pose a challenge in distinguishing sustainable trajectories of social-ecological system dynamics from unsustainable ones.

The aim of this study is to investigate the range of transient dynamics that could unfold in human consumer-renewable resource systems, and explore potential windows of opportunity to successfully intervene in systems that are currently on a trajectory toward an irreversible loss of natural resources and its concomitant negative impacts on society, specifically the number of people the social-ecological system is able to provide for. We explore how these dynamics depend on the presence of depensation within the renewable resource's regeneration process. Specifically, we contrast analyses of a baseline model, i.e., a consumer-resource system without depensation (see "Methods" and Supplementary Methods 1 for details), to analyses of an extended model, i.e., a system with a critical depensation threshold in renewable resource dynamics (see "Methods" and Supplementary Methods 1 and 2 for details).

As noted above, the analyses are focused on human populations that are relatively isolated and interacting within confined locations such as island states (see "Methods" and Supplementary Methods 1 for details). Therefore, we also examine to what extent the modeled relationships between productivity of the environment, harvesting regime, and human population dynamics corresponded to historical reconstructions of human population dynamics and resource extraction in island states with various climates. Although we analyze these patterns in conceptually bounded island state systems, the consequences of resource consumption have manifested itself as a global driver of earth system change in the Anthropocene[5,6,42]. Hence, the type of system dynamics studied here may become increasingly relevant at larger spatial scales and higher levels of societal organization[4,49].

## Results

The first step of the analysis was to identify the conditions under which both resources and human consumers cannot persist in a stable equilibrium, and the conditions under which they can (see "Methods", Supplementary Methods 3 and 4, and Supplementary Table 1 for details). Using isocline analysis of the two model equations (describing human population and resource dynamics, respectively, see Table 1), each set of conditions could then be further divided into two scenarios that differ in the transient dynamics toward the (same) asymptotic equilibrium state. The resulting four scenarios occurred in both the baseline and the extended model, and are referred to as cases I–IV from here. Each case is described in further detail in the next two Results sections. In the third Results section, we analyze how resource productivity and harvest regime determine which type of transient system dynamics occur, thereby constraining the possibilities for sustainable development. In the fourth Results section, we show how inclusion of depensation in the extended model leads to counterintuitive observations regarding the impact of system interventions, and the substantial time lags that may occur between interventions and their effect on social-ecological outcomes.

**Table 1 Description of the model equations, and interpretation of the system state variables and parameters.**

Model equations

| | |
|---|---|
| Population dynamics: | $\frac{dP}{dt} = rP\left(1 - \frac{P}{qR}\right)$ |
| Renewable resource dynamics: | $\frac{dR}{dt} = f_i(R) - hP$ |
| Resource growth (baseline model): | $f_1(R) = cR\left(1 - \frac{R}{K_{max}}\right)$ |
| Resource growth (extended model): | $f_2(R) = cs^*R\left(1 - \frac{R}{K_{max}}\right)\left(\frac{R}{K_{min}} - 1\right)$ |

Interpretation of symbols

| Symbol | Interpretation | Unit | Value | References |
|---|---|---|---|---|
| $r$ | Relative population growth rate | $\text{Year}^{-1}$ | 0.0044 | 10 |
| $q$ | Per capita dependency on the renewable resource | Individuals # resource units$^{-1}$ | 1 | 10 |
| $h$ | Per capita exploitation rate | Individual$^{-1}$ year$^{-1}$ | Varied | This study |
| $c$ | Relative resource growth rate | $\text{Year}^{-1}$ | Varied | This study |
| $K_{max}$ | Carrying capacity of the resource | # Resource units | 70,000 | 10 |
| $K_{min}$ | Critical resource level | # Resource units | $\frac{K_{max}}{10}$ | e.g., ref. 35 |
| $s^*$ | Scaling factor setting $\max(f_2(R)) \equiv \max(f_1(R))$ | Unitless | For given $K_{max}$, $K_{min}$: $\approx 0.198$ | e.g., ref. 58; Supplementary Methods 2 |
| $P$ | Population size | Individuals | State variable | - |
| $R$ | Resource availability | # Resource units | State variable | - |

Finally, we compare model expectations to historical data of human population and harvesting dynamics in island states, using the HYDE database[50–52].

**Scenarios of human population decline: crumble or collapse?** When a sustainable equilibrium cannot be attained, and the system is initialized with high resource availability and a small human consumer population, the population overshoots, after which a trajectory of decline follows (Fig. 1). The overshoot phase is followed by collapse of the population when overharvesting leads to complete exhaustion of the resource (case I, Fig. 1a, b). Alternatively, the overshoot phase may be followed by a so-called "crumble" process: a decelerating decline of resources and the consumer population, both components approaching zero more gradually (case II, Fig. 1c, d). Which of these two transient trajectories will occur can be inferred from projections of the isoclines and a so-called crumbling trajectory in the state space of resources and human consumers (Fig. 1 and Supplementary Methods 5). Along a crumbling trajectory, the consumer: resource ratio is fixed (Fig. 1c). As a result, the decline of the consumer population is proportional to its current size: the smaller the current population size, the smaller the population decline. This proportionality explains the crumbling process of decelerating decline described above. A requirement for the system to approach the crumbling trajectory is that the consumer:resource ratio along this trajectory exceeds the corresponding ratio along the human consumer population isocline (Fig. 1b, d and Supplementary Methods 5). If the latter ratio is larger, the transient dynamics are characterized by collapse (i.e., case I) instead. The system properties differentiating between overshoot and crumble versus overshoot and collapse dynamics were similar for the baseline and extended model versions (Fig. 1, Supplementary Methods 4, 5, and Supplementary Fig. 1).

**Scenarios toward equilibrium: (damped) oscillations or logistic growth?** In the baseline model, the shapes of the resource and consumer isoclines determine that there can only be a single isocline intersection, and thus equilibrium point, at which both resources and human consumers are present in non-zero densities (Fig. 2a). At the critical point where this equilibrium becomes stable, sustained oscillations occur (labeled as case III at the critical point, i.e., case $\text{III}_C$; Fig. 2c). Beyond this critical point, the equilibrium state of the system is reached via damped oscillations (case III Fig. 2d). Damped oscillations occur when the slope of the resource isocline at the equilibrium state is either weakly positive or weakly negative (Fig. 2a, d). The equilibrium state is reached through logistic growth of the consumer population when the slope of the resource isocline at the equilibrium state is strongly negative (case IV, Fig. 2b, e).

In the extended model, depensation reduces the slope of the resource isocline at low densities. As a result, there are either zero isocline intersections (yielding either case I or case II systems as shown above) or two isocline intersections, and thus equilibrium points, at which both resources and human consumers are present in non-zero densities (Fig. 2b). At the critical point between these two situations, there is a single isocline intersection. In contrast to the baseline model, this single intersection comprises a stable equilibrium point that is reached through damped oscillations (case III; Fig. 2c), rather than sustained oscillations around a neutrally stable equilibrium point. Beyond this critical point, the slope of the resource isocline at the equilibrium state determines whether the equilibrium is also reached through damped oscillations or logistic growth, similar to the baseline model (Fig. 2a, b).

**Resource productivity and harvest regime constrain possibilities for sustainable development**. In the baseline model, the classical overshoot and collapse dynamics occur in systems where the regeneration rate of the resource is slow, and the harvesting regime is intense (case I; Fig. 3a). The overshoot and crumble dynamics occur under slightly more benign conditions – a higher resource regeneration rate or less intense harvesting regime (case II; Fig. 3a). A stable equilibrium is reached through damped oscillations when conditions improve even further (case III; Fig. 3a). Finally, under the most benign conditions, the equilibrium point is reached through logistic consumer population growth (case IV; Fig. 3a). One caveat here is that under intense harvesting regimes, there is always a risk of overexploitation at low resource levels, regardless of the system's productivity and the existence of a stable equilibrium point (Fig. 3a).

In the extended model, the range of social-ecological conditions generating overshoot and collapse dynamics drastically increases

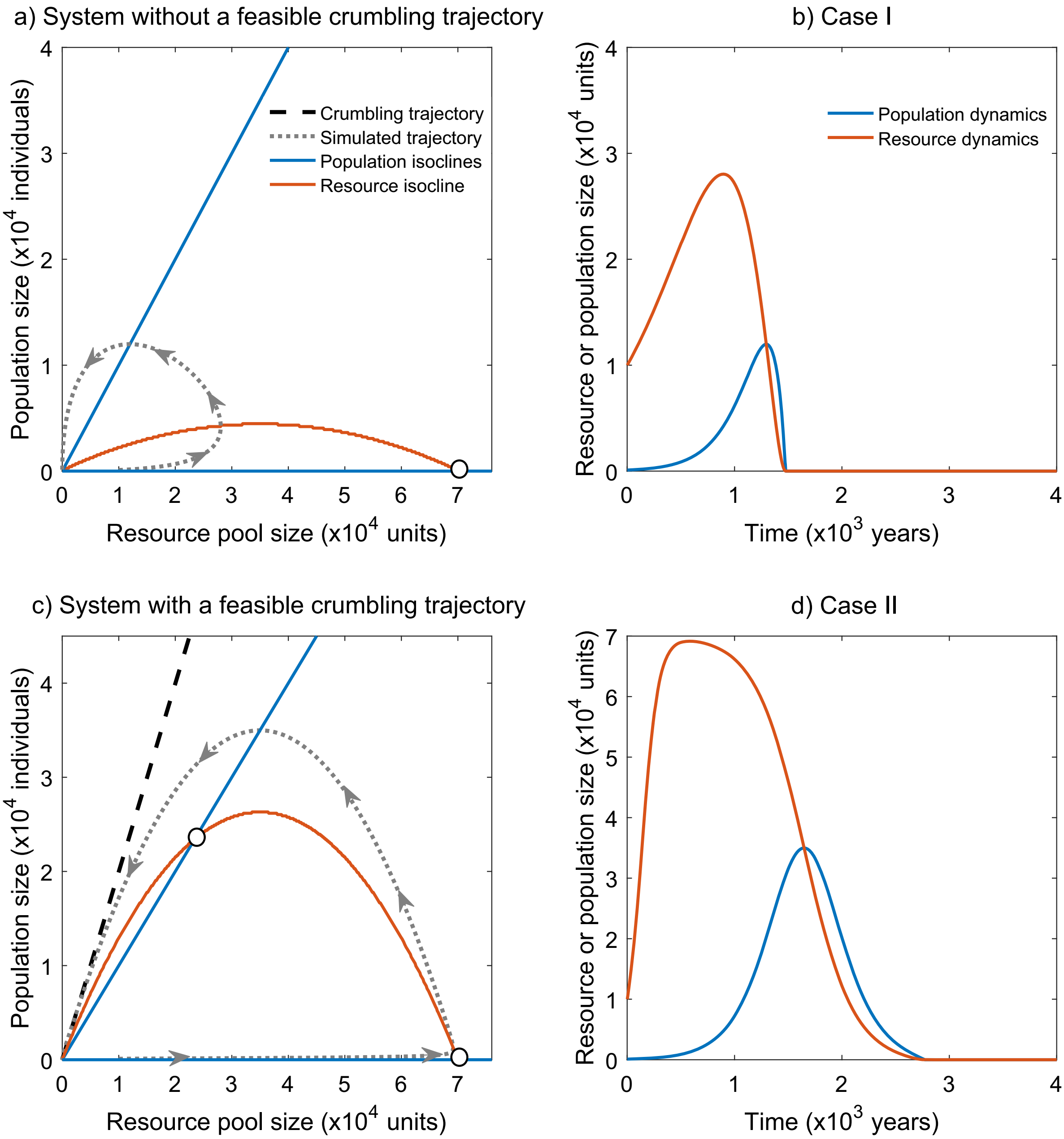


**Fig. 1 Overview of the possible transient system dynamics in the absence of a stable equilibrium point.** The transient dynamics of the human consumer-renewable resource system exhibit either overshoot and collapse dynamics (case I; **a**, **b**), or overshoot and crumble dynamics (case II; **c**, **d**). **a** State space portrait showing the population isoclines and resource isocline of a system exhibiting overshoot and collapse dynamics. For this system, the slope of the crumbling trajectory is negative, and therefore not appearing in the positive quadrant of the state space. **b** Temporal dynamics of overshoot and collapse scenario. **c** State space portrait showing the population isoclines and resource isocline of a system exhibiting overshoot and crumble dynamics. For this system, the slope of the crumbling trajectory is larger than the slope of the population isocline, facilitating the crumbling dynamics. **d** Temporal dynamics of overshoot and crumble scenario. Here, the baseline model system is shown, but dynamics are similar for the extended model (Supplementary Fig. 1). Parameter values: Overshoot and collapse: $c = 0.0022$ year$^{-1}$, $h = 0.0088$ individual$^{-1}$ year$^{-1}$; Overshoot and crumble: $c = 0.0131$ year$^{-1}$, $h = 0.0088$ individual$^{-1}$ year$^{-1}$; other parameters as in Table 1.

(Fig. 3b). In contrast, the range of conditions generating overshoot and crumble dynamics substantially decreases, becoming limited to regimes with low harvesting rates (Fig. 3b and Supplementary Methods 5). Furthermore, the asymmetry in the resource growth function creates a relatively steep slope at high renewable resource levels, which has a stabilizing effect on the equilibrium points (Fig. 2b). Therefore, the extended model has a larger range of social-ecological conditions that develop straightforwardly toward a sustainable equilibrium point (Figs. 2 and 3b). Finally, the inclusion of depensation in the renewable resource dynamics means that renewable resource will decline to zero when the resource availability falls below a critical level needed for recovery (see Methods), even in the absence of resource harvesting by consumers. Thus, in the extended model, degradation is always possible; even in systems with little or no harvesting (Fig. 3b).

**System interventions to avert crises: some counter-intuitive observations.** We analyzed the potential effects of interventions within the extended model framework, focusing on an interesting

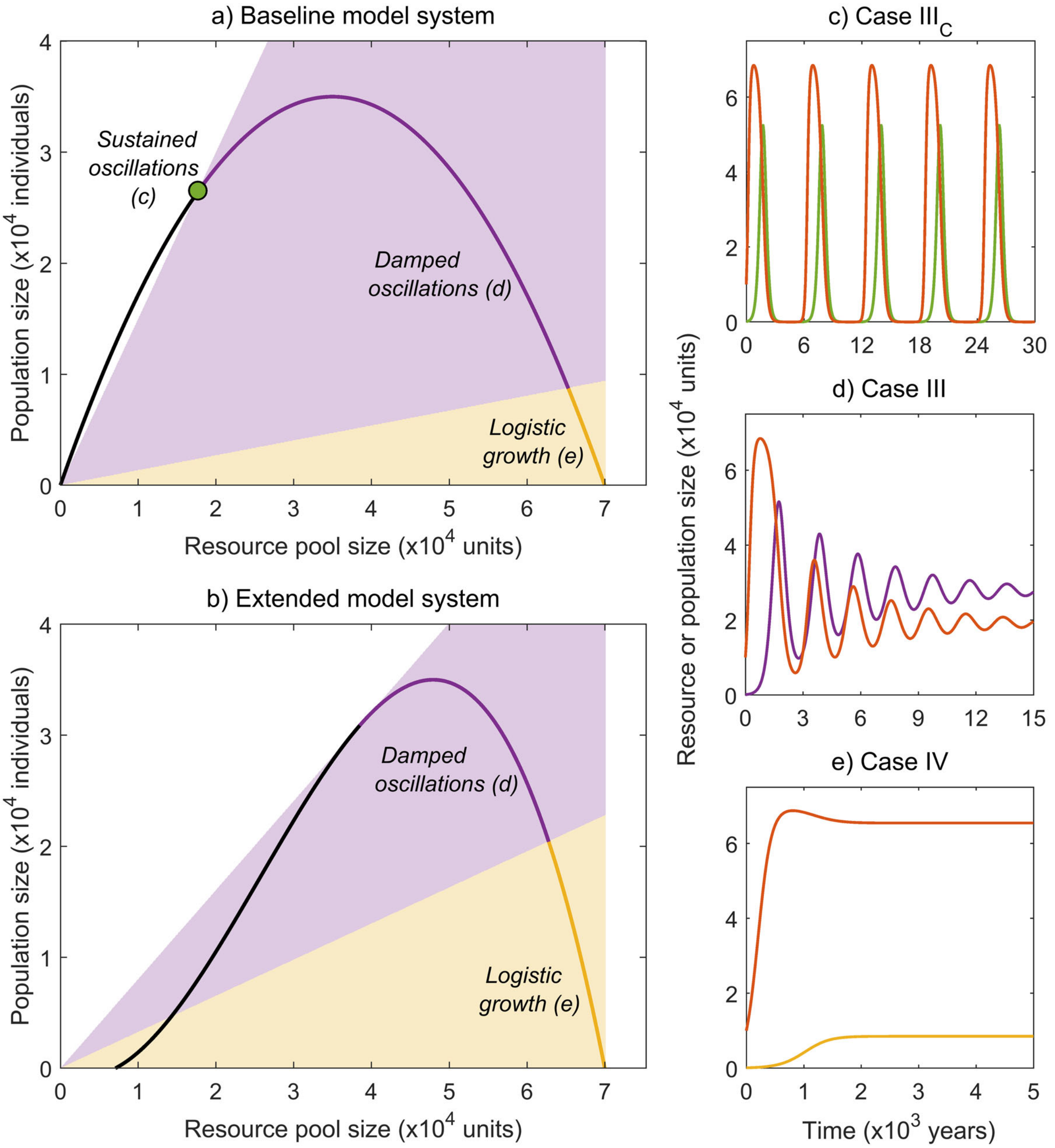


**Fig. 2 Overview of the possible transient system dynamics in the presence of a stable equilibrium point.** The transient dynamics of the human consumer-resource system may approach the equilibrium point through damped oscillations (case III; **d**), or through logistic growth of the human consumer population (case IV; **e**). At the critical point where the equilibrium becomes stable (**a**, **b**), both the baseline and extended model system exhibit sustained oscillations (case $III_C$; **c**), just for one unique harvest intensity value (when other parameter are fixed). **a** State space portrait showing when cases III and IV occur in the baseline model. **b** State space portrait showing when cases III and IV occur in the extended model. **c** Temporal dynamics of sustained oscillations. **d** Temporal dynamics of dampening oscillations. **e** Temporal dynamics of logistic growth toward the equilibrium. In the dynamics simulations, red lines indicate resource dynamics, whereas population dynamics are shown in green (**c**), purple (**d**) and ochre (**e**), corresponding to the color scheme used in panels **a** and **b**. Parameter values (baseline model simulations): Sustained oscillations: $c = 0.0088$ year$^{-1}$, $h = 0.0044$ individual$^{-1}$ year$^{-1}$, $q = 1.5$ individuals #resource units$^{-1}$; Dampened oscillations: $c = 0.0088$ year$^{-1}$, $h = 0.0044$ individual$^{-1}$ year$^{-1}$, $q = 1.45$ individuals #resource units$^{-1}$; Logistic growth toward the equilibrium: $c = 0.0088$ year$^{-1}$, $h =$ 0.0044 individual$^{-1}$ year$^{-1}$, $q = 0.13$ individuals #resource units$^{-1}$; other parameters as in Table 1.

case where a sustainable equilibrium could be reached through oscillations (i.e., case III). The type of dynamics discussed below occur more generally at the upper edge of the case III parameter region (Fig. 3b), for most of the resource productivity gradient considered (see Supplementary Discussion 1 and Supplementary Fig. 2 for details). Numerical analyses reveal that reaching this sustainable equilibrium requires a relatively delicate balance between renewable resource availability and consumer population size (Fig. 4a). Even slight differences in initial conditions can lead to divergent dynamics that bring about either a sustainable or a degraded system (Fig. 4b). Interestingly, a new type of dynamics emerges in the extended model, where systems "crawl by" (cf. ref. [46]) the unstable saddle equilibrium point created by the second isocline intersection (Fig. 2). During this crawl-by, systems go through a long period of apparent stability, followed by a relatively rapid transition toward a degraded state (Fig. 4b). The emergence of an unstable saddle equilibrium point and the associated crawl-by is due to the depensation mechanism

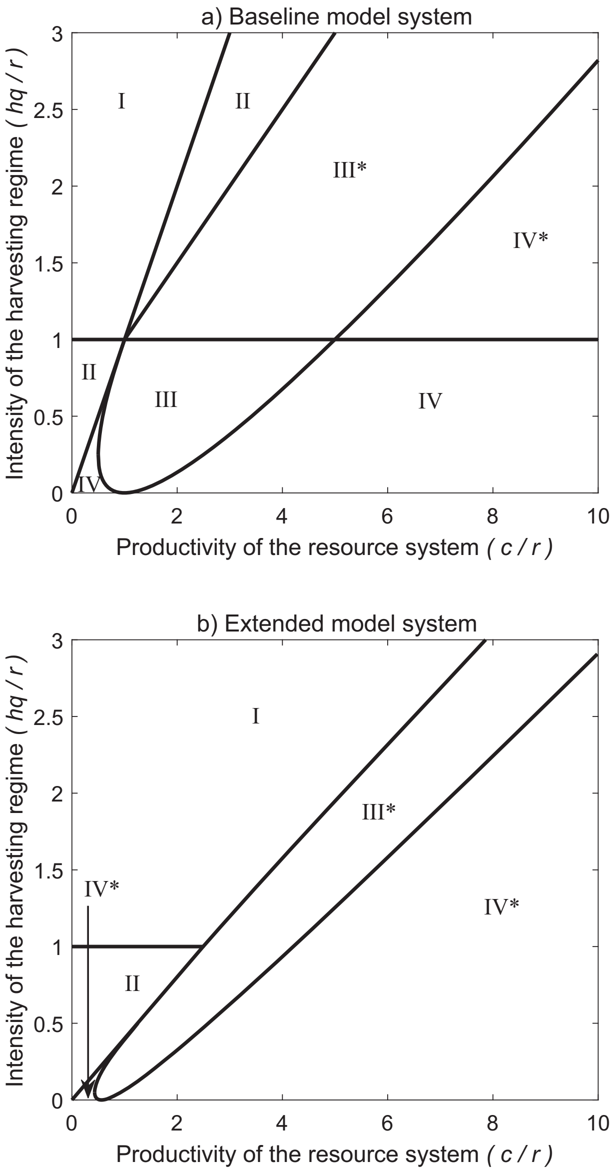


**Fig. 3 Quantitative analysis of the influence of environmental conditions and human harvesting strategy on the emerging model dynamics.** Panels show the results for the baseline consumer-renewable resource model (**a**), and the extended model version (**b**) Roman numerals indicate cases I–IV as shown in detail in Figs. 1 and 2. Note that case $III_C$ (Fig. 2c) occurs along the lines separating the case II and case III regions in the baseline model system (**a**). Asterisks indicate systems in which overexploitation may prevent reaching a sustainable equilibrium. In the extended consumer-renewable resource model, overexploitation is always a possibility, regardless of the system's productivity and regardless of the harvest intensity. Moreover, the parameter space in which an overshoot and crumble scenario occurs drastically decreases as compared to the baseline model system. In contrast, the parameter space in which an overshoot and collapse scenario occurs drastically increases.

included in the renewable resource dynamics, which creates the possibility of having two isocline intersections instead of one (Fig. 2). Thus, the long-term transients observed cannot occur within the baseline model framework (see Supplementary Discussion 2 and Supplementary Fig. 3 for details).

Successful interventions are perturbations that move the system from a trajectory outside the so-called basin of attraction, i.e., the set of system states that will develop toward the equilibrium point, to a trajectory within this basin of attraction. These successful interventions (i.e., a change in renewable resource availability, or a change in consumer population size) can be quite counter-intuitive. For example, the degradation case discussed can be circumvented by increasing the population, and hence resource consumption in the early growth phase (Fig. 4c). Alternatively, degradation of this system can be prevented by removing resources (i.e., not using them for human sustenance and growth) when renewable resource availability is at its peak (Fig. 4d). However, the windows of opportunity to avoid crises may be limited, meaning that appropriate timing of a particular intervention within such windows can be critical to its success. Moving toward the basin of attraction of the sustainable equilibrium (the shaded green regions in Fig. 4c, d) may require an increase of a state variable at some points in time, and a decrease at other points in time (Fig. 4c, d). Hence, when the successful interventions discussed above are executed at a different moment in time, they may only move the system farther away from the basin of attraction, accelerating the loss of resources and its consumer population rather than avoiding it (Fig. 4c, d).

In addition, one may intuitively expect that the earlier interventions are implemented in systems on unsustainable trajectories, the more likely it is that these interventions will be successful. This intuitive expectation, however, may not be correct for unsustainable trajectories undergoing phases of rapid population growth under relatively high resource availability, for example. Under these conditions, immigration events may only accelerate the eventual decline of resources and the population (Fig. 5). Moreover, migration events would only lead to a temporal setback followed by a very similar, unsustainable system trajectory (Fig. 5). Instead, for the latter type of interventions to be successful, their implementation may need to be delayed until the system reaches a window of opportunity when it is already in a declining phase of the trajectory (Fig. 5). In summary, the lagged response of the human consumer population to changes in resource availability provides a major constraint to the opportunities for reaching a sustainable equilibrium. If the population: resource ratio is too large, both the population and resources will decline, but the population decline will not be fast enough to halt further decline of resources (Figs. 1 and 4). Alternatively, if the population:resource ratio is too small, the population will increase rapidly and by the time it starts declining the population:resource ratio is again too high (Figs. 4 and 5), leading to the same outcome as described above. Hence, interventions that force the system to more balanced population:resource ratios are more likely to be successful (Figs. 4 and 5).

**Climate and harvest intensity affect historical consumer-renewable resource dynamics**. Historical reconstructions of population dynamics showed the same range of dynamical behavior observed in model simulations (Fig. 6). For example, in Australia, a stable population started to grow exponentially for more than 1500 years, after which it rapidly declined to the smallest population numbers in thousands of years (Fig. 6). In Iceland, the decline was more gradual (Fig. 6), resembling the overshoot and crumble dynamics observed in model simulations (Fig. 1c, d). Interestingly, both island states experienced a relatively intense harvesting regime, and environments with relatively low productivity, consistent with the regions in the productivity-harvesting intensity parameter space where overshoot and collapse/crumble dynamics would be expected (Figs. 3 and 6). In contrast, Cyprus, Japan and Taiwan experienced lower harvesting intensities (Fig. 6). Climatic conditions on Cyprus are harsher, and hence its productivity is lower. Consistent with model

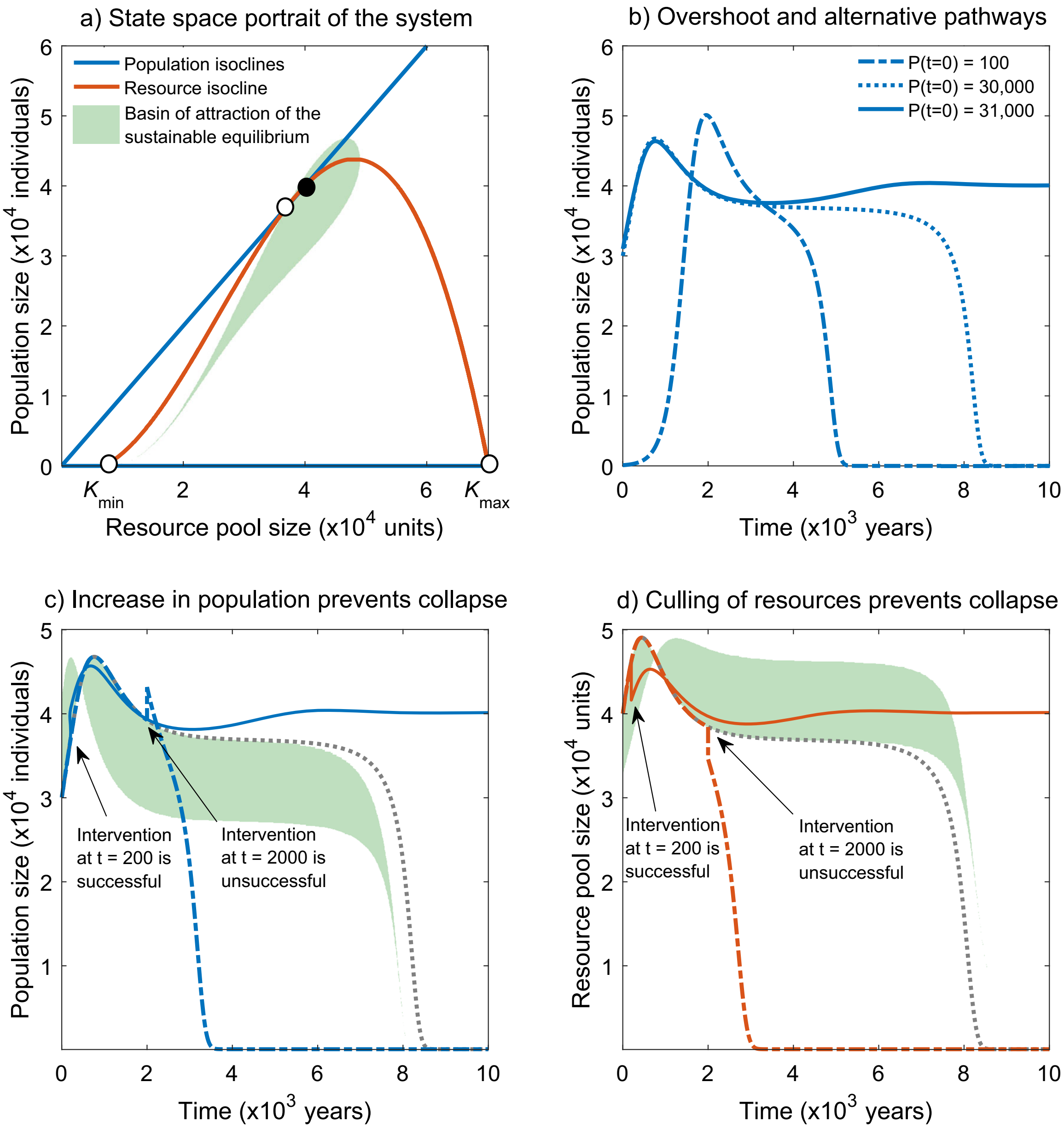


**Fig. 4 Numerical investigation of the transient dynamics of a consumer-renewable resource system that contains a stable (spiral) equilibrium. a** Graph showing the isoclines of the system and the basin of attraction of the stable equilibrium point (green shaded region; numerically derived with $c = 0.0088$ year$^{-1}$, $h = 0.0035$ individual$^{-1}$ year$^{-1}$, and other parameters as in Table 1). The relatively small size of this basin of attraction suggests that any given resource availability strongly constrains the population range that will develop towards the stable equilibrium, and vice versa. **b** Transient dynamics show that collapsing systems may undergo a relatively long phase of apparent stability, before a relatively rapid collapse occurs. In contrast, initial conditions that are within the basin of attraction will develop towards a stable equilibrium point. **c** Example showing how an immigration event (adding 10% to the population at $t = 200$ years after initialization) can move the system into the sustainable equilibrium's basin of attraction (green shaded region), and save the system from collapsing on the longer term. However, when the same perturbation is applied at a different moment in time ($t = 2000$ years) it accelerates the decline of consumers and resources. In panels **c** and **d**, the gray dotted line shows the default simulation from panel **b**, with initial population size $P(t = 0) = 30{,}000$ individuals. **d** Example showing how a resource culling event (removing 10% of the resource at $t = 200$ years after initialization) can move the system into the sustainable equilibrium's basin of attraction (green shaded region) save the system from collapsing on the longer term. However, when the same perturbation is applied at a different moment in time ($t = 2000$ years) it accelerates the decline of consumers and resources.

predictions, population dynamics on Cyprus showed more of an oscillatory behavior, while population dynamics on Japan and Taiwan approached relatively stable population numbers in a logistical fashion (Fig. 6). For the latter two island states, a new phase of rapid growth at the onset of the approach to the Industrial Revolution could also be observed. Finally, climatic conditions in New Zealand are comparable to those in Japan, but a more intensive harvest regime was present. Model simulations suggested that such intense harvesting regimes could lead to oscillating dynamics (Fig. 6). Although such oscillations were not observed in the time period considered, the population decline observed in the 18th century for New Zealand is distinctly different from dynamics observed in Japan and Taiwan (Fig. 6). In summary, the range of historical population dynamics of island states is similar to the range observed in the model framework, and differences in population dynamics are consistent with the

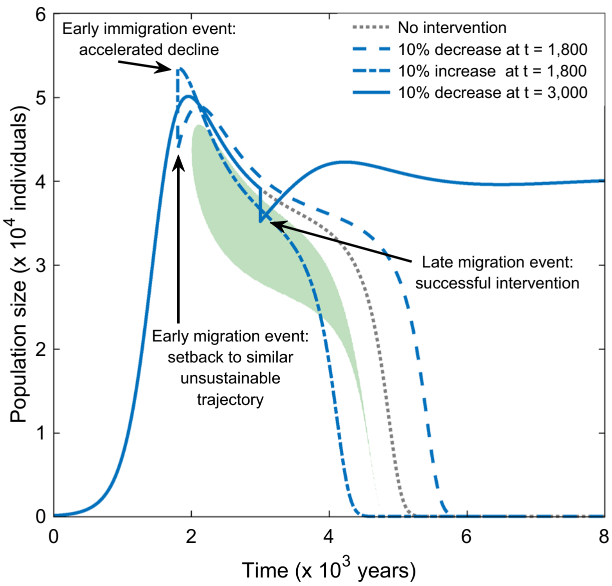


**Fig. 5 Averting crises in systems on unsustainable trajectories may require holding off of interventions until a window of opportunity emerges.** In systems experiencing rapid population growth under relatively high resource availability, timely interventions may not be successful, as it may not be possible to move the system into the sustainable equilibrium's basin of attraction in this stage. Note that this basin of attraction (green region) is drawn for the "no intervention" simulation; in the early immigration scenario, lower resource availability means that the system is no longer within the basin of attraction at the same population sizes. Parameter values as in Fig. 4, with initial conditions: $P(t=0)=100$ individuals, $R(t=0)=50{,}000$ resource units.

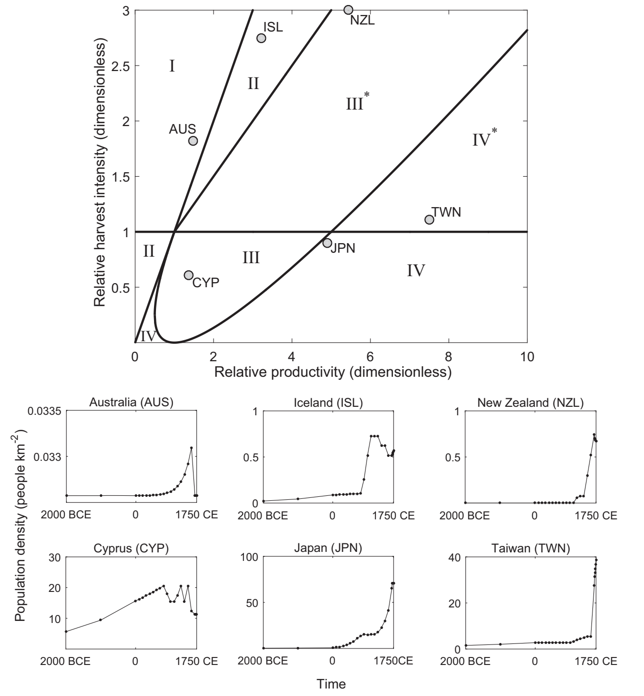


**Fig. 6 Projection of six island states and the social-ecological system dynamics map for the baseline model onto a dimensionless (*productivity*, *harvest intensity*) parameter space.** As all population showed recovery during the Industrial Revolution[52], it was assumed that the resources in the system did not exhibit the depensation mechanisms that were included to generate Fig. 3b). Population dynamics (from ref. [52]) showed a similar range of dynamics as observed in model simulations, and this variation closely corresponded to the expected variation due to relative differences in productivity and harvesting regime in the systems considered.

model-inferred relationships with the productivity of the environment and the intensity of the harvesting regime (Figs. 3 and 6).

## Discussion

The mechanisms driving overshoot and collapse dynamics in past and current societies, while a popular archetype for human-renewable resource interactions, are heavily debated[23–25,53,54]. When searching for causal mechanisms driving rapid transitions in social-ecological systems, an intuitive approach is to search for changes in internal or external forcings that occurred close to the transition point (e.g., refs. [55–57]). Using a stylized theoretical modeling framework, our study illustrated how rapid transitions of seemingly stable human consumer-renewable resource systems toward a degraded state can be the result of long transients that occur without any change in forcing (Fig. 4). Instead, these transient dynamics emerged from depensation, i.e., a reduction in the regeneration rate of the renewable resource at low levels (Fig. 2 and Supplementary Discussion 2). Depensation created an unstable equilibrium that systems crawl by during a long period of apparent stability[46,47]. Depensation mechanisms may be particularly relevant when considering biotic resources[27,34,35,41,58]. Recent research has emphasized that observed regime shifts in ecological systems may reflect long transients[46], rather than a response to a gradual change in environmental conditions or exploitation pressure. Our study highlights that such long-term transients may also provide a relevant yet largely unexplored perspective on human consumer population—renewable resource systems. Although these interactions were studied here within confined system settings as found in island states, global impacts of resource consumption on human populations are highlighting the need to consider these interactions at the earth system level as well[4,6,59,60]. Despite the relative simplicity of the model frameworks considered, the emerging dynamics revealed some counter-intuitive consumer-renewable resource dynamics. Specifically, we found that the basin of attraction of sustainable equilibrium points may comprise a relatively narrow range around a certain consumer population:resource ratio (Fig. 4a). This means that for a given current level of renewable resources, both a too large, and too small, population would prevent sustainable development. Similarly, for a given current population size, the amount of renewable resources may be too small to ensure sustainable development, but the amount could also be too large. Hence, either the removal of renewable resources or a sudden increase in consumer population size could provide a means to avert environmental crises in some cases (Fig. 4c, d). Although it may be difficult to implement these types of interventions as management strategies, it is important to note that sudden, short-term system perturbations can have lasting, long-term consequences for the direction in which the consumer-resource system develops, even though these effects remain largely hidden in the system's transient dynamics (Fig. 4c, d). In this context, previous studies have suggested that windows of opportunity for successful interventions may arise from climatic fluctuations[61], or rapid changes in environmental conditions[62,63]. Indeed, considering external perturbations driven by climate may become increasingly important when longer periods of time are considered[64]. Here, we show that the occurrence of such windows of opportunity may also arise from the nature of the sustainable equilibrium point itself, even in the absence of external changes (Fig. 4). Our numerical approach to identify basins of attraction around stable equilibrium points provides an effective way to identify such windows, and is readily applicable to similar stylized models of social-ecological systems (e.g., refs. [3,8,9,11,12,27,29]).

The relationships between productivity of the environment, harvesting regime and human population dynamics, as inferred from the model analyses (Fig. 3), provided a useful explanatory framework for diverging population dynamics in island states (Fig. 5;[52]). It should be noted that many other societal processes contribute to population dynamics (e.g., refs. [25,28,53]), suggesting that productivity and harvesting intensity may not always be sufficient to describe and project population dynamics. We should also stress that our approach used relatively rough indicators for resource regeneration capacity and harvesting intensity[52,65], which are subject to increased uncertainty moving further back in time (e.g., ref. [51]). While the correspondence between historical dynamics and expectations derived from our modeling approach (Fig. 6) is not meant to be an argument for environmental determinism of human-environment relationships, we can note that different human-environment interactions may drive a range of dynamics broader than a dichotomy of collapsing and succeeding societies (Figs. 1, 2, 6). Our results may also motivate the formulation of alternative hypotheses to event-based explanations of societal changes. For example, whereas human population dynamics on Iceland could be interpreted as three events of population decline caused by famine[66], it could also be seen as a long transient overshoot and crumble process that may be typical for systems with intermediate productivity and relatively intense harvesting regimes (Figs. 1c, d, 3, and 6).

**Limitations and outlook to future research**. This study built on the framework presented in ref. [10], considering one essential renewable resource that constrains the growth of the consumer population. We extended this baseline model by considering that the renewable resource may be subject to depensation, an extension that has been considered in similar models[27,34,35,58], but not within the particular model structure considered here. One limitation of the current study is that in both the baseline and extended models, we assumed that renewable resource availability and maximal regeneration rate are uniform in space and time (Supplementary Methods 1). Previous studies have shown how heterogeneity in resource availability in space (e.g., ref. [67]) and time (e.g., refs. [61,62,68]) may affect transient system dynamics, reducing the abruptness of transitions or obscuring the transition to the basin of attraction of an alternative equilibrium point. Alternatively, when including heterogeneity in the baseline model through a meta-population approach that allows for import and export of resources, transitions may also be accelerated[69]. In addition, heterogeneity may also arise from the use of multiple, substitutable resources. Alternative modeling approaches have previously considered multiple alternative resources, showing that resource-switching may increase the abruptness of system transitions (e.g., refs. [9,12,29,70]). Obtaining a systematic overview of how spatial and temporal heterogeneity in the availability of multiple resources may mediate transient dynamics in social-ecological systems is, therefore, an interesting avenue for further research.

Similarly, we made the simplifying assumption that the per capita harvest rate of the human consumer population was constant over time. Technological developments and societies' capabilities to institutionally adapt would allow for this characteristic to change over time. On the one hand, technological developments may enable an increase in per capita harvest rates, which may pose a challenge for timely institutional adaptation[12]. On the other hand, technological developments can also promote higher resource efficiency and increasing the possibilities for developing towards a stable equilibrium (Fig. 3;[3,12]). Apart from technological developments, previous studies have also demonstrated how stylized models including human population dynamics can be expanded to include more detailed demographic processes (e.g., ref. [71]), multiple consumer behaviors (e.g., ref. [11]) and more explicit consideration of general consumer behavior[19] or individual consumer behavior (using agent-based modeling, e.g., ref. [72]). Societal dynamics and related institutional processes (e.g., ref. [73]) can be included in more detail as well. Again, resolving the appropriate intervention strategies for these different cases would provide an important area of future research on management of social-ecological systems, which is particularly relevant for modern societies aiming to develop strategies for sustainable development within regional or planetary boundaries[6,74–76]. Although complete analytical analysis of further expanded models may not be possible anymore, numerical simulations of more complicated models could easily be compared to the quantitative maps of possible social-ecological scenarios presented here (Figs. 1, 2, 3). Such an "exploratory modeling approach" (cf. ref. [15]), may provide a more detailed understanding of which (set of alternative) mechanism(s) can explain a specific type of dynamics within consumer-renewable resource systems.

Stylized models provide a useful means to explore the potential consequences of human-environment feedbacks for the sustainable development of social-ecological systems[12]. However, results from these exercises need to be interpreted with caution. Although the emerging dynamics in model systems can be well attributed to specific underlying processes, such observations are unlikely to yield simple and universal solutions to sustainability challenges experienced in consumer-renewable resource systems around the globe[77]. For instance, even in common pool resource systems accessible to multiple users, extraction behavior might change in response to changing environmental conditions, from independent utilization to cooperation with other users (although such adaptation may be most likely for small-scale systems[14,18]). Hence, assessing to what extent theoretical mechanisms drive dynamics within a specific social-ecological system requires complementary empirical work[78]. Models can then also assist in explaining the context-dependent outcomes that can be observed in comparisons between such case studies. For example, even in the relatively simple systems analyzed here, context-dependent effects of interventions can already be observed; just the timing of an intervention can create drastically different outcomes in otherwise identical systems (Figs. 4 and 5). Although it may be difficult to fully deduct this type of dynamical system behavior by trial and error, analytical approaches as utilized here can provide a more fundamental understanding of the underlying geometry of the consumer-renewable resource system[12,79]. Following this approach, our current study showed that even in relatively simple model systems, a broad range of consumer-renewable resource dynamics may be possible (Figs. 1, 2, 3) and that substantial time lags between interventions and system responses may occur (Fig. 4). In real systems, the presence of such time lags may hamper the inference of social-ecological impacts of human-nature couplings by direct observation[80], further highlighting how models can serve as an integrative framework to synthesize empirical observations and theoretical predictions[15,81,82].

## Methods

**Main assumptions regarding consumer-resource interactions in island states**. Our framework builds on previous studies modeling dynamics between humans and the resources they depend on. These mathematical models are often inspired by the well-known Lotka-Volterra predator-prey model, where the label of "humans" is assigned to the predator (consumer) and "resources" to the prey (e.g., refs. [8–10,27,73,83,84]). The Lotka-Volterra framework can then be modified to include specific characteristics of the human population considered, or their resource environment (e.g., refs. [10,12,27]).

We consider a human consumer population which, confined to an island, fully depends on the availability of a renewable resource for its sustenance and growth. A detailed derivation of the model equations is presented in Supplementary Methods 1. In summary, we assume that the amount of energy and time spent on harvesting and consuming the renewable resource is dependent on resource availability, and that consumers divide harvesting activities in space according to an ideal free distribution. We also assume that the marginal benefit of resource gains will decrease with the total amount of resources already harvested, and that there will be a point at which the marginal cost of investing more time in resource harvesting exceeds the marginal benefit of the additional resources acquired. As shown in Supplementary Methods 1, two important constraints for subsequent model analyses emerge from these assumptions. First, the per capita resource consumption rate can be considered to be constant. Second, the human population's carrying capacity becomes proportional to the island's resource availability. We note that this latter assumption is equivalent to the notion of planetary boundaries at the global scale[5,6], where the system's ability to provide resources (and assimilate waste products resulting from its consumption) constrains the trajectory of population development[59,60,85].

**Baseline model framework**. Following the perspective of an island state, the model framework includes a carrying capacity constraining the total amount of resources that can persist in the system. In the baseline model version, it is assumed that development of the resource toward carrying capacity (in the absence of human harvesting) can be described by the standard logistic growth equation, meaning that resource growth is maximal when resource availability is half of the carrying capacity (see function $f_1(R)$ in Table 1). Together with the two constraints mentioned above, this stylized model can then be defined as two coupled ordinary differential equations that describe the dynamics of the resource $R$ (unit: # resource units), and the human consumer population $P$ (# individuals):

$$\frac{\mathrm{d}R}{\mathrm{d}t} = f_1(R) - hP = cR\left(1 - \frac{R}{K_{\max}}\right) - hP \qquad (1)$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = rP\left(1 - \frac{P}{qR}\right) \qquad (2)$$

in which $c$ represents the maximum relative growth rate of the resource (year$^{-1}$), $K_{\max}$ is the resource's carrying capacity (# resource units), $h$ is the longer-term per capita harvest rate (# resource units individual$^{-1}$ year$^{-1}$), $r$ is the maximum relative growth rate of the consuming population (year$^{-1}$) and $t$ represents time (years). The specific variation on the Lotka-Volterra predator-prey model described by Eqs. (1) and (2) was previously proposed in ref. [10].

**Extended model framework**. Logistic resource growth dictates that the relative resource regeneration rate approaches its maximum rate (here defined by the parameter $c$ in Eq. (1)) when resource availability is close to zero. For biotic resources, this description may not always be accurate, as reproduction can become more difficult when populations reach small numbers or densities[33,41]. This effect can be included in a phenomenological way by modifying the first term on the right-hand side of Eq. (1) (following e.g., refs. [27,35,37,58]). Specifically, the modified renewable resource dynamics can be described by

$$\frac{\mathrm{d}R}{\mathrm{d}t} = f_2(R) - hP = cs^{*}R\left(1 - \frac{R}{K_{\max}}\right)\left(\frac{R}{K_{\min}} - 1\right) - hP \qquad (3)$$

in which $K_{\min}$ represents a critical level of resource availability (# resource units) below which the rate of change in the renewable resource becomes negative. To improve the comparability between the baseline model and the extended model, we also introduced a scaling factor $s^*$ (following e.g., ref. [58]), which ensures that the maximal amount of resource growth is the same in both model versions (see Supplementary Methods 2 for details). Although previous social-ecological models did include depensation in the resource dynamics[27,86], this extension has to our knowledge not yet been considered in the specific model framework studied here.

**Transient dynamics and asymptotic states in different social-ecological scenarios**. We used linear stability analyses of asymptotic states in the baseline model (Eqs. (1) and (2)) and the extended model (Eqs. (2) and (3)) to identify the conditions under which both resources and human consumers can persist in a stable equilibrium, and the conditions under which such a stable equilibrium is absent (see Supplementary Methods 3, 4 for details). Each set of conditions could be further divided into two scenarios that differ in the transient dynamics toward the (same) asymptotic equilibrium state.

In the absence of a stable equilibrium, the human consumer population and the renewable resource will not persist. The transient consumer-resource dynamics, however, may follow either an overshoot and collapse scenario (case I), or an overshoot and crumble scenario (case II). In the former scenario, the human consumer population crashes rapidly after peaking and exhaustion of the resource drives a complete extinction of the population. In the latter scenario, the population declines more gradually after peaking, thus approaching zero more gradually. We distinguished between these two scenarios through identification of a crumbling trajectory involving a fixed ratio of the number of human consumers and available resources (see Supplementary Methods 5 for details).

In the presence of a stable equilibrium, both humans and resources may persist. The transient dynamics toward this equilibrium may be characterized either by damped oscillations (case III) or logistic growth of the human consumer population to the equilibrium point (case IV). We distinguished between these two scenarios through identification of the presence or absence of an imaginary part in the eigenvalues of the Jacobian matrix associated with each set of differential equations (Eqs. (1), (2) for the baseline model; Eqs. (2), (3) for the extended model), evaluated at the equilibrium point (see Supplementary Methods 3, 4 for details). For both model versions, we used this catalog of four possible scenarios (i.e., cases I–IV) to analyze the set of natural conditions (i.e., productivity of the renewable resource) and anthropogenic conditions (i.e., intensity of the harvest regime) in which each of the four cases could be observed. We also ran numerical simulations to illustrate the transient dynamics for each of the four cases.

**System interventions to avert crises**. Linear stability analysis identifies whether system equilibrium points are resilient to small perturbations in consumer population size or renewable resource availability. However, it does not provide insight into the maximum perturbation to which a stable equilibrium is resilient. Therefore, we used simulations to derive numerically the so-called basin of attraction, i.e., the full set of system states that will develop toward a stable equilibrium state. We performed this analysis for both the baseline and the extended model (see Supplementary Discussion 2 and Supplementary Fig. 3 for details). Once this basin of attraction has been derived, it is possible to assess how system interventions can move systems within it. Here, we focus specifically on interventions manipulating the amount of resources present in the system (e.g., by culling or importing) or the number of individuals present (e.g., through migration or immigration). All simulations were carried out using a fifth-order Runge-Kutta integration method as implemented in MATLAB (ode45, v.9.0, MathWorks, 2016).

**Comparison to historical consumer-renewable resource dynamics**. We compared states that comprise a (small number of) large island(s), as these could be considered relatively isolated systems. In addition, we only considered human population dynamics on these islands before the onset of the approach to the Industrial Revolution (1750 CE), starting at 2000 BCE. Finally, we selected island states that showed during this time period either: (i) period(s) of population decline; (ii) period(s) of prolonged stable population size. The following island states fulfilled these criteria: Australia, Cyprus, Iceland, Japan, New Zealand, and Taiwan.

The History Database of the Global Environment (HYDE) provides internally consistent estimates of historical human population dynamics and land use[51]. The most recent version of the dataset (HYDE 3.2) spans the past 12,000 years, and provides data in gridded form, and in aggregated form at the country level (using contemporary administrative boundaries[50,52]). In this study, we used historical estimates of population density (#people km$^{-2}$), and the per capita use of pasture area (ha #people$^{-1}$) from HYDE 3.2. In the dataset, historical estimates of population density are obtained by combining global and regional reconstructions that used historical and archeological data (e.g., ref. [87]). Historical estimates of per capita use of pasture area were obtained through a combination of hindcasting recent per capita use rates and estimations based on regional historical data of dietary habits and farming practices, for example[51,52]. In addition, as the productivity of a given area depends on climate, we estimated the maximum annual net primary productivity (ANPP, in $10^4$ g ha$^{-1}$ year$^{-1}$; which depends on parameter $c$ in the model framework) of a country following ref. [65]:

$$\mathrm{ANPP} = 4000\left(1 - \mathrm{e}^{-4.77\times10^{-5}\times\mathrm{MAP}}\right) \qquad (4)$$

in which MAP is the mean annual precipitation (in mm year$^{-1}$ (ref. [88])). Equation (4) estimates the aboveground productivity of lower vegetation (i.e., excluding trees[65]). The selected island countries were then ranked along a dimensionless productivity axis that was defined as:

$$X = \frac{X_{\mathrm{Scale}}\,\mathrm{ANPP}}{\max(\mathrm{ANPP})} \qquad (5)$$

where $X_{\mathrm{Scale}}$ is a dimensionless scaling parameter. In addition, multiplying ANPP with the per capita area use then yields a measure of per capita harvest intensity (similar to model parameter $h$). Again, the selected island countries were then ranked along a dimensionless harvest intensity axis, which was defined as:

$$Y = \frac{Y_{\mathrm{Scale}}(\mathrm{ANPP\ PastureUse})^{0.25}}{\max\left((\mathrm{ANPP\ PastureUse})^{0.25}\right)} \qquad (6)$$

where PastureUse is the per capita area used for pasture as reported in the HYDE 3.2 database[52], and $Y_{\mathrm{Scale}}$ is a scaling parameter. The relative rates in Eq. (5) and (6) were rescaled to fit the system dynamics map showed in Fig. 3a, by setting $X_{\mathrm{Scale}} = 7.5$ and $Y_{\mathrm{Scale}} = 3$, respectively.

To transform the system dynamics map of the baseline model shown in Fig. 3a to the same dimensionless coordinate system, we used the following equations:

$$X_{\mathrm{M}} = \frac{X_{\mathrm{M,Scale}}\left(\frac{c(x)}{r}\right)}{\max\left(\frac{c(x)}{r}\right)} \quad (7)$$

$$Y_{\mathrm{M}} = \frac{Y_{\mathrm{M,Scale}}\left(\frac{h(y)q}{r}\right)}{\max\left(\frac{h(y)q}{r}\right)} \quad (8)$$

in which the dimensionless parameters were set at $X_{\mathrm{M,Scale}} = 10$ and $Y_{\mathrm{M,Scale}} = 3$, corresponding numerically to the maximum values in Fig. 3a of $\frac{c(x)}{r}$ on the $x$-axis and $\frac{h(y)q}{r}$ on the $y$-axis, respectively.

Hence, using Eqs. (5)–(8), we were able to assign each island state a relative position in a dimensionless ($c$, $h$) parameter space, similar to the model analyses and providing a qualitative model-data comparison between productivity, harvesting regime and the resulting consumer population dynamics.

## Data availability
The HYDE database[50–52] that was used in this study (version 3.2) is publicly available at https://dataportaal.pbl.nl/downloads/HYDE/HYDE3.2/, under the Creative Commons License (CC BY 3.0).

## Code availability
The MATLAB scripts written for this study only contain standard functions and analysis methods. A model script using the fifth-order Runge-Kutta integration for the baseline and extended model versions is available (Supplementary Software 1).

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## References
1. Meadows, D. H., Meadows, D. L., Randers, J. & Behrens, W. W. *The Limits to Growth: A Report for the Club of Rome's Project on the Predicament of Mankind*. (Earth Island, 1972).
2. Peretto, P. & Valente, S. Growth on a finite planet: resources, technology and population in the long run. *J. Econ. Growth* **20**, 305–331 (2015).
3. Lafuite, A.-S. & Loreau, M. Time-delayed biodiversity feedbacks and the sustainability of social-ecological systems. *Ecol. Modell.* **351**, 96–108 (2017).
4. Xu, C., Kohler, T. A., Lenton, T. M., Svenning, J.-C. & Scheffer, M. Future of the human climate niche. *Proc. Natl Acad. Sci. USA* **117**, 11350–11355 (2020).
5. Rockström, J. et al. A safe operating space for humanity. *Nature* **461**, 472–475 (2009).
6. Steffen, W. et al. Planetary boundaries: guiding human development on a changing planet. *Science* **347**, 1259855 (2015).
7. O'Neill, D. W., Fanning, A. L., Lamb, W. F. & Steinberger, J. K. A good life for all within planetary boundaries. *Nat. Sustain.* **1**, 88–95 (2018).
8. Anderies, J. M. Culture and human agro-ecosystem dynamics: the Tsembaga of New Guinea. *J. Theor. Biol.* **192**, 515–530 (1998).
9. Brander, J. A. & Taylor, M. S. The simple economics of Easter Island: a Ricardo–Malthus model of renewable resource use. *Am. Econ. Rev.* **88**, 119–138 (1998).
10. Basener, B. & Ross, D. S. Booming and crashing populations and Easter Island. *SIAM J. Appl. Math.* **65**, 684–701 (2005).
11. Lafuite, A.-S., de Mazancourt, C. & Loreau, M. Delayed behavioural shifts undermine the sustainability of social–ecological systems. *Proc. R. Soc. Lond. B* **284**, 20171192 (2017).
12. Anderies, J. M. On modeling human behavior and institutions in simple ecological economic systems. *Ecol. Econ.* **35**, 393–412 (2000).
13. Schlüter, M. et al. New horizons for managing the environment: a review of coupled social-ecological systems modeling. *Nat. Resour. Model.* **25**, 219–272 (2012).
14. Schlüter, M. et al. Capturing emergent phenomena in social-ecological systems: an analytical framework. *Ecol. Soc.* **24**, 11 (2019).
15. Larsen, L. G., Thomas, C., Eppinga, M. B. & Coulthard, T. Exploratory modelling: extracting causality from complexity. *Eos* **95**, 285–292 (2014).
16. Krutilla, K. & Reuveny, R. A renewable resource-based Ramsey model with costly resource extraction. *Environ. Resour. Econ.* **27**, 165–185 (2004).
17. Oostdijk, M., Santos, M. J., Agnarsson, S. & Woods, P. J. Structure and evolution of cod quota market networks in Iceland over times of financial volatility. *Ecol. Econ.* **159**, 279–290 (2019).
18. Ostrom, E. A general framework for analyzing sustainability of social–ecological systems. *Science* **325**, 419–422 (2009).
19. Freeman, J. & Anderies, J. M. Intensification, tipping points, and social change in a coupled forager-resource system. *Human Nat.* **23**, 419–446 (2012).
20. Hardin, G. H. The tragedy of the commons. *Science* **162**, 1243–1248 (1968).
21. Berkes, F. et al. Globalization, roving bandits and marine resources. *Science* **311**, 1557–1558 (2006).
22. Kirch, P. V. In *Island Societies: Archaeological Approaches to Evolution and Transformation* (ed. Kirch, P. V.) 1–5 (Cambridge University Press, 1986).
23. Ponting, C. *A Green History of the World*. (Penguin Books, 1993).
24. Diamond, J. M. *Collapse: How Societies Choose to Fail Or Succeed*. (Penguin Books, 2005).
25. Tainter, J. A. Archaeology of overshoot and collapse. *Ann. Rev. Anthropol.* **35**, 9–74 (2006).
26. Weiss, H. & Bradley, R. S. What drives societal collapse? *Science* **291**, 609–610 (2001).
27. Taylor, M. S. Environmental crisis: past, present, and future. *Can. J. Econ.* **42**, 1240–1275 (2009).
28. Middleton, G. D. Nothing lasts forever: environmental discourses on the collapse of past societies. *J. Archaeol. Res.* **20**, 257–307 (2012).
29. Anderies, J. M. Robustness, institutions, and large-scale change in social-ecological systems: the Hohokam of the Phoenix Basin. *J. Institutional Econ.* **2**, 133–155 (2006).
30. Daly, H. E. Toward some operational principles of sustainable development. *Ecol. Econ.* **2**, 1–6 (1990).
31. Hilborn, R., Walters, C. J. & Ludwig, D. Sustainable exploitation of renewable resources. *Ann. Rev. Ecol. System.* **26**, 45–67 (1995).
32. Bretschger, L. & Smulders, S. Sustainable resource use and economic dynamics. *Environ. Resour. Econ.* **36**, 1–13 (2007).
33. Allee, W. C. *Animal Aggregations, A Study in General Sociology*. (University of Chicago Press, 1931).
34. Clark, C. W. *Mathematical Bioeconomics: The Optimal Management of Resources*. (John Wiley and Sons, 1976).
35. Haider, H. S. et al. Incorporating Allee effects into the potential biological removal level. *Nat. Resour. Model.* **30**, 1–16 (2017).
36. De Roos, A. M. & Persson, L. Size-dependent life history traits promote catastrophic collapses of top predators. *Proc. Natl Acad. Sci. USA* **99**, 12907–12912 (2002).
37. Basnet, K., Likens, G. E., Scatena, F. N. & Lugo, A. E. Hurricane Hugo: damage to a tropical rain forest in Puerto Rico. *J. Trop. Ecol.* **8**, 47–55 (1992).
38. Jones, C. G., Lawton, J. H. & Shachak, M. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* **78**, 1946–1957 (1997).
39. Scheffer, M., Carpenter, S. R., Foley, J. A., Folke, C. & Walker, B. Catastrophic shifts in ecosystems. *Nature* **413**, 591–596 (2001).
40. Anderies, J. M., Janssen, M. A. & Walker, B. H. Grazing management, resilience, and the dynamics of a fire driven rangeland system. *Ecosystems* **5**, 23–44 (2002).
41. Clark, C. W. Possible effects of schooling on the dynamics of exploited fish populations. *ICES J. Mar. Sci.* **36**, 7–14 (1974).
42. Lenton, T. M. Environmental tipping points. *Ann. Rev. Environ. Resour.* **38**, 1–29 (2013).
43. Blenckner, T. et al. Climate and fishing steer ecosystem regeneration to uncertain economic futures. *Proc. R. Soc. Lond. B* **282**, 20142809 (2015).
44. Stephens, P. A. & Sutherland, W. J. Consequences of the Allee effect for behaviour, ecology, and conservation. *Trend. Ecol. Evol.* **14**, 401–405 (1999).
45. Biggs, R., Carpenter, S. R. & Brock, W. A. Turning back from the brink: detecting an impending regime shift in time to avert it. *Proc. Natl Acad. Sci. USA* **106**, 826–831 (2009).
46. Hastings, A. et al. Transient phenomena in ecology. *Science* **361**, eaat6412 (2019).
47. Morozov, A. et al. Long transients in ecology: theory and applications. *Phys. Life Rev.* **32**, 1–40 (2020).
48. Jäger, C. G., Diehl, S., Matauschek, C., Klausmeier, C. A. & Stibor, H. Transient dynamics of pelagic producer-grazer systems in a gradient of nutrients and mixing depths. *Ecology* **89**, 1272–1286 (2008).
49. Seidl, R. et al. Science with society in the Anthropocene. *AMBIO* **42**, 5–12 (2013).
50. Klein Goldewijk, K., Beusen, A., van Drecht, G. & de Vos, M. The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. *Glob. Ecol. Biogeogr.* **20**, 73–86 (2011).
51. Klein Goldewijk, K. & Verburg, P. H. Uncertainties in global-scale reconstructions of historical land use: an illustration using the HYDE data set. *Landsc. Ecol.* **28**, 861–877 (2013).
52. Klein Goldewijk, K., Beusen, A., Doelman, J. & Stehfest, E. Anthropogenic land use estimates for the Holocene–HYDE 3.2. *Earth Syst. Sci. Data* **9**, 927–953 (2017).

53. McAnany, P. A. & Yoffee, N. *Questioning Collapse: Human Resilience, Ecological Vulnerability, and the Aftermath of Empire*. (Cambridge University Press, 2009).
54. Boersema, J. J. *The Survival of Easter Island: Dwindling Resources and Cultural Resilience*. (Translated by Webb, D., first published in Dutch: Beelden van Paaseiland). (Cambridge University Press, 2015).
55. Tinner, W. et al. Climatic change and contemporaneous land-use phases north and south of the Alps 2300 BC to 800 AD. *Quat. Sci. Rev.* **22**, 1447–1460 (2003).
56. Van Egmond, N. D. & de Vries, B. J. M. Sustainability: the search for the integral worldview. *Futures* **43**, 853–867 (2011).
57. Armit, I., Swindles, G. T., Becker, K., Plunkett, G. & Blaauw, M. Rapid climate change did not cause population collapse at the end of the European Bronze Age. *Proc. Natl Acad. Sci. USA* **111**, 17045–17049 (2014).
58. Lewis, M. A. & Kareiva, P. Allee dynamics and the spread of invading organisms. *Theor. Popul. Biol.* **43**, 141–158 (1993).
59. Anderies, J. M., Carpenter, S. R., Steffen, W. & Rockström, J. The topology of non-linear carbon dynamics: from tipping points to planetary boundaries. *Environ. Res. Lett.* **8**, 044048 (2013).
60. Fujimori, S. et al. A multi-model assessment of food security implications of climate change mitigation. *Nat. Sustain.* **2**, 386–396 (2019).
61. Holmgren, M. & Scheffer, M. El Niño as a window of opportunity for the restoration of degraded arid ecosystems. *Ecosystems* **4**, 151–159 (2001).
62. Scheffer, M., Van Nes, E. H., Holmgren, M. & Hughes, T. Pulse-driven loss of top-down control: the critical rate hypothesis. *Ecosystems* **11**, 226–237 (2008).
63. Siteur, K., Eppinga, M. B., Doelman, A., Siero, E. & Rietkerk, M. Ecosystems off track: rate-induced critical transitions in ecological models. *Oikos* **125**, 1689–1699 (2016).
64. Dermody, B. J. et al. A seesaw in Mediterranean precipitation during the Roman Period lined to millennial-scale changes in the North Atlantic. *Clim. Past* **8**, 637–651 (2012).
65. Del Grosso, S. et al. Global potential net primary production predicted from vegetation class, precipitation and temperature. *Ecology* **89**, 2117–2126 (2008).
66. Zhang, D. D. et al. Climate change and large-scale human population collapses in the pre-industrial era. *Glob. Ecol. Biogeogr.* **20**, 520–531 (2011).
67. Martin, P. V., Bonachela, J. A., Levin, S. A. & Muñoz, M. A. Eluding catastrophic shifts. *Proc. Natl Acad. Sci. USA* **112**, E1828–E1836 (2015).
68. Medeiros, E. S., Caldas, I. L., Baptista, M. S. & Feudel, U. Trapping phenomenon attenuates the consequences of tipping points for limit cycles. *Sci. Reports* **7**, 42351 (2017).
69. Dockstadter, Z., Bauch, C. T. & Anand, M. Interconnections accelerate collapse in a social-ecological metapopulation. *Sustainability* **11**, 1852 (2019).
70. Freeman, J., Peeples, M. A. & Anderies, J. M. Toward a theory of non-linear transitions from foraging to farming. *J. Anthropol. Archaeol.* **40**, 109–122 (2015).
71. Anderies, J. M. Economic development, demographics, and renewable resources: a dynamical systems approach. *Environ. Dev. Econ.* **8**, 219–246 (2003).
72. Le, Q. B., Seidl, R. & Scholz, R. W. Feedback loops and types of adaptation in the modelling of land-use decisions in an agent-based simulation. *Environ. Modell. Softw.* **27-28**, 83–96 (2012).
73. Pezzey, J. C. V. & Anderies, J. M. The effect of subsistence on collapse and institutional adaptation in population-resource societies. *J. Dev. Econ.* **72**, 299–320 (2003).
74. Barnosky, A. D. et al. Approaching a state shift in Earth's Biosphere. *Nature* **486**, 52–58 (2012).
75. Desing, H. et al. A Circular Economy within the planetary boundaries: towards a resource-based, systemic approach. *Resour. Conserv. Recycl.* **155**, 104673 (2020).
76. Rockström, J., Edenhofer, O., Gaertner, J. & DeClerck, F. Planet-proofing the global food system. *Nat. Food* **1**, 3–5 (2020).
77. Ostrom, E., Janssen, M. A. & Anderies, J. M. Going beyond panaceas. *Proc. Natl Acad. Sci. USA* **104**, 15176–15178 (2007).
78. Ostrom, E. A diagnostic approach for going beyond panaceas. *Proc. Natl Acad. Sci. USA* **104**, 15181–15187 (2007).
79. Vandermeer, J. H. Loose coupling of predator-prey cycles: entrainment, chaos and intermittency in the classic MacArthur consumer-resource equations. *Am. Nat.* **141**, 687–716 (1993).
80. Liu, J. et al. Complexity of coupled human and natural systems. *Science* **317**, 1513–1516 (2007).
81. Schlüter, M., Hinkel, J., Bots, P. W. G. & Arlinghaus, R. Application of the SES framework for model-based analysis of the dynamics of social-ecological systems. *Ecol. Soc.* **19**, 36 (2014).
82. Eppinga, M. B. et al. Frequency-dependent feedback constrains plant community coexistence. *Nat. Ecol. Evol.* **2**, 1403–1407 (2018).
83. Eberhardt, L. L. Is wolf predation ratio-dependent? *Can. J. Zool.* **75**, 1940–1944 (1997).
84. Reuveny, R. Taking stock of Malthus: modelling the collapse of historical civilizations. *Ann. Rev. Resour. Econ.* **4**, 303–329 (2012).
85. Samir, K. C. & Lutz, W. The human core of the shared socioeconomic pathways: population scenarios by age, sex and level of education for all countries to 2100. *Glob. Environ. Chang.* **42**, 181–192 (2017).
86. D'Alessandro, S. Non-linear dynamics of population and natural resources: the emergence of different patterns of development. *Ecol. Econ.* **62**, 473–481 (2007).
87. McEvedy, C. & Jones, R. *Atlas of World Population History* (Penguin Books, 1978).
88. FAO. *AQUASTAT Main Database, Food and Agriculture Organization of the United Nations* (FAO, 2016). Website last accessed on: 23 December 2020.


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## Competing interests

The authors declare no competing interests.

## Additional information

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