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Agricultural land use and the sustainability of social-ecological systems

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Abstract

Agricultural land expansion and intensification, driven by human consumption of agricultural goods, are among the major threats to environmental degradation and biodiversity conservation. Land degradation can ultimately hamper agricultural production through a decrease in ecosystem services. Thus, designing viable land use policies is a key sustainability challenge. We develop a model describing the coupled dynamics of human demography and landscape composition, while imposing a trade-off between agricultural expansion and intensification. We model land use strategies spanning from low-intensity agriculture and high land conversion rates per person to high-intensity agriculture and low land conversion rates per person; and explore their consequences on the long-term dynamics of the coupled human-land system. We seek to characterise the strategies' viability in the long run; and understand the mechanisms that potentially lead to large-scale land degradation and population collapse due to resource scarcity. We show that the viability of land use strategies strongly depends on the land's intrinsic recovery rate. We also find that socio-ecological collapses occur when agricultural intensification is not accompanied by a sufficient decrease in land conversion. Based on these findings we stress the dangers of uninformed land use planning and the importance of precautionary behaviour for land use management and land use policy design.

Keywords: Socio-ecological modelling, Land use planning, Agricultural intensification, Agricultural expansion, Socio-ecological collapse, Policies for sustainability

1. Introduction

Food production is the most basic and tangible example of humans' dependence on nature. From Paleolithic hunter-gatherers, who relied on direct harvest from nature, to contemporary complex societies that rely on agriculture and livestock, human survival ultimately depends on what the land provides. An ever growing population and demand for food are putting unprecedented pressure on the environment (Tschardt et al., 2012). Increased food consumption necessitates agriculture expansion; however, the last IPBES report (Bongaarts, 2019) highlights the role of agricultural land expansion as the main threat to

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29 biodiversity loss, mediated by the fragmentation and degradation of habitats (Corvalán et al., 2005; Jacobson
30 et al., 2019; Nowosad and Stepinski, 2019). Degradation of the natural environment brings societal and
31 economic consequences for human populations, as it can result in decreasing agricultural yields (Mitchell
32 et al., 2014) and public health issues (Power, 2010). Conservation of biodiversity and natural spaces are
33 often considered secondary objectives when compared to food security, but biodiversity and ecosystem
34 services play an integral role in maintaining food supply. Agricultural productivity is strongly dependent on
35 ecosystem services, such as pollination, nutrient cycling and pest control, that surrounding natural spaces
36 provide (Mitchell et al., 2013). Therefore, conservation goals should not be seen as opposed to agricultural
37 production or human well-being, as natural land is essential to provisioning services (Cazalis et al., 2018;
38 Braat and de Groot, 2012). Allying natural and agricultural lands is the key to achieve sustainability and
39 avoid a potential socio-ecological collapse.

40 The introduction of agriculture permitted the apparition of the first permanent human settlements. How-
41 ever, Neolithic settlements quickly became heavily reliant on the agricultural system and, as a result, when
42 environmental disasters struck, the food supply and the population suffered (Downey et al., 2016). In some
43 cases, as much as 60% of the population was lost due to failed crops. Over time technological developments
44 made it possible for human societies to adopt more intense forms of agriculture, which increased resource
45 production and food security. Agricultural production enabled the population to grow and allowed the de-
46 velopment of complex societies via social differentiation and territorial expansion (Kuijt and Goring-Morris,
47 2002). This drive to increase agricultural production, however led to deforestation (DeFries et al., 2010),
48 excessive freshwater use (Lilienfeld and Asmild, 2007), soil biodiversity loss (Tsiafouli et al., 2015), altered
49 nutrient (Quinton et al., 2010) and water cycles (Davidson et al., 2012), decreased pollinator abundance,
50 and increased vulnerability to environmental change, all of which can have deleterious effects on agricultural
51 production. Agriculture is thus dependent on the natural environment, but it also heavily transforms this
52 environment. The aim of future societies is to have agriculture improve social welfare, but how to achieve
53 this, while limiting environmental degradation, is a major unknown.

54 Agriculture has been responsible for both the rise and fall of societies. Historical examples of societal
55 collapse are geographically diverse and have occurred over various time scales (Cumming and Peterson, 2017).
56 Several social, political and economical mechanisms have been proposed to explain such collapses (Tainter,
57 1988). However, for a number of them, the roots of societal decline can be traced back to ecological
58 problems caused by resource over-exploitation and poor agricultural land management. The Mayan and
59 the Anasazi collapses are two classic examples. In both cases, collapse is thought to have resulted from
60 feedbacks between population growth and agricultural expansion and intensification, which led to greater
61 environmental degradation and made the food production system unviable (Diamond, 2005; Cumming and
62 Peterson, 2017; Roman et al., 2018). Food scarcity sows the seeds of economic trouble, social unease and
63 political instability, which trap societies in positive feedback loop leading to collapse.

64 The current environmental crisis has reignited scientific interest in societal collapse. There is a general
65 agreement that overpopulation and overconsumption are the main threats to environmental conservation
66 and sustainability (Barrett et al., 2020). Thus, recent studies have addressed sustainability questions by
67 explicitly considering human demography and consumption behaviour. In particular, modelling approaches
68 have shown great potential to shed light on sustainability challenges, as they allow the exploration of
69 different scenarios that would be impossible to reproduce experimentally. In a recent study, Motesharrei
70 et al. (2014) used a dynamical model to show how social inequalities, in terms of resource consumption and
71 contribution to labour, can undermine sustainability and cause societal collapses. This finding can be linked
72 to other issues such as population growth (Kentor, 2001) and over-consumption (Ceballos et al., 2017), which
73 contribute to environmental degradation and social instability. More recently, Henderson and Loreau (2018)
74 and Henderson and Loreau (2019) proposed a general theoretical framework to explain human demography
75 across history in relation to resource accessibility, which can be used to explain the population explosion in
76 the last century and potential future scenarios. Broadening the spectrum of possible connections between
77 nature and human populations, Cazalis et al. (2018) built a model to explore socio-ecological dynamics
78 through the dependence of humans on several ecosystem services. Through an economic-ecological model
79 Lafuite and Loreau (2017), Lafuite et al. (2017) and Lafuite et al. (2018) investigated how time lags in the
80 response of biodiversity to anthropic perturbations can feedback on the human population via shortages in
81 food production and undermine the sustainability of the socio-ecological system. These studies provide the
82 basis for our work, showing a link between humans and the environment through food consumption, which
83 we represent by feedbacks between human population growth and agricultural land use.

84 Research on sustainable agricultural land use has led to the land sharing-sparing debate (Grau et al.,
85 2013; Power, 2010). Whether it is better to protect larger areas of natural land and cultivate high-intensity
86 fields on the remaining land; or protect smaller areas of natural land while practicing wild-life friendly, low-
87 intensity agriculture, is a question that has not yet been fully answered. Different authors often arrive at
88 different conclusions, some defending the sparing/intensification paradigm (Phalan et al., 2011a,b; Balmford
89 et al., 2019) and others the sharing or agroecological one (Perfecto and Vandermeer, 2010; Power, 2010).
90 The sparing-sharing debate has been criticized for omitting the coupling between land use and human
91 demography (Phalan, 2018). Furthermore, the discussion generally examines discrete, opposing strategies,
92 yet there is an entire spectrum between these two extremes. The impact of agricultural intensification on
93 sustainability is an important issue at present, as in the developing countries foreign demand is fueling the
94 conversion of large areas of natural land into intensively cultivated monocultures (Fearnside, 2001; Pengue,
95 2005; Reboratti, 2010; Soares-Filho et al., 2006). The result is a uniform landscape that is highly vulnerable
96 to environmental fluctuations, destruction of natural habitats, fragmentation, contamination of underground
97 water sources and nutrient runoff. These practices are detrimental to the environment, but agriculture is
98 necessary to feed the population. It is obvious that a balance needs to be achieved between food production

99 and natural land conservation, as the actions taken today could jeopardize the population's viability in the
100 long run.

101 Here we build a model to explore the effects of different agricultural land use strategies on long-term
102 human-environment dynamics. Through a simple and tractable model accounting for the interaction between
103 human demography and land dynamics, we study the viability of agricultural socio-ecological systems under
104 different land use strategies along an intensification-expansion spectrum. We introduce a trade-off between
105 intensification and the land conversion effort and investigate for which land use strategies the population
106 collapses due to land degradation. Our central premise is that increasing agricultural production can promote
107 further population growth. Thus, agricultural intensification, via increasing agricultural yields, can have
108 a positive feedback on human demography, initiating the need for larger production and therefore causing
109 further natural land conversion to agriculture, which eventually leads to a more degraded landscape. We
110 test the conditions under which increasing agricultural intensification fails to spare enough natural land and
111 promotes unsustainable population growth, pushing the environment through a tipping point and ultimately
112 leading the social-ecological system to collapse.

113 **2. Model description**

114 *2.1. Bidirectional coupling between human demography and land dynamics*

115 Our model considers the conversion of natural land to agricultural land in relation to the demand from the
116 human population. As population dynamics are driven by the resources humans can access and consume,
117 they ultimately depend on the landscape's composition. Resource production depends on the landscape
118 composition but also on agricultural intensity. We conceive agricultural land use along two dimensions:
119 the conversion effort, which controls the spatial extension of agricultural land, and agricultural intensity.
120 In the model, humans adopt a land use strategy ranging from low intensity and high land conversion
121 rates, to high intensity and low land conversion rates. This negative relation between agricultural intensity
122 and the land conversion effort is grounded in the land sparing-sharing debate. Highly expansive and intense
123 agricultural land uses have been identified as unsustainable. Hence, the debate is whether the focus to achieve
124 sustainability should be put on increasing intensification to reduce the converted areas or extensification to
125 have a wildlife friendly agricultural landscape. We aim to reproduce these two strategic poles by imposing
126 a trade-off between agricultural intensity and land conversion effort, hence reducing the two strategical
127 dimensions to a single parameter. In this study, we do not consider the evolution of the strategy over time
128 and assume it remains constant.

129 Agricultural land is exhausted and degraded, at different rates depending on the surrounding landscape,
130 and ultimately becomes unproductive (Henderson and Loreau, 2019; Cramer et al., 2008). Natural land
131 contributes to the recovery of surrounding land, acting, for example, as a species pool necessary for recolo-
132 nization by native species (Cramer et al., 2008; Baeten et al., 2010). Hence, fragmentation of natural areas

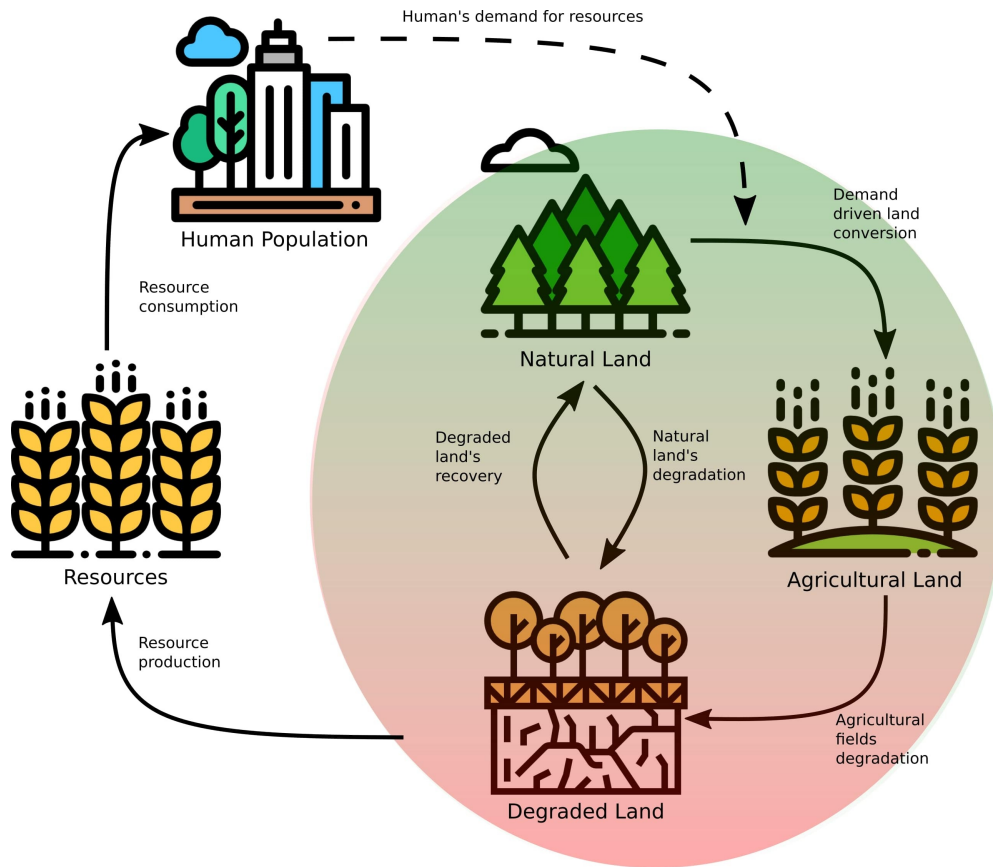


Figure 1: Model's graphical representation. The right part of the diagram represents the landscape, composed of natural land, agricultural land and degraded land. The arrows between the three land types represent the possible land transformations we consider (conversion, recovery, degradation). Both the agricultural intensity and the landscape composition determine the number of resources that are produced and consumed by the human population. Human demography is entirely determined by resource access. Changes in the human population size modify the population's demand for resources and feedback on the landscape's composition by increasing or decreasing the conversion of natural land for agricultural purposes.

133 and degradation of natural patches surrounding degraded land can obstruct its spontaneous recovery. On
 134 the other hand, natural land can also become degraded. Indeed, a degraded state of land can propagate
 135 into a natural one, as is the case with a desertification front that propagates on semi-arid landscapes (Zelnik
 136 et al., 2017; Zelnik and Meron, 2018). The balance between the recovery and degradation processes depends
 137 not only on the extension of both natural and degraded land, but also on the borders between the two types
 138 of lands and on the level of degradation (Cramer et al., 2008).

139 2.2. Human demography

140 A number of studies have discussed the idea of a human carrying capacity and pointed to food supply
 141 as one of the main constraints to human population growth (Cohen, 1995; Hopfenberg, 2003; Fanta et al.,
 142 2018). In this study, we follow the same reasoning and assume human population size p follows logistic

143 growth with a carrying capacity that evolves over time subject to changes in food supply.

144 The use of the logistic equation to describe the dynamics of human populations has been previously
145 criticized (Mote et al., 2020; Board on Environmental Change and Society et al., 2014) and other studies
146 have opted to explicitly model fertility and mortality processes by various functions related to consumption
147 levels (Motesharrei et al., 2014; Lafuite and Loreau, 2017; Henderson and Loreau, 2019). Furthermore,
148 Cohen (1995) has stressed the difficulties of estimating a human carrying capacity given that several bio-
149 physical and social mechanisms that might constrain human population growth are dynamically evolving
150 and possibly unidentified. However, historical population trends have been well recovered by logistic models
151 using food-dependent carrying capacities (Goldberg et al., 2016; Fanta et al., 2018). Additionally, the
152 unprecedented population increase of the 1960s to 2000s was also modelled using a logistic model, where
153 Hopfenberg (2003) quantified the human carrying capacity using food production, showing good agreement
154 with empirical data. More recently, Suweis et al. (2013) used the link between water availability and food
155 production to calculate a human carrying capacity based on access to water resources, using population
156 data from 1970 to 2011.

157 We assume the human carrying capacity to be the ratio between total resource production and per capita
158 consumption $K_p = Y/C$, where Y is total resource production, depending on the landscape's composition,
159 and C is per capita resource consumption. As such, the carrying capacity endogenously changes over
160 time as food production changes driven by the feedbacks between humans and the landscape. For a given
161 consumption intensity, the maximum number of humans that can be sustained is then given by the ratio of
162 production over per capita consumption:

$$\frac{dp}{d\tau} = r_0 p \left(1 - \frac{p}{K_p} \right) = r_0 p \left(1 - \frac{Cp}{Y} \right), \quad (1)$$

163 where r_0 is the population's growth rate at very low densities. We assume that r_0 and C remain constant
164 over time. This is a simplification, as it is known that technological developments and cultural evolution
165 have driven changes in human fertility and consumption, as well as in agricultural productivity, which
166 inevitably impact the human carrying capacity. However, in this study we do not consider the role of
167 cultural and technological evolution, instead we focus on the land dynamics. Based on a previous model of
168 socio-ecological interactions that included variations in food production efficiency (Cazalis et al., 2018), the
169 inclusion of technology in the carrying capacity would likely shift the onset of collapse, vary the size of the
170 collapse range and alter the viability range of parameters, but would not change the overall or long term
171 trends.

172 2.3. Agricultural production

173 The number of resources produced (Y) depends on the area of agricultural land (a), but also on that of
174 natural (n) and degraded (d) land, as well as on agricultural intensity, β . Noncultivated land, whether natural

175 or degraded, provides ecosystem services that are crucial for agricultural production, such as pollination,
 176 nutrient cycling, pest control and water quality regulation (Mitchell et al., 2014). However, greater land
 177 degradation leads to fewer and lower-quality ecosystem services. Therefore, we do not consider natural
 178 and degraded land to contribute equally to agricultural production. Instead, we introduce an effective
 179 land function $\epsilon_l(n, d, \beta)$, which represents the effective area of non-cultivated land that provides ecosystem
 180 services to agricultural land:

$$\epsilon_l = n + (1 - \beta) d. \quad (2)$$

181 The contribution of degraded land to effective land decreases with its level of deterioration, which in turn
 182 depends on the level of agricultural intensification (β). We assume that more intensive agriculture results in
 183 higher degrees of land degradation and as such intensive agriculture transitions to highly degraded land. For
 184 simplicity, the contribution of degraded land to effective land decreases linearly with agricultural intensity.

185 We model agricultural resource production Y as the sum of the contributions from the total cultivated
 186 area (area contribution) and from the border of agricultural land with non-cultivated land, both natural
 187 and degraded, represented by the effective land ϵ_l (border contribution). Therefore, the “area contribution”
 188 scales with agricultural land area and the “border contribution” with the square root of agricultural land
 189 area. Furthermore, we assume the relative weights of area, and border contributions in production depend
 190 on agricultural intensity (β). As agricultural intensification grows, production, Y , becomes less dependent
 191 on the ecosystem services provided by the surrounding non-agricultural land and more dependent on human
 192 inputs. Hence, increasing intensification diminishes the border contribution and increases the area contribu-
 193 tion on production. Therefore, we assume the area contribution increases linearly with agricultural intensity,
 194 β , while the border contribution decreases linearly with β .

195 The amplitude of the area and border contributions is modulated by the functions $Y_A(\beta)$ and $Y_B(\beta)$.
 196 These two functions can be interpreted as the characteristic productivity of the area and border contribu-
 197 tions, respectively. For a given agricultural intensity (β), $Y_A(\beta)$ is the production per unit area of agricultural
 198 land and $Y_B(\beta)$ is the production per unit area of effective land per unit length of the agricultural land’s
 199 border.

$$Y = \underbrace{Y_A(\beta) \beta a}_{\text{Area contribution}} + \overbrace{Y_B(\beta) (1 - \beta) \epsilon_l \sqrt{a}}^{\text{Border contribution}} = y_A \beta (\beta a + Q \epsilon_l (1 - \beta) \sqrt{a}) \quad (3)$$

200 Agricultural intensity (β) ranges from 0 to 1, 0 being extreme low-intensity agriculture and 1 extreme high
 201 intensity. As intensification increases agricultural yields, we model the characteristic productivity of the area
 202 (Y_A) and border (Y_B) contributions as increasing functions of agricultural intensification. For simplicity, we
 203 assume a linear dependency, i.e., $Y_A(\beta) = y_A \beta$ and $Y_B(\beta) = y_B \beta$. The parameters y_A and y_B are then

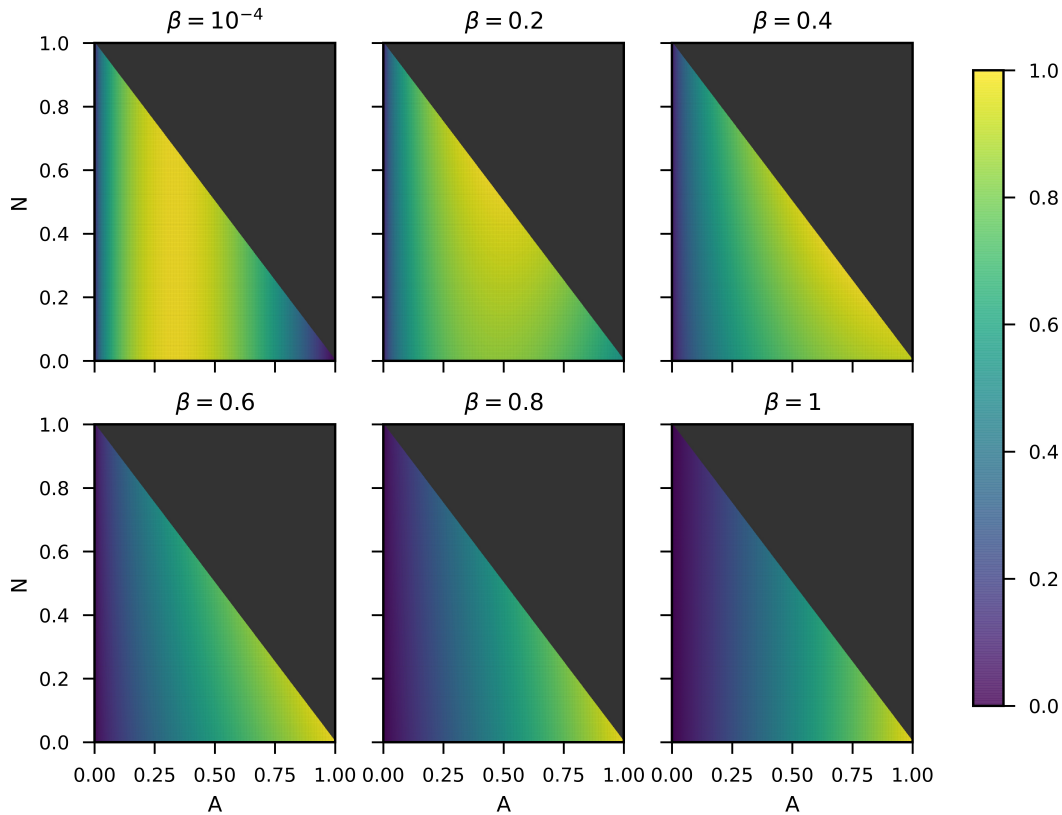


Figure 2: Agricultural production as a function of landscape composition for different agricultural intensities. The x and y axis correspond to the fraction of agricultural and natural land respectively. Each subplot corresponds to a different agricultural intensity (β). The production is normalised for each case, hence comparison of agricultural production’s magnitude between strategies is not possible. Instead, the figure shows the different effect that landscape composition has on each case. When agricultural intensity is very low ($\beta = 10^{-2}$), production strongly depends on the services provided by the non-agricultural landscape, hence it decreases when the fraction of agricultural becomes bigger than a certain threshold ($A \simeq 0.4$ in the plot). As intensification grows, natural land’s importance for production diminishes ($\beta = 0.2, 0.4, 0.6, 0.8$). On the high intensification extreme ($\beta = 0.99$), the production becomes exclusively dependent on human inputs, hence it grows monotonically with agricultural area.

204 the productivities per unit of intensification. We introduce the parameter $Q = y_B/y_A$, which represents the
 205 relative importance of the border and area contribution to resource production.

206 Figure 2 shows the magnitude of agricultural resource production as a function of landscape composition.
 207 When β is close to 0, maximum production is obtained in a landscape where about a third of the land is
 208 agricultural. The food production is exclusively dependent on the services provided by the non-anthropogenic
 209 landscape. As we assume the services that non-cultivated land provides to agricultural land depend both on
 210 the area and quality of non-cultivated land and on the length of the border between them, at this extreme
 211 of the spectrum production scales with the square root of agricultural area. At the extreme, the fraction of

212 natural land is not important because the degradation caused by the agricultural activity is extremely low,
 213 such that natural and degraded land contribute equally to effective land. As β grows, the fraction of natural
 214 land starts to have an impact, as degraded and natural land are not interchangeable anymore. When β
 215 approaches 1, production becomes exclusively dependent on agricultural land area. This is a scenario of
 216 extremely high agricultural intensity, where agricultural yields become independent of the services provided
 217 by the non-agricultural landscape, and rely exclusively on human inputs, such as fertilizers or pesticides. In
 218 the high intensity case, production is proportional to the area of agricultural land. Figure 2 also shows that
 219 yields increase with intensification, as maximum attainable production (yellow areas in the figure) grows
 220 with β .

221 2.4. Land dynamics: agricultural land equation

222 Land conversion is driven by the human population's demand for agricultural goods, which results
 223 on the conversion of natural land to agriculture. We assume that demand is equal to the total desired
 224 food consumption (Cp). Since we aim to investigate the impact of different land use strategies along the
 225 intensification-extensification spectrum on human-land dynamics, we impose a trade-off between agricul-
 226 tural intensity and land conversion rate. We model land conversion rate as a decreasing affine function
 227 of agricultural intensity (β). Nutrient runoff and soil erosion cause agricultural land degradation, which
 228 increases with intensity. Therefore, we model the degradation rate of agricultural land as a linear function
 229 of β , capturing the fact that high-intensity agriculture degrades the land faster than does low intensity
 230 agriculture. The dynamical equation for the agricultural land area is given by

$$\frac{da}{d\tau} = \underbrace{[K_0 + (K - K_0)(1 - \beta)] Cp n}_{\text{Conversion}} - \overbrace{E\beta a}^{\text{Degradation}} . \quad (4)$$

231 Parameters K_0 and K are the minimum and maximum conversion rates per unit of demanded resources
 232 Cp , respectively. As the demand for resources is proportional to population density, K_0 and K are also
 233 per capita rates of conversion. Therefore, in the following we will call them per capita conversion rates. In
 234 the extreme high intensity scenario ($\beta = 1$), the conversion rate per person is at its minimum K_0 . In the
 235 extreme low intensity scenario ($\beta = 0$), the conversion rate per person is at its maximum K .

236

237 2.5. Land dynamics: natural land equation

238 Apart from being converted to agriculture, natural land area can either increase through the spontaneous
 239 recovery of degraded land or decrease by the propagation of the degraded state of land. The natural land
 240 at the edges of degraded land fosters its spontaneous recovery through both biotic and abiotic processes.
 241 It acts as a species pool, promoting native species recolonization, or as a source of good quality water or

Parameter name	Parameter description	Dimension	Nondimensional	Value
r_0	Population growth rate at low densities	time ⁻¹		
y_A	Maximum production per cultivated area	mass/area		
C	Resources consumption per person	mass/person		
K_0	Minimum land conversion rate per resources demand	mass ⁻¹	k_0	0.5
K	Maximum land conversion rate per resources demand	time ⁻¹		
E	Maximum agricultural fields degradation rate	mass ⁻¹	k	4.5
Q	Ratio between area and border contribution	time ⁻¹	e	1.0
R	Recovery rate of degraded land per length of frontier with natural land	length ⁻¹	q	1.0
D	Maximum degradation rate of natural land per length of frontier with degraded land	length ⁻¹	r	[0.1 – 3.5]
β	Land use strategy parameter	time ⁻¹	d	[0.1 – 3.5]
			β	[0 – 1]

Table 1: Description of the model's parameters.

242 chemical compounds to restore soil chemistry (Cramer et al., 2008; Baeten et al., 2010). The size of the
243 natural patches is also important as larger patches foster more species and are more resilient to abiotic
244 fluctuations (Mitchell et al., 2013, 2015). Hence, the recovery process depends both on the area of natural
245 patches and on the size of their border with degraded land. We propose a spontaneous recovery term that
246 scales both with natural land area n and with degraded land's border $\propto \sqrt{d}$ (Mitchell et al., 2015). The
247 propagation of degraded land's occurs through a symmetric mechanism, where the potential for degradation
248 grows with degraded land area and with the natural land's border. Therefore, the equation for the change
249 in natural land is

$$\frac{dn}{d\tau} = \underbrace{R n \sqrt{d}}_{\text{Recovery}} - \underbrace{D \beta d \sqrt{n}}_{\text{Degradation}} - \underbrace{[K_0 + (K - K_0)(1 - \beta)] C p n}_{\text{Conversion}}. \quad (5)$$

250 The parameters R and $D\beta$ are the recovery and degradation rates, respectively. The degradation rate scales
251 linearly with the agricultural intensification, such that more intensive agricultural land is more heavily
252 degraded. Furthermore, heavily degraded land contributes to a greater extent to the degradation of natural
253 land.

254 2.6. Nondimensionalization

255 We rescale the dynamical system by introducing the non-dimensional variables P , N , A and t , for
256 population, natural land area, agricultural land area and time respectively:

$$t = \frac{\tau}{T_0} = r_0 \tau, \quad N = \frac{n}{A_0}, \quad A = \frac{a}{A_0}, \quad P = \frac{p}{P_0} = p \frac{C}{y_A A_0}. \quad (6)$$

257 Time is rescaled to the characteristic timescale of human demography $T_0 = 1/r_0$. Parameter A_0 is the total
258 amount of land, hence variables N and A represent the fraction of natural and agricultural land in the
259 landscape, respectively. We normalize the population by $P_0 = y_A A_0 / C$. P_0 represents the population size
260 that could be sustained if the whole landscape was cultivated with the highest intensity agriculture $\beta = 1$,
261 given per capita consumption C . Indeed, when $\beta = 1$, if the whole landscape is cultivated, production is
262 $Y = \beta^2 y_A A_0 = y_A A_0$. The following dimensionless parameters emerge from the non-dimensionalisation:
263 k_0 – minimum land conversion rate, k – maximum land conversion rate, e – agricultural land degradation
264 rate, r – spontaneous recovery rate of degraded land, d – degradation rate of natural land, and q – the
265 relative importance of the border contribution to agricultural production.

$$k_0 = \frac{K_0 y_A A_0}{r_0}, \quad k = \frac{K y_A A_0}{r_0}, \quad e = \frac{E}{r_0}, \quad q = Q \sqrt{A_0}, \quad r = \frac{R \sqrt{A_0}}{r_0}, \quad d = \frac{D \sqrt{A_0}}{r_0} \quad (7)$$

266 The dynamical equations describing the non-dimensional system behaviour are

$$\begin{cases} \frac{dP}{dt} &= P \left(1 - \frac{P}{Y}\right) \\ \frac{dA}{dt} &= [k_0 + (k - k_0)(1 - \beta)] P N - e \beta A \\ \frac{dN}{dt} &= r N \sqrt{1 - A - N} - d \beta (1 - A - N) \sqrt{N} - [k_0 + (k - k_0)(1 - \beta)] P N \\ \mathcal{Y} &= \beta \left(\beta A + q(1 - \beta)(N + (1 - \beta)(1 - A - N)) \sqrt{A} \right) \end{cases} \quad (8)$$

267 3. Results

268 3.1. Exploitation of a pristine landscape: sustainable vs. unsustainable land use strategies

269 We first look at the dynamics that follow the introduction of a small population in a pristine landscape.
270 The time series are depicted in Figure 3. No matter the land use strategy, the early transient dynamics
271 are identical. The human population converts the natural land into agricultural fields, thus increasing
272 resource production, which positively feeds back on the human population. The increased population, in
273 turn, accelerates land conversion. This positive feedback loop causes a population explosion accompanied
274 by a transformation of the landscape. Agricultural land expansion fuels an increase in degraded land. Both
275 land conversion and increasing amounts of degraded land contribute to the decline of natural land. The
276 decrease in natural land area ultimately causes a deceleration of agricultural expansion until no more land
277 is converted. The human population peaks with the agricultural area.

278 Degraded land cannot be converted back to agricultural land. This introduces a time delayed feedback
279 as the stock of natural land is not instantaneously regenerated. The time delayed feedback causes the
280 population to overshoot its carrying capacity. After the overshoot, the socio-ecological system can reach
281 two different equilibria depending on the land use strategy β . We call *viable equilibrium* the one where

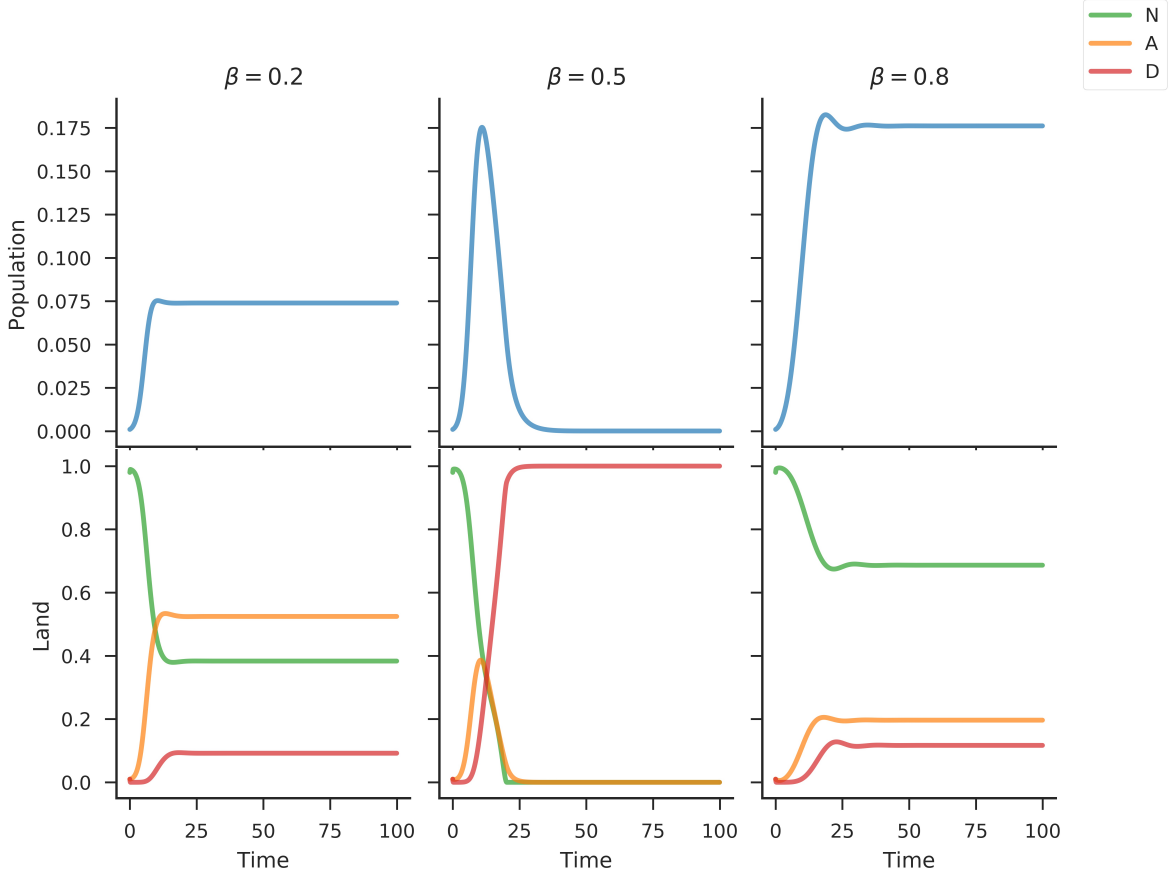


Figure 3: Temporal dynamics of the socio-ecological system for different agricultural land use strategies. *On the left:* dynamics emerging from low intensity agriculture and a high land conversion effort. The socio-ecological system reaches a viable equilibrium. *Center:* dynamics emerging from intermediate agricultural intensity and conversion effort. The socio-ecological system collapses. *On the right:* dynamics emerging from high intensity agriculture and low land conversion effort. A viable equilibrium is reached again. *Parameter values:* $r = 1.0$, $d = 1.0$, $k = 4.5$, $e = 1.0$, $k_0 = 0.5$, $q = 1.0$.

282 the human population exists in the long term, and *collapse equilibrium* the one where the population goes
 283 extinct. In the viable equilibrium, the human population exists within a complex landscape, composed of
 284 a natural, agricultural and degraded land mosaic. In contrast, the landscape in the collapse equilibrium is
 285 fully degraded. Without agriculture, there is no resource production and the human population cannot be
 286 maintained.

287 The land use strategy spectrum can be divided into three regions according to the system's asymptotic
 288 behaviour, as a function of the strategy β . The first region corresponds to values of β between 0 and the
 289 transition to the collapse equilibrium at the critical point $\beta = \beta_{c,1}$. We call this region the *sharing* side of
 290 the spectrum, as land use strategies in that range mimic land-sharing kinds of strategy (e.g. low intensity
 291 agriculture over large areas). The *collapse range* (referred to as $\Delta\beta$ later in the text) refers to the region

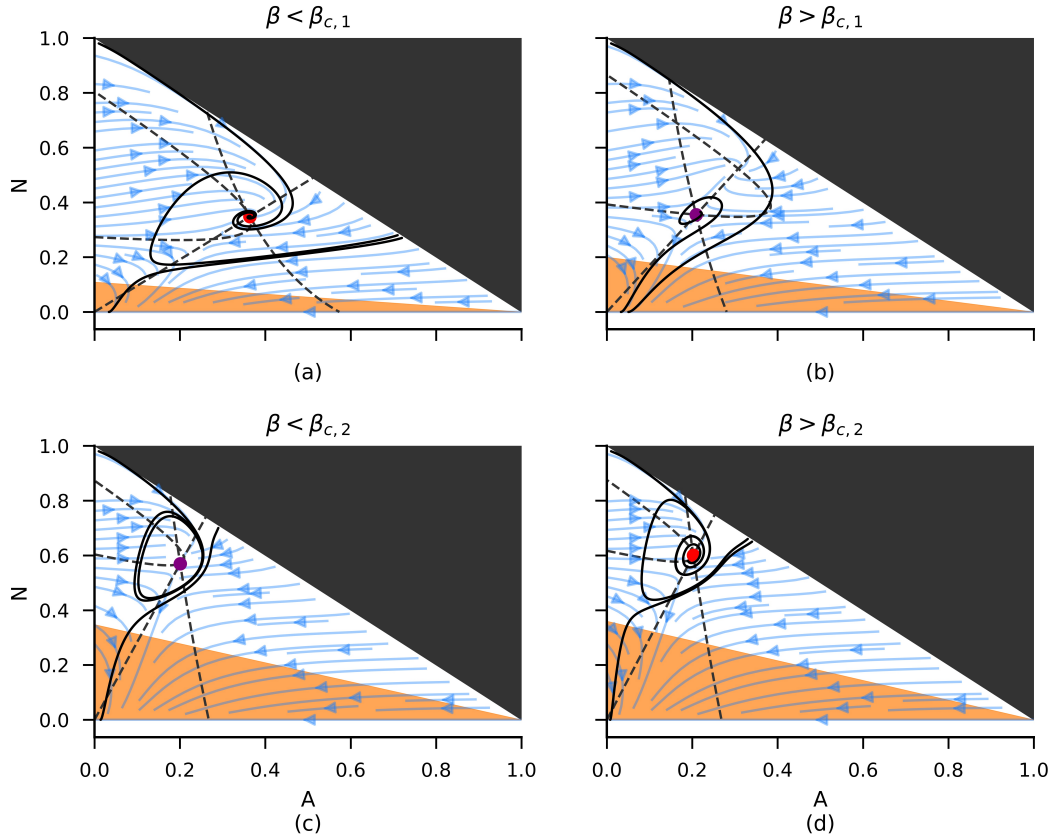


Figure 4: Phase representations of the socio-ecological system for strategies in the viable and collapse regions of the strategy spectrum. The plots correspond to particular landscape planes of the three-dimensional phase space. The chosen planes are the ones containing the system's viable equilibrium, hence determined by setting the population at its viable equilibrium value. The dotted grey lines are projections of the null planes for the population, the natural land and the agricultural land on the chosen landscape plane. The black solid lines are projections of simulated trajectories. The vector field depicted with blue arrows indicates the landscape's direction of change for each landscape composition given a population at equilibrium. *On the top:* before (a) and after (b) the first transition to collapse. A subcritical Hopf bifurcation causes the stability loss of the viable equilibrium explaining the transition to collapse. *On the bottom:* emergence of a stable limit cycle (c) from a stable focus node (d) after a supercritical Hopf bifurcation. *Parameter values:* $r = 1.0$, $d = 1.0$, $k = 4.5$, $e = 1.0$, $k_0 = 0.5$, $q = 1.0$.

292 of the spectrum where strategies lead to the collapse equilibrium. When land use strategies are inside the
 293 collapse range, the degraded land propagates into the whole landscape, leading to a population collapse. The
 294 region between the collapse range and the viable equilibrium is designated the sparing side of the spectrum,
 295 as the strategies in this region mimic land-sparing kind of strategies (e.g. high intensity agriculture over
 296 small areas).

297 3.2. On the path to socio-ecological collapse

298 The existence of the collapse range is due to changes in the stability of the viable equilibrium as a
 299 function of the agricultural land use strategy β . On the sharing side of the spectrum, the viable equilibrium

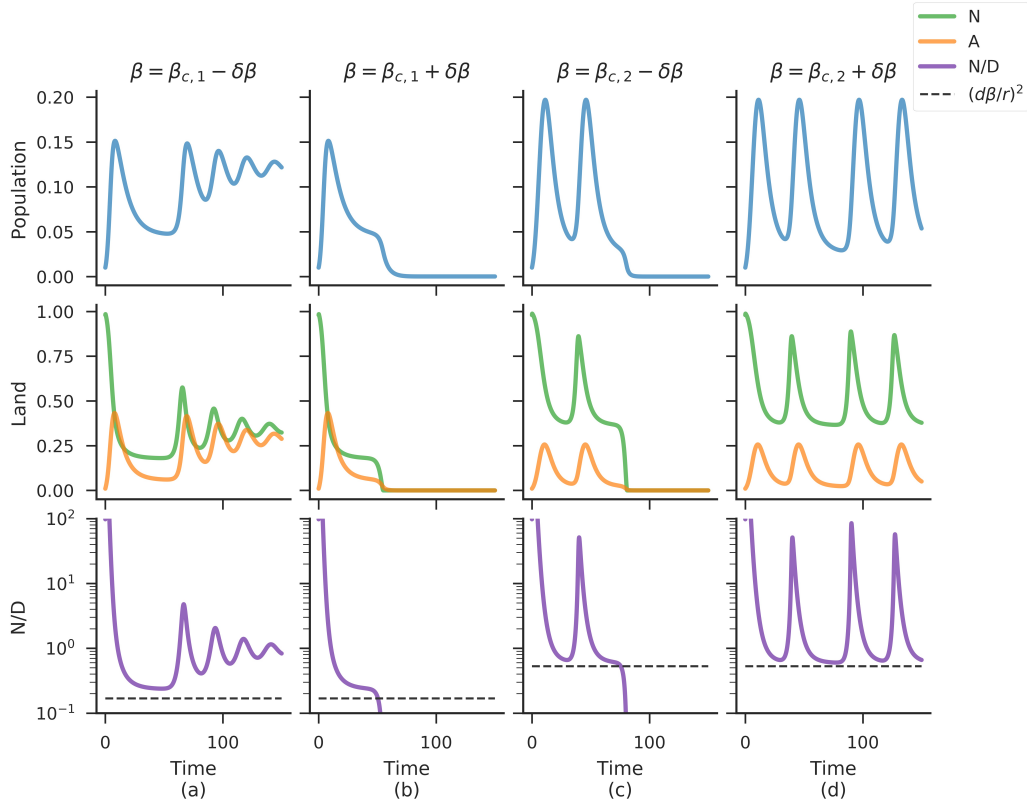


Figure 5: Temporal dynamics of the socio-ecological system at the edges of the collapse range. *Column (a):* dynamics before the first transition to collapse. The equilibrium is reached after large amplitude damped oscillations. *Column (b):* dynamics after the first transition to collapse. *Column (c):* dynamics after the second transition to collapse. The growth of the oscillations' amplitude pushes the system through a threshold and causes the collapse (bottom plot). *Column (d):* dynamics before the second transition to collapse. The collapse is avoided as the system oscillates around the equilibrium without reaching it. *Parameter values:* $\beta_{c,1} = 0.4106108$, $\beta_{c,2} = 0.7272030$, $\delta\beta = 10^{-7}$, $r = 1.0$, $d = 1.0$, $k = 4.5$, $e = 1.0$, $k_0 = 0.5$, $q = 1.0$.

300 is a stable focus-node. Hence, in the phase space, trajectories follow spirals before reaching the fixed point
301 (Figure 4 (a)), which translate into damped oscillations over time (column (a) of Figure 5). As land use
302 strategies come closer to the collapse range (β increases), the amplitude of the oscillations grow, which
303 delays the system's convergence to the viable equilibrium. When the land use strategy enters the collapse
304 range, the viable equilibrium becomes a saddle-focus and loses stability (Figure 4 (b)). The stability loss is
305 caused by a subcritical Hopf bifurcation which leaves the collapse equilibrium as the sole stable attractor
306 for the socio-ecological system.

307 On the sparing side of the spectrum, the transition to collapse has a different origin. As for the sharing
308 side of the spectrum, the system converges to a viable equilibrium via damped oscillations (Figure 4 (a))
309 which grow in amplitude as the collapse range is approached. However, in this case the system undergoes
310 a supercritical Hopf transition when the critical point is reached. Hence, the stability loss of the viable
311 equilibrium is accompanied by the birth of a stable limit cycle, which allows the socio-ecological system

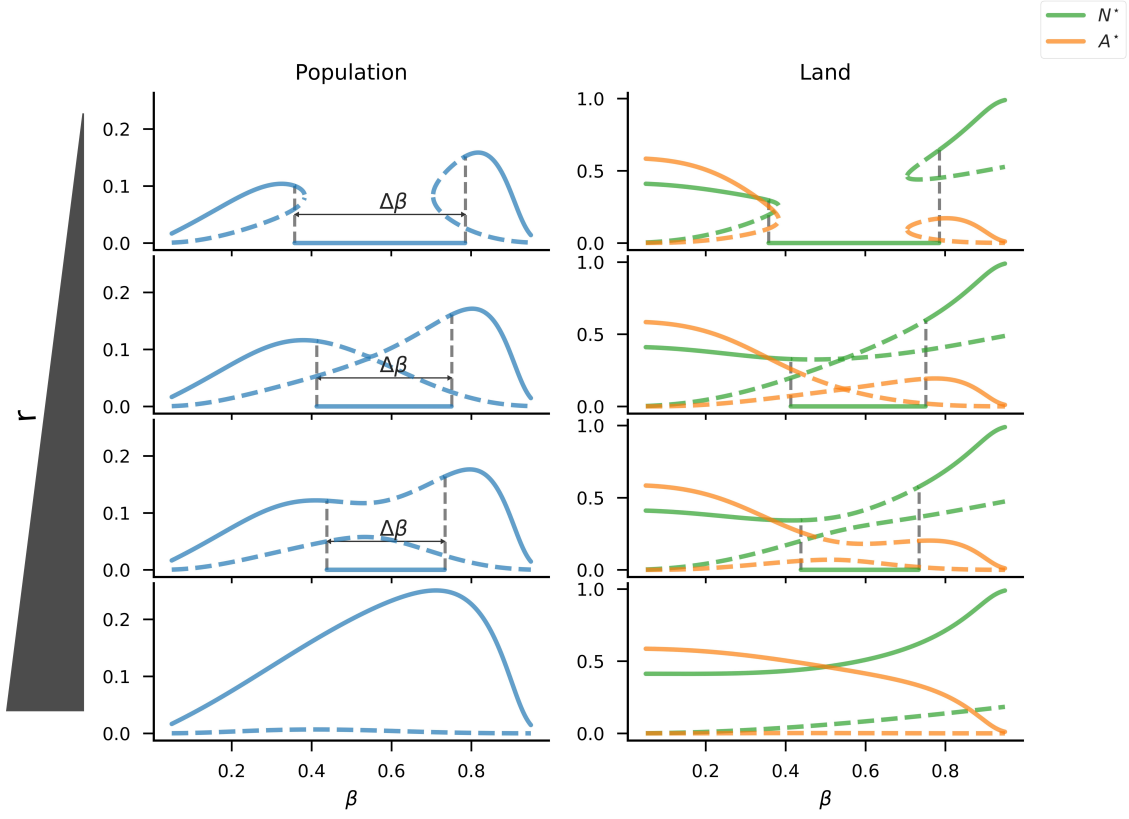


Figure 6: Bifurcation diagrams for the land use strategy parameter β and for different values of natural land's recovery capacity. Socio-ecological steady states are plotted as a function of the land use strategy. The dotted lines correspond to the unstable equilibria and the solid ones to the stable ones. The size of the collapse region is $\Delta\beta$. From the top to the bottom, the natural land's recovery capacity increases. The values of the recovery capacity increase from top to bottom and were chosen to give a full picture of the steady state branches' behaviour. $\Delta\beta$ decreases until disappearance as the recovery rate r increases. Parameter values for these simulation are $r = 0.9, 0.97139, 1, 2, d = 1.0, k = 4.5, e = 1.0, k_0 = 0.5$ and $q = 1.0$.

312 to potentially escape the collapse equilibrium (Figure 4 (c)) and oscillate around the viable equilibrium.
 313 However, the amplitude of the oscillations grows as the land use strategy moves in the sharing direction (β
 314 decreases). Eventually, the oscillations become large enough to push the system through a tipping point
 315 provoking a socio-ecological collapse (bottom of column (c) in Figure 5).

316 Analytically, we can determine a threshold landscape composition after which socio-ecological collapse
 317 is unavoidable. Analysis of the natural land's dynamical equation gives the following condition

$$\frac{N}{D} \leq \left(\frac{d\beta}{r} \right)^2, \quad (9)$$

318 where $D = 1 - A - N$ is the fraction of degraded land. The threshold depends on the land recovery potential
 319 r , as well as on the degradation potential $d\beta$. The threshold represents the point at which the landscape
 320 is so deteriorated that the remaining fraction of natural land is not sufficient to recover the degraded land

321 nor to maintain its natural state. Hence, degraded land starts propagating into the natural land, resulting
 322 in the complete degradation of the landscape and population extinction. Close to the second transition to
 323 collapse, oscillations approach the previous threshold (column (d) of Figure 5). A small change in the land
 324 use strategy increases the oscillations' amplitude and pushes the system through the tipping point, driving
 325 it to collapse (column (c) of Figure 5).

326 *3.3. Role of land recovery potential on the size of the collapse range*

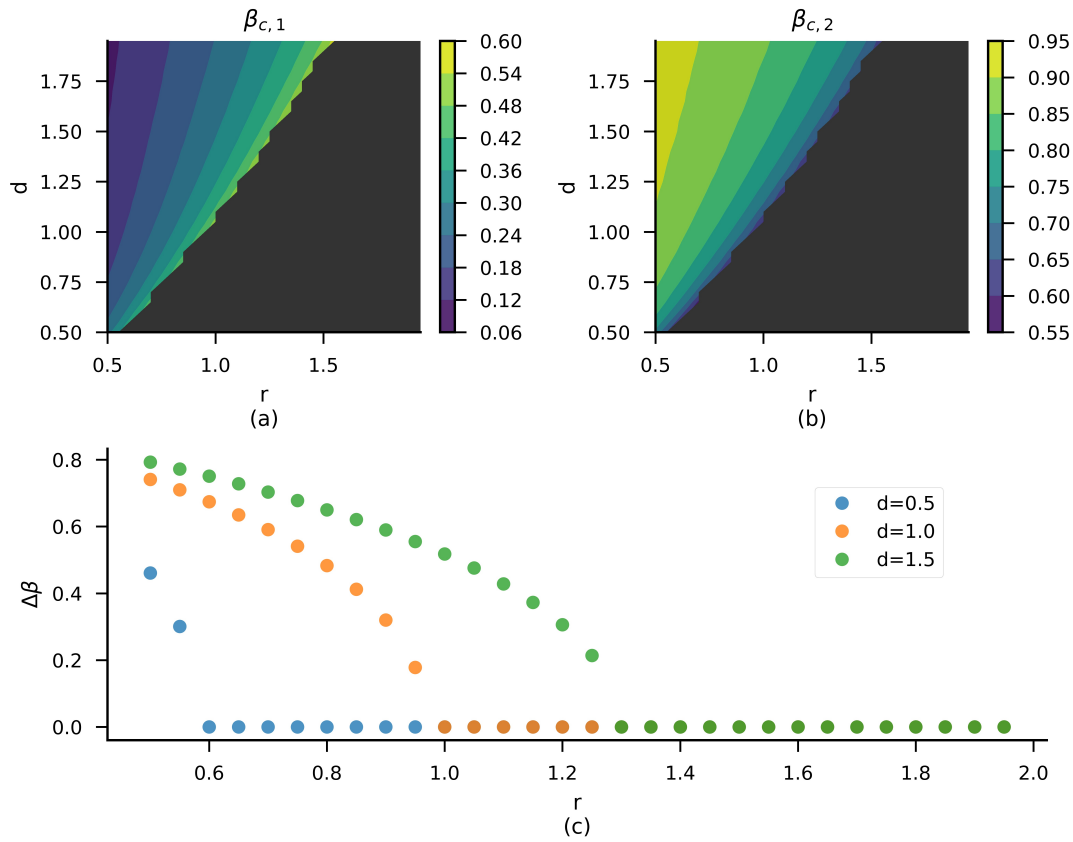


Figure 7: Collapse range size $\Delta\beta$ in function of landscape's intrinsic characteristics. *On the top:* critical values $\beta_{c,1}$ (a) and $\beta_{c,2}$ (b) in function of the land's recovery r and degradation d rates. The black colour depicts the region of the parameter space (r, d) where the human population is viable no matter the land use strategy. *On the bottom:* Size of the collapse range $\Delta\beta = \beta_{c,1} - \beta_{c,2}$ in function of the land's recovery rate for different degradation rates. The amplitude of the collapse region sharply increases when r decreases. The parameter values are $k = 4.5$, $e = 1.0$, $k_0 = 0.5$ and $q = 1.0$.

327 The size of the collapse range $\Delta\beta = \beta_{c,2} - \beta_{c,1}$ is highly dependent on the degraded land's recovery
 328 potential (r), as Figures 6 and 7 show. As the land recovery potential increases, the size of the collapse
 329 range decreases until it disappears. It is interesting to note that on the sharing side of the spectrum,
 330 when $\beta < \beta_{c,1}$, an increase in β leads to higher agricultural yields and larger populations. However, the

331 decrease in the land conversion effort is not high enough to prevent the fraction of natural land to decrease.
 332 Indeed, agricultural intensification increases the natural land's degradation rate βd , increasing the potential
 333 of degraded land to propagate into the rest of the landscape. When agricultural intensification is not
 334 accompanied by a sufficiently large reduction in the conversion effort, the system enters the path to collapse.
 335 At the critical point, the levels of degradation are sufficiently high to cause a socio-ecological collapse.

336 On the sparing side of the spectrum, when $\beta > \beta_{c,2}$, the decrease in the land conversion effort that
 337 accompanies the increase of intensification succeeds in sparing natural land and allows larger populations to
 338 exist in a landscape with a higher fraction of natural area. At the extreme of the sparing strategy spectrum,
 339 populations decrease when β rises. This is due to the decrease in the land conversion effort. Only a small
 340 fraction of land is converted to agriculture and as such a much lower population can be sustained with the
 341 same consumption level.

342 We investigated in more detail the relationship between the size of the critical region $\Delta\beta$ and the
 343 landscape intrinsic parameters r and d (Figure 7). The contour plots of Figure 7 show the variation of the
 344 critical values $\beta_{c,1}$ and $\beta_{c,2}$ as a function of r and d . For a given natural land degradation rate (d), increasing
 345 the recovery rate of degraded land (r) rises $\beta_{c,1}$ and diminishes $\beta_{c,2}$. When the difference between the two
 346 critical values reaches 0, the collapse range ceases to exist (black region in contour plots of Figure 7). The
 347 non-linearity of the edge between the coloured ($\Delta\beta > 0$) and black regions ($\Delta\beta = 0$) of the contour plots
 348 shows that the collapse frontier is more sensitive to r than d , such that when an increase in degradation
 349 requires a smaller increase in r to off-set the increase in degradation.

350 3.4. *The dangers of naive agricultural land use planning*

351 As it is formulated, our model does not allow us to know how much the land conversion effort should
 352 diminish for a given increase in agricultural intensification, in order to avoid socio-ecological collapse. This is
 353 because we fixed a linear trade-off between the conversion effort and the intensity. In reality, the relationship
 354 between them can be highly nonlinear. In order to address the question, we release the linear trade-off
 355 assumption and let the land conversion effort to be independent of agricultural intensity. We then explore
 356 land use strategies along the two dimensions of intensification and extensification. In practice, this means
 357 we now have two parameters K (land conversion effort) and β (agricultural intensity) to describe a land use
 358 strategy instead of a single one. Hence, the equations for land become:

$$\begin{cases} \frac{dA}{dt} = K P N - e \beta A \\ \frac{dN}{dt} = r N \sqrt{1 - A - N} - d \beta (1 - A - N) \sqrt{N} - K P N \end{cases} \quad (10)$$

359 In Figure 8 we plot the regions of the land use strategy space, defined by the land conversion effort K and
 360 the agricultural intensity β where either the collapse equilibrium or the viable equilibrium are attained. The
 361 border between the two regions is concave rather than linear, which explains the existence of the collapse

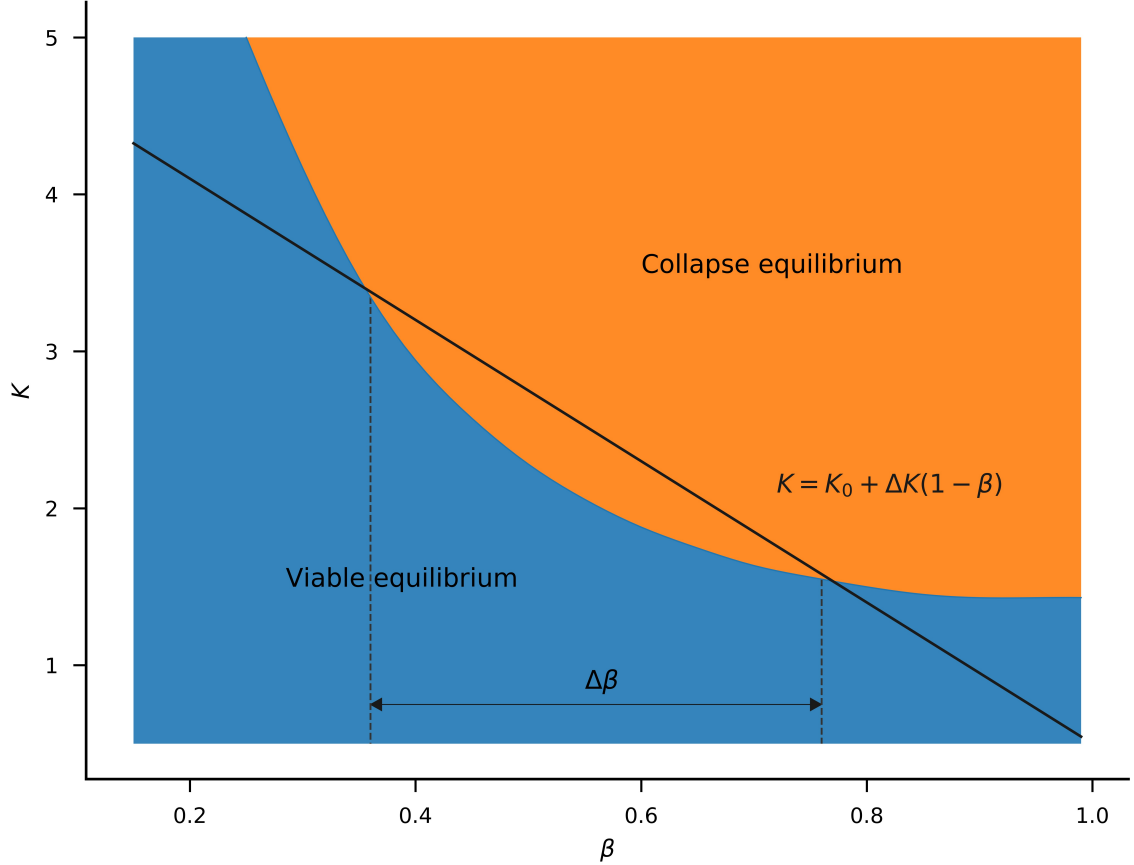


Figure 8: Long-term system’s behaviour in the two-dimensional land use strategy space. Land use strategy is defined by the couple intensification β and conversion effort K . The blue region corresponds to the set of strategies leading to a viable socio-ecological equilibrium, and the orange region corresponds with the ones leading to socio-ecological collapse. The solid black line depicts the linear trade-off between intensification and conversion effort that we were previously assuming. The border between the two regions is non-linear, which explains the existence of the collapse range $\Delta\beta$.

range $\Delta\beta$ we previously described. A linear decrease in the conversion effort in relation to agricultural intensity (solid black line in the graph) makes it unavoidable to cross the border between the viable and collapse equilibria. This result shows the non-triviality of designing sustainable land use strategies.

4. Discussion

We investigated the impact of different land use strategies on the long-term sustainability of an agriculturally based human society. We considered agricultural land use planning along two strategical dimensions: expansion and intensification. Inspired by the land sparing-sharing debate we introduced in our model a

369 land use strategy parameter (β) that controls the trade-off between agricultural intensity and land conver-
370 sion effort, thus reducing the two dimensions of the strategy to a single parameter. We then studied the
371 behaviour of the coupled socio-ecological system across a continuum of strategies ranging from low agricul-
372 tural intensity and high conversion effort ($\beta = 0$) to high agricultural intensity and low conversion effort
373 ($\beta = 1$). We find that agricultural intensification leads to irreversible land degradation and population
374 collapse when not accompanied by a strong reduction of the land conversion effort. Furthermore, the rela-
375 tionship between agricultural intensification and conversion effort is not straightforward. Uninformed land
376 use planning can drive the socio-ecological system to a critical transition that undermines sustainability and
377 leads to irreversible collapse.

378 Our model predicts that the most suitable strategy to ally a large population and nature conservation
379 is to practice extremely intense agriculture and minimise the conversion of natural land to agriculture.
380 Alternatively, low agricultural intensification and high conversion efforts (i.e., extensive agriculture) lead to
381 preserved landscapes, but with significantly lower population sizes. Therefore, for our current population
382 the model seems to support the advocates of the sparing hypothesis. However, the existence of a collapse
383 region in the middle of the strategy spectrum suggests that it is not simply a question of sparing.

384 Gradual increases in intensification eventually cause the adoption of land use strategies within the collapse
385 region of our model. Therefore, if technological development in the agriculture sector stagnates, there is a
386 greater risk of getting trapped in the collapse region. Furthermore, technology is not a panacea for all socio-
387 ecological issues, as technology can lead to greater environmental degradation through what is known as ‘the
388 Jevons paradox’ (Alcott et al., 2012). With reference to this paradox, increasing agricultural production
389 efficiency has the potential to increase demand which ultimately degrades more land and drives the system
390 towards collapse. Socio-ecological collapse can be avoided in the model by changing land use strategies
391 quickly. Whether the levels of intensification required to overcome the collapse region are attainable or how
392 to accurately measure intensity to know where we are on the spectrum are unclear.

393 It is evident that simultaneous increases in both agricultural expansion and intensification cannot be
394 viable in the long term. However, current practices favour both intensification and expansion. The last
395 century’s Green Revolution is a recent and striking example of how agricultural intensification can increase
396 yields and food security. However, this was also the period of fastest population growth in history, which fur-
397 ther increased demand and motivated agricultural intensification and expansion. The societal and economic
398 benefits of agricultural intensification that ensure food security are undeniable. However, agricultural inten-
399 sification and expansion have caused several environmental problems such as soil erosion, nutrient runoff,
400 water pollution or habitat destruction and fragmentation. It has also caused profound societal transfor-
401 mations, in particular the disappearance of small agricultural producers, that fuel urbanisation and change
402 consumption patterns.

403 Agricultural intensification is considered a plausible explanation of past societal collapses, such as in the

404 Roman or Mayan examples ([Diamond, 2005](#)). Population collapse emerges from our model as a consequence
405 of large-scale land degradation, which impairs agricultural production in two ways: first, the deterioration
406 of the landscape critically depletes the stock of natural land, which is the primary source for conversion to
407 agriculture; second, natural land depletion reduces the provision of ecosystem services to existing agricultural
408 areas. Since land degradation can critically decrease agricultural production, it seems ironic that agricultural
409 land use is nowadays considered to be among the major causes of land degradation. This dangerous feedback
410 loop poses a serious threat to sustainability as agricultural expansion and/or intensification to cope with
411 reduced production can further reduce production in the long term by accentuating land degradation.
412 Thus, we stress the major importance that agricultural land use planning has on the sustainability of socio-
413 ecological systems.

414 Furthermore, our results also highlight the importance of socio-ecologically informed agricultural land
415 use policies to achieve sustainability. By removing the trade-off between land conversion and agricultural
416 intensity in our model, we showed that sustainable land use strategies can be obtained for the entire spectrum
417 of intensification we consider. However, the frontier between unsustainable and sustainable land use is far
418 from trivial. The existence of unsustainable land use strategies comes from a bad evaluation of the needed
419 reduction of land conversion for a given increase on intensification. As our model is a simplification of
420 real population dynamics and land use planning, we do not claim that the frontier between sustainable and
421 collapse paths is as we describe. However, we show that it is very likely for this frontier to be far from trivial,
422 hence making it easy for uninformed land use planning to fail. Much the same way that science-based policies
423 are considered crucial for climate change mitigation or human population sustainability ([Motesharrei et al.,
424 2016](#)), our work stresses the need to incorporate informed agricultural land use planning into the policy
425 agenda to achieve sustainability.

426 Globally, at an aggregated scale, it could be argued that we have not yet reached a critical point or
427 planetary boundary ([Steffen et al., 2015](#)), however at a local scale this might not be true. Agricultural
428 land use is not spatially homogeneous and agricultural production is often strongly localised: the Pampas
429 in South America and the Great Plains in the United States are two examples. Moreover, these major
430 agricultural regions are mostly expansive and intensive monocultures. Hence, at a regional scale there is
431 neither sparing nor sharing, rather extensive exploitation, which makes the landscape highly susceptible to
432 irreversible ecological degradation. In South American grasslands and forests, these practices have already
433 caused major environmental degradation ([Guerschman and Paruelo, 2005](#); [Fearnside, 2001](#); [Pengue, 2005](#)), in
434 addition to societal problems ([Pengue, 2005](#)). Agricultural expansion has already destroyed most of Brazil's
435 Atlantic Forest ([Centre for Applied Biodiversity Science, 2003](#); [Ribeiro et al., 2011](#)), and now it is advancing
436 over the Amazon Forest, one of the world's biodiversity hotspots ([Soares-Filho et al., 2006](#); [Davidson et al.,
437 2012](#); [Lovejoy and Nobre, 2018](#); [Nepstad et al., 2008](#)). The variations in land management practices highlight
438 the interest of considering a continuous range of both agricultural expansion and intensification rather than

439 discrete levels of intensity (Roman et al., 2018) in modelling studies. The possibility of local collapses poses
440 a threat to global sustainability, as it is unclear how these local collapses can propagate over the world, via
441 environmental degradation but also via changes in trade or migration networks.

442 Our model is a simplified representation of agricultural practices, human demography and social struc-
443 ture, which allows us to explore a range of scenarios and understand the behaviours within the model, but
444 it also omits details of our complex society. For example, it does not account for social and economic in-
445 equalities, which have been recognized as important drivers of socio-ecological dynamics (Motesharrei et al.,
446 2016). Social and economic inequalities push the system away from a sustainable human-nature equilibrium
447 (Cumming and von Cramon-Taubadel, 2018), thus would likely have an amplifying effect on the results. Ad-
448 ditionally, the logistic model we use to describe human population dynamics is heuristic and does not reflect
449 the actual mechanisms responsible for variations in human fertility and mortality (Mote et al., 2020). Lastly,
450 we have assumed that humans cannot adapt to environmental degradation by changing land use strategies
451 or fertility and consumption behaviours over time. This is a major limitation, as adaptive strategies could
452 potentially prevent the predicted population collapse. However, these simplifications do not reduce the per-
453 tinence of our results, as the current trends have the potential to cause a collapse, if habits go unchanged.
454 Moreover, if humans succeed, through changes in cultural patterns, to avoid a drastic population reduction,
455 it is very likely that the changes will be dramatic and involve, for example, a complete socio-economical
456 restructuring (Cumming and Peterson, 2017). Hence, our results highlight that our current socio-ecological
457 system might be heading towards dramatic changes, even though it is hard to predict the form they will
458 take.

459 5. Conclusions

460 By exploring a continuum of land use strategies, our work differentiates from previous models of coupled
461 human-land dynamics and shows the importance of quantifying agricultural expansion and intensification
462 levels to assess sustainable land use strategies. We modelled agricultural land use planning along two
463 dimensions: expansion, given by the population’s conversion effort, and intensification. Expansion and
464 intensification can act in synergy to increase landscape degradation, but there are also trade-offs between
465 them. Agricultural expansion increases the stock of potential degraded land, while agricultural intensification
466 can both speed and deepen agricultural land’s degradation.

467 Our results show how increasing agricultural intensification leads to socio-ecological collapse when there
468 is an insufficient reduction of the land conversion effort. Agricultural intensification increases agricultural
469 production, hence human population size, if consumption levels are kept equal. Population growth feeds
470 back on the landscape’s composition by further accelerating land conversion. Eventually, land degradation
471 reduces resource production and causes the population to overshoot its carrying capacity and ultimately
472 decline.

473 It could be argued that technological development has the potential to stave off collapse, however the
474 impact of new technologies on the environment is ambiguous. Technology has the potential to increase
475 production efficiency, but could also further decouple food production from nature by replacing ecosystem
476 services with synthetic inputs. The cure-all technology argument neglects feedbacks between technology
477 and human behaviour, as well as its underlying dependence on the environment. Future work will put a
478 greater focus on the links between changes in technology and behaviour and its impact on socio-ecological
479 dynamics.

480 Our model illustrates a potential mechanism that may explain the decline of past societies but also a
481 possible future collapse. As the global human population is projected to keep growing in the coming decades
482 adapted agriculture management will become more important and reduce the potential risks of future socio-
483 ecological collapse. Our model points to agriculture intensification as a possible solution, however it is
484 imperative that this is not in combination with expansion. However, we also stress that determining the
485 limits to agricultural expansion that are necessary to achieve sustainability is not a trivial task. Hence
486 precautionary land use planning should be accompanied by changes in social norms, such as a reduction of
487 consumption to increase the likelihood of a sustainable future.

488 By modelling the bi-directional feedbacks between human demography and land use, we have shown
489 how misguided or uninformed agricultural land use planning can lead a socio-ecological system to collapse.
490 This stresses the importance of informed land use planning to achieve sustainability. Through evidence
491 based policy design, humans have the tools to modify precarious land use patterns and reduce the impact
492 of agriculture on the environment, setting our socio-ecological system on a more sustainable path.

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499 **Code accesibility**

500 All the open-source software to reproduce our analysis and the associated plots is available at <https://doi.org/10.5281/zenodo.3988256>.
501

502 **References**

503 Teja Tschardtke, Yann Clough, Thomas C. Wanger, Louise Jackson, Iris Motzke, Ivette Perfecto, John Vandermeer, and
504 Anthony Whitbread. Global food security, biodiversity conservation and the future of agricultural intensification. *Biological*
505 *Conservation*, 151(1):53–59, July 2012. ISSN 0006-3207. doi: 10.1016/j.biocon.2012.01.068.

- 506 John Bongaarts. IPBES, 2019. Summary for policymakers of the global assessment report on biodiversity and ecosystem services
507 of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. *Population and Development*
508 *Review*, 45(3):680–681, 2019. ISSN 1728-4457. doi: 10.1111/padr.12283.
- 509 C. Corvalán, Simon Hales, A. J. McMichael, Millennium Ecosystem Assessment (Program), and World Health Organization,
510 editors. *Ecosystems and Human Well-Being: Health Synthesis*. Millennium Ecosystem Assessment. World Health Organi-
511 zation, Geneva, Switzerland, 2005. ISBN 978-92-4-156309-3.
- 512 Andrew P. Jacobson, Jason Riggio, Alexander M. Tait, and Jonathan E. M. Baillie. Global areas of low human impact
513 (‘Low Impact Areas’) and fragmentation of the natural world. *Sci Rep*, 9(1):1–13, October 2019. ISSN 2045-2322. doi:
514 10.1038/s41598-019-50558-6.
- 515 J. Nowosad and T. F. Stepinski. Stochastic, Empirically Informed Model of Landscape Dynamics and Its Application to Defor-
516 estation Scenarios. *Geophysical Research Letters*, 46(23):13845–13852, 2019. ISSN 1944-8007. doi: 10.1029/2019GL085952.
- 517 Matthew G. E. Mitchell, Elena M. Bennett, and Andrew Gonzalez. Forest fragments modulate the provision of multiple
518 ecosystem services. *Journal of Applied Ecology*, 51(4):909–918, August 2014. ISSN 00218901. doi: 10.1111/1365-2664.12241.
- 519 Alison G. Power. Ecosystem services and agriculture: Tradeoffs and synergies. *Philosophical Transactions of the Royal Society*
520 *B: Biological Sciences*, 365(1554):2959–2971, September 2010. doi: 10.1098/rstb.2010.0143.
- 521 Matthew G. E. Mitchell, Elena M. Bennett, and Andrew Gonzalez. Linking Landscape Connectivity and Ecosystem Service
522 Provision: Current Knowledge and Research Gaps. *Ecosystems*, 16(5):894–908, August 2013. ISSN 1432-9840, 1435-0629.
523 doi: 10.1007/s10021-013-9647-2.
- 524 Victor Cazalis, Michel Loreau, and Kirsten Henderson. Do we have to choose between feeding the human population and
525 conserving nature? Modelling the global dependence of people on ecosystem services. *Science of The Total Environment*,
526 634:1463–1474, September 2018. ISSN 0048-9697. doi: 10.1016/j.scitotenv.2018.03.360.
- 527 Leon C. Braat and Rudolf de Groot. The ecosystem services agenda: bridging the worlds of natural science and economics,
528 conservation and development, and public and private policy. *Ecosystem Services*, 1(1):4–15, July 2012. ISSN 2212-0416.
529 doi: 10.1016/j.ecoser.2012.07.011.
- 530 Sean S. Downey, W. Randall Haas, and Stephen J. Shennan. European Neolithic societies showed early warning signals of
531 population collapse. *Proceedings of the National Academy of Sciences*, 113(35):9751–9756, August 2016. ISSN 0027-8424,
532 1091-6490. doi: 10.1073/pnas.1602504113.
- 533 Ian Kuijt and Nigel Goring-Morris. Foraging, Farming, and Social Complexity in the Pre-Pottery Neolithic of the Southern
534 Levant: A Review and Synthesis. *Journal of World Prehistory*, 16(4):361–440, December 2002. ISSN 1573-7802. doi:
535 10.1023/A:1022973114090.
- 536 Ruth S. DeFries, Thomas Rudel, Maria Uriarte, and Matthew Hansen. Deforestation driven by urban population growth and
537 agricultural trade in the twenty-first century. *Nature Geosci*, 3(3):178–181, March 2010. ISSN 1752-0894, 1752-0908. doi:
538 10.1038/ngeo756.
- 539 Amy Lilienfeld and Mette Asmild. Estimation of excess water use in irrigated agriculture: A Data Envelopment Analysis
540 approach. *Agricultural Water Management*, 94(1):73–82, December 2007. ISSN 0378-3774. doi: 10.1016/j.agwat.2007.08.005.
- 541 Maria A. Tsiafouli, Elisa Thébault, Stefanos P. Sgardelis, Peter C. de Ruiter, Wim H. van der Putten, Klaus Birkhofer,
542 Lia Hemerik, Franciska T. de Vries, Richard D. Bardgett, Mark Vincent Brady, Lisa Bjornlund, Helene Bracht Jørgensen,
543 Sören Christensen, Tina D’ Hertefeldt, Stefan Hotes, W. H. Gera Hol, Jan Frouz, Mira Liiri, Simon R. Mortimer, Heikki
544 Setälä, Joseph Tzanopoulos, Karoline Uteseny, Václav Pižl, Josef Stary, Volkmar Wolters, and Katarina Hedlund. Intensive
545 agriculture reduces soil biodiversity across Europe. *Global Change Biology*, 21(2):973–985, 2015. ISSN 1365-2486. doi:
546 10.1111/gcb.12752.
- 547 John N. Quinton, Gerard Govers, Kristof Van Oost, and Richard D. Bardgett. The impact of agricultural soil erosion on
548 biogeochemical cycling. *Nature Geosci*, 3(5):311–314, May 2010. ISSN 1752-0908. doi: 10.1038/ngeo838.
- 549 Eric A. Davidson, Alessandro C. de Araújo, Paulo Artaxo, Jennifer K. Balch, I. Foster Brown, Mercedes M. C. Bustamante,
550 Michael T. Coe, Ruth S. DeFries, Michael Keller, Marcos Longo, J. William Munger, Wilfrid Schroeder, Britaldo S. Soares-
551 Filho, Carlos M. Souza, and Steven C. Wofsy. The Amazon basin in transition. *Nature*, 481(7381):321–328, January 2012.
552 ISSN 1476-4687. doi: 10.1038/nature10717.
- 553 Graeme S. Cumming and Garry D. Peterson. Unifying Research on Social–Ecological Resilience and Collapse. *Trends in*
554 *Ecology & Evolution*, 32(9):695–713, September 2017. ISSN 0169-5347. doi: 10.1016/j.tree.2017.06.014.
- 555 Joseph Tainter. *The Collapse of Complex Societies*. Cambridge University Press, 1988. ISBN 978-0-521-38673-9.
- 556 Jared M. Diamond. *Collapse: How Societies Choose to Fail or Succeed*. New York: Viking, 2005.
- 557 Sabin Roman, Erika Palmer, and Markus Brede. The Dynamics of Human–Environment Interactions in the Collapse of the
558 Classic Maya. *Ecological Economics*, 146:312–324, April 2018. ISSN 0921-8009. doi: 10.1016/j.ecolecon.2017.11.007.
- 559 Scott Barrett, Aisha Dasgupta, Partha Dasgupta, W. Neil Adger, John Anderies, Jeroen van den Bergh, Caroline Bledsoe,
560 John Bongaarts, Stephen Carpenter, F. Stuart Chapin, Anne-Sophie Crépin, Gretchen Daily, Paul Ehrlich, Carl Folke, Nils
561 Kautsky, Eric F. Lambin, Simon A. Levin, Karl-Göran Mäler, Rosamond Naylor, Karine Nyborg, Stephen Polasky, Marten
562 Scheffer, Jason Shogren, Peter Sögaard Jørgensen, Brian Walker, and James Wilen. Social dimensions of fertility behavior
563 and consumption patterns in the Anthropocene. *Proceedings of the National Academy of Sciences*, 117(12):6300–6307,
564 March 2020. ISSN 0027-8424, 1091-6490. doi: 10.1073/pnas.1909857117.
- 565 Safa Motesharrei, Jorge Rivas, and Eugenia Kalnay. Human and nature dynamics (HANDY): Modeling inequality and use of
566 resources in the collapse or sustainability of societies. *Ecological Economics*, 101:90–102, May 2014. ISSN 0921-8009. doi:
567 10.1016/j.ecolecon.2014.02.014.
- 568 Jeffrey Kentor. The Long Term Effects of Globalization on Income Inequality, Population Growth, and Economic Development.
569 *Soc Probl*, 48(4):435–455, November 2001. ISSN 0037-7791. doi: 10.1525/sp.2001.48.4.435.
- 570 Gerardo Ceballos, Paul R. Ehrlich, and Rodolfo Dirzo. Biological annihilation via the ongoing sixth mass extinction signaled

by vertebrate population losses and declines. *Proc Natl Acad Sci USA*, 114(30):E6089–E6096, July 2017. ISSN 0027-8424, 1091-6490. doi: 10.1073/pnas.1704949114.

Kirsten Henderson and Michel Loreau. How ecological feedbacks between human population and land cover influence sustainability. *PLOS Computational Biology*, 14(8):e1006389, August 2018. ISSN 1553-7358. doi: 10.1371/journal.pcbi.1006389.

Kirsten Henderson and Michel Loreau. An ecological theory of changing human population dynamics. *People and Nature*, 1(1):31–43, 2019. ISSN 2575-8314. doi: 10.1002/pan3.8.

A. S. Lafuite and M. Loreau. Time-delayed biodiversity feedbacks and the sustainability of social-ecological systems. *Ecological Modelling*, 351:96–108, May 2017. ISSN 0304-3800. doi: 10.1016/j.ecolmodel.2017.02.022.

A.-S. Lafuite, C. de Mazancourt, and M. Loreau. Delayed behavioural shifts undermine the sustainability of social-ecological systems. *Proceedings of the Royal Society B: Biological Sciences*, 284(1868):20171192, December 2017. ISSN 0962-8452, 1471-2954. doi: 10.1098/rspb.2017.1192.

A. S. Lafuite, G. Denise, and M. Loreau. Sustainable Land-use Management Under Biodiversity Lag Effects. *Ecological Economics*, 154:272–281, December 2018. ISSN 0921-8009. doi: 10.1016/j.ecolecon.2018.08.003.

Ricardo Grau, Tobias Kuemmerle, and Leandro Macchi. Beyond ‘land sparing versus land sharing’: Environmental heterogeneity, globalization and the balance between agricultural production and nature conservation. *Current Opinion in Environmental Sustainability*, 5(5):477–483, October 2013. ISSN 18773435. doi: 10.1016/j.cosust.2013.06.001.

Ben Phalan, Malvika Onial, Andrew Balmford, and Rhys E. Green. Reconciling Food Production and Biodiversity Conservation: Land Sharing and Land Sparing Compared. *Science*, 333(6047):1289–1291, September 2011a. ISSN 0036-8075, 1095-9203. doi: 10.1126/science.1208742.

Ben Phalan, Andrew Balmford, Rhys E. Green, and Jörn P.W. Scharlemann. Minimising the harm to biodiversity of producing more food globally. *Food Policy*, 36:S62–S71, January 2011b. ISSN 03069192. doi: 10.1016/j.foodpol.2010.11.008.

Ben Balmford, Rhys E. Green, Malvika Onial, Ben Phalan, and Andrew Balmford. How imperfect can land sparing be before land sharing is more favourable for wild species? *Journal of Applied Ecology*, 56(1):73–84, January 2019. ISSN 00218901. doi: 10.1111/1365-2664.13282.

I. Perfecto and J. Vandermeer. The agroecological matrix as alternative to the land-sparing/agriculture intensification model. *Proceedings of the National Academy of Sciences*, 107(13):5786–5791, March 2010. ISSN 0027-8424, 1091-6490. doi: 10.1073/pnas.0905455107.

Benjamin T. Phalan. What Have We Learned from the Land Sparing-sharing Model? *Sustainability*, 10(6):1760, June 2018. doi: 10.3390/su10061760.

Philip M. Fearnside. Soybean cultivation as a threat to the environment in Brazil. *Environmental Conservation*, 28(1):23–38, March 2001. ISSN 1469-4387, 0376-8929. doi: 10.1017/S0376892901000030.

Walter A. Pengue. Transgenic Crops in Argentina: The Ecological and Social Debt. *Bulletin of Science, Technology & Society*, 25(4):314–322, August 2005. ISSN 0270-4676. doi: 10.1177/0270467605277290.

Carlos Reboratti. Un mar de soja: La nueva agricultura en Argentina y sus consecuencias. *Revista de geografía Norte Grande*, (45):63–76, May 2010. ISSN 0718-3402. doi: 10.4067/S0718-34022010000100005.

Britaldo Silveira Soares-Filho, Daniel Curtis Nepstad, Lisa M. Curran, Gustavo Coutinho Cerqueira, Ricardo Alexandrino Garcia, Claudia Azevedo Ramos, Eliane Voll, Alice McDonald, Paul Lefebvre, and Peter Schlesinger. Modelling conservation in the Amazon basin. *Nature*, 440(7083):520–523, March 2006. ISSN 1476-4687. doi: 10.1038/nature04389.

Viki A. Cramer, Richard J. Hobbs, and Rachel J. Standish. What’s new about old fields? Land abandonment and ecosystem assembly. *Trends in Ecology & Evolution*, 23(2):104–112, February 2008. ISSN 0169-5347. doi: 10.1016/j.tree.2007.10.005.

Lander Baeten, Darline Velghe, Margot Vanhellefont, Pieter De Frenne, Martin Hermy, and Kris Verheyen. Early Trajectories of Spontaneous Vegetation Recovery after Intensive Agricultural Land Use. *Restoration Ecology*, 18:379–386, March 2010. ISSN 1526-100X. doi: 10.1111/j.1526-100X.2009.00627.x.

Yuval R. Zelnik, Hannes Uecker, Ulrike Feudel, and Ehud Meron. Desertification by front propagation? *Journal of Theoretical Biology*, 418:27–35, April 2017. ISSN 0022-5193. doi: 10.1016/j.jtbi.2017.01.029.

Yuval R. Zelnik and Ehud Meron. Regime shifts by front dynamics. *Ecological Indicators*, 94:544–552, November 2018. ISSN 1470-160X. doi: 10.1016/j.ecolind.2017.10.068.

J. Cohen. Population growth and earth’s human carrying capacity. *Science*, 269(5222):341–346, July 1995. ISSN 0036-8075, 1095-9203. doi: 10.1126/science.7618100.

Russell Hopfenberg. Human Carrying Capacity Is Determined by Food Availability. *Population and Environment*, 25(2):109–117, November 2003. ISSN 1573-7810. doi: 10.1023/B:POEN.0000015560.69479.c1.

Václav Fanta, Miroslav Šálek, Jan Zouhar, Petr Sklenicka, and David Storch. Equilibrium dynamics of European pre-industrial populations: The evidence of carrying capacity in human agricultural societies. *Proceedings of the Royal Society B: Biological Sciences*, 285(1871):20172500, January 2018. doi: 10.1098/rspb.2017.2500.

Safa Mote, Jorge Rivas, and Eugenia Kalnay. A Novel Approach to Carrying Capacity: From a priori Prescription to a posteriori Derivation Based on Underlying Mechanisms and Dynamics. *Annu. Rev. Earth Planet. Sci.*, 48(1):657–683, May 2020. ISSN 0084-6597. doi: 10.1146/annurev-earth-053018-060428.

Board on Environmental Change and Society, Committee on Population, Division of Behavioral and Social Sciences and Education, Board on Life Sciences, Division on Earth and Life Studies, and National Research Council. *Can Earth’s and Society’s Systems Meet the Needs of 10 Billion People? Summary of a Workshop*. National Academies Press (US), Washington (DC), 2014. ISBN 978-0-309-30634-8.

Amy Goldberg, Alexis M. Mychajliw, and Elizabeth A. Hadly. Post-invasion demography of prehistoric humans in South America. *Nature*, 532(7598):232–235, April 2016. ISSN 1476-4687. doi: 10.1038/nature17176.

Samir Suweis, Andrea Rinaldo, Amos Maritan, and Paolo D’Odorico. Water-controlled wealth of nations. *Proceedings of the National Academy of Sciences*, 110(11):4230–4233, March 2013. ISSN 0027-8424, 1091-6490. doi: 10.1073/pnas.1222452110.

- 636 Matthew G. E. Mitchell, Andrés F. Suarez-Castro, Maria Martinez-Harms, Martine Maron, Clive McAlpine, Kevin J. Gaston,
637 Kasper Johansen, and Jonathan R. Rhodes. Reframing landscape fragmentation's effects on ecosystem services. *Trends in*
638 *Ecology & Evolution*, 30(4):190–198, April 2015. ISSN 0169-5347. doi: 10.1016/j.tree.2015.01.011.
- 639 Blake Alcott, Mario Giampietro, Kozo Mayumi, and John Polimeni. *The Jevons Paradox and the Myth of Resource Efficiency*
640 *Improvements*. Routledge, April 2012. ISBN 978-1-136-55336-3.
- 641 Safa Motesharrei, Jorge Rivas, Eugenia Kalnay, Ghassem R. Asrar, Antonio J. Busalacchi, Robert F. Cahalan, Mark A. Cane,
642 Rita R. Colwell, Kuishuang Feng, Rachel S. Franklin, Klaus Hubacek, Fernando Miralles-Wilhelm, Takemasa Miyoshi,
643 Matthias Ruth, Roald Sagdeev, Adel Shirmohammadi, Jagadish Shukla, Jelena Srebric, Victor M. Yakovenko, and Ning
644 Zeng. Modeling Sustainability: Population, Inequality, Consumption, and Bidirectional Coupling of the Earth and Human
645 Systems. *National Science Review*, page nww081, December 2016. ISSN 2095-5138, 2053-714X. doi: 10.1093/nsr/nww081.
- 646 Will Steffen, Katherine Richardson, Johan Rockström, Sarah E. Cornell, Ingo Fetzer, Elena M. Bennett, ReINETTE Biggs,
647 Stephen R. Carpenter, Wim de Vries, Cynthia A. de Wit, Carl Folke, Dieter Gerten, Jens Heinke, Georgina M. Mace,
648 Linn M. Persson, Veerabhadran Ramanathan, Belinda Reyers, and Sverker Sörlin. Planetary boundaries: Guiding human
649 development on a changing planet. *Science*, 347(6223), February 2015. ISSN 0036-8075, 1095-9203. doi: 10.1126/science.
650 1259855.
- 651 Juan Pablo Guerschman and José María Paruelo. Agricultural impacts on ecosystem functioning in temperate areas of North
652 and South America. *Global and Planetary Change*, 47(2):170–180, July 2005. ISSN 0921-8181. doi: 10.1016/j.gloplacha.
653 2004.10.021.
- 654 Centre for Applied Biodiversity Science. *The Atlantic Forest of South America: Biodiversity Status, Threats, and Outlook*.
655 Island Press, 2003. ISBN 978-1-55963-989-7.
- 656 Milton Cezar Ribeiro, Alexandre Camargo Martensen, Jean Paul Metzger, Marcelo Tabarelli, Fábio Scarano, and Marie-Josée
657 Fortin. The Brazilian Atlantic Forest: A Shrinking Biodiversity Hotspot. In Frank E. Zachos and Jan Christian Habel,
658 editors, *Biodiversity Hotspots: Distribution and Protection of Conservation Priority Areas*, pages 405–434. Springer, Berlin,
659 Heidelberg, 2011. ISBN 978-3-642-20992-5. doi: 10.1007/978-3-642-20992-5.21.
- 660 Thomas E. Lovejoy and Carlos Nobre. Amazon Tipping Point. *Science Advances*, 4(2):eaat2340, February 2018. ISSN
661 2375-2548. doi: 10.1126/sciadv.aat2340.
- 662 Daniel C Nepstad, Claudia M Stickler, Britaldo Soares Filho, and Frank Merry. Interactions among Amazon land use, forests
663 and climate: Prospects for a near-term forest tipping point. *Philosophical Transactions of the Royal Society B: Biological*
664 *Sciences*, 363(1498):1737–1746, May 2008. doi: 10.1098/rstb.2007.0036.
- 665 Graeme S. Cumming and Stephan von Cramon-Taubadel. Linking economic growth pathways and environmental sustain-
666 ability by understanding development as alternate social–ecological regimes. *Proc Natl Acad Sci USA*, 115(38):9533–9538,
667 September 2018. ISSN 0027-8424, 1091-6490. doi: 10.1073/pnas.1807026115.