

Abundance patterns in multi-species communities exposed to habitat destruction

Andrew Morozov^{a,b,*}, Bai-Lian Li^{a,c}

^aEcological Complexity and Modeling Laboratory, University of California, Riverside, CA 92521-0124, USA

^bShirshov Institute of Oceanology, Russian Academy of Science, Moscow, Russia

^cCAU-UCR International Center for Ecology and Sustainability, University of California, Riverside, CA 92521, USA

Received 21 June 2007; received in revised form 10 October 2007; accepted 16 January 2008

Available online 20 January 2008

Abstract

Habitat destruction resulting from human activity is a serious threat to biodiversity. The model developed by Tilman et al. [Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. *Nature* 371, 65–66] has become an important tool for analyzing persistence of species in habitats under destruction. However, most analysis and applications of this model have been limited to the studies of species richness and the order of extinction. In this paper, we address other important issues related to succession of species abundances. We are interested in how the abundance ranking (i.e., the ranking of species according to their relative abundances), the rank–abundance curve and the community diversity alter in habitats under destruction. We treat analytically the model of Tilman et al. and investigate three different scenarios. We consider that before destruction: (i) best competitors are most abundant; (ii) all species are equally abundant; (iii) poor competitors are most abundant. In each case, we have derived explicit expressions for equilibrium species abundances depending on proportion of destroyed sites. Then we follow analytically alteration in the initial abundance ranking, show complex patterns of succession of species abundances and consider transformations in the rank–abundance curve. We demonstrate patterns of self-organization in abundance distributions emerging as a response to habitat destruction. We show non-monotonic dependence of community diversity and community evenness on proportion of destroyed sites.

© 2008 Elsevier Ltd. All rights reserved.

Keywords: Habitat destruction; Metapopulation model; Rank–abundance curve; Evenness; Diversity

1. Introduction

Habitat destruction due to anthropogenic factors is a major threat to biodiversity (Wilson, 1992). The metapopulation model developed by Tilman et al. (1994, 1997) has become an important tool for analysis of persistence in habitats under destruction. This model (based on earlier models developed by Hastings, 1980; Nee and May, 1992) considers a metacommunity as a collection of a large number of patches. Each patch can be empty, permanently destroyed or inhabited by an individual of species i ($i = 1, n$). The species are in competition for space and ranked according to their competitive ability: when a propagule of

species j lands on a patch, it can colonize it either if the patch is empty or if it is inhabited by species j having a lower rank ($i < j$). The strongest competitor has rank 1. The equation for the proportion of habitat p_i occupied by species i is given by

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

where m_i is the mortality rate, c_i is the specific colonization rate, D is the proportion of permanently destroyed sites.

In real ecosystems, the value of D is being constantly increased and the central questions addressed with Eq. (1) include alteration in the community richness (the number of persisting species) and the order of extinction. Analytical studies (Stone, 1995; Tilman et al., 1997; Klausmeier, 1998) have revealed conditions which guarantee that the species

*Corresponding author at: Ecological Complexity and Modeling Laboratory, University of California, Riverside, CA 92521-0124, USA. Tel.: +7495 124 6392; fax: +7495 124 5983.

E-mail address: morozov_andrew@yahoo.com (A. Morozov).

will go extinct according to their competitive ranking. In particular, in communities with equal mortalities ($m_i = m$), extinction would take place first for species having poor dispersal abilities. Those species are often supposed to be strongest competitors due to the so-called competition-colonization trade-off (Klausmeier and Tilman, 2002). Later works (Lin, 2005; Liu et al., 2007) pointed out, as well, the importance of some other issues: the existence of a minimal threshold p^0 of abundances and the influence of transition time from an intact habitat $D = 0$ to a habitat with $D = D^* > 0$.

However, species richness is not the only key component of community diversity. Another major constituent includes species evenness which shows how equally populations are represented within a community (Magurran, 1988; Weiher and Keddy, 1999). It is usually measured with an index which is varying from near 0 (high single-species dominance) to 1 (equal abundance of all species) and higher values of evenness correspond to higher values of diversity (Stirling and Wilsey, 2001). Habitat destruction and human caused disturbance result in alteration of species evenness as well. However, contrary to the well-known patterns of richness decline, species evenness may show both a decrease (Hill and Hamer, 1998; Mac Nally, 2007) and an increase (Bohning-Gaese and Bauer, 1996; Cushman and McGarigal, 2003; Seigel et al., 2005); the latter case being a rather common phenomenon. Therefore, the resultant change in community diversity will depend on relative proportion between a decrease in richness and an increase in evenness.

From the other hand, both species richness and species evenness are integral characteristics of a community. A more detailed description of the impact of habitat destruction would include the dependence of abundances of all persisting species on the proportion D of destroyed sites (Mac Nally, 2007). In particular, it is important to know the succession in the abundance ranking of persisting species. In this paper, by ‘the abundance ranking’ we understand the ranking of species according to their relative abundances p_i (regardless of their competitive hierarchy). An alteration in the initial abundance ranking can disrupt the ecosystem integrity (Bolger, 2001; Mac Nally, 2007). In particular, the relevant question is: what will be the most abundant species in a destroyed habitat: poor or strong competitors?

Model (1) allows to follow successions in the abundance ranking and to make predictions regarding alteration of species evenness and diversity in communities exposed to habitat destruction. We should note that the mentioned questions have not been addressed properly in the current literature yet. In our paper, we apply model (1) for studying the above issues. Also, we consider transformation of rank–abundance curves (also called ‘rank–abundance distributions’) when proportion of destroyed sites is being increased. Note that alteration in a rank–abundance curve is often considered as an important indicator of the impact of habitat fragmentation (Stone et al., 1996;

Mouquet and Loreau, 2003), habitat disturbance (Hill and Hamer, 1998) or pollution (Gray, 1979).

We treat analytically model (1) and investigate the three situations suggested in Tilman et al. (1997). Namely, we consider that in the intact habitat: (1) best competitors are most abundant; (2) all species are equally abundant; (3) poor competitors are most abundant. We analyze the situation when mortality rates are equal. In each case, we have derived explicit expressions for equilibrium abundances of species within the whole range of destruction ($0 < D < 1$). This allowed us to follow analytically alterations in the initial abundance ranking and show self-organization patterns of succession of abundance distributions. We show non-monotonic dependence of community diversity and community evenness on the proportion D of destroyed sites and study transformations of the rank–abundance curve. We discuss implications of our results for the ecology of biodiversity, in particular, the eventual relationship between species evenness and community richness.

2. Parameterization of colonization rates

The model equations are given by Eq. (1). We consider the mortalities to be the same for all species: $m_i = m$. We will address briefly the case of different mortalities in Section 4. For an intact habitat ($D = 0$), we consider three following possibilities suggested by Tilman et al. (1997).

2.1. Best competitors are most abundant

Following Tilman et al. (1997), we consider that the equilibrium abundances in an intact habitat form a geometric progression. In this case, the abundances \hat{p}_i and the colonization rates c_i are given by

$$\hat{p}_i = q(1 - q)^{i-1}, \quad c_i = \frac{m}{(1 - q)^{2i-1}}, \quad i = 1, n, \quad (2)$$

where q is the abundance of the strongest competitor; there is not limitation to the number n of species in the community. Note that here and further, expressions for c_i are derived from the abundance distribution \hat{p}_i which is assumed (*a priori*) to hold for $D = 0$.

2.2. All species are equally abundant

The equilibrium abundances \hat{p}_i in an intact habitat and the corresponding colonization rates c_i are given by

$$\hat{p}_i = q, \quad c_i = \frac{m}{(qi - 1)[q(i - 1) - 1]}, \quad i = 1, n. \quad (3)$$

The number of competitors should satisfy the condition: $n < 1/q$.

2.3. Poor competitors are more abundant

In this paper, we consider in detail the simplest case of a linear increase in abundances (Tilman et al., 1997). The equilibrium abundances and the colonization rates are given by

$$\hat{p}_i = iq, \quad c_i = \frac{4m}{[2 - qi(i - 1)][2 - qi(i + 1)]}, \quad i = 1, n. \tag{4}$$

Note that we have corrected a misprint in Tilman et al. (1997) in the formula for c_i . The number of competitors should satisfy the condition: $n(n + 1) < 2/q$.

We also address briefly the case when the rate of increase of \hat{p}_i in an intact habitat is faster than linear. We shall consider the following parameterization given by a power function:

$$\hat{p}_i = i^r q, \quad i = 1, n, \tag{5}$$

where $r > 1$; for n we have the condition: $(1^r + 2^r + 3^r + \dots + n^r)q < 1$.

Note that the order of extinction in model (1), with c_i given by Eqs. (2)–(4), has been investigated by Tilman et al. (1997). It was shown that the expression $D_i = 1 - m/c_i$ provides the smallest values of D_i such as for $1 > D > D_i$ persistence of species i is impossible. Since for all above cases we have $c_{i+1} > c_i$, the order of extinction becomes equivalent to the competitive ranking order. However, a more strict definition of extinction order (see Klausmeier, 1998) takes into account possible extinction of species for some intermediate values of $D < D_i$ (with their further reestablishment for some higher values of D). In other words, a strict equivalence of the competitive order and the order of extinction would signify that species i may not go extinct before any stronger competitor (species 1, 2, ..., $i - 1$). Some rules providing the equivalence between the competitive order and the order of extinction have been established (Klausmeier, 1998). By applying the mentioned rules, one can prove the equivalence between the extinction and competition order for Eqs. (2)–(4). We should note that, however, the question about the order of extinction in a more general case (Eq. (5)) has not been studied yet and we shall address this issue in the paper along with analysis of succession in species abundances.

In our study, we use expressions for equilibrium abundances obtained in (Klausmeier, 1998):

$$\begin{aligned} \hat{p}_{i,odd} &= \frac{c_1 c_2 \dots c_{i-2}}{c_2 c_4 \dots c_{i-1}} (1 - D) - \frac{c_2 c_4 \dots c_{i-1}}{c_1 c_3 \dots c_i} m, \\ \hat{p}_{i,even} &= \frac{c_1 c_3 \dots c_{i-1}}{c_2 c_4 \dots c_i} (D - 1) + \frac{c_2 c_4 \dots c_{i-2}}{c_1 c_3 \dots c_{i-1}} m. \end{aligned} \tag{6}$$

The above expressions hold for $0 < D < q$.

From these formulae one can see that destroying a proportion of sites would result in a decrease in the abundances of species having odd ranks and an increase of those having even ranks. It is a generic property of model (1).

3. Analysis of the model and results

3.1. Best competitors are most abundant

Let us consider first $0 < D < q$, which is equivalent to $D \in (0, 1 - m/c_1)$. By applying Eq. (6) with c_i defined by Eq. (2) we have obtained (by induction) that the equilibrium abundances are given by

$$\begin{aligned} \hat{p}_{2k-1} &= (q - D)(1 - q)^{2k-2}, \\ \hat{p}_{2k} &= (q + D - qD)(1 - q)^{2k-1}, \quad k = 1, 2, \dots, k_0. \end{aligned} \tag{7}$$

(Without losing generality, we may consider that the number of species in the habitat is even, i.e. $n = 2k_0$.)

It is easy to see that the destruction of the habitat for $0 < D < q$ results in an increase of species abundances having even ranks and in a decrease of those having odd ranks and abundances within both the odd and even subsequences decrease with increasing of rank.

When D crosses the critical value $D = q$, the best competitor ($i = 1$) cannot survive in the system any more. The new best competitor becomes species 2. To obtain the equilibrium abundances, we apply Eq. (6) by replacing c_1 by c_2 , c_3 by c_4 , etc. This gives

$$\begin{aligned} \hat{p}_{2k} &= [1 - D - (1 - q)^3](1 - q)^{2k-2}, \\ \hat{p}_{2k+1} &= (D - q)(1 - q)^{2k}, \quad k = 1, 2, \dots \end{aligned} \tag{8}$$

The total number of species is now: $2k_0 - 1$. Expressions (8) hold for $D \in (q, 1 - (1 - q)^3)$, since they provide positive values of abundances; this is equivalent to $D \in (1 - m/c_1, 1 - m/c_2)$. Destruction of habitat within the considered range results in a decrease of abundances of species having even competitive ranks and an increase of those having odd ranks.

By induction, we have derived that for $D \in (1 - m/c_i, 1 - m/c_{i+1})$ the best competitor becomes species $i + 1$ (first i competitors cannot survive in the system) and equilibrium abundances of the persisting species are defined by

$$\begin{aligned} \hat{p}_{i+2k-1} &= [1 - D - (1 - q)^{2i+1}](1 - q)^{2k-2}, \\ \hat{p}_{i+2k} &= (1 - q)^{2k} [D - 1 + (1 - q)^{2i-1}], \quad k = 1, 2, \dots \end{aligned} \tag{9}$$

The total number of species in the habitat is now: $2k_0 - i$. Note that Eqs. (7) and (8) follow from Eq. (9) as particular cases for $i = 0$ and $i = 1$, respectively.

It can be seen from Eq. (9) that for every i , the equilibrium abundances form two subsequences which are geometric progressions with the same common ratio $(1 - q)^2$ but with different initial terms. Since the progression ratio is less than unity, both subsequences are monotonically decreasing. However, an increase of D within the considered range results in a decrease of \hat{p}_{i+2k-1} (the new best competitor belongs to this subsequence) and in an increase of \hat{p}_{i+2k} . Note that for $D = 1 - m/c_i$ all equilibrium abundances \hat{p}_{i+2k} become equal to zero. The latter property seems to be a mathematical artifact of the model.

Expressions (7)–(9) allow us to follow the succession in the abundance ranking. Here and further we ascribe rank 1 (in the abundance ranking) to the most abundant species. Let us follow the succession when D is being varied within the range $(1-m/c_i, 1-m/c_{i+1})$, the new best competitor being species $i+1$. For the sake of simplicity, we may consider that the number of persisting species is even and equal to $2k_i$; the rank of the poorest competitor is $n=i+2k_i$. For D close to the left end of the range we have: $\hat{p}_{i+2l-1} > \hat{p}_{i+2s}$ for all $l, s=1, 2, \dots, k_i$. This can be seen from the fact that for $D \approx 1-m/c_i = 1-(1-q)^{2i-1}$ all \hat{p}_{i+2k} tend to zero, whereas all \hat{p}_{i+2k-1} are bounded by a positive number. We have the following abundance ranking: $i+1, i+3, \dots, i+2k_i-1, i+2, i+4, i+6, \dots, i+2k_i$. The most abundant is the best competitor. For an increase in D , the abundances of species with competitive ranks $i+1, i+3, \dots, i=2k_i-1$ decrease monotonically, whereas those with ranks $i+2, i+4, i+6, \dots, i+2k_i$ increase monotonically. For a certain value of D (it can be found from Eq. (9)), we have $\hat{p}_{i+2k_i-1} = \hat{p}_{i+2}$. After crossing this value, the abundance ranking becomes $i+1, i+3, \dots, i+2k_i-3, i+2, i+2k_i-1, i+4, i+6, \dots, i+2k_i$.

In case that D is such that $\hat{p}_{i+2l+1} < \hat{p}_{i+2} < \hat{p}_{i+2l-1}$, the abundance ranking is

$$\begin{aligned}
 & i+1, i+3, \dots, i+2l-1, \dots, i+2, i+2l+1, i+4, \\
 & i+2l+3, i+6, \dots, i+2k_i-1, i+2(k_i-l), \\
 & i+2(k_i-l)+2, \dots, i+2k_i-2, i+2k_i, \quad \text{where } 1 \leq l < k_i.
 \end{aligned}
 \tag{10}$$

Note that the terms with even and odd competitive ranks in Eq. (10) strictly alternate since both subsequences (Eq. (9)) constitute geometric progressions with the same ratio.

While the habitat destruction is increasing, the two subsequences defined by Eq. (9) ‘pass through’ each other and for a certain D they coincide (i.e., we have $\hat{p}_{i+2k-1} = \hat{p}_{i+2k}$ for all k). For a further progressing of habitat destruction, the most abundant species becomes the one with competitive rank $i+2$. For the values of D satisfying $\hat{p}_{i+2l} < \hat{p}_{i+1} < \hat{p}_{i+2l-2}$, the abundance ranking is the following:

$$\begin{aligned}
 & i+2, i+4, i+6, \dots, i+2l, i+1, i+2(l+1), i+3, \\
 & i+2(l+2), i+5, \dots, i+2k_i, i+2(k_i-l)-1, \dots, \\
 & i+2k_i-3, i+2k_i-1, \quad \text{with } 1 \leq l < k_i.
 \end{aligned}
 \tag{11}$$

Finally, after the abundance of the best competitor becomes smaller than that of the poorest competitor (the both subsequences have ‘passed’ through each other), we have the following abundance ranking: $i+2, i+4, i+6, \dots, i+2k_i, i+1, i+3, i+5, \dots, i=2k_i-1$. This order is the opposite to the one we observe for $D \approx 1-m/c_i$ and will remain until $D = 1-m/c_{i+1}$.

For a better visualization of successions in the abundance ranking, we give an illustration in Table 1 for $n = 16$ for the case when the best competitor has rank 3 ($q = 0.3$). The values of D are calculated by using Eq. (9). The

Table 1

Succession in the abundance ranking in model (1) with colonization rates given by Eq. (2) (best competitors are most abundant) obtained for $q = 0.3, n = 16$

Habitat destruction	Abundance ranking (from the most abundant to the least abundant)
0.657 < D < 0.662	4, 6, 8, 10, 12, 14, 16, 3, 5, 7, 9, 11, 13, 15
0.662 < D < 0.667	4, 6, 8, 10, 12, 14, 3, 16, 5, 7, 9, 11, 13, 15
0.667 < D < 0.675	4, 6, 8, 10, 12, 3, 14, 5, 16, 7, 9, 11, 13, 15
0.675 < D < 0.691	4, 6, 8, 10, 3, 12, 5, 14, 7, 16, 9, 11, 13, 15
0.691 < D < 0.715	4, 6, 8, 3, 10, 5, 12, 7, 14, 9, 16, 11, 13, 15
0.715 < D < 0.744	4, 6, 3, 8, 5, 10, 7, 12, 9, 14, 11, 16, 13, 15
0.744 < D < 0.774	4, 3, 6, 5, 8, 7, 10, 9, 12, 11, 14, 13, 16, 15
0.774 < D < 0.798	3, 4, 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16
0.798 < D < 0.814	3, 5, 4, 7, 6, 9, 8, 11, 12, 13, 14, 15, 14, 16
0.814 < D < 0.822	3, 5, 7, 4, 9, 6, 11, 8, 13, 10, 15, 12, 14, 16
0.822 < D < 0.827	3, 5, 7, 9, 4, 11, 6, 13, 8, 15, 10, 12, 14, 16
0.827 < D < 0.830	3, 5, 7, 9, 11, 4, 13, 6, 15, 8, 10, 12, 14, 16
0.830 < D < 0.831	3, 5, 7, 9, 11, 13, 4, 15, 6, 8, 10, 12, 14, 16
0.831 < D < 0.832	3, 5, 7, 9, 11, 13, 15, 4, 6, 8, 10, 12, 14, 16

demonstrated patterns of succession can be considered as patterns of self-organization in metacommunities under habitat destruction.

3.1.1. Alterations in the rank–abundance curve

We shall address this issue briefly. Suppose that D is varied within $(1-m/c_i, 1-m/c_{i+1})$. For $D \approx 1-m/c_i$, a typical shape of the rank–abundance curve is shown in Fig. 1a (obtained for $q = 0.2, i = 1, D = 0.2002$). In a logarithmic scale, the rank–abundance curve (solid line) consists of two pieces of straight lines corresponding to subsequences (Eq. (9)) with odd and even competitive ranks. The upper piece is constituted by \hat{p}_{i+2k-1} . The rank–abundance curve for the intact habitat is presented by a dashed line. Note that the slope of the new curve is twice greater than in case when $D = 0$. It can be easily understood from the fact that the both sequences (Eq. (9)) have common ratio $(1-q)^2$ instead of $(1-q)$ for $D = 0$. We show the species abundances, as well, plotted according to their competitive ranks (Fig. 1b).

For an increase in D , both subsequences with odd and even competitive ranks are passing through each other (in terms of their abundance ranking) and the rank–abundance curve consists now of three parts (see Fig. 1c obtained for $D = 0.230$). The central part corresponds to alternation of both subsequences in Eq. (9) and it can be approximated by a straight line. In Fig. 1d we show abundances plotted according to their competitive ranks. For an increase in D , the central part of the curve becomes larger and its slope approaches $(1-q)$. For D when the abundance ranking coincides with the competitive ranking, the rank–abundance curves in destroyed and intact habitats have the same slope (Fig. 1e, $D = 0.357$). For a further increase in D , the rank–abundance curve exhibits the opposite transformations and, for $D \approx 1-m/c_{i+1}$, the shape of the curve is similar to that shown in Fig. 1a (the upper part is formed now by \hat{p}_{i+2k}).

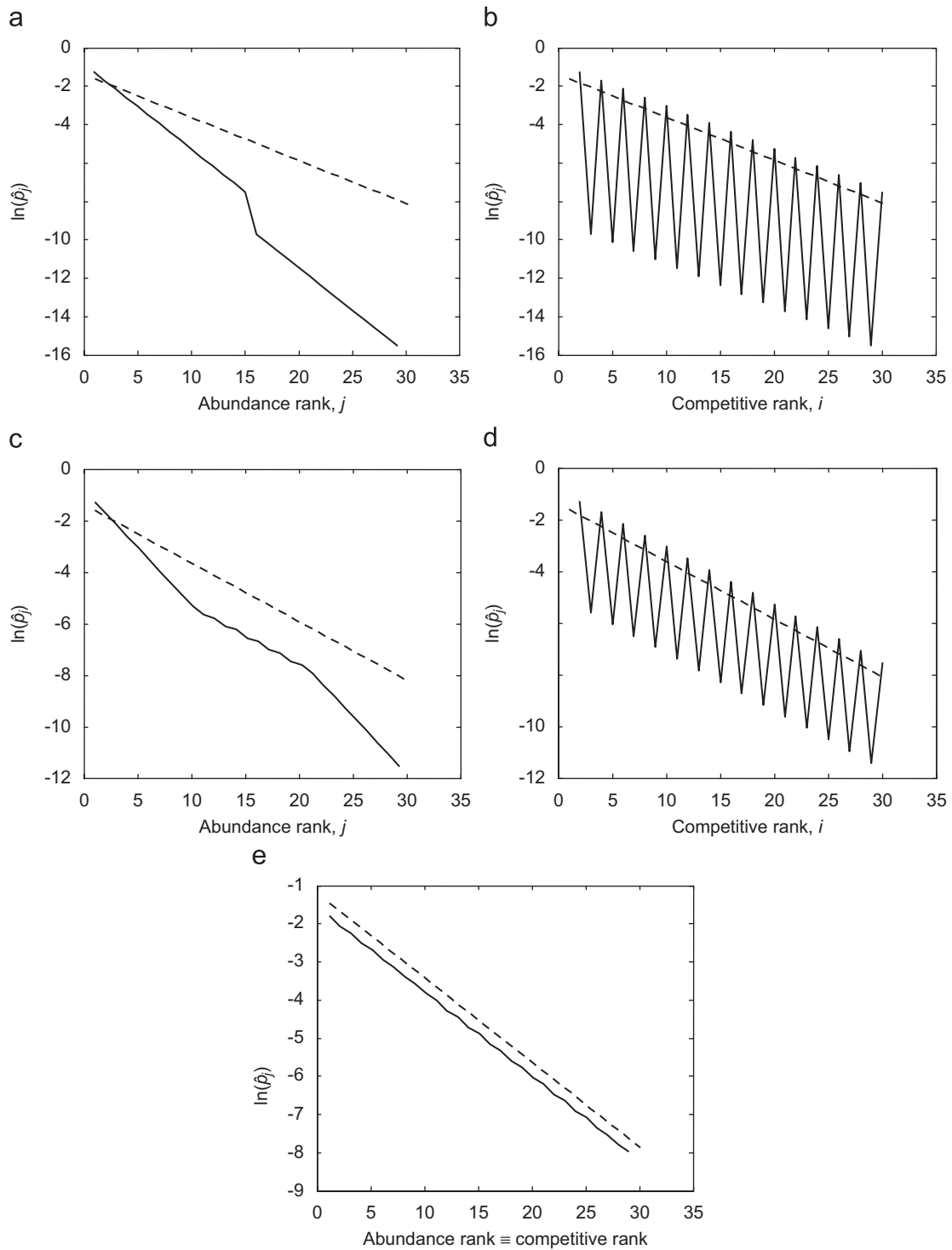


Fig. 1. Successions in the rank–abundance curve and abundance distribution in habitats under destruction with best competitors initially most abundant. We consider $D \in (0.2, 0.488)$ which is equivalent to species 2 as the best competitor ($q = 0.2$, the initial number of species $n = 30$). (a) Rank–abundance curve and (b) equilibrium abundances obtained for $D = 0.2002$. (c) Rank–abundance curve and (d) equilibrium abundances obtained for $D = 0.230$. (e) Rank–abundance curve and equilibrium abundances obtained for $D = 0.357$ (abundance ranking and competitive ranking coincide). In all cases, the rank–abundance curve for an intact habitat is shown by a dashed line.

3.2. All species are equally abundant

We consider first that $0 < D < q$, which is equivalent to $D \in (0, 1 - m/c_1)$. By applying Eq. (6) with c_i defined by

Eq. (5) we have derived that the abundances are given by

$$\begin{aligned} \hat{p}_{2k-1} &= D[2(k-1)q - 1] + q, \\ \hat{p}_{2k} &= D(1 - 2kq) + q, \quad k = 1, 2, \dots, k_0. \end{aligned} \tag{12}$$

(Without losing generality, we may consider that the number of species in the habitat is even, i.e. $n = 2k_0$.) We remind, as well, that $2kq < 1$.

By induction, we have derived that for $D \in (1 - m/c_i, 1 - m/c_{i+1})$ the best competitor becomes species $i+1$ (first i competitors cannot survive in the system) and equilibrium abundances of persisting species are defined by

$$\begin{aligned} \hat{p}_{i+2k-1} &= \frac{1 - (i + 2k - 2)q}{1 - qi} (1 - D) - [1 - (i + 2k - 1)q](1 - qi), \\ \hat{p}_{i+2k} &= \frac{1 - (i + 2k)q}{1 - qi} (D - 1) + [1 - (i + 2k - 1)q](1 - qi), \\ k &= 1, 2, \dots \end{aligned} \tag{13}$$

Note that Eq. (12) follows from Eq. (13) by assuming $i = 0$.

The equilibrium species abundances form two arithmetic progressions: $\{\hat{p}_{i+2k-1}\}$ and $\{\hat{p}_{i+2k}\}$.

This follows from

$$\begin{aligned} \hat{p}_{i+2(k+1)-1} - \hat{p}_{i+2k-1} &= \Delta_1 = \frac{2q(D - 2qi + q^2i^2)}{1 - qi}, \\ \hat{p}_{i+2(k+1)} - \hat{p}_{i+2k} &= \Delta_2 = -\frac{2q(D - 2qi + q^2i^2)}{1 - qi}. \end{aligned} \tag{14}$$

The common differences Δ_1, Δ_2 of the progressions have the same absolute value, but the opposite signs: $\Delta_1 = -\Delta_2$.

Expressions (13) and (14) help us follow the succession in species abundances for variation of D . First, we consider that $0 < D < q$. It can be easily proved that the abundance ranking is the following: 2, 4, 6, 8, ..., $2k_0, 2k_0 - 1, \dots, 7, 5, 3, 1$. This order remains till $D = q$.

Let us follow the succession in species abundances when $D \in (1 - m/c_i, 1 - m/c_{i+1}), i \geq 1$. For the sake of simplicity, we consider that the number of persisting species is even and equal to $2k_i$; the rank of the poorest competitor is $i + 2k_i$. For D close to the left end of the range, we have $\Delta_1 < 0$; for D close to the right end, we have $\Delta_1 > 0$; moreover, Δ_1, Δ_2 become zero at

$$D = \hat{D}_i = qi(2 - qi). \tag{15}$$

It can be proven that $\hat{D}_i \in (1 - m/c_i, 1 - m/c_{i+1})$. As such, for $D \in (1 - m/c_i, \hat{D}_i)$ the abundance ranking is the following:

$$\begin{aligned} i + 1, i + 3, i + 5, \dots, i + 2k_i - 3, i + 2k_i - 1, \\ i + 2k_i, i + 2k_i - 2, \dots, i + 6, i + 4, i + 2. \end{aligned} \tag{16}$$

The most abundant is the best competitor; the least abundant is the species next to the best competitor. For $D = \hat{D}_i$ all equilibrium abundances are equal each other: $\hat{p} = q(1 - qi)$. For $D \in (\hat{D}_i, 1 - m/c_{i+1})$ the order of abundance is

$$\begin{aligned} i + 2, i + 4, i + 6, \dots, i + 2k_i - 2, i + 2k_i, \\ i + 2k_i - 1, i + 2k_i - 3, \dots, i + 5, i + 3, i + 1. \end{aligned} \tag{17}$$

The best competitor becomes the least abundant and the most abundant is the species next to the best competitor. Thus, after achieving the critical value (Eq. (16)) of destruction, the abundance ranking becomes exactly the opposite to the previous one.

3.2.1. Alterations in the rank–abundance curve

Consider that $D \in (1 - m/c_i, 1 - m/c_{i+1})$. The shape of the rank–abundance curve is qualitatively the same for all $D \neq \hat{D}_i$ (where \hat{D}_i is given by Eq. (15)) and consist of two pieces of straight lines (see Fig. 2a obtained for $q = 0.03, i = 1, D = 0.0306$). For $D \in (1 - m/c_i, \hat{D}_i)$ the upper piece is constituted by \hat{p}_{i+2k-1} . The rank–abundance curve for an intact habitat is presented by a dashed line. In Fig. 2b we show the species abundances plotted according to their competitive ranks. With an increase in D , the slope of the rank–abundance curve diminishes and, for $D = \hat{D}_i$, the curve becomes degenerated since all species are equally abundant. For $D \in (\hat{D}_i, 1 - m/c_{i+1})$ the rank–abundance curve is qualitatively the same to the one shown in Fig. 2a; however, the upper piece is formed now by \hat{p}_{i+2k} . With a further increase in D , the slope of the curve increases and attains its maximum at $D = 1 - m/c_{i+1}$.

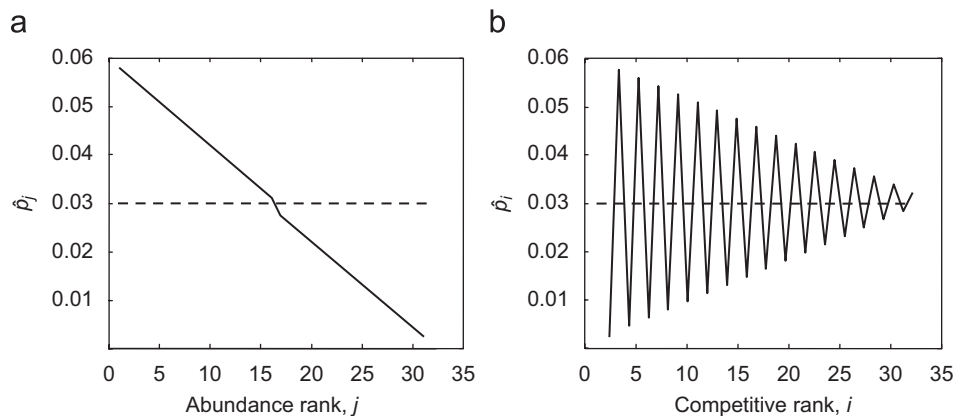


Fig. 2. Typical behavior of the rank–abundance curve (a) and abundance distribution (b) in habitat under destruction in case when all species are initially equally abundant ($q = 0.03, D = 0.0306$; the best competitor is species 2, the initial number of species $n = 32$). The rank–abundance curve for an intact habitat is shown by a dashed line.

3.3. Poor competitors are more abundant

3.3.1. Abundance of poor competitors increases linearly

First, we consider the case of the linear increase in species abundances in an intact habitat. By applying Eq. (6) with c_i defined by Eq. (4) we have derived by induction that the equilibrium abundances for $0 < D < q$ are given by

$$\begin{aligned} \hat{p}_{2k-1} &= -D + q(2k - 1) + qD(2k - 1)(k - 1), \\ \hat{p}_{2k} &= D + q2k - qD(2k + 1)k, \quad k = 1, 2, \dots, k_0. \end{aligned} \quad (18)$$

By induction, we have derived that for $D \in (1 - m/c_i, 1 - m/c_{i+1})$ the best competitor becomes species $i+1$ and the equilibrium abundances of the remaining species are defined by

$$\begin{aligned} \hat{p}_{i+2k-1} &= \frac{1 - q(i + 2k - 2)(i + 2k - 1)/2}{1 - qi(i + 1)/2} (1 - D) \\ &\quad - [1 - qi(i + 1)/2][1 - q(i + 2k - 1)(i + 2k)/2], \\ \hat{p}_{i+2k} &= \frac{1 - q(i + 2k)(i + 2k + 1)/2}{1 - qi(i + 1)/2} (D - 1) \\ &\quad + [1 - qi(i + 1)/2][1 - q(i + 2k - 1)(i + 2k)/2]. \end{aligned} \quad (19)$$

Note that Eq. (18) follows from Eq. (19) by putting $i = 0$.

Our analysis shows that abundances (Eq. (19)) within each subsequence increase with increasing of rank number: $\hat{p}_{i+2(k+1)} - \hat{p}_{i+2k} > 0$ and $\hat{p}_{i+2(k+1)-1} - \hat{p}_{i+2k-1} > 0$. However, this increase is not linear, but described by a quadratic parabola. An increase in D over the considered range will result in a decrease of \hat{p}_{i+2k-1} and in an increase of \hat{p}_{i+2k} .

Next step is to follow the successions in the abundance ranking. We should say that compared to the two previous cases, this order seems to be much more complex. The expressions and rules of succession that we obtained analytically are too cumbersome and of little practical use. In this paper, we give only a general idea on succession in the abundance ranking without going into details. Let us consider $D \in (1 - m/c_i, 1 - m/c_{i+1})$. Without losing generality, the main structure of the pattern can be understood from a particular example. As an illustration, we consider $n = 28$; $i = 4$; $q = 0.0025$. The new best competitor has rank $i + 1 = 5$; the poorest competitor has rank 28; this takes place for $D \in (0.0400, 0.0615)$.

For the values of D close to the left end of the considered range, we have the following abundance ranking ($0.0400 < D < 0.0406$, from the most abundant to the least abundant):

$$28, 27, 25, 26, 23, 24, 21, 19, 22, 17, 20, 15, 13, 18, 11, 16, 9, 14, 7, 5, 12, 10, 8, 6. \quad (20)$$

In other words, l species with the least abundances ($l = 4$ in the given example) belong to the subsequence \hat{p}_{i+2k} ; after the appearance of the best competitor (first member of \hat{p}_{i+2k-1}) species with even and odd competitive ranks generally alternate, but not in a strict way. It can be proven analytically that the length of clusters containing only odd (or even) ranks is smaller than l . For an increase in D , the

abundances of species $i + 1, i + 3, i + 5, \dots, i = 2k_i - 1$ decrease monotonically, whereas those of species $i + 2, i + 4, i + 6, \dots, i + 2k_i$ increase monotonically; we have progressively: $\hat{p}_5 = \hat{p}_{12}$, then $\hat{p}_5 = \hat{p}_{10}$, etc. Thus, first members of the odd and even subsequences pass through each other in their abundance ranking order, whereas the most abundant ones conserve their positions.

In the given example, we found about 40 different bifurcations in the abundance ranking while D is being varied within $(0.04, 0.0615)$. It can be proven analytically, as well, that for each $(1 - m/c_i, 1 - m/c_{i+1})$ there exists a certain range of D where the abundance ranking corresponds to the one in the intact habitat.

For D close to the right end of $(0.0400, 0.0615)$ the less abundant species becomes the best competitor. For $D \rightarrow 0.0615 = 1 - m/c_{i+1}$, the order of persistence becomes the following:

$$28, 26, 27, 24, 22, 25, 20, 23, 18, 16, 21, 14, 12, 19, 10, 17, 8, 15, 6, 13, 11, 9, 7, 5. \quad (21)$$

Thus, first least abundant l species ($l = 5$ in the given example) belong to $\{\hat{p}_{i+2k-1}\}$. After the appearance (we go from the right-hand end to left-hand end) of the first member from $\{\hat{p}_{i+2k}\}$, species with even and odd competitive ranks generally alternate, but not in a strict way; the length of clusters containing only odd (or even) ranks is smaller than l . We should emphasize that the described above properties hold for all i, q, n .

3.3.2. Abundance of poor competitors increases faster than linearly

Let us consider now a more generic case when the abundances of species in an intact habitat are described by a power function (5). In Appendix we show that in case of equal mortality rates, the colonization rates c_i can be derived from the following expression:

$$c_i = \frac{m}{[1 - F(i)][1 - F(i - 1)]}, \quad (22)$$

where $F(i) = \hat{p}_1 + \hat{p}_2 + \hat{p}_3 + \dots + \hat{p}_i$. The total number n of species is limited by $F(n) < 1$.

Since there is no explicit formula for the sum $1^r + 2^r + 3^r + \dots + i^r$ for an arbitrary r , we cannot derive an explicit expression for c_i . However, for $r = 2$ and $r = 3$ one can easily get

$$c_i = \frac{36m}{[6 - i(i + 1)(2i + 1)q][6 - i(i - 1)(2i - 1)q]}, \quad \hat{p}_i = qi^2, \quad (23)$$

$$c_i = \frac{16m}{[4 - i^2(i + 1)^2q][4 - i^2(i - 1)^2q]}, \quad \hat{p}_i = qi^3. \quad (24)$$

Analytical treatment of the model with c_i given by Eqs. (23) and (24) shows that even for the simplest case $r = 2$, the explicit expressions for the equilibrium abundances for $D > q$ are extremely cumbersome. Further, we will utilize mostly numerical simulations.

First, we analyze whether the extinction order in a habitat under destruction is equivalent to the competition ranking. We remind that here we use the concept suggested by Klausmeier (1998), i.e., the equivalence between the competition and extinction orders would signify that for every D , the species with the rank i goes extinct only in case that all stronger competitors cannot persist. It was shown (Klausmeier, 1998) that this takes place when $c_{i+1}/c_i > c_i/c_{i-1}$. Our analytical verification of this condition (leading to rather cumbersome expressions) shows that for Eqs. (23) and (24) it always holds. Moreover, we applied numerical simulations and obtained that $c_{i+1}/c_i > c_i/c_{i-1}$ holds for the range $1 < r < 10$ (we considered non-integer values of r , as well). This means that the extinction order (in its strictest sense) in model (1), when initial abundances are given by a power function, corresponds to the competitive ranking.

Second, we investigated the succession in the abundance ranking. The results of numerical simulations show that patterns of succession are qualitatively similar to those arising in the case of linear increase (illustrated by Eqs. (20) and (21)). In other words, for every $D \in (1 - m/c_i, 1 - m/c_{i+1})$

there are two subsequences: $\{\hat{p}_{i+2k-1}\}$ and $\{\hat{p}_{i+2k}\}$, each of them is increasing with k . An increase in D results in an increase of \hat{p}_{i+2k-1} and in a decrease of \hat{p}_{i+2k} . For $D \approx 1 - m/c_i$, l the least abundant species belong to \hat{p}_{i+2k} ; then the species from both subsequences alternate (not in a strict way) in the abundance ranking. With an increase of D , the first members of both subsequences pass through each other in the abundance ranking, whereas the most abundant competitors conserve their abundance ranks. When approaching $D \approx 1 - m/c_{i+1}$, the best competitor becomes the least abundant. The other least abundant species belong to the subsequence $\{\hat{p}_{i+2k-1}\}$. Note that with an increase of r (all other conditions being equal), difference between modified and the initial abundance ranking starts with a higher i in $D = 1 - m/c_i$. For instance, for $r = 3$ there is no disturbance of the initial abundance ranking order until $D > 1 - m/c_3$ (for $r = 1$ this happens already for $D > 1 - m/c_1$).

3.3.2.1. Alterations in the rank–abundance curve. Our analysis shows that in the studied case, habitat destruction

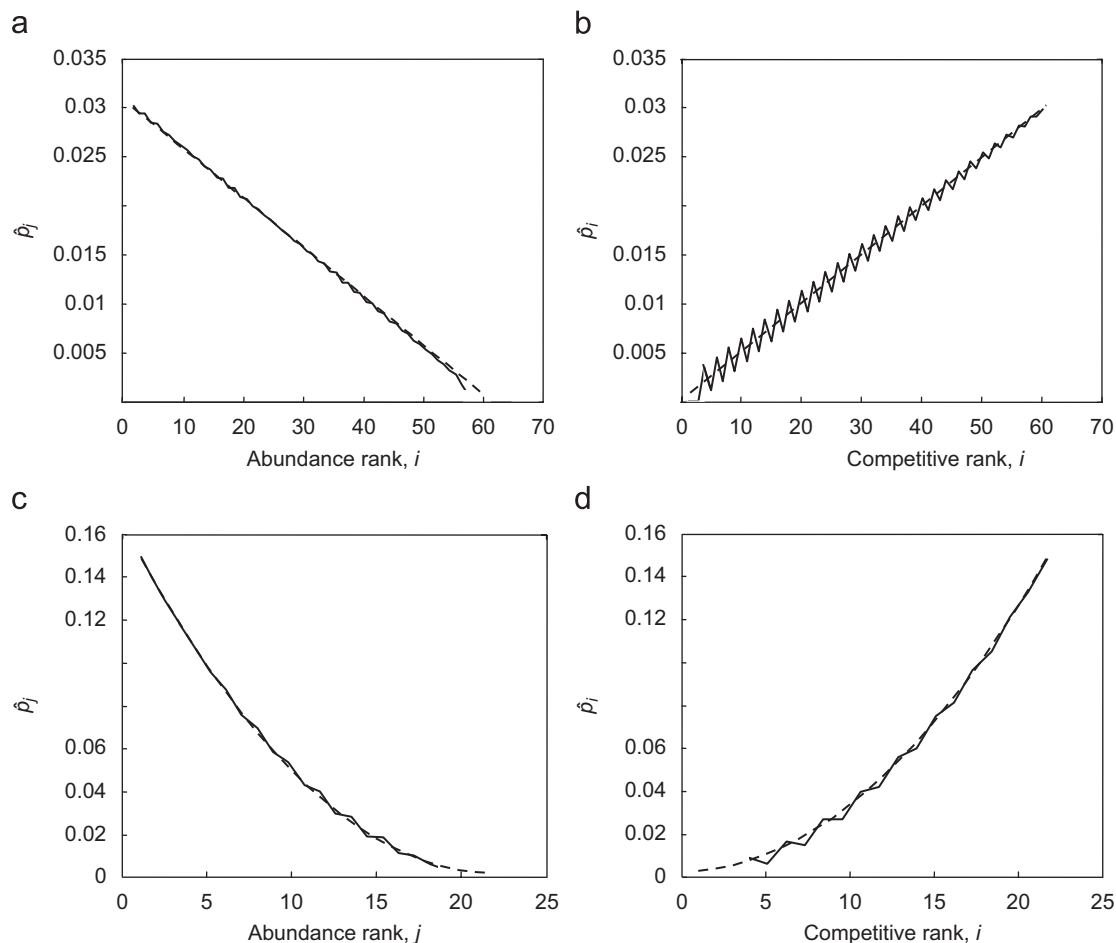


Fig. 3. Rank–abundance curves (a, c) and abundance distributions (b, d) in habitats under destruction with poor competitors initially more abundant. (a, b) Abundances of species in an intact habitat increase linearly. The curves are obtained for $D = 0.0047$, $q = 0.0005$, $n = 60$. (c, d) Abundances of species in an intact habitat increase faster than linearly. We consider quadratic increase (Eq. (23)) and show the curves obtained for $D = 0.0058$, $q = 0.0003$, $n = 22$. In both cases, the rank of the best competitor $i = 4$. Rank–abundance curve for intact habitats are shown by dashed lines.

does not lead to significant changes in the rank–abundance curve (see Fig. 3). Fig. 3a and b ($q = 0.0005$, $D = 0.0047$, the best competitor is species 4) represent the situation when initial species abundances increase linearly. Fig. 3c and d ($q = 0.0003$, $D = 0.0058$, the best competitor is species 4) are plotted for a quadratic increase of initial abundances (described by Eq. (23)). In both cases, the rank–abundances curves and the abundances for $D = 0$ are represented by dashed lines. One can easily see that although the initial order in the abundance ranking may be perturbed (especially, in the linear case), the new rank–abundance curve is situated rather close to the one plotted for the intact habitat. Our study shows that this property always holds when abundances in an intact habitat are described by a power function (5).

Completing the current section, it is worth to mention one important property of model (1) generic for all studied cases. In Appendix, it is shown that for every D the remnant intact part of the habitat ($1-D$) is large enough to provide space for all persisting species, i.e., an increase of abundances of some species is compensated by a decrease of abundances of others.

4. Discussion

Despite some criticism (McCarthy et al., 1997), the metapopulation model developed by Tilman et al. (1994) remains an important tool for exploring consequences of habitat loss in multi-species communities with competition (Loehle and Li, 1996; Stone et al., 1995; Stone et al., 1996; Klausmeier, 1998; Lin, 2005; Liu et al., 2007). In this paper, we address the issues related to succession in species abundances in such habitats: alterations of the abundance ranking, changes in the rank–abundance curve, variation in species evenness and diversity (see below). To the best of our knowledge, these important issues are rarely taken into consideration in the literature.

In each case suggested earlier by Tilman et al. (1997), the obtained above analytical expressions provide an explicit demonstration that the order of extinction coincides with the competitive ranking order in the model. Moreover, we show that in a more general case (Eq. (5)) such equivalence also takes place.

We found that the most severe alterations of abundance ranking arise in communities where either best competitors are initially most abundant or all species are initially equally abundant. For those communities, destruction of a portion of habitat leads to a complete re-organization of initial abundance hierarchy, as well as, to transformation of the rank–abundance curve. Thus, complex successions in the abundance ranking may be considered as self-organization process induced by external forcing of the system (habitat destruction). From this point of view, the most resistant are communities with poor competitors initially more abundant (e.g. coral reefs, see Stone et al., 1996). We should note that, however, in terms of species richness,

those communities are less resistant than the others (Stone, 1995; Tilman et al., 1997).

Note that successions of abundances in model (1) were partially studied by Lin (2005). By applying numerical simulations, the author considered the situation with best competitors most abundant. Our analytical treatment shows that the mentioned study is rather incomplete. In particular, a lot of patterns of succession were missed and the whole mechanism of succession was somewhat misinterpreted. This emphasizes once again the importance of analytical methods compared to numerical simulations.

The obtained expressions for equilibrium abundances allowed us to follow alterations in rank–abundance curves. We found that within every range of constant species richness, the curves exhibit symmetrical transformations. In other words, the curves become most altered for D situated close to the ends of the range; the slope of a curve becomes steeper. An interesting observation is that such transformations may result in the appearance of a Z-shaped distribution (see Fig. 1c) which visually resembles the well-known rank–abundance distributions of log-series or broken stick models, obtained from different assumptions (Magurran, 1988). While D approaches the middle of a constant richness range, the shape of the curve becomes closer to the one for an intact habitat. The dependence of rank–abundance distributions on D can be characterized quantitatively via evaluating community diversity and evenness.

To calculate the diversity index H we used the following expression (Shannon's diversity index, see Magurran, 1988):

$$H = - \sum_{i=1}^s n_i \ln(n_i), \quad n_i = \frac{\hat{p}_i}{\sum_{i=1}^s \hat{p}_i}, \quad (25)$$

where s is the number of persisting species. The corresponding index of evenness E is given by the Shannon–Wiener formula:

$$E = \frac{H}{\ln(s)}. \quad (26)$$

Fig. 4 shows variations in H and E within the whole range $0 < D < 1$ constructed for the three cases of abundance distributions in an intact habitat. From Fig. 4a one can see that for the same initial number of species, the fastest decline in biodiversity occurs for communities with poor competitors more abundant. This is due to a quicker loss rate of species for those communities for small D (Tilman et al., 1997). Another important conclusion is that the dependence $H(D)$ is non-monotonic. Every local minimum in the graph corresponds to extinction of a species. Within each range of constant richness, H attains its maximum for D situated close to the middle of the range. For example, in case of initially equal abundances (Eq. (3)), all abundances become equal for $D = \hat{D}_i$ ($H_{max} = \ln(s)$, \hat{D}_i is defined by Eq. (15)). Thus, surprisingly, the model predicts that an increase in D within some

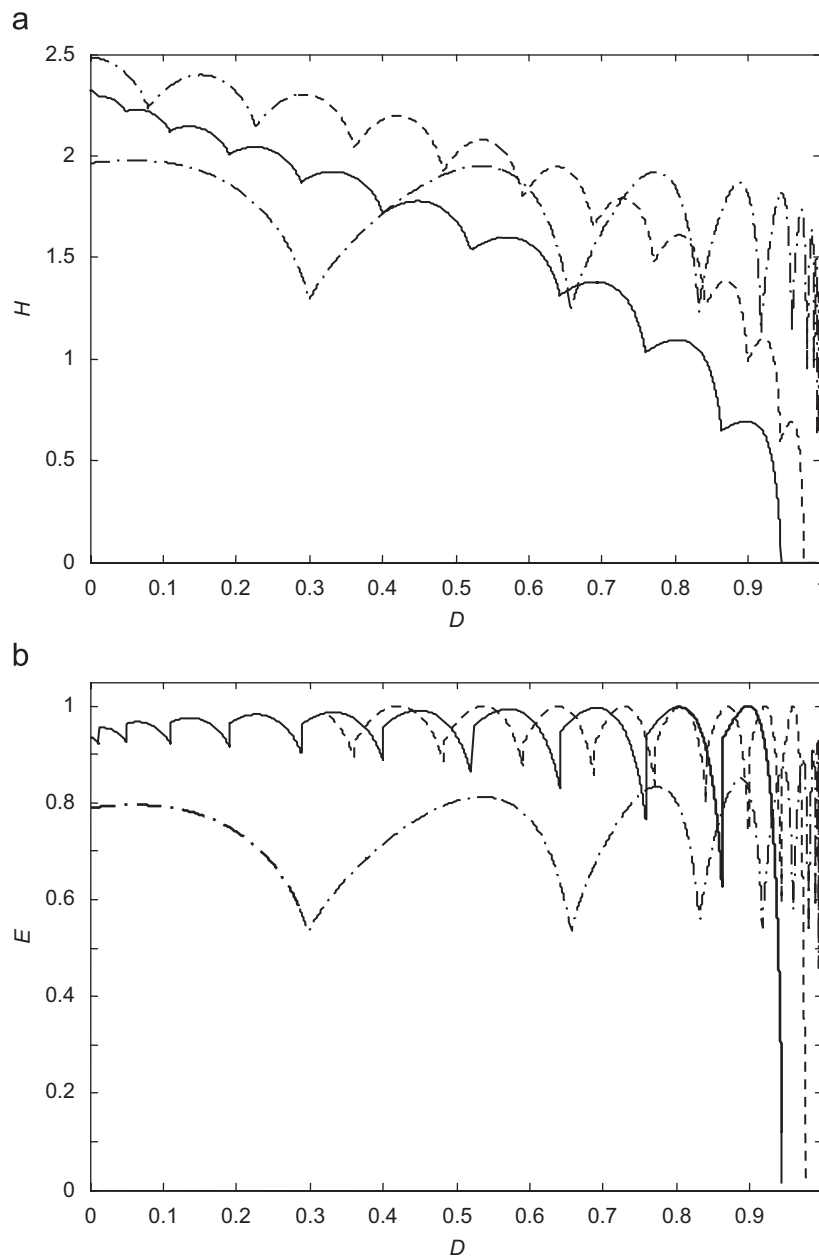


Fig. 4. (a) Diversity index H and (b) evenness index E as functions of proportion D of destroyed sites. Dashed-dotted line corresponds to the case with best competitors initially most abundant ($q = 0.3$); dashed line corresponds to the case with all species initially equally abundant ($q = 0.08$); solid line corresponds to the case with poor competitors initially most abundant ($q = 0.0125$). The number of species in an intact habitat is the same for all distributions ($n = 12$). Every local minimum in H and E is related to extinction of a species.

ranges may lead to a counter-intuitive amelioration in terms of ecosystem biodiversity (cf. Nee and May, 1992). Note that this property is rather similar to conclusions based on the intermediate disturbance hypothesis (Connell, 1978). Therefore, restoration of a portion of destroyed habitat may result in an unexpected decline in biodiversity.

Fig. 4b shows that the evenness index E exhibits a non-monotonic behavior as well. Consecutive maxima of E are slightly increasing with D (in case of initially equal abundances $E_{max} \equiv 1$). Actually, increasing in E within the ranges of constant richness (related to decreasing in single-

species dominance) is the main cause of intermediate maxima in H observed in Fig. 4a. In case when the loss of species in the community is not large, such an increase in evenness can somewhat compensate an eventual decrease in biodiversity. This is sometimes observed in ecological practice. For example, in Bohning-Gaese and Bauer (1996) it was found that biodiversity of some avian communities had increased (due to an increase in species evenness) despite a decline in species richness caused by landscape fragmentation. However, in case of dramatic loss of species (e.g. communities with initially abundant poor

competitors, see Fig. 4a), slight increase in evenness cannot ameliorate the situation.

Fig. 4b allows to address another fundamental ecological issue: an eventual relationship between the species richness and the species evenness. There is a large body of literature discussing whether such a relation exist and, if the answer is positive, whether we should consider the evenness as an independent characteristics of a community (see Gosselin, 2006, for a review). In particular, for some basic rank–abundance distributions, a negative relationship between richness and evenness was found. However, consideration of communities exposed to habitat destruction allows to address this question from another point of

view. In the previous studies, comparison was made among communities having similar rank–abundance distributions and different numbers of species. This approach may be inapplicable for studying changes of diversity of the same community, where rank–abundance distributions can vary considerably with species richness. For example, for a community with initial abundance distribution (Eq. (2)), referred as ‘geometric’ in the literature, we do not observe a pronounced increase in evenness with a decrease of richness which was found in Gosselin (2006).

Throughout the paper, we considered the mortality rate to be exactly equal for all competitors. In a real ecosystem this is not true even though mortalities may be close to each

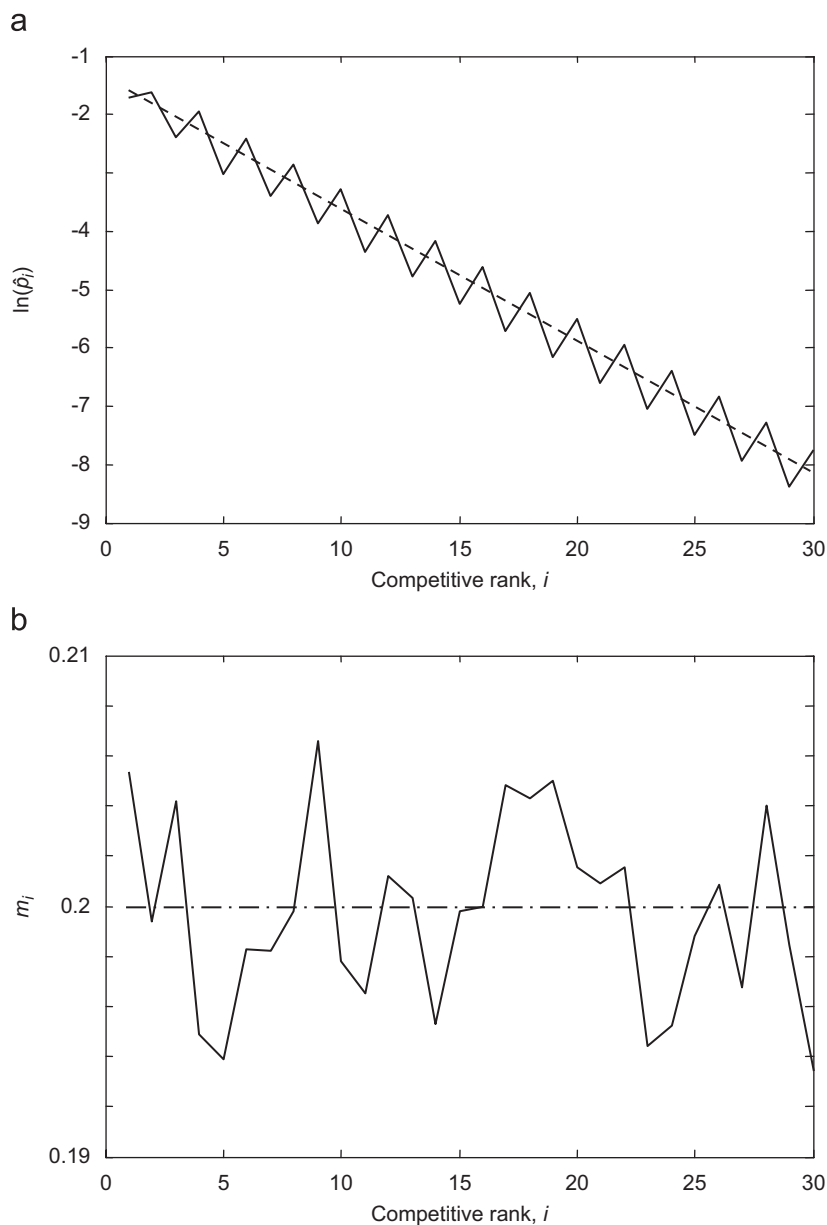


Fig. 5. Pattern of self-organization in species abundance distribution in an intact habitat ($D = 0$) induced by a random perturbation of the mortality rate ($\eta = 0.05$), i.e., random perturbation of m_i would result in a strict alternation in \hat{p}_i with odd and even ranks. We show the situation with best competitors most abundant ($q = 0.2$). (a) Abundance distribution of species. Dashed line represents the case when $m_i = m_0 = 0.2$. (b) Mortality rates of species.

other. We explored the situation when m is slightly perturbed:

$$m_i = m_0(1 + \eta\alpha_i), \tag{27}$$

where α_i is a random variable with a uniform distribution over the range $(-0.5, 0.5)$, η is a positive coefficient. Thus, the mean mortality rate is m_0 and the standard deviation is $(\eta m_0)^2/12$. In our study, we consider that is η rather small: $\eta < 0.05$.

For each set of (q, m_0) , we generated about 50 different sets of $\{m_i\}$ and followed the succession in species abundances for an increase in D for all cases (Eqs. (2)–(4)). Our simulations show that patterns of succession in the abundances ranking, in general, exhibit behavior similar to the one observed for $m_i = m_0$. Some disturbances in the patterns of succession take place, as well. However, pronounced alterations occur only in the vicinity of $D = 1 - m/c_i$.

Another interesting observation is that even for $D = 0$, random perturbation (Eq. (27)) of mortality would result in system’s self-organization. After a few ‘random’ oscillations in abundances of best competitors, the densities of species with odd and even competitive ranks strictly alternate (see Fig. 5a), although the corresponding values of mortality do not behave in a similar way (Fig. 5b). This phenomenon took place for more than 80% simulations (we have done about 100 simulations in total).

Note that there are some possible constrains for observing the complex patterns obtained in the paper in real ecosystems. The point is that we consider here species abundances at equilibrium. The process of transition in habitats under destruction may require long time (Diamond, 1972; Fahrig, 1992). Thus, transients observed in ecosystems might have nothing to do with the final abundance distribution; one of the consequences is the extinction debt phenomenon (Tilman et al., 1994, 1997). Another reason is possible extinction of some less abundant species due to a sharp destroying of a portion of the habitat (Lin, 2005). Species densities decrease beyond a certain threshold and the species go extinct; only a later re-colonization from other habitats would result in their reestablishment. Finally, a very important aspect is the impact of spatial heterogeneity (Neuhauser, 1998; Huxel and Hastings, 1999; Ovaskainen et al., 2002). It was shown that considering local dispersals, clamped remnant sites and finite habitat dimensions may somewhat alter predictions made based on the spatially implicit model (1) (Tilman et al., 1997; Klausmeier, 1998).

Acknowledgments

We highly appreciated our long-term collaborator Dr. Sergei V. Petrovskii for comments. This research was partially supported by the US National Science Foundation’s Biocomplexity Program (DEB-0421530) and Long-Term Ecological Research Program (Sevilleta LTER,

DEB-027774) and the University of California Agricultural Experiment Station.

Appendix

Here we prove two important properties of model (1).

- *Property 1.* In case of equal mortalities, the colonization rates c_i are given by

$$c_i = \frac{m}{[1 - F(i)][1 - F(i - 1)]}, \tag{A.1}$$

where $F(i) = \hat{p}_1 + \hat{p}_2 + \hat{p}_3 + \dots + \hat{p}_i$; \hat{p}_j are the equilibrium abundances in an intact habitat.

To prove this property, we use Eq. (6) with $D = 0$ and perform summation of the abundances over all species 1, 2, ..., i . For the sake of simplicity, we assume that $i = 2k + 1$ (for $i = 2k$ the proof is similar). We obtain

$$\begin{aligned} F(2k) &= \hat{p}_1 + \hat{p}_2 + \hat{p}_3 + \dots + \hat{p}_{2k} \\ &= 1 - \frac{c_1 c_3 c_5 \dots c_{2k-1}}{c_2 c_4 c_6 \dots c_{2k}}, \\ F(2k + 1) &= \hat{p}_1 + \hat{p}_2 + \hat{p}_3 + \dots + \hat{p}_{2k+1} \\ &= 1 - \frac{c_2 c_4 c_6 \dots c_{2k}}{c_1 c_3 c_5 \dots c_{2k-1} c_{2k+1}} m. \end{aligned} \tag{A.2}$$

From expressions (A.2), one can easily derive that

$$c_{2k+1} = \frac{m}{[1 - F(2k + 1)][1 - F(2k)]}. \tag{A.3}$$

Thus, we arrive at Eq. (A.1). For $i = 2k$ the proof is the same.

- *Property 2.* Suppose that $D \in (1 - m/c_i, 1 - m/c_{i+1})$, where c_i is given by Eqs. (2)–(5). For any $i < n$, we have

$$1 - D - (\hat{p}_{i+2k-1} + \hat{p}_{i+2k} + \hat{p}_{i+2k+1} + \dots + \hat{p}_n) > 0. \tag{A.4}$$

As it is shown in the paper, within the considered range of D , the strongest competitor is species $i + 1$. We use Eq. (6) again (with a substitution of c_1 by c_{i+1}) and perform summation over all species remaining in the community. We obtain that

$$\begin{aligned} \hat{S}_1 &= \hat{p}_{i+2k-1} + \hat{p}_{i+2k} + \hat{p}_{i+2k+1} + \dots + \hat{p}_n \\ &= 1 - D - (1 - D) \frac{c_{i+1} c_{i+3} c_{i+5} \dots c_{n-1}}{c_{i+2} c_{i+4} c_{i+6} \dots c_n}, \\ \hat{S}_2 &= \hat{p}_{i+2k-1} + \hat{p}_{i+2k} + \hat{p}_{i+2k+1} + \dots + \hat{p}_n \\ &= 1 - D - \frac{c_{i+2} c_{i+4} c_{i+6} \dots c_{n-1}}{c_{i+1} c_{i+3} c_{i+5} \dots c_n} m, \end{aligned} \tag{A.5}$$

where \hat{S}_1 corresponds to an even number and \hat{S}_2 corresponds to an odd number of remnant species.

From Eq. (A.5) it is easy to see that $1 - D - \hat{S}_1 > 0$ and $1 - D - \hat{S}_2 > 0$, i.e., property (A.4). In other words, the undestroyed part $(1 - D)$ of the habitat is still large enough to provide space for the remaining $n - i$ species in the community.

References

- Bohning-Gaese, K., Bauer, H.-G., 1996. Changes in species abundance, distribution, and diversity in a central European bird community. *Conserv. Biol.* 10, 175–187.
- Bolger, T., 2001. The functional value of species biodiversity—a review. *Proc. R. Irish Acad.* 101, 199–224.
- Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs—high diversity of trees and corals is maintained only in a non-equilibrium state. *Science* 199, 1302–1310.
- Cushman, S.A., McGarigal, K., 2003. Landscape-level patterns of avian diversity in the Oregon Coast Range. *Ecol. Monogr.* 73, 259–281.
- Diamond, J.M., 1972. Biogeographic kinetics: estimation of relaxation times for avifaunas of south-west Pacific Islands. *PNAS* 69, 3199–3203.
- Fahrig, L., 1992. Relative importance of spatial and temporal scales in a patchy environment. *Theor. Popul. Biol.* 41, 300–329.
- Gosselin, F., 2006. An assessment of the dependence of evenness indices on species richness. *J. Theor. Biol.* 242, 591–597.
- Gray, J.S., 1979. Pollution-induced changes in populations. *Phil. Tran. R. Soc. B* 286, 545–557.
- Hastings, A., 1980. Disturbance, coexistence, history, and competition for space. *Theor. Popul. Biol.* 18, 363–373.
- Hill, J.K., Hamer, K.C., 1998. Using species-abundance models as indicators of habitat disturbance in tropical forests. *J. Appl. Ecol.* 35, 458–460.
- Huxel, G., Hastings, A., 1999. Habitat Loss, Fragmentation, and Restoration. *Restorat. Ecol.* 7, 309–315.
- Klausmeier, C.A., 1998. Extinction in multispecies and spatially explicit models of habitat destruction. *Am. Nat.* 152, 303–310.
- Klausmeier, C.A., Tilman, D., 2002. Spatial models of competition. In: Sommer, U., Worm, B. (Eds.), *Competition and Coexistence*. Ecological Studies, vol. 161. Springer, Berlin, pp. 43–78.
- Lin, Z.S., 2005. The ecological order of persisting species during habitat destruction. *Ecol. Model.* 184, 249–256.
- Liu, H.Y., Lin, Z.S., Wen, T., 2007. Responses of metapopulation dynamics to two different kinds of habitat destruction caused by human activities. *Plant Ecol.* 188, 53–65.
- Loehle, C., Li, B.-L., 1996. Habitat destruction and the extinction debt revisited. *Ecol. Appl.* 6, 784–789.
- Mac Nally, R., 2007. Use of the abundance spectrum and relative-abundance distributions to analyze assemblage change in massively altered landscapes. *Am. Nat.* 170, 319–330.
- Magurran, A.E., 1988. *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, NJ.
- McCarthy, M.A., Lindenmayer, D.B., Drechsler, M., 1997. Extinction debts and risks faced by abundant competitive communities. *Conserv. Biol.* 11, 221–226.
- Mouquet, N., Loreau, M., 2003. Community patterns in sourcesink metacommunities. *Am. Nat.* 162, 544–557.
- Nee, S., May, R., 1992. Dynamics of metapopulations: habitat destruction and competitive coexistence. *J. Anim. Ecol.* 61, 37–40.
- Neuhauser, C., 1998. Habitat destruction and competitive coexistence in spatially explicit models with local interactions. *J. Theor. Biol.* 193, 445–463.
- Ovaskainen, O., Sato, K., Bascompte, J., Hanski, I., 2002. Metapopulation models for extinction threshold in spatially correlated landscapes. *J. Theor. Biol.* 215, 95–108.
- Seigel, A., Hatfield, C., Hartman, J.M., 2005. Avian response to restoration of urban tidal marshes in the Hackensack Meadowlands, New Jersey. *Urban Habitats* 3, 87–116.
- Stirling, G., Wilsey, B., 2001. Empirical relationships between species richness, evenness and proportional diversity. *Am. Nat.* 158, 286–299.
- Stone, L., 1995. Biodiversity and habitat destruction: a comparative study of model forest and coral reef ecosystems. *Proc. R. Soc. B* 261, 381–388.
- Stone, L., Eilam, E., Abelson, A., Ilan, M., 1996. Modelling coral reef biodiversity and habitat destruction. *Mar. Ecol. Prog. Ser.* 134, 299–302.
- Tilman, D., May, R.M., Lehman, C.L., Nowak, M.A., 1994. Habitat destruction and the extinction debt. *Nature* 371, 65–66.
- Tilman, D., Lehman, C.L., Yin, C., 1997. Habitat destruction, dispersal, and deterministic extinction in competitive communities. *Am. Nat.* 149, 407–435.
- Weiher, E., Keddy, P.A., 1999. Relative abundance and evenness patterns along diversity and biomass gradients. *Oikos* 87, 355–361.
- Wilson, E.O., 1992. *The Biodiversity of Life*. Belknap Press of Harvard University Press, Cambridge, MA.