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Biodiversity Response to Human-Caused Habitat Destruction in Different Eras

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Abstract: A non-autonomous multi-time-scale n-population dynamical model has been introduced to study how biodiversity responds to human-caused habitat destruction in different historical eras. The simulated results show that under continuous habitat destruction at different time scales such as ten-thousand time scale in the primitive Agriculture Era, millenary time scale in the Agricultural Revolution Era and Industrial Era, species in different metacommunities will go extinct from the best to the poorest before complete destruction. The survival species will go extinct collectively when habitat is destroyed completely. If continuous habitat destruction only last a short period of time, no species will go extinct. Instantaneous destruction brought by human activities such as in the rapid urban expansion period has long-term influences on the abundances of all species, i.e., the time debt for species to respond to habitat destruction would be very long. When the amount of habitat destruction exceeds the threshold value, it will result in 'extinction debts'.

Key words: Biodiversity, era, continuous destruction, instantaneous destruction, multi-time-scale

Introduction

Planning and decision-making can be improved by access to reliable forecasts of ecosystem state. Availability of new models, together with progress in computation and statistics, will increase our ability to forecast or simulate the ecosystem change (Clark *et al.*, 2001). Human-caused habitat destruction declines biodiversity by destroying species, disrupting community interactions and interrupting evolutionary processes (Pimm and Raven, 2002; Solé and Alonso, 2004). Various researchers have put forward different numerical models to simulate and predict the effects of habitat destruction. Levins (1969), Hanski (1991), Nee and May (1992), Tilman *et al.* (1994, 1997), Neuhauser (1998) and Lin (2003) simulated the effects of habitat destruction on species abundances with different population dynamical models. Melian and Bascompte (2002) and Murdoch *et al.* (2002) analyzed how metacommunity structure affected species response to habitat loss. Despite these, the bulk of these studies have a common assumption that the amount of habitat destruction is a constant, i.e., they focus on instantaneous destruction. Although Tilman *et al.* (1997) have a primary study on the effects of continuous destruction on species extinction, they have not explored the multi-time-scale characteristics of continuous destruction. In fact human-caused habitat destructions are different at various time scales, such as ten-thousand-year time scale in the Primitive-Agriculture Epoch, millenary scale in the Agricultural Revolution and Industrial Epoch and year time scale in the city and town

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expansion period (Niu *et al.*, 1993). So the scientific problems have been raised that how human activities in different historical epochs affect biodiversity or how biodiversity responds to human activities in different eras. A non-autonomous n-population dynamical model is introduced in the second part. Some simulation results of biodiversity disturbed by human activities in different eras are given in the third part.

Materials and Methods

We have noticed that the model applied to simulate the species extinction by Tilman *et al.* (1994, 1997), Loehle and Li (1996), Neuhauser (1998) and Lin (2003) is an autonomous one:

$$\frac{dp_i}{dt} = c_i p_i (1 - D - \sum_{j=1}^i p_j) - m_i p_i - \sum_{j=1}^{i-1} c_j p_j p_i \tag{1}$$

Where, *i* refers to the *i*th species in the competitive hierarchy, *j* indexes the other species competing with species *i*; *p_i* is the proportion of patches occupied by species *i* (proportion abundance of species *i*); *c_i* is species-specific colonization rate; *m_i* is the mortality (or local extinction) rates and *D* is the proportion of sites destroyed permanently which is a given constant and does not change with time. At the same time, superior competitors can invade the sites occupied by the inferior competitors, but inferior competitors can not invade those of the superiors and the patches permanently destroyed can never be occupied. The first term on the right hand side of Eq. 1 thus describes the colonization of inhabitable sites which are either vacant or occupied by an inferior species, the second term describes the mortality of species *i* and the third term describes the invasion of superior competitors into patches occupied by species *i* which results in the death of species *i* upon invasion. Those three factors lead to the changes of the proportions of sites occupied by all species in community.

Because the amount of habitat destroyed by human activities are different in different eras such as in the Agriculture Revolution and Industrial Era and during different time of the same era (e.g., continuous habitat destruction, large scale exploitation on habitat), we introduce *H(t)* to represent the amount of human-caused habitat destruction at different time scales. Firstly, we introduce δ function to represent instantaneous destruction induced by most drastic human activities:

$$H(t) = D_0 \delta(t), \quad \delta(t) = \begin{cases} 1, & t = t_j \\ 0, & t \neq t_j \end{cases} \tag{2}$$

Where, *D₀* denotes the fraction of habitat destroyed by human activities permanently, *t* is the integral time (the time human acting on habitat) and *t_j* is the time when habitat is destroyed instantaneously.

To describe human-caused continuous destruction at different time scale during different periods in history, we introduce scale function *f(t/T)*, where, *T* denotes time scale, representing different time scales or different periods in history by giving different values such as ten-thousand, thousand, one hundred years and so forth and *t* is the integral time or the duration of human activities. The scale function *f(t/T)* can be linear or exponential to describe different kinds of human activities such as linear, nonlinear or exponential activities. Therefore, we use the following function to represent continuous destruction (linear, nonlinear and exponential).

$$H(t) = f(t/T), \quad t \leq T \tag{3}$$

For a primary study, we just consider $f(t/T)$ to be linear, that is,

$$H(t) = f(t/T) = t/T, \quad t \leq T \quad (4)$$

So we just study the responses of species diversity to continuous linear-destruction by human activities at different time scales.

Substitute Eq. (2) or (3) into Eq. (1), we extend Tilman's none time scale n-Population model to Multi-time-Scale n-population Competition Model as follows:

$$\frac{dp_i}{dt} = c_i p_i (1 - H(t) - \sum_{j=1}^i p_j) - m_i p_i - \sum_{j=1}^{i-1} c_j p_i p_j \quad (5)$$

Obviously, if $H(t) = D_0 \delta(t)$, $t_j =$ starting time and then Eq. 5 is simplified into Tilman's (1997), i.e., Eq. 1. Therefore, the model we have put forward is not only of multi-time scales, but also includes n-species competitive coexistence model.

We choose the hypotheses taken by Tilman *et al.* (1997). Hereby, m_i is the mortality of different species which is identical, p_i^0 is the occupation proportion of the species community on undestroyed habitat, c_i is the colonization rates and q denotes habitat occupancy of the best species in the metapopulation (representing different metapopulation structures). They meet the following relationship:

$$m_i = m, \quad p_i^0|_{D=0} = q(1-q)^{i-1}, \quad c_i = m/(1-q)^{2i-1} \quad (6)$$

For this case, the species abundances in an intact habitat are taken to be a geometrically decreasing function of competitive rank, i.e., the better competitors are assumed to be the more abundant species (Tilman *et al.*, 1997).

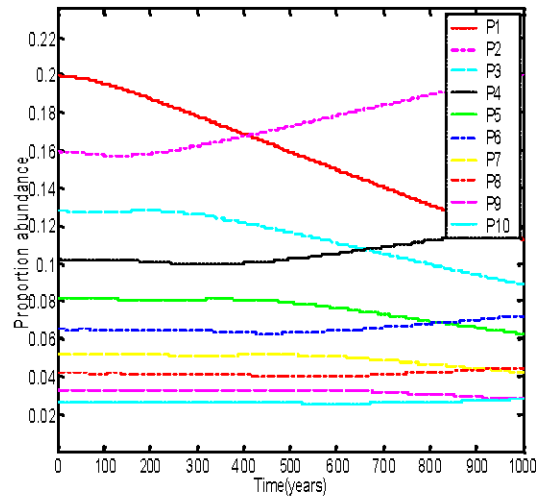
Results

Effects on Species Diversity of Human-caused Habitat Destruction in the Primitive Agriculture Era

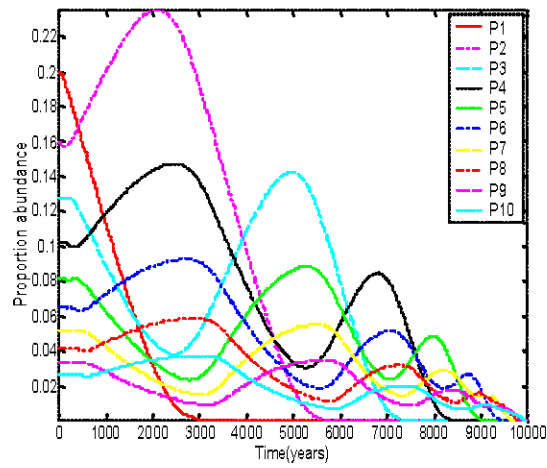
To begin with, let us study the effects on species diversity of human-caused habitat destruction in the Primitive Agriculture Era. The speed of destroying habitat is very low and the amount of resulting habitat destruction is limited due to the low productivity in the Primitive Agriculture Era. Therefore, we assume that human-caused habitat destruction is of a millenary time scale, i.e., $T = 10000$, $H(t) = f(t/T) = f(t/10000)$, $t \leq 10000$. Substituting Eq. 4 and 6 into model (5), the simulation results of effects on species diversity are shown in Fig. 1 with $m_i = m = 0.05$, $q = 0.2$ and $n = 10$ (with lots of simulations, we find when other parameters remain unchanged, the increase in the number of species will not change the results of the response of superior competitors to human-caused habitat destruction. For simplicity, we only simulate the former strongest 10 species).

As shown from Fig. 1 a and b, the simulations are based on the conditions that the duration of human activities is 1000 and 10000 years, respectively, i.e., $t = 1000$ (a) and $t = 10000$ (b).

As illustrated in Fig. 1a, Human destructive activities of millenary-year duration in the Primitive Agriculture Era do not lead to species extinction (in this paper, when species abundance is lower than 10^{-7} , we consider it to be extinct). Even and odd levels in the competitive hierarchy respond as groups: even number species decline, while odd number species decline firstly and then rise. As shown in Fig. 1b, if human primitive farming lasts for a period of ten thousands years, species would fluctuate

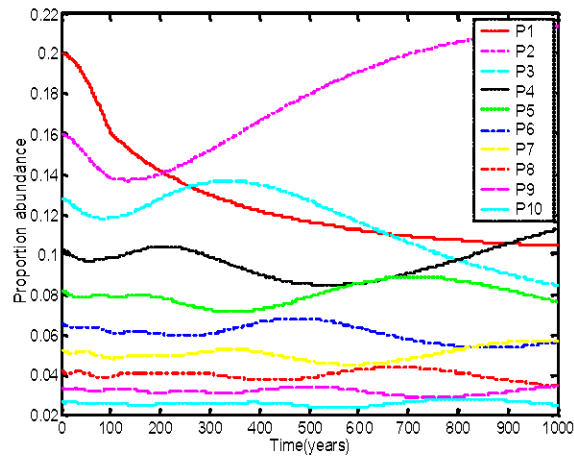


(a)

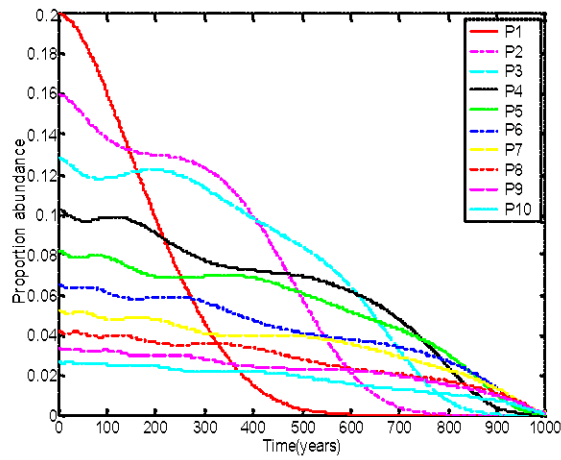


(b)

Fig. 1: Biodiversity response to human activities in the Primitive Farming Era with the parameters, $q = 0.2$, $m = 0.05 \text{ years}^{-1}$, $n = 10$. $n_1, n_2, n_3, n_4, n_5, n_6, n_7, n_8, n_9, n_{10}$ are, respectively species 1, 2, 3, 4, 5, 6, 7, 8, 9 and 10. (a) $t = 1000$ years, $H(t) = t/10000 = 0.1$, (b) $t = 10000$ years, $H(t) = t/10000 = 1$



(a)



(b)

Fig. 2: Biodiversity response to human activities in the Agriculture Revolution and Industry Era with the parameters $q = 0.2$, $m = 0.05 \text{ yr}^{-1}$, $n = 10$. $n_1, n_2, n_3, n_4, n_5, n_6, n_7, n_8, n_9, n_{10}$ are, respectively species 1, 2, 3, 4, 5, 6, 7, 8, 9, 10. (a) $t = 100$ years, $H(t) = t/1000 = 0.1$, (b) $t = 1000$ years, $H(t) = t/1000 = 1$

with amplitude decreasing and then decline to extinction at end. The order of species extinction ranks from the best to the poorest competitors before complete habitat destruction. The extinction time of the most competitive species is about 3276 years, while that of the poorest is about 9975 years.

Effects on Species Diversity of Human-caused Habitat Destruction in the Agriculture Revolution and Industrial Era

Because of the rapid development of productivities in the Agriculture Revolution and Industrial Era, the effect of human-caused habitat destruction on biodiversity is great. We consider habitat destruction to be at millenary scale in the Agriculture Revolution and Agriculture Era, i.e., $T = 1000$, $H(t) = f(t/T) = t/1000$, $t \leq 1000$. From model (4), Eq. 5-6, the simulation results are shown in Fig. 2 with the integral time, $t = 100$ (a) and $t = 1000$ (b), respectively, i.e., $H(t) = 0.1$ and $H(t) = 1$. The rest parameters are $m_1 = m = 0.05$, $q = 0.2$ and $n = 10$, respectively.

As shown in Fig. 2. If the duration of human activities is only 100 years in the Agriculture Revolution and Industrial Era (i.e., continuous habitat destruction ceases at 100 years), species will not be driven to extinction and relative abundance of each species in the community will take on irregular periodic fluctuation (Fig. 2a), which reveals some internal mechanisms of complexity of species diversity. As shown from Fig. 2b, under a continue and complete habitat destruction, species decline gradually to extinction with small fluctuations. Before complete habitat destruction, species 1, 2, 3, 4 will go extinct from the best to poorest. The survival species will go extinct collectively when habitat is destroyed completely, because the survival are better dispersers and more resistive to habitat destruction with time debts of species extinction being longer than the time for complete destruction.

Effects on Species Diversity of Human-caused Habitat Destruction in the Contemporary City Construction Era

In contemporary city construction era, human destructive activities on habitat is unprecedented and a certain proportion of habitat can be destroyed quickly in very short time, so we consider human-caused habitat destruction to be year time scale. That is:

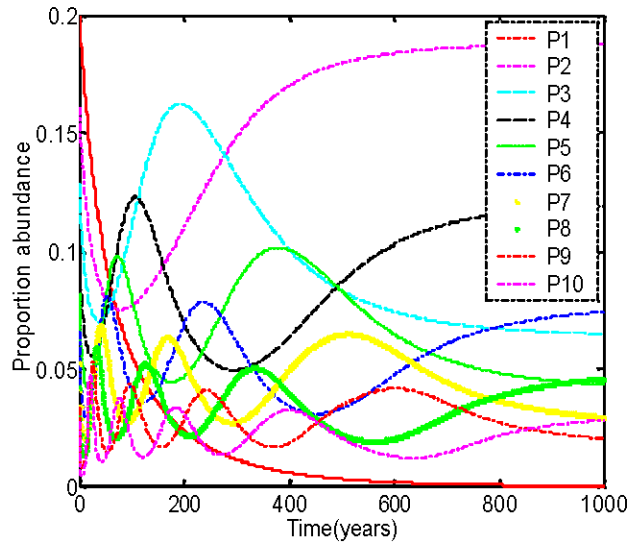
$$H(t) = D_0 \delta(t), \delta = \begin{cases} 1, t = t_0 \\ 0, t \neq t_0 \end{cases}$$

For such cases, the model is a very close approximation to Tilman's.

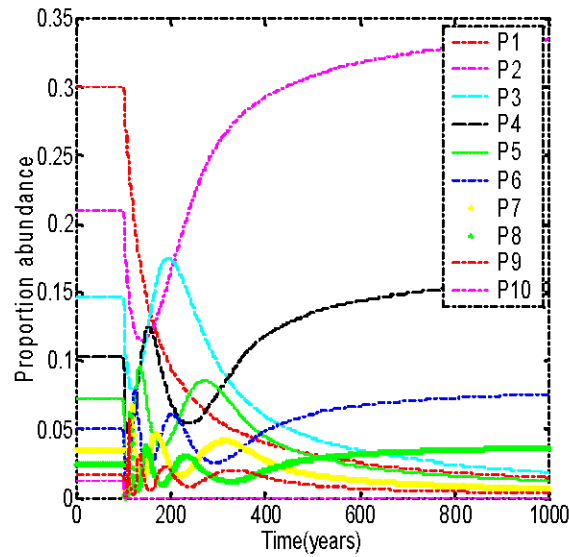
As shown in Fig. 3, how species diversity varies with time has been simulated in different communities with $q = 0.2$ (Fig. 3a) and $q = 0.31$ (Fig. 3b), respectively when 30% of habitat has been destroyed and $m_1 = m = 0.05$ /years. Human activities happen instantaneously (i.e., $t_0 = 0$) in Fig. 3a, while human activities take place at 100 years (i.e., $t_0 = 100$) in Fig. 3b.

The simulated results in Fig. 3 indicated that:

As shown in Fig. 3, if human destroyed 30% of habitat in very short time such as during the rapid urban expansion period, the instantaneous destruction has a long-term influence on all species, i.e., the time it takes for species to respond to sudden habitat loss is especially long. The survival species undergo three phases: decrease in abundance, adjustment with quasi-periodic oscillation, new equilibrium. As Tilman *et al.* (1994, 1997) pointed out, there is a "competitive cascade", i.e., species of even levels in the competitive hierarchy increase in species abundance, while odd number species decrease in abundance. Tilman *et al.* (1994, 1997) thought, if and only if $D_0 > q$, will species go extinct in ranked competitive order from the best to the poorest as habitat destruction increases. As shown in Fig. 3a, the best competitor goes extinct about 860 years later, which is the so-called 'extinction



(a)



(b)

Fig. 3: Biodiversity response to human activities in the rapid urban expansion period with the parameters (a) $q = 0.2$, $m = 0.05 \text{ years}^{-1}$, $n = 10$, $t_0 = 0$, $D_0 = 30\%$. (b) $q = 0.31$, $m = 0.05 \text{ years}^{-1}$, $n = 10$, $t_0 = 100$, $D_0 = 30\%$. $n_1, n_2, n_3, n_4, n_5, n_6, n_7, n_8, n_9, n_{10}$ are, respectively species 1, 2, 3, 4, 5, 6, 7, 8, 9, 10

debts' (Tilman *et al.*, 1994). However, shown from Fig. 3b, it is species 10 (not the best competitor, but the poorest one) that go extinct when $D_0 = 0.3 < q = 0.31$. It is because the oscillation amplitude of species 10 is so large that when species abundance is too low to recover. Moreover, although the species abundance is very low but not equal to zero, if we take Allee effect and other stochasticity into consideration, species is doomed to extinction. In the meanwhile, the time lag of species extinction is very short, that is, species extinction was almost simultaneous with habitat destruction. By analogy, all the inferior competitors of species 10 will go extinct more quickly, thus, we consider such a mechanism of species extinction to be short-time collective extinction of inferior competitors.

Discussion

The simulated results in Fig. 1 to 3 showed that. Under continuous destruction at different time scales in different eras, before complete habitat destruction, species go extinct from the best to the poorest and the survival species will go extinct collectively when habitat has been destroyed completely. Under instantaneous habitat destruction, when $D_0 > q$, species will go extinct from the best to poorest, while when $D_0 < q$, when the oscillation amplitudes of poor competitors are very big, it is possible to drive poor competitors go extinct collectively in very short time.

The conclusions are drawn from the condition that $q = 0.2$. Then, will these conclusions be compatible when q is different (i.e., in different metacommunities with different structures)?

The time it takes for the species abundances to reduce to 1/2, 1/e and species extinction are, respectively defined as T_{half} , T_e and T_{extine} . Table 1 shows T_{half} , T_e and T_{extine} of the 10 species metapopulation ($q = 0.03$, $m = 0.05/\text{years}$) response to the habitat destruction in different historical epochs.

Sustained human activities at any time scale, if not ceased and continued to a complete destruction would inevitably drive species extinct from the best to the poorest (Table 1). The time of species extinction due to human reclamation at ten-thousand-year time scale is far shorter than 10000 years and the extinction time at millenary scale is close to 1000 years, while most species do not go extinct on the condition that the amount of habitat destruction is a given constant (Tilman *et al.*, 1994, 1997; Lin, 2003).

The adaptability of inferior competitors are stronger than those of superior ones in response to human reclamation at ten-thousand-year time scale and millenary time scale, which obviously represents that T_{half} , T_e and T_{extine} of inferior competitors are much longer than those of superior species. It is because superior competitors have poorer dispersal abilities, leading to superior competitors being more susceptible to habitat destruction (Table 1).

The influence on biodiversity is significant and catastrophic when it is exerted by a short-time (such as one-year time scale) and large-area reclamation (such as $D_0 = 30\%$), which obviously represents that T_e and T_{extine} is very short. That is to say, biodiversity is highly sensitive to large-scale and drastic human activities (Table 1). Instantaneous and large-scale reclamation will drive some species go extinct after hundreds of years, which is called as "extinction debts".

In sum, under continuous habitat destruction at different time scales, species in different metacommunities will go extinct from the best to the poorest before complete destruction. The survival species will go extinct collectively when habitat is destroyed completely. Generally-speaking, at the same time scale, if q is smaller, i.e., all species in the whole community have poorer dispersal abilities. They will be more susceptible to habitat destruction, which leads to time debt of species extinction to be shorter. In contrast, when q is bigger, all species have better dispersal abilities and can endure more habitat destruction, which result in longer time lag of species extinction. These are why some

Table 1: T_{half} , T_e and T_{extine} of the 10 species metapopulation ($q = 0.03$, $m = 0.05/\text{years}$) response to the habitat destruction at different time scales

Species	Ten thousand-year time scale (the Primitive- Agriculture Epoch)			Thousand-year time scale (the Agriculture Revolution and Industry Epoch)			Year time scale (cities and towns extending period, $D_0 = 0.3$)		
	T_{half}	T_e	T_{extine}	T_{half}	T_e	T_{extine}	T_{half}	T_e	T_{extine}
n1	583	709	2230	171	206	656	48	69	404
n2	815	1014	2692	179	218	682	47	70	460
n3	1409	1599	3186	190	233	708	47	71	549
n4	1954	2121	3640	203	252	735	47	73	709
n5	2342	2533	4054	221	277	762	47	76	1093
n6	2802	2985	4450	246	309	789	47	80	3438
n7	3223	3399	4819	282	349	816	47	87	∞
n8	3560	3754	5165	328	393	842	48	103	∞
n9	3941	4128	5489	377	436	863	48	∞	∞
n10	4284	4468	5793	419	473	888	49	∞	∞

n1, n2, n3, n4, n5, n6, n7, n8, n9, n10 are, respectively species 1, 2, 3, 4, 5, 6, 7, 8, 9, 10

species will survive before complete destruction and go extinct collectively due to complete destruction. For instantaneous and great-scale habitat destruction, there are two mechanisms of species extinction. The former refers to extinction in order from the best competitors to the poorest; the latter refers to short-time extinction of inferior competitors.

In this study, we just modified the parameter D (i.e., the fraction of destroyed habitat caused by human) as linear function or δ function of time, that is to say, we only consider the temporal effects and ignore the spatial ones. In fact, species diversity is sensitive to spatial effects; on the other hand, the temporal characteristic is not only linear, but also periodic or nonlinear. From the point of view of modeling, it is not difficult to study the periodic or nonlinear temporal effects, but to study the spatial effects of human activities is absolutely difficult. In theory, we can modify parameter D as spatial function and introduce spatial heterogeneity as differential operators, but such attempts are very tough because of the peculiarity of landscape and the difficulty in describing physical field of habitat elements. In addition, we have only considered case 1 of Tilman's (1997) four analytical cases, mainly the geometric rank-abundance relationship for a perfect hierarchy of competitors. A different assumption may result in a different output. Interested reader can have some further simulations under the six assumptions advanced by Lin and Wang (2002) for some comparisons.

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