

ANALYSIS

Environmental change and ecosystem functioning drive transitions in social-ecological systems: A stylized modelling approach

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ABSTRACT

Sustainable management of social-ecological systems requires an understanding of how anthropogenic climate- and land use change may disrupt interactions between human societies and the ecosystem processes they depend on. In this study, we expand an existing stylized social-ecological system model by explicitly considering how urbanizing societies may become less dependent on local ecosystem functioning. This expansion is motivated by a previously developed conceptual framework suggesting that societies may reside in either a green loop and be strongly dependent on local ecosystem processes, or in a red loop where this dependency is weaker due to imports of natural resources from elsewhere. Analyzing the feasibility and stability of local social-ecological system states over a wide range of environmental and socio-economic conditions, we observed dynamics consistent with the notion of green loop-dominated and red loop-dominated societies comprising alternate stable social-ecological states. Based on systems' inherent dependencies on local ecosystem processes, responses to environmental change could comprise either transitions between green loop- and red loop-dominated states, or collapse of either of these states. Our quantitative model provides an internally consistent mapping of green loop- and red loop-dominated states, as well as transitions between or collapses of these states, along a gradient of environmental conditions.

1. Introduction

Current anthropogenic climate- and land use change may disrupt connections between human societies and the ecosystem processes they depend on (Schröter et al., 2005; Metzger et al., 2006; Kubiszewski et al., 2017; Hasan et al., 2020). How such disruptions affect the dynamics and functioning of social-ecological systems remains a challenging research topic, as these consequences are governed by complex feedbacks between the social and ecological subsystems (Liu et al., 2007; Ostrom, 2009; Raudsepp-Hearne et al., 2010; Domp tail et al., 2013; Levin et al., 2013; Sachs et al., 2019; Donges et al., 2021). For example, feedbacks between biotic and abiotic ecological system components may drive abrupt and drastic responses to gradual changes in anthropogenic pressure (Levin, 1998; Scheffer et al., 2001; Rietkerk et al., 2004). On the other hand, feedbacks between the adaptive capacity of governance structures and the robustness provided by the system's institutions may drive divergent responses to changes in environmental conditions

(Olsson et al., 2004; Armitage, 2005; Berkes and Turner, 2006; Cifdaloz et al., 2010; Moritz et al., 2018). Understanding these social-ecological feedbacks becomes even more challenging when small-scale (local) social-ecological systems develop stronger ties to larger-scale (i.e. regional or global) systems (Anderies et al., 2013; Fader et al., 2013; Cumming et al., 2017; Sterk et al., 2017; Peng et al., 2020).

Cumming et al. (2014) proposed a conceptual framework describing how agricultural transitions and urbanization within a local social-ecological system interact with the system's connection to larger-scale systems. The strength of this connection to larger-scale systems mediates the dependency of the socio-economic subsystem on local ecosystem functioning. When this larger-scale connection is relatively weak, the human population depends predominantly on local ecosystem processes and the system may reside within a green loop: a negative feedback between human population size and the availability of local ecosystem processes that this population depends on (Lima and Berryman, 2011; Alados et al., 2014). This feedback may then stabilize human

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population dynamics and the state of the local natural environment (Cumming et al., 2014). The green loop may become disrupted by the emergence of alternative livelihoods that generate income and enable the import of natural resources from beyond the local system boundary (Cumming et al., 2014; Schröter et al., 2018; Dorninger et al., 2021). In this way, importable ecosystem processes yielding resources such as fish (Dajka et al., 2020), timber (Grêt-Regamey et al., 2014) or crops (Dermody et al., 2014) no longer need to be supplied by the local ecosystem (Cumming et al., 2014). Consequently, the local population becomes less dependent on local ecosystem processes driving natural resource dynamics, enabling the population to grow beyond the carrying capacity of the local ecosystem. These alternate means of generating income enable the import of natural resources from elsewhere and subsequently increase the strength of the connection to larger-scale systems, while further reducing the dependence on local ecosystem processes. This development can allow the system to enter a red loop: a positive feedback between urban population size and the system's capacity to trade with and import natural resources from elsewhere (Cumming et al., 2014). It should be noted that not all ecosystem processes can be imported from elsewhere. For example, (spatial) demands for regulating processes such as erosion control and flood protection (Grizzetti et al., 2019) or cultural ones such as recreation and spiritual inspiration (Bagstad et al., 2017) can only be met through local supply. Moreover, meeting the demand of importable ecosystem processes may be constrained by the larger-scale, regional carrying capacity of natural resource use (Dermody et al., 2014). Hence, these characteristics will constrain the red loop's strength, meaning that at a certain size of the urban population, further growth will not be achieved through increased imports of natural resources (Cumming et al., 2014).

The green loop-red loop framework thereby highlights how human-environment connections may become obscured by separation in both time and space (Cumming et al., 2014; Hamann et al., 2015; Lapointe et al., 2019). This separation provides a potential explanation of the Environmentalist's Paradox (Raudsepp-Hearne et al. 2010), which refers to observations of increased human well-being even as the functioning of ecosystems declines. However, the framework also identifies the possibility of social-ecological systems entering traps that can lead to a system collapse (Cumming et al., 2014). More specifically, collapse of a green loop-dominated state may be driven by rural poverty and ecological degradation reinforcing each other, while collapse of a red loop-dominated state may be driven by overconsumption and a failure to regulate ecological decline (Cumming et al., 2014). When social-ecological systems have entered such a green trap or red trap, they must reorganize to prevent collapse (Cumming et al., 2014).

The notion of positive feedback driving the transition from green loop-dominated to red loop-dominated states implies the possibility of these social-ecological states being alternative stable equilibria (Cumming et al., 2014). This prediction of the conceptual framework has been tested with country-level data, showing bimodal distributions of Human Development Index (HDI) scores, with the two modalities exhibiting contrasting relationships between population growth rate and per capita Gross Domestic Product (GDP) (Cumming and Von Cramon-Taubadel, 2018; but see O'Sullivan, 2018). These observations suggest that one group of countries currently resides in a green loop, where economic dependence on local ecosystem processes is reflected in a negative correlation between per capita income and population growth (Cumming and Von Cramon-Taubadel, 2018; O'Sullivan, 2018). A second group of countries may reside in a red loop, where population growth increases the capacity to produce manufactured goods and services and is therefore positively correlated with per capita GDP (Cumming and Von Cramon-Taubadel, 2018).

While a differential equation model can explain why both the green loop-dominated state and the red loop-dominated state may be stable equilibria (Cumming and Von Cramon-Taubadel, 2018), this model formulation does not capture the positive feedback dynamics that may drive system transitions from a green loop-dominated to a red loop-

dominated state (O'Sullivan, 2018). In addition, an expanded model formulation would be needed to explicitly identify when such transitions are not possible, and systems may collapse instead (Cumming et al., 2014). Expanding dynamical models in this manner has the potential to increase our understanding of critical social-ecological system thresholds, and provide a catalogue of potential dynamical system responses to projected environmental changes or crises (Anderies, 2000; Larsen et al., 2014, 2016; Lade et al., 2017; Schlüter et al., 2019; Eppinga et al., 2021).

Explicit modelling of adaptation and transformations of social-ecological systems remains challenging and increased research efforts are needed to fully realize the potential of dynamical models (Schlüter et al., 2019; Donges et al., 2021). Stylized theoretical models provide a valuable step in this process, as they allow for the study of feedbacks and transitions in social-ecological systems in an analytically tractable way (Anderies, 2000; Schlüter et al., 2012; Lafuite et al., 2017; Eppinga et al., 2021). Previous stylized model studies have typically focused on relatively isolated social-ecological systems, more frequently found in the distant past (Anderies, 1998, 2006; Brander and Taylor, 1998; Basener and Ross, 2005; Eppinga et al., 2021). In this study we extend this stylized approach, by including a dynamical connection between the local social-ecological system and large-scale systems that mediates the local system's dependence on local ecosystem processes. Importantly, this coupling strength between the local and larger-scale systems is dependent on the current socio-economic state of the local system. With this approach, we aim to connect local environmental conditions with green loop and red loop dynamics, including the identification of when transitions between these dynamical regimes are possible or not. By incorporating local and larger-scale coupling in a phenomenological way, we use a minimal modelling approach that retains sufficient tractability to analyze analytically a broad range of scenarios and local environmental conditions (Anderies, 2003; Lade et al., 2013). Specifically, our model analysis focuses on answering the following research questions: 1) Under which environmental conditions will social-ecological systems reside in either a green loop-dominated or a red loop-dominated state, and which environmental conditions allow for transitions between these states?; 2) Under which conditions may social-ecological systems residing in a green loop-dominated state collapse, and how is this process reflected in the system's transient dynamics?; 3) Under which conditions may social-ecological systems residing in a red loop-dominated state collapse, and how is this process reflected in the system's transient dynamics?

2. Material and methods

2.1. Model assumptions and derivation of the local social-ecological system dynamics

We considered a local social-ecological system in which the socio-economic state, S_L , influences the degree of modification activities, M_L (Fig. 1). Here, modification activities refer to anthropogenic actions that change the state of the system's natural environment, N_L . These modification activities may be driven by the demand for a subset of local ecosystem processes that can sustain local resource-based livelihoods (Fig. 1a). The state of the natural environment, and changes therein caused by modification activities, determine the supply of the subset of local ecosystem processes that support livelihoods, E_L , which affects the socio-economic state and thereby closes a loop of interactions between these system components (Fig. 1). The demand for this subset of ecosystem processes, however, is not necessarily fully met through the local natural environment and the ecosystem processes therein, but may partly depend on imports from outside the local system boundary (Fig. 1a). The total capacity to sustain livelihoods is then the sum of the supplies generated by local ecosystem processes and imports, i.e. $E = E_L + E_G$ (Fig. 1a).

In this study, we operationalized the socio-economic state as the size

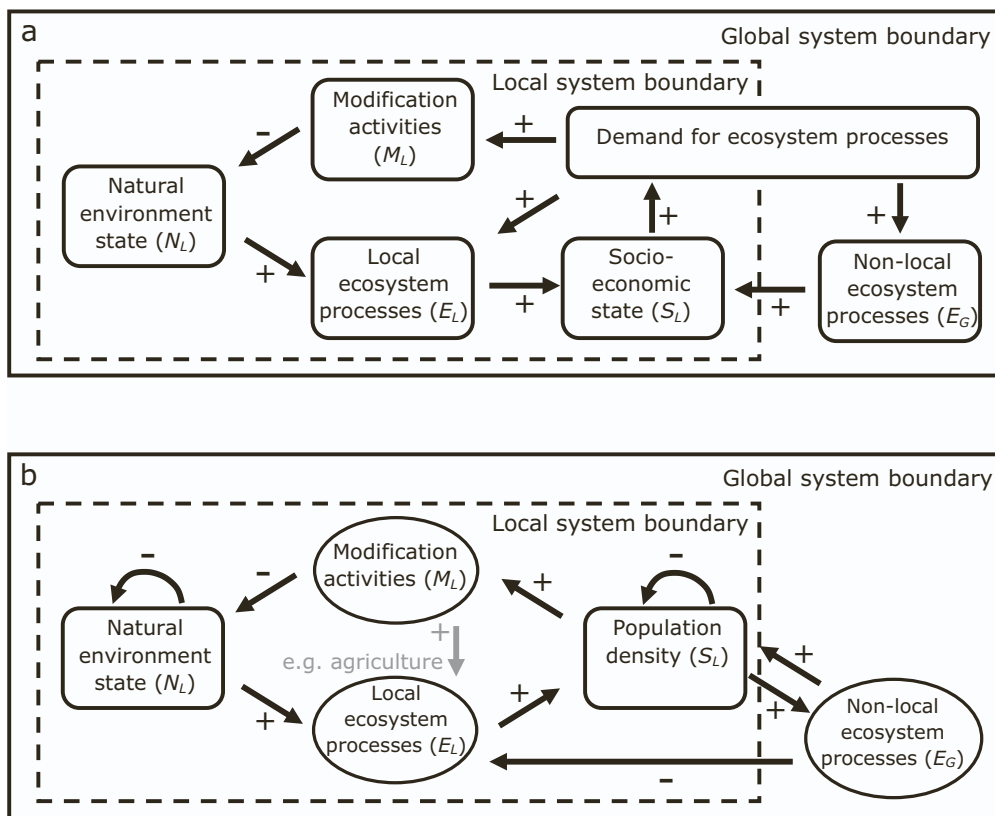


Fig. 1. Schematic overview of the interactions between main components of the local social-ecological systems considered. a) General system description. b) Specific system description, based on the model assumptions described in sections 2.1 and 2.2. Here, rounded rectangles indicate state variables that are explicitly modelled, whereas ovals indicate system characteristics that are implicitly modelled. This specific description shows how larger human populations may benefit from economies of scale, and create opportunities for livelihoods that are less dependent on local ecosystem processes, E_L . These systems may enter a red loop: a positive feedback between population size (S_L) and the system's capacity to sustain livelihoods that depend on the import of natural resources generated by ecosystem processes elsewhere (E_G). Eventually, the strength of this red loop will be constrained by external resource availability, or constraints for other resources within the local social-ecological system.

of the human population residing within the system, which equates to population density within a spatially bounded system (i.e. number of people per area, Fig. 1b). Describing the socio-economic state by a single state variable inevitably excludes possibilities to study complexity emerging within the socio-economic subsystem, such as the distribution of wealth and resources within the society, the development of technological capabilities or the creation of institutions to manage natural resources (Anderies, 2000; Pezzey and Anderies, 2003; Cifdaloz et al., 2010; Lafuite and Loreau, 2017; Lafuite et al., 2017; Scheffer et al., 2017). Yet, within the limitations of a single-variable description, population density fits our purpose, as it has been proposed as an indicator for societal responses to changing environmental conditions in general (Zhang et al., 2011; Haldon et al., 2018; Xu et al., 2020) and to distinguish green loop-dominated systems from red loop-dominated systems in particular (Cumming et al., 2014; Hamann et al., 2015; Cumming and Von Cramon-Taubadel, 2018).

Furthermore, we assumed that the extent of modification activities is directly proportional to the current human population density. This assumption was motivated by previous approaches to quantify modification activities, such as the Human Footprint Index (HFI, Venter, 2014, Venter et al., 2016) and the Human Modification Index (HMI, Theobald, 2013; Kennedy et al., 2019). The HFI and HMI indices describe cumulative anthropogenic pressure on the environment that originates from multiple sources. For each source, one or multiple indicators quantify its contribution to the total anthropogenic pressure, typically assuming proportional (i.e. linear) relationships between indicator and pressure scores (Theobald, 2013; Venter, 2014). Importantly, within these analyses, population density emerged as the dominant source explaining variation in modification activity across the globe (Kennedy et al., 2019), suggesting that population density provides an appropriate indicator for modification activity. Therefore, within a local, spatially bounded system, the magnitude of modification activity is proportional to the current population density:

$$M_L(t) = \alpha S_L(t) \tag{1}$$

In which α specifies the per capita modification activity. We focused on human benefits from ecosystem processes involving extractable biotic resources, such as trees used for timber production or fish used for consumption (e.g. Palacios-Agundez et al., 2015). Hence, we operationalized the state of the natural environment as the size of the biotic resource stock, which equates to resource density within a spatially bounded system (i.e. number of resource units per area). Single-variable descriptions of the natural environment face similar limitations as described above for the socio-economic sub-system. For example, it excludes the possibility to consider synergies and trade-offs between the supply and demand of different ecosystem processes (Reader et al., 2022, 2023). However, given these limitations, our focus on extractable biotic resource dynamics warrants description of the state of the natural environment using ecological principles of (logistic) population growth (Brander and Taylor, 1998; Anderies, 2000; Basener and Ross, 2005; Haider et al., 2017). The amount of biotic resources is then proportional to the local supply of the subset of ecosystem processes that support livelihoods:

$$E_L(t) = \beta N_L(t) \tag{2}$$

In which β specifies the potential benefits provided per unit of the biotic resource stock (i.e. biomass, reflecting the current state of the natural environment). By keeping these per capita benefits constant, we are assuming that the density of the biotic resource stock does not affect its quality. Human effort is needed to convert potential into realized benefits, where these realized benefits comprise a positive impact on the socio-economic system state (Fig. 1; Anderies et al., 2016; Costanza et al., 2017). Thus, the extent to which potential benefits are converted into realized benefits depends not only on the natural resource stock itself, but also on the human and social capital that can be utilized (Anderies, 2003; Anderies et al., 2016; Costanza et al., 2017). It should be noted that our model formulation made a simplifying assumption by

not explicitly considering direct impacts of modification activities on local ecosystem processes (the grey arrow in Fig. 1b). Such direct connections could emerge in a variety of ways, such as agricultural technology-driven increases in productivity (Boserup, 1965; Lafuite et al., 2017; Ellis et al., 2018; Reader et al., 2022).

In summary, the above assumptions lead to a description of the social-ecological system with two variables that quantify the states of the socio-economic system and the natural environment. The two variables are linked through the generation of benefits from local ecosystem processes, which involves the harvesting/reduction of biotic resources and associated human capital costs (i.e. labor) and the gains obtained from consuming or capitalizing these resources.

As noted by Eppinga et al. (2021), over short (i.e. daily) timescales it is reasonable to assume that labor input generates gains according to a fixed proportions production function, i.e. the gains increase linearly with labor time invested (e.g. Anderies, 2000). The slope of this production function will depend on the amount of natural resources available and the density of the population utilizing these resources. Adopting the functional forms for these dependencies as described in Eppinga et al. (2021), two important constraints emerge for the longer-term dynamics of the system: i) the per capita resource consumption rate, h , is considered to be constant; ii) the human population's carrying capacity is proportional to the natural resource availability within the local social-ecological system (see Appendix A for details). Including these constraints, the resulting model can then be written as:

$$\frac{dS_L}{dt} = rS_L \left(1 - \frac{1}{q} \frac{S_L}{N_L} \right) \quad (5)$$

$$\frac{dN_L}{dt} = cN_L \left(1 - \frac{N_L}{K} \right) - h_{max} S_L \quad (6)$$

In which S_L is the human population density (# individuals km^{-2}), r is the human population growth rate (month^{-1}), N_L indicates the natural resource stock (# resource units km^{-2}), q is the number of humans that can be sustained per unit of the natural resource stock (# individuals # resource units $^{-1}$), c indicates the natural resource productivity (month^{-1}), K quantifies the system's carrying capacity for the natural resource (# resource units km^{-2}), and h_{max} is the long-term consumption rate of the natural resource per human capita (# resource units # individuals $^{-1}$ month $^{-1}$). As the above processes describe internal system dynamics, the model formulated by eqs. (5) and (6) describes the local system dynamics. This model is part of a broader class of models inspired by the well-known Lotka-Volterra predator-prey model, with the label of "humans" being assigned to the predator (consumer) and "resources" to the prey (e.g., Eberhardt, 1997; Anderies, 1998; Brander and Taylor, 1998; Pezzey and Anderies, 2003; Basener and Ross, 2005; Taylor, 2009; Reuveny, 2012). The Lotka-Volterra framework can be modified to include specific characteristics of the human population considered, or their resource environment (e.g., Anderies, 2000; Basener and Ross, 2005; Taylor, 2009). The two specific modifications included in Eqs. (5) and (6) are the natural resource-dependent carrying capacity of the human population, and the natural resource consumption being only dependent on the human population density (i.e. and not on the size of the natural resource pool). These modifications were first proposed by Basener and Ross (2005) as a description of local social-ecological system dynamics. The derivations of these modifications, including the assumptions made about the social-ecological systems considered, were described in a previous study (Eppinga et al., 2021) and are briefly recapped in Appendix A. The consequences of these modifications for the emerging system dynamics, have subsequently been studied in detail in a number of studies (Basener and Ross, 2005; Nucci and Sanchini, 2015, 2016; Güngör and Torres, 2019; Güngör et al., 2020; Eppinga et al., 2021). In section 2.2, we will expand this framework by considering that natural resources may be imported from elsewhere, depending on the state of the socio-economic subsystem (Fig. 1b).

2.2. Incorporating urbanization and associated import of natural resources

Within the local system dynamics described above, the entire supply of natural resources originates from within the system. When population centers expand, increases in economies of scale can be obtained through labor specialization, which can lead to urbanization and the spatial decoupling of natural resource production and consumption (Fig. 1b; Fader et al., 2013; Cumming et al., 2014; Schröter et al., 2018; Dörninger et al., 2021). However, to benefit from such economies of scale and the resulting ability to import natural resources at competitive cost, the system needs to invest human capital to generate the infrastructure, governance system and additional institutions needed to develop and maintain a more complex societal structure (Cumming et al., 2014). We mimicked this constraint by assuming that spatial decoupling and the associated externalization of natural resource production (i.e. the ability to import resources at competitive cost from elsewhere) proceed at an accelerating rate when small populations increase in density (Fig. 2). When the population density increases, we assumed that the contribution of local resources to overall consumption eventually approaches a minimum level that is only a small fraction of the natural resource consumption needed for sustenance (Fig. 2).

Specifically, the local per capita harvest rate can then be written as:

$$h_L(S_L) = h_{min} + (h_{max} - h_{min}) \frac{P^2}{S_L^2 + P^2} \quad (7)$$

In which h_{max} and h_{min} are the maximum and minimum levels of consumption of the local natural resource (# resource units # individuals $^{-1}$ year $^{-1}$), and P specifies the human population density at which half of the maximum reduction in local natural resource consumption occurs (# individuals km^{-2}). Eq. (7) establishes a deterministic relationship between the ability to extract resources from elsewhere and human population size, thus following a Boserupian rather than a Malthusian description (Freeman et al., 2019). In addition, we made a simplifying assumption by presuming that the local social-ecological systems studied are relatively small compared to regional and global trade markets, meaning that the characteristics of the latter are not significantly affected by changes within the local system. For a given state of the socio-economic sub-system, i.e. a given population density, the dependency of the system on local natural resources can now be quantified as the ratio between this modified resource harvest term (Eq. (7)) and the former resource harvest term (the last term in Eq. (6)):

$$\delta(S_L) = \frac{h_L(S_L)S_L}{h_{max}S_L} = \frac{h_{min}S_L^2 + h_{max}P^2}{h_{max}(S_L^2 + P^2)} \quad (8)$$

Where $\delta(S_L)$ is a dimensionless property that approaches a value of 1 at very low human population densities, corresponding to a maximum per capita harvest intensity of local resources, h_{max} (Fig. 2a). At the other extreme, $\delta(S_L)$ approaches a value of $\frac{h_{min}}{h_{max}}$ at very large human population densities, corresponding to a minimum per capita harvest intensity of local resources, h_{min} (Fig. 2a). Thus, in this latter case, there is a minimum dependence on local natural resources, as the import of natural resources from elsewhere is maximized. By substituting the constant parameter h_{max} with the function $h_L(S_L)$ in Eq. (6), we can modify the human population's utilization of local natural resources (Fig. 2a). In addition, this reduced utilization also implies a reduced dependency of human population dynamics on local natural resource availability (Fig. 2b).

Furthermore, now that the system may no longer be strongly limited by local natural resource availability, additional constraints on human population density need to be considered. As described in the Introduction, these additional constraints can be posed by non-importable resources, local regulatory and cultural ecosystem processes, or regional (i.e. larger scale) resource constraints. We incorporated this constraint by including an additional, generic limitation term within the

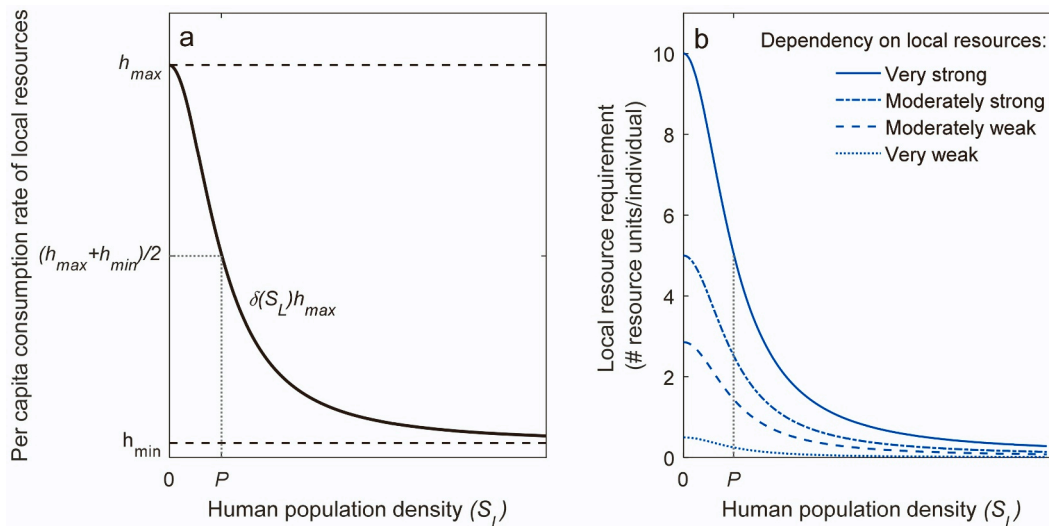


Fig. 2. Spatial decoupling of natural resource supply and demand can be incorporated in the model by modifying the per capita resource consumption rate (see Eq. (7) in section 2.2). a) When the supply is entirely local, the per capita consumption rate is constant, i.e. independent of the current population density (upper dashed line). Larger populations may increase their capacity to import natural resources from elsewhere, reducing the per capita consumption rate of local resources (solid line). An inverse sigmoidal response is assumed, with half the maximum reduction in the local per capita consumption rate occurring at the population density P (dotted lines). b) Through the model parameter q , the strength of the local resource constraint on the population can be varied (see Eq. (9) in section 2.2), with smaller values of q yielding stronger constraints. Parameter values shown: very strong: $q = 0.1$; moderately strong: $q = 0.2$, moderately weak: $q = 0.35$, very weak: $q = 2$.

human population dynamics. In summary, the above modifications yielded the following model system:

$$\frac{dS_L}{dt} = rS_L \left(1 - \frac{\delta(S_L) S_L}{q N_L} - \frac{S_L}{\sigma_{max}} \right) \quad (9)$$

$$\frac{dN_L}{dt} = cN_L \left(1 - \frac{N_L}{K} \right) - \delta(S_L) h_{max} S_L \quad (10)$$

In which σ_{max} indicates the maximum population density of the local socio-economic system (# individuals km^{-2}), as constrained by other factors than (importable) natural resources. While the strength of this latter constraint is monotonically increasing with human population density, the strength of the local natural resource constraint may decrease with increasing human population density, as the enhanced ability to import natural resources from elsewhere may outweigh the increased demand of a larger population (see Appendix B for details). All model parameters are listed in Table 1, and further motivation of the parameter values is provided in Appendix C.

2.3. Analyses

We analyzed the model system described by Eqs. (8), (9) and (10) using a combination of analytical and simulation approaches. Preparatory analytical analyses revealed that the model extension described above increased model complexity. While only one steady social-ecological system state occurs in the simpler model described by Eqs. (5) and (6) (Eppinga et al., 2021), we found that four real, non-negative steady social-ecological system states (i.e. equilibrium points) occur in the extended model system described by Eqs. (8), (9), and (10), for the parameter space considered in this study. The equilibrium point $(\hat{S}_L, \hat{N}_L) = (0, K)$ was always feasible and unstable, provided that the maximum human population growth rate is positive ($r > 0$), a condition fulfilled in all cases considered in this study. Hence, we focused our results on the feasibility and stability analyses of the remaining three equilibria of the model system.

For these remaining three equilibria, feasibility and stability were analyzed using linear stability analysis (e.g. Edelstein-Keshet, 1988). To answer our first research question, we studied how the feasibility and

stability of equilibrium points depended on productivity of the local natural resource. We repeated this analysis for four scenarios that varied in the extent of the system's inherent dependency on local natural resources. While the system's dependency on local natural resources changes with population density, as specified by the parameter δ introduced above, Eq. (9) shows that the per capita dependency on local natural resources is quantified by the ratio $\frac{\delta(S_L)}{q}$ (# resource units # individuals $^{-1}$). Hence, smaller values of q indicate a stronger inherent dependency on local natural resources. In the analyses we use this characteristic of the parameter q to create four scenarios that span a gradient ranging from strong dependence ($q = 0.1$) to weak dependence ($q = 2$) on local natural resources (Fig. 2b).

To answer our second and third research questions, we simulated system dynamics under changing environmental conditions. Specifically, we varied the productivity of the local natural resource, specified by the parameter c in Eq. (10), over time. In these simulations, we aimed for identifying changes in transient system dynamics that could be attributed to altered internal social-ecological system processes. Hence, we focused on gradual, monotonic changes in local natural resource productivity over time. To study transitions away from a green loop-dominated state, systems were initialized with intermediate densities of human populations ($S_L(t = 0) = 100$ individuals km^{-2}) and resources ($N_L(t = 0) = 300$ resource units km^{-2}) and a level of resource productivity where a green-loop dominated state was stable ($c = 0.009$ month $^{-1}$). After a brief period of constant productivity, a linear decrease in productivity over time was simulated. To study transitions away from a red loop-dominated state, systems were initialized in the same state, but first exposed to a linear increase in productivity over time. After systems had transitioned from a green loop-dominated state to a red loop-dominated state, productivity was again decreased linearly over time (Table 1). From the analyses answering our first research question, it became clear that system responses to the described changes in environmental conditions depended on the strength of the local natural resource constraint, $\frac{\delta(S_L)}{q}$. In the main text, we focused on studying transient system responses under moderately weak dependency on local natural resources ($q = 0.35$), while responses under moderately strong dependency on local natural resources ($q = 0.2$) are presented in

Table 1
Description of the model parameters and the system state variables.

Symbol	Interpretation	Unit	Value	References*
r	Relative population growth rate	month ⁻¹	0.0044	1,2,3
q	Strength of the natural resource constraint on human population growth	# individuals # resource units ⁻¹	0–2	1,3
h_{max}	Maximum per capita consumption rate of the local natural resource	# individuals ⁻¹ month ⁻¹	0.0176	6
h_{min}	Minimum per capita consumption rate of the local natural resource	# individuals ⁻¹ month ⁻¹	$\frac{h_{max}}{100}$	6
P	Human population density at which half of the resources is imported	# individuals km ⁻²	200	5,6
σ_{max}	Maximum population density for the local system	# individuals km ⁻²	1450	1,3,4,5
K	Carrying capacity of the local system for the natural resource	# resource units km ⁻²	700	1,3
S_L	Human population density	# individuals km ⁻²	State variable	–
N_L	Natural resource stock	# resource units km ⁻²	State variable	–
c	Productivity of the natural resource	month ⁻¹	0–0.044	3,6

Bifurcation analyses: varied over entire range; Green loop collapse analyses: reduced from 0.009 to 0.007 month⁻¹, Fig. 5b, d, f; Red loop collapse analyses: increased from 0.009 to 0.13 month⁻¹, subsequently reduced to 0.003 (slow change, Fig. 6b), 0.0018 (intermediate change, Fig. 6d) or 0 (fast change, Fig. 6f).

* References: 1: Basener and Ross (2005); 2: Cumming and von Cramon-Taubadel (2018); 3: Eppinga et al. (2021); 4: Cumming et al. (2014); 5: Reader et al. (2023); 6: This study (see Appendix C for details).

Appendix D for comparison. For all scenarios, we compared system responses for different rates of environmental change, as previous studies have shown that responses of systems that exhibit alternative stable states may critically depend on the rate (rather than the magnitude) of environmental change experienced (Ashwin et al., 2012; Siteur et al., 2016a; Bastiaansen et al., 2020). Model simulations were carried out using a fifth-order Runge-Kutta integration method as implemented in MATLAB (ode45, v.9.0, MathWorks, 2016). Scripts reproducing the analyses (Figs. 3–6) are provided as Supplementary Information.

3. Results

3.1. Social-ecological equilibrium states vary with dependence on the local environment

Before describing the existence and stability of social-ecological equilibrium states as a function of resource productivity, we briefly illustrate how a system with constant productivity within the local environment develops over time toward these equilibrium states (Fig. 3). Under low resource productivity, a low-density human population typically develops logistically toward the (relatively low) equilibrium population density (Fig. 3a). For initial conditions exceeding the

equilibrium population density, the population decreases toward the equilibrium population density (Fig. 3a). Under high resource productivity, similar dynamics occur, but the population stabilizes at much higher population densities (Fig. 3b). Depending on other characteristics of the system, like its dependency on local natural resource availability, the two equilibrium points discussed above can be of the same type, i.e. both are green loop-dominated, or both are red loop-dominated states, but may also be of different types. For a green loop-dominated state, an increase in population density above the equilibrium state increases the strength in the local natural resource constraint, which forces a subsequent return to the equilibrium state (see Appendix B for details). In contrast, for a red loop-dominated state, such an increase in population density would reduce the strength of the natural resource constraint, and a return to the equilibrium state is due to the increasing strength of other constraints on the population (Appendix B).

In the case where a green loop-dominated state occurs at low productivity and a red loop-dominated state at high productivity, there is also an intermediate range of resource productivities where the initial conditions of the system determine which of these states the system develops toward over time (Fig. 3c). These temporal dynamics can be summarized in a bifurcation diagram, which shows the existence and stability of equilibrium points as a function of local environmental conditions, i.e. natural resource productivity. For environmental conditions where two stable states occur, an unstable equilibrium in between (i.e. the dashed line in Fig. 3d) separates the basins of attraction of each equilibrium point. Here, basin of attraction refers to the set of system states that will develop toward the equilibrium point. Thus, for a given initial condition and a given level of natural resource productivity, the transient dynamics can be inferred from the bifurcation diagram (Fig. 3d).

Bifurcation diagrams showed that the existence and stability of social-ecological equilibrium states changed as a function of the system's dependency on local resource availability (Fig. 4).

As noted above, this dependency could be varied through the parameter q in Eq. (9), with low values of q indicating that human population dynamics are strongly constrained by local resource availability. Under these conditions, only a low-density population could be maintained (Fig. 4a), which required a relatively high level of natural resources being present within the system (Fig. 4b). These results can be interpreted as the system dynamics being controlled by a green loop, regardless of the natural resource productivity of the system (Fig. 4a, b). When the control of the population by local natural resource availability is slightly weaker, increasing resource productivity can trigger a transition toward a higher-density population state (Fig. 4c). This higher-density population is able to import resources into the system, reducing the dependence on and use of local natural resources (Fig. 2, 4d). These system states comprise the upper branch of equilibrium solutions in the bifurcation diagram (Fig. 4c, d). For these states, their system dynamics can be interpreted as being controlled by a red loop (Fig. 4c, d). However, maintaining a red loop-dominated state due to an increase in resource productivity does partly depend on local resource supply. This dependency exhibits itself by the system returning to a green loop-dominated state when resource productivity subsequently decreases (Fig. 4c, d).

When the control of the population by local resource availability is further weakened, the red loop-dominated state becomes more resilient to subsequent decreases in local resource productivity (Fig. 4e, f). More specifically, once the red loop-dominated state has been reached, it can even be sustained for resource productivity levels where a green loop-dominated state is no longer feasible (Fig. 4e, f). Finally, when the control of the population by local resource availability is weakened even further, the red loop-dominated state becomes the only stable state (Fig. 4g, h). The limited dependence of the population on local resources is in this case reflected by the equilibrium population size being nearly constant along a local resource productivity gradient (Fig. 4g). The very limited consumption of local resources only becomes problematic under

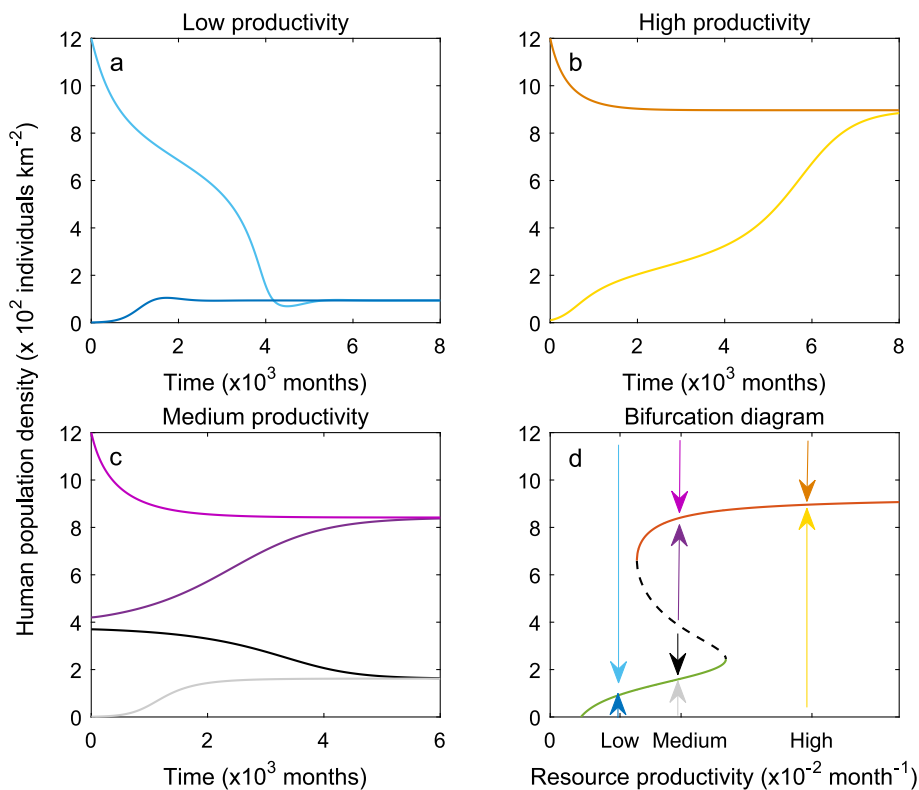


Fig. 3. Temporal dynamics of the human population under different levels of resource productivity. a) Under low resource productivity, the human population develops to a relatively low population density. b) Under high resource productivity, the human population develops to a relatively high population density. c) Under medium resource productivity, the population can develop to either a low or a high population density, depending on initial conditions. d) Dynamics as observed in cases a) – c) can be summarized in a bifurcation diagram showing the existence and stability (solid lines are stable, dashed lines are unstable equilibria) of equilibrium population densities, using resource productivity as the bifurcation parameter. Arrow colors correspond to the temporal dynamics shown with the same-colored lines in panels a) – c). Simulations were started at extreme values of population size (1 or 1200 individuals km⁻²), and at values near thresholds (350 and 450 individuals km⁻²), in order to show the full range of transient population dynamics. Parameter values: $q = 0.2$, other parameters as in Table 1. Initial conditions for the natural resource availability (100, 350, 450 and 700 resource units km⁻², respectively) were correlated positively with initial population density.

very low resource productivity levels, where this consumption is no longer replenished and the sustainable level of local natural resource availability rapidly decreases (Fig. 4h). In summary, these results highlight that transitions away from green loop- and red loop-dominated states are most likely to occur at intermediate levels of dependence on local resource supply (Fig. 4).

3.2. Counter-intuitive responses of green loop-dominated systems to decreasing resource productivity

Unexpected responses to decreasing local natural resource productivity were observed in systems with strong feedbacks between population density and resource imports (Fig. 5). These responses could be partly explained by the green loop-dominated state becoming unstable when a critical threshold in resource productivity was passed (Fig. 5a). How the system dynamics developed after passing this threshold depended on the relative rate of change in resource productivity (Fig. 5b, c, d). Surprisingly, the most drastic responses were observed when the decrease in resource productivity was rather slow and thus more gradual (Fig. 5b). While the response to passing the critical productivity threshold was delayed in systems experiencing slow and gradual change, the response itself exhibited oscillations of increasing amplitude (Fig. 5b). Thus, counter-intuitively, the decisive collapse of the system was preceded by the largest boom in population growth (Fig. 5b). Technically, this response can be understood as the system passing a sub-critical Hopf bifurcation (see Appendix E). When the same decrease in resource productivity occurs more rapidly, the amplitude of the boom-and-bust cycles decreases (Fig. 5c), while only a gradual decline in population density and local resource availability is observed under rapid change (Fig. 5d). Under these latter conditions, the system responds more quickly to passing the critical threshold in resource productivity (indicated with the green dashed lines in Fig. 5b, c, d). Contrasting these dynamics, systems that are more strongly constrained by local resource availability show a gradual population decline under declining natural resource productivity (see Appendix D for details).

3.3. Green loop to red loop transitions and the collapse of red loop-dominated states

With increasing resource productivity, strong population-resource import feedbacks enabled a transition from a green loop-dominated state to a red loop-dominated state (Fig. 6a). This transition comprised a rapid increase in population density, yet a reduced dependence on local resources (Fig. 6b, c, d). Due to this reduced dependence on local resources, subsequent decreases in local resource productivity had little effect on the population density and natural resource stock of the system (Fig. 6).

This red loop-dominated state could then persist below the minimum resource productivity levels observed in the green loop-dominated systems, and even below the resource productivity levels in systems where the green loop-dominated state was feasible but unstable, as explained above (red shaded region in Fig. 6a). While reaching this red loop-dominated state at low resource productivity may be difficult, it is a relatively robust state after a transition that previously occurred under high productivity (Fig. 6a). Although robust, the capacity of this state to adapt at low resource productivity levels is limited in that no alternative stable system equilibria are feasible under these conditions (Fig. 6a). Furthermore, when the resilience of the red loop-dominated state begins to decrease as productivity reaches very low levels, it does so rather abruptly (Fig. 6a). As a result, the system response to a gradual decrease in productivity over time is characterized by a prolonged period of stability, followed by a very abrupt deterioration of the system (Fig. 6b, c, d). The abruptness of this transition toward a deteriorated state occurred similarly fast for the different rates of environmental change considered; even with a slow decrease in productivity, a rapid decline in population and resources was observed (Fig. 6b, c, d). Technically, this response can be understood as the system passing a saddle node (also called a fold) bifurcation (Fig. 6; Appendix E). Contrasting these dynamics, systems that are more strongly constrained by local resource availability show that red loop-dominated systems can transition (back) to a green-loop dominated state under declining natural resource

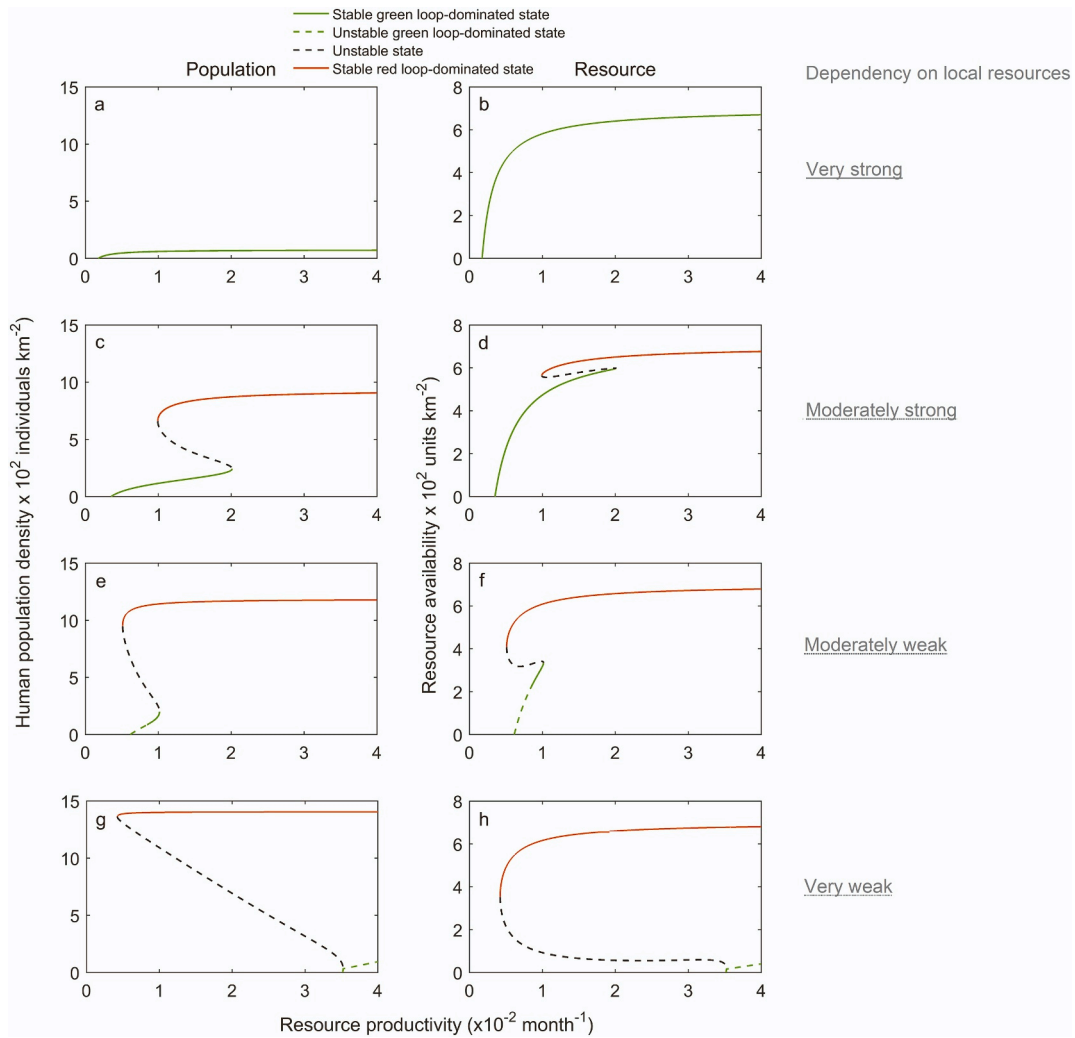


Fig. 4. Overview of the feasibility and stability of equilibrium states of the local social-ecological system, over a gradient of natural resource productivity. Four scenarios were considered, which varied in the degree of inherent dependency on local natural resources. a, b) Under strong dependency on local resources, the only stable equilibrium state is a green loop-dominated state (green solid line). c, d) Under moderately strong dependency on local resources, the green loop-dominated state is the only stable state under low productivity, the red loop-dominated state (red solid line) is the only stable state under high productivity, and in an intermediate range of productivity both states are stable, and separated by an unstable equilibrium (black dashed line). e, f) Under moderately weak dependency on local resources, the red loop-dominated state is the only stable state under both low and high productivity, whereas in an intermediate range of productivity the green loop-dominated state is stable as well, the states being separated by an unstable equilibrium. g, h) Under weak dependency on local resources, the only stable equilibrium state is a red loop-dominated state. Parameter values of q were varied between rows as in Fig. 2b (a,b: $q = 0.1$; c,d: $q = 0.2$, e,f: $q = 0.35$, g,h: $q = 2$); other parameters as in Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

productivity (see Appendix D for details).

4. Discussion

4.1. Using stylized models to catalogue social-ecological system transitions

We present a stylized mathematical model to study the dynamics of socio-ecological systems and, specifically, study the system behavior when socio-economic dynamics become less dependent on local ecosystem processes. Our results identify conditions under which systems may transition between green loop- and red loop-dominated states, or when these states may collapse in response to degrading environmental conditions. The latter type of observed dynamics provide a link to the conceptual framework of Cumming et al. (2014), who identified how social-ecological systems may enter green traps or red traps, requiring reorganization to prevent collapse. In this context, it is of interest to note that our observed model dynamics associated with

collapse of the green-loop dominated state, i.e. rapid population growth and subsequent deterioration, are in line with descriptions of green trap dynamics (Figs. 5, 7; Cumming et al., 2014; see Appendix F for details). Moreover, our observed model dynamics associated with collapse of the red-loop dominated state, i.e. a large population becoming independent on local conditions, until a very degraded local environmental state starts posing problems, is in line with descriptions of red trap dynamics (Cumming et al., 2014). According to this conjecture, systems would enter a red trap once equilibrium states associated with green loop dynamics are no longer feasible (Fig. 6; see Appendix E for details). Using these operationalizations of green and red traps, the presented model captures the six types of social-ecological system transitions identified in a previously proposed conceptual framework linking societal transformations and local ecosystem processes. These transitions occur between five dynamical regimes: (1) Green loop, (2) Green trap, (3) Red loop, (4) Red trap and (5) Collapse and famine (Fig. 7; Cumming et al., 2014).

Within this set of social-ecological system transitions, two types of

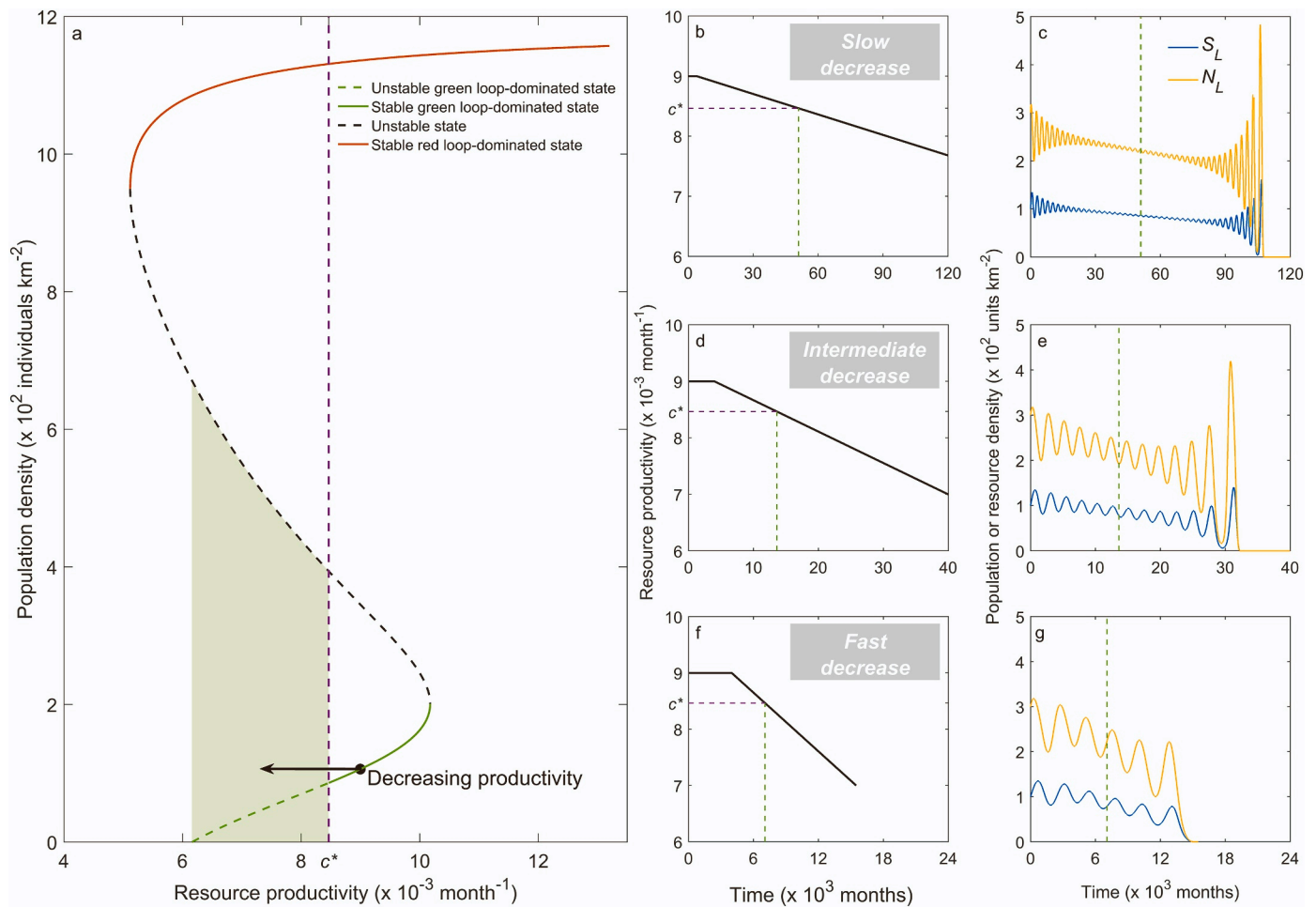


Fig. 5. Temporal dynamics showing the response of a system residing in the green loop-dominated state to a decrease in resource productivity. a) There exists a critical threshold in resource productivity, c^* , (purple dotted line) below which the green loop-dominated state becomes unstable (green shaded region). b) A relatively slow change in resource productivity is considered, with the green dotted line indicating the moment in time where the critical threshold c^* was passed. c) The system response under this scenario of slow change, showing cycles of increased amplitude when approaching the critical threshold. d) Resource productivity is reduced more quickly in this scenario of an intermediate rate of change. e) When the system is responding to this intermediate rate of change, the amplitude of the cycles is smaller as compared to the slow change scenario. f) Resource productivity is reduced at the highest rate in this scenario of fast change. g) When the population (S_L , blue lines) and natural resources (N_L , gold lines) are responding to this fast rate of change, no cycles appear when crossing the critical threshold in productivity, c^* , but a gradual decline in human population density and natural resource availability is observed instead. Parameter values: $q = 0.35$, other parameters as in Fig. 4 and Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

emergent phenomena can be distinguished. First, a positive feedback between population density and the capacity to obtain resources from elsewhere explained the occurrence of a green loop-dominated state and red loop-dominated state as alternative stable equilibria under intermediate levels of resource productivity (Figs. 4, 7). Within this range of productivity, transitions between green and red loop-dominated states could be driven by perturbations of the system state. In this study, however, we focused on transitions driven by gradual environmental changes (operationalized as changes in natural resource productivity). In the absence of system perturbations, these latter types of transitions may take substantially longer as compared to systems experiencing gradual environmental changes and system perturbations simultaneously (Siteur et al., 2014; Siero et al., 2019). Moreover, our results show that the rate of environmental change may substantially alter the system dynamics during the transition trajectory (Figs. 5, 6). Hence, more detailed assessments of the timespans involved in the transitions identified in Fig. 7 would require explicit consideration of the relative influence of gradual environmental change and system state perturbations, and the rate of the former and the magnitude of the latter (Arani et al., 2021).

While consistent with the conceptual framework, this emergent

phenomenon is not a very distinctive feature of the specific model considered; positive feedback and alternate stable states are common features of stylized consumer-resource models and positive feedback can emerge in both growth and loss functions, for both the consumer and its resource (e.g. DeAngelis et al., 1975; May, 1977; Rietkerk and van de Koppel, 1997; Scheffer et al., 2001). The second type of emergent phenomena are the relatively large and abrupt transitions from green loop to green trap, and red loop to red trap states in response to gradual changes in resource productivity (Fig. 7). Although regime shifts are a common emergent response of social-ecological systems to gradual environmental changes as well (Schlüter et al., 2019; Biggs et al., 2022), the transitions into the identified green and red trap states are more distinctive for the particular model framework considered. Our results suggest that this type of green and red trap states are a robust feature of the system dynamics of coupled socio-ecological systems that depend on natural resources from distinct local and non-local sources.

More specifically, we observed that with decreasing local resource productivity, the green loop-dominated state may become unstable, rather than gradually approaching a population density of zero (Fig. 7). The transition from the stable green loop-dominated state to the unstable green trap state (see Appendix E for technical details) leads to

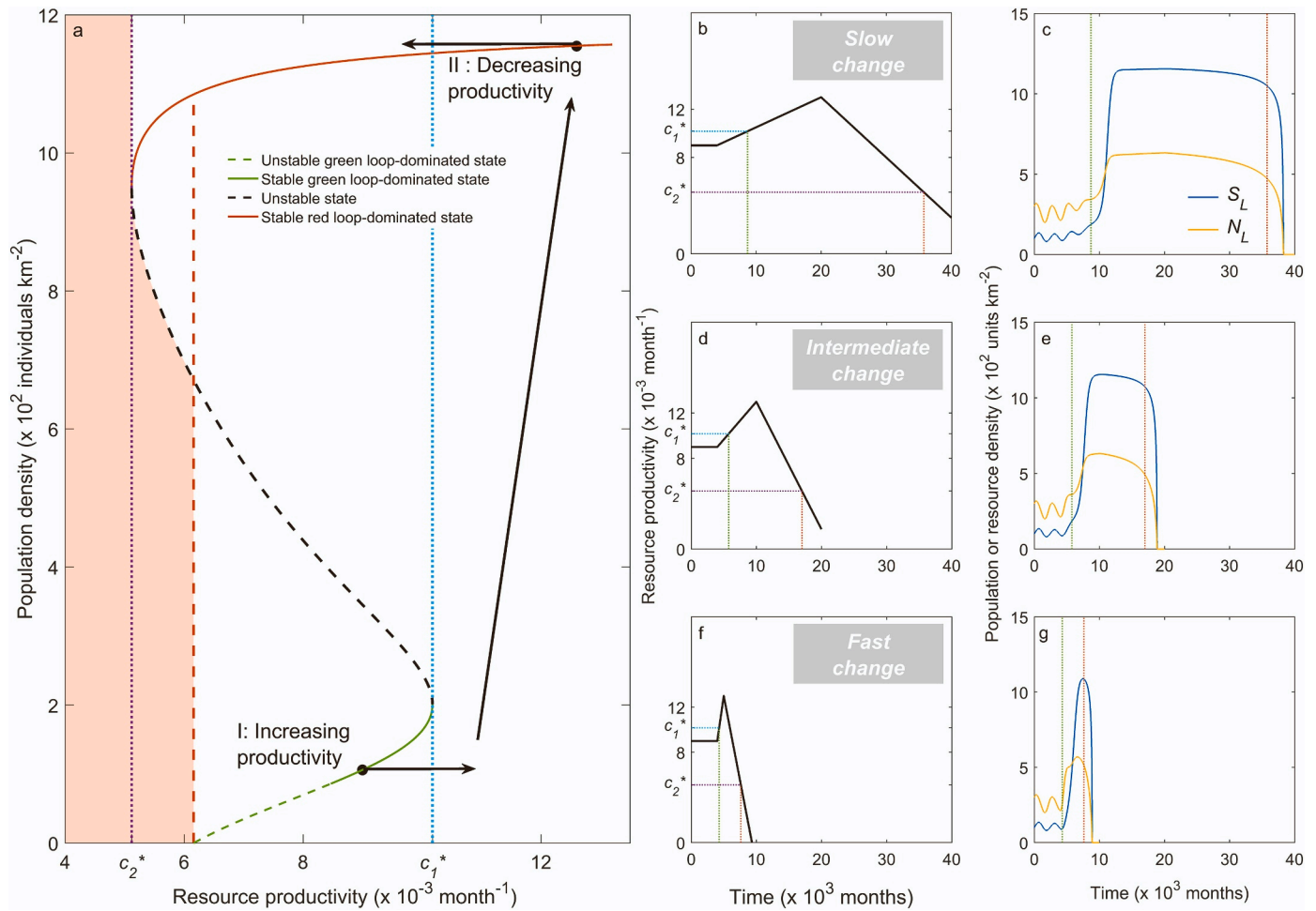


Fig. 6. Temporal dynamics showing the response of a system residing in the green loop-dominated state to an increase, and a subsequent decrease in resource productivity. a) There exists a critical threshold in resource productivity (c_1^* , blue dotted line) above which the green loop-dominated state becomes unstable, and the system transitions to a red loop-dominated state. When decreasing resource productivity from this point, the system state loses stability when a critically low resource productivity level, c_2^* , is crossed (purple dotted line). In the simulations shown, natural resource productivity is increased until threshold c_1^* is passed, and subsequently decreases until threshold c_2^* is passed. These changes occur as b) slow, c) intermediate, or d) fast changes. Green dotted lines indicate the time points in simulations when threshold c_1^* is passed, red dotted lines indicate time points when threshold c_2^* is passed. The decline in population (S_L , blue lines) and natural resources (N_L , gold lines) is abrupt when crossing the critical productivity level, not depending on whether it is exposed to: c) Slow change e) Intermediate change; or g) Fast change. Parameters as in Fig. 5 and Table 1. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

large and rather counterintuitive oscillations in human population density once the population resides in the green trap state (Fig. 5). In contrast, we observed that red loop-dominated states could undergo two different types of transition when natural resource productivity decreases (Figs. 4, 6, see Appendix E for technical details). First, a transition may occur to a green loop-dominated state, provided that this state is stable under the current level of resource productivity (Fig. 4c, d; Appendix D). A second type of transition occurs when the red loop-dominated state is feasible and stable at both lower and higher levels of resource productivity as compared to both the green loop-dominated and green trap states (Figs. 4, 6, 7). A prerequisite for this second type of dynamics is that the inherent dependence on local natural resources is relatively weak (Fig. 4). Under these conditions, a system residing in a red loop-dominated state may not transition (back) toward a green loop-dominated state in response to declining resource productivity (Fig. 6). Here, a more distinct feature of the model is that under these conditions, none of the theoretical equilibria, including the trivial equilibrium point, is stable. Hence, the deterioration of the system from the red trap comprises accelerated decline over time, rather than asymptotically approaching the trivial equilibrium, suggesting that this transition would comprise a rather abrupt process (Figs. 6, 7; Appendix F). These

findings from our theoretical analysis provide several opportunities to inform interpretations of empirical observations, as outlined in the next subsection.

4.2. Opportunities to connect theoretical findings to empirical observations

Previous empirical studies have distinguished green loop- and red loop-dominated (administrative) regions through quantification of their direct dependence on local ecosystem processes (Hamann et al., 2015), and correlations between these dependencies and human well-being indicators (Hamann et al., 2016). These previous studies utilized cluster analyses to distinguish systems with low, medium and high dependence on local ecosystem processes and levels of human well-being, yielding categorizations consistent with green-loop dominated, red loop-dominated and transitioning systems (Hamann et al., 2015, 2016). Our study suggest that an interesting complementary approach could be provided by analyzing the frequency distribution of administrative regions along the ecosystem process dependency and human well-being axes, and how this varies with the state of the local natural environment. Such an analysis may provide an empirical test for the occurrence

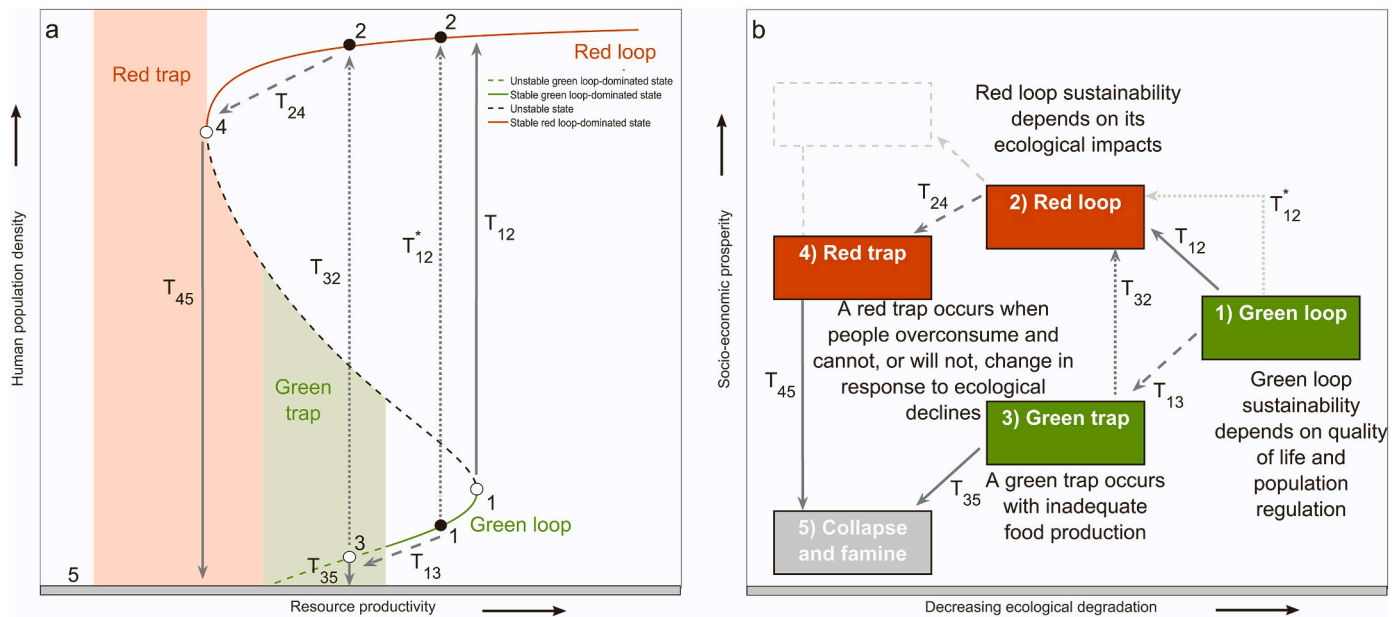


Fig. 7. Overview of the ways in which the model (panel a) captures the five types of local social-ecological system states and six types of transitions between these states as identified in a previously proposed conceptual framework (panel b; Cumming et al., 2014). Numbers indicate the five types of system states that can be distinguished: 1: Green loop-dominated state; 2: Red loop-dominated state; 3: Green trap state; 4: Red trap state; 5: A degraded state (no sustainable equilibrium with human population and natural resources present is possible). A transition from state x to state y is indicated as T_{xy} . In the bifurcation diagram, two types of transitions are distinguished. The first type of transition is driven by a perturbation of the current system state, and in these cases the system develops to either the green loop-dominated, red loop-dominated or degraded state (transitions T_{12}^* , T_{32} , T_{35} , T_{45}). The second type of transition is driven by changes in environmental conditions (resource productivity within our mathematical model), and in these cases the system develops to either the green trap or red trap state (transitions T_{12} , T_{13} , T_{24}). The dashed box in panel b) indicates the position of the red trap state in the original version of the figure in Cumming et al. (2014). The grey dotted arrow associated with transition T_{12}^* shows a type of transition not identified in the original version of the same figure. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

of alternate stable states (e.g. Staver et al., 2011), but may also highlight conditions where these dynamics are not expected (i.e. at either very low or very high inherent resource dependencies, Fig. 4) and uniform distributions would be expected as a counterexample.

Theoretical studies can also shed light on how empirically observed interacting socio-ecological stressors may affect the ability of systems to develop or maintain trajectories within a safe operating space (Vörösmarty et al., 2010; Carpenter et al., 2015; Anderies et al., 2019; Eppinga et al., 2021). Scenarios of gradual declines of natural resource productivity, as considered in our study, may provide relevant analogues for local social-ecological system dynamics in the Anthropocene, such as coral reef fisheries (Kroeker et al., 2017). Specifically, concern has risen that climate change-driven loss of living reef structures may negatively affect community structure at higher trophic levels and associated provisioning of local ecosystem processes (Mellin et al., 2022). Moreover, it has been suggested that coral reef fisheries may reside in and transition between green loop-dominated, red loop-dominated and associated trap states (Dajka et al., 2020). While empirical observations are consistent with productivity being higher in green loop-dominated and red loop-dominated states as compared to green trap states (Fig. 7; Cinner et al., 2009; Steneck, 2009), trajectories toward a green trap may not necessarily be environmentally driven. Here, alternative drivers include changes in technology that increase per capita harvest rates, or socio-economic developments that lead to dietary shifts (Steneck, 2009). These observations suggest potential relevant extensions of the model presented in this study, as explained in the section 4.3 below.

4.3. Opportunities for further expansion of the theoretical framework

The assumptions and simplifications made in our stylized modelling approach yielded a theoretical framework with analytical solutions of

equilibrium states, enabling an assessment of the feasibility and stability of these solutions over a wide range of environmental conditions (Fig. 4; Appendix B, E, F). Relaxing some of our assumptions in future modelling exercises would therefore create additional opportunities for theoretical investigation. For example, in our current approach the system's maximum resource productivity was considered to be independent of other system components within our current model. Plausible refinements here could include technology-driven increases in productivity (Boserup, 1965; Ellis et al., 2018), but also decreases in productivity through prolonged overexploitation (Kosmas et al., 2015). This latter process would allow for a more explicit consideration of the degree of ecological degradation in local social-ecological systems, consistent with the focus of the previously proposed conceptual framework for green loop and red loop dynamics (Fig. 7; Cumming et al., 2014). Such an extension could add dynamics occurring on a separate timescale, which may lead to repeated transitions between different states on longer timescales (e.g. Turchin, 2009; Siteur et al., 2016b).

In addition, processes associated with human behavior and decision making were implemented through model parameters that were considered constant over time. An important extension of the current model would be the explicit consideration of adaptation, which combines coping with changes in values, knowledge, institutions and technology, as well as changes in behaviors in response to environmental change (Fedele et al., 2019; Bruley et al., 2021). For example, the per capita dependency on local natural resources (i.e. model parameter q) may not be fixed, but may change over time due to switches in diet, fuel sources or ecosystem utilization that are motivated by the current state of the natural environment or by socio-economic incentives (Balvanera et al., 2017; Dajka et al., 2020; Fedele et al., 2020). Similarly, the per capita harvest rate may depend on the current state of technology, where technology may either allow for higher harvesting rates, or more efficient use of the resource (Janssen et al., 2007). Our model analyses

suggest that the feasibility and stability of social-ecological system states may strongly depend on the strength of these dependencies (Fig. 4). Hence, changes in these dependencies over time would imply that the feasibility and stability of social-ecological states would not only depend on local environmental conditions, but also on the extent to which the system has adapted to changing conditions in the past.

It would be of particular interest to examine how the above modifications may affect the existence and stability of the identified green trap and red trap states. It should be noted that in this study, we followed the conceptual definition of Cumming et al. (2014) identifying traps as transient states that require reorganization of systems to prevent collapse. Other definitions, more aligned with poverty trap concepts originating from developmental economics, conceptualize traps as stable states, which are self-perpetuating unless critical thresholds (e.g. in physical, natural or cultural capitals) are passed (Lade et al., 2017; Haider et al., 2018). While our current identification of traps aligns more closely to the former conceptualization, the red trap as identified in this study is not necessarily a transient state, as it could be maintained in the absence of further environmental degradation (Figs. 6, 7). Introduction of (one or some of) the above model extension(s) may create additional feedbacks, for example between local environmental conditions and human modification activities, which may either stabilize or destabilize the social-ecological states identified and possibly create alternative (stable) equilibrium states. Such systematic exploration of the potential role of different socio-economic and ecological processes in driving social-ecological system dynamics may contribute to the development of social-ecological systems theory that provides testable hypotheses and opportunities for synthesizing findings of empirical case studies (Schlüter et al., 2019; Siegel et al., 2022).

Finally, it should be noted that in our current model, the impacts of the local social-ecological system on larger-scale systems is negligible. While this may be a reasonable approximation for a single local system, the cumulative pressure of externalized impacts on the natural environment, especially in an age of technological prowess and globally operating markets, may significantly alter dynamics at the Earth system level (Steffen et al., 2015; Rocha et al., 2015). Explicit consideration of natural resources at larger-scale levels could thus inform potential future pathways emerging from the interaction between local social-ecological systems (Dockstader et al., 2019). Within this context, it should also be noted that the current approach did not distinguish between multiple ecosystem processes, and the potential synergies and trade-offs in the supply of these processes (Reader et al., 2022, 2023). For example, in cases where the import of one type of ecosystem process trades off with another needed process, this may limit a local social-ecological system's capacity to reduce its dependency on local natural resources and ecosystem processes (e.g. Hoekstra and Wiedmann, 2014; Cottrell et al., 2018).

The potential model refinements outlined above may identify alternative environmental and socio-economic drivers of social-ecological system transitions, and possibly provide alternative realizations of the conceptual framework proposed by Cumming et al. (2014). An advantage of mathematical models is that alternative formulations can be systematically compared to each other, in order to formulate alternative hypotheses (e.g. Larsen et al., 2014). These alternative hypotheses enable the use of empirical data to infer which driving mechanism(s) are consistent with these observations, and therefore most plausible (Eppinga et al., 2009, 2010; Larsen et al., 2016). Such empirical tests can then guide further model development with increasing levels of detail. Importantly, more detailed system descriptions are more reliant on system-specific input for accurate parameterization. The performance of such high-fidelity models may then also be evaluated in terms of their ability to reproduce empirically observed system dynamics. In this sense, the modelling process can be seen as an iterative process starting with stylized models making general inferences toward system-specific, high fidelity models that can inform policy processes and decision-making procedures in specific systems (Larsen et al., 2014, 2016).

5. Conclusion

Understanding the interactions between human societies and the ecosystem processes they depend on is of key importance to the promotion of sustainability transformations within the Anthropocene. As these interactions become increasingly decoupled across spatio-temporal scales, theoretical frameworks provide a useful tool to relate empirically observed patterns to their drivers and processes. The mathematical model we present in this study highlighted the additional complexity that emerges from the spatial decoupling of natural resource utilization and environmental impacts (Fig. 1). Starting from a model that did not consider natural resource imports from elsewhere, and in which only one stable equilibrium state existed (Eppinga et al., 2021), inclusion of resource imports (Fig. 2) drastically changed local social-ecological system characteristics (Figs. 3, 4, 5, 6). Specifically, we identified green loop-dominated states that strongly depend on local natural resource supply and red loop-dominated states strongly depending on resource imports as alternative social-ecological system states. Under intermediate levels of local natural resource requirements, transitions between these states or conditions leading to their collapse could be identified (Fig. 7; Appendix D). Hence, we conclude that our study provides a framework to synthesize social-ecological system responses to changes in environmental conditions to specific transitions between states that differ in their dependence on local ecosystem processes (Fig. 7).

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Model code needed to reproduce the simulation results has been provided as supplementary information

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolecon.2023.107861>.

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