

1 **Malthusian Catastrophe: Species Extinction Caused by Oversized Population**

2 Xubin Pan^{1*}

3 ¹Institute of Plant Quarantine, Chinese Academy of Inspection and Quarantine,

4 Beijing 100029, China

5 *To whom correspondence should be addressed. E-mail: xubin.hu.pan@gmail.com

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9

10 **Abstract**

11 There is one pseudo-extinction debt and four occurring conditions for real extinction
12 debt. Since small and oversized populations have a high extinction risk, Pan threshold
13 (upper limit) was calculated for Verhulst-Pear “logistic” growth model and logistic
14 model with the Allee effect, an important parameter corresponding to Allee threshold
15 (lower limit).

16

17 **Keywords** Allee threshold, Pan threshold, carrying capacity, disturbance, species
18 immigration

19

20 The prediction and management of population dynamic is central to human
21 sustainable development and ecosystem protection. We have been aware that small
22 population has a high risk of extinction rate [1] and our society has utilized many
23 resources to save endangered species. However, if we overlooked the extinction risk
24 caused by oversized population, Malthusian catastrophe would happen [2].

25

26 The extinction of most species was a long-term process, and few species suddenly
27 became extinct. The phenomenon has been coined as extinction debt in ecology,
28 which is worth investigating due to its application in wildlife conservation and
29 invasive species management. Particularly, species extinction rate has been

30 accelerated due to climate change [3]. If we understand well the occurring conditions
31 of extinction debt, we will be able to slow down the extinction of or even save
32 endangered species, or eliminate undesired alien species in someplace.

33

34 Several studies are available on the mechanism of extinction debt caused by changes
35 in habitat quality/quantity/connectivity [4,5]. Habitat loss or degradation might repel
36 one species and favor another. Furthermore, little research has been conducted on the
37 link between habitat change and population change embedded in the context of
38 extinction debt. Thus, it is necessary to explore the occurring conditions of extinction
39 debt for specific species and how the extinction debt will be affected by forcing
40 events. Unfortunately, few records have been found on the occurring conditions
41 taking into account population dynamics. To simplify population dynamics, we
42 proposed a framework with the fluctuation of population size (N) around carrying
43 capacity (K) with self-adjustment as a quasi-steady state. If the population size falls
44 below the Allee threshold (A), extinction debt will occur, the process of which will be
45 irreversible. Normally, the species' population can sustain continuously until the
46 population and/or the habitat are highly impacted by external disturbances.

47

48 One type of direct extinction occurs when a species disappear immediately due to the
49 disturbance at time t , when the population size is decreased to 0 (Figure 1A, $N_t=0$). As
50 for another type of direct extinction or pseudo-extinction debt, the species population
51 can sustain for a short period of time after the disturbance, since population does not

52 have any new individuals but old, injured or gender-imbalanced individuals. In this
53 case, the time interval from N_t to 0 (extinction) is shorter than the life span of the
54 species (Figure 1B, $N_t > 0$).

55

56 For the occurrence of extinction debt, there are two typical conditions. One is that N_0
57 decreases to N_t due to the disturbance at time t , which is less than A (Figure 1C). The
58 other is that K shrink to less than A due to the disturbance at time t (Figure 1D). Then
59 N_t follows K and falls below A eventually.

60

61 When the population size is larger than K , it will decrease or regress to K , leading to
62 fluctuation of N around K under normal conditions. If the population size is too large
63 (here we define the existing limit as the Pan threshold, P), the call-back of N can be
64 zero or less than A , resulting in an extinction debt finally. Two conditions might lead
65 to such an outcome. One condition is that K is suppressed by the disturbance so that
66 N_t is higher than P (Figure 1E, P is a function of K and positively correlated with K).
67 The other is that N_0 is raised to N_t by external force, which is higher than P (Figure
68 1F).

69

70 The formula for calculating Pan threshold (P) of the two typical population growth
71 models, Verhulst-Pear “logistic” growth model [6] and logistic model with the Allee
72 effect [7], is as follows:

73 For the Verhulst-Pear “logistic” growth model,

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right)$$

74 where r is the growth rate. When $N + \frac{dN}{dt} * 1 = 0$, we get the Pan threshold

$$N + rN \left(1 - \frac{N}{K}\right) = N \left(1 + r - \frac{rN}{K}\right) = 0$$

$$P = \frac{K}{r} (1 + r) = \left(1 + \frac{1}{r}\right)K$$

75 For the logistic model with the Allee effect,

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) \left(\frac{N - A}{K}\right)$$

76 When $N + \frac{dN}{dt} * 1 = A$, we get the Pan threshold

$$N + rN \left(1 - \frac{N}{K}\right) \left(\frac{N - A}{K}\right) = A$$

$$(N - A) + rN \left(1 - \frac{N}{K}\right) \left(\frac{N - A}{K}\right) = 0$$

$$(N - A) \left(1 + N \frac{r}{K} \left(1 - \frac{N}{K}\right)\right) = 0$$

77 $N > A$ and $K > 0$, $\left(1 + N \frac{r}{K} \left(1 - \frac{N}{K}\right)\right) = 0$, $K^2 + Nr(K - N) = 0$

$$rN^2 - rKN - K^2 = 0$$

$$P = \frac{rK + \sqrt{r^2K^2 + 4rK^2}}{2r} = \frac{1 + \sqrt{1 + \frac{4}{r}}}{2} K$$

78 For both growth models, P increases with the increase of K or the decrease of r . And

79 P is not relevant to A in both models.

80

81 There are two dead zones for species population, meaning either small population or

82 oversized population can lead to species extinction. One is below the Allee threshold,

83 and the other is above the Pan threshold. If the population size falls within these two

84 dead zones, the species will be in the process of extinction debt. Thus, appropriate

85 population size should be within $[A, P]$ (Figure 2a). Both A and K are equilibrium

86 points, and the point P will transform to A soon. Others points in the interval will

87 fluctuate around the point K . Both extremely small ($N < A$) and extremely large ($N > P$)
88 population will go extinct eventually. Thus we can adjust the population (r) or
89 carrying capacity (K) to control the occurrence of extinction debt according to policy
90 goals. Species immigration, which is not considered in the above simplified frame,
91 also exerts a significant impact on the extinction debt. Based on our analysis, in
92 Figure 1C, species immigration can help increase the population size and produce a
93 credit, especially when considering the effect of genetic exchange of species on the
94 Allee threshold (A) [4]. However, Figure 1E and 1F reveal that, species immigration
95 can become a burden for existing large-sized population.

96

97 Therefore, the Allee threshold [8], or the Pan threshold can be utilized to improve
98 endangered species conservation and invasive species control. For example, there is a
99 lag between the peaks of the two species in the prey-predator (Lotka–Volterra)
100 equations [9] (Figure 2b). Allee effect can be employed to control the predator
101 population directly, while Pan threshold to regulate the prey population (K). When the
102 predator population size is large, and the prey population is continuously decreased
103 due to natural or anthropogenic disturbances, the population of predator can easily
104 surpass the Pan threshold and become extinct. This might be the possible mechanism
105 of extinction for many flourishing species in the geological history.

106

107 **Conclusions**

108 There is one pseudo-extinction debt and four occurring conditions for real extinction

109 debt in the frame with Allee threshold, carrying capacity and exogenous disturbance.
110 For Verhulst-Pear “logistic” growth model and logistic model with the Allee effect,
111 Pan threshold (upper limit) is proposed as an important parameter corresponding to
112 Allee threshold (lower limit). The measures considering the occurring conditions of
113 extinction debt would further improve biodiversity conservation and bio-invasion
114 control.

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135 **Figure legends**

136 Figure 1. The occurring conditions of extinction debt in a habitat due to the

137 disturbance impact in time t on the population size N_0 (Fig. 1A, 1B and 1C), carrying

138 capacity (Fig. 1D and 1E) and population dynamics (Fig. 1F).

139 Figure 2. Allee threshold (A), carrying capacity (K) and Pan threshold (P) (2A). The

140 population size can be divided into three sections: survival interval and two extinction

141 intervals (2A). Population dynamics of prey and predator species (2B). There is a lag

142 between the prey population peak and the predator population peak (2B).

143

144 **Declarations section**

145 *Ethics approval and consent to participate*

146 Not applicable.

147 *Consent for publication*

148 All author agrees this submission.

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155 *Conflict of Interest*

156 The authors declare that they have no conflict of interest.

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