Supplementary Note C

Kin-selection model for the intergenerational common-pool resource game

The niche-construction models of Lehmann (2007) and Lehmann and Rousset (2010) can be adapted to model an ICPR scenario. The starting point is Wright's infinite islands model (Wright 1931). We consider a landscape with an infinite number of common-pool resources ("islands"), each with the capacity to support N adults. Adults harvest the resource, which they use to produce clonal offspring, and then they die (non-overlapping generations). It is assumed that the number of juveniles produced per adult is large. Juveniles may stay at their natal resource pool or disperse to another pool with probability m. Each juvenile that settled at a pool has an equal chance of becoming one of the N adults who obtain a territory and produce the next generation. Juveniles that miss out on a territory die.

We consider a baseline scenario where the resource-use strategy y is sustainable, and we consider a mutant strategy z that over-exploits the resource pool and harms future generations. We ask, under what conditions can the over-exploiting strategy invade?

Relative fecundity and fitness function

Because $1 - m$ proportion of juveniles do not disperse, relatedness builds up between individuals at a pool, and therefore individuals' resource-use strategies are also related. Let $z_{\bullet}$ be the phenotype of the focal individual (the mutant), z_R be the average phenotype of all individuals at the pool including the focal individual, and z_t be the average phenotype of individuals at the pool t generations ago.

Over-exploitation of the pool benefits the individual but has a cost to future generations at the pool. Let B be the incremental benefit of over-exploiting the pool, and C_t be the cost of over-exploitation that occurred t generations ago. In contrast to the niche-construction models in Lehmann (2007) and Lehmann and Rousset (2010), this model assumes that over-exploitation has no direct effects on other individuals sharing the pool in the current generation. The relative fecundity of the focal individual is

$$f_{\bullet} = 1 + Bz_{\bullet} - \sum_{t=1}^{\infty} C_t \, z_t, \qquad \text{(SI A.1)}$$

where $Bz_{\bullet}$ represents the benefit of over-exploiting the pool, and $-Cz_t$ is the cost of overexploitation that occurred t generations ago on the current generation.

The relative fecundity in the landscape is

$$f_y = 1 + By + \sum_{t=1}^{\infty} C_t\, y_t \tag{SI A.2}$$

where y is the average phenotype in the landscape.

The relative fecundity in the focal deme — including the focal individual's fecundity — is

$$f_R = 1 + Bz_R - \sum_{t=1}^{\infty} C_t\, z_t. \tag{SI A.3}$$

The non-dispersing portion of the locally produced juveniles will compete with the focal individual's offspring for territories at the pool.

The fitness of the focal individual is therefore (A-30 Lehmann and Rousset 2010)

$$w = \frac{(1-m)f_{\bullet}}{(1-m)f_R + mf_y} + \frac{mf_{\bullet}}{f_y}. \tag{SI A.4}$$

The first term is for offspring who stay at the natal pool, and the second term is for offspring who disperse. Each term is the proportion of offspring in each scenario (staying home, $1 - m$; or dispersing, m) multiplied by the chance of winning a territory in that scenario.

Relatedness calculations

Expressions for three different types of relatedness are needed before we can evaluate the inclusive fitness effect (in the next subsection). Relatedness is calculated as the probability that two individuals are identical by descent. Rousset (2013, p. 23–28) provides the general approach to relatedness calculations; here, we will focus on our particular scenario.

Let R be the relatedness between two different adults randomly chosen from the same pool (i.e. chosen without replacement). Let R_R be the relatedness between any two adults randomly chosen from the same pool, including the possibility of choosing the same individual twice (i.e. chosen with replacement). Then

$$R_R = \frac{1}{N} + \left(\frac{N-1}{N}\right) R, \tag{SI A.5}$$

where the first term is when the same individual is chosen again (an individual has relatedness 1 to itself), and the second term is when a different individual is chosen.

To obtain an expression for R, we follow the lineages of two adults backwards in time. In an infinite landscape, two adults will only have have non-zero relatedness if their current pool is also their natal pool, i.e. both did not disperse, which has probability $(1-m)^2$. Therefore the relatedness between two pre-dispersal juveniles at the same pool is

$$R_{JJ} = \frac{1}{N} + \left(\frac{N-1}{N}\right) R,$$

where the first term is when both juveniles have the same parent, and the second term is when they have different parents. R_{JJ} is also equal to R_R so

$$R = (1-m)^2 R_R. \tag{SI A.6}$$

Let R_t be the relatedness between an adult in the present generation and an adult residing at the same pool t generations ago. To find R_t, we follow the lineage of the present-generation individual back in time. In an infinite landscape, the present-generation adult will only have non-zero relatedness to the $-t$-generation adult if the lineage of the present-generation adult resided at the current pool for t generations, which has probability $(1-m)^t$. This calculation takes us back in time to a particular pre-dispersal juvenile who is the offspring of some adult t generations ago. The relatedness between a pre-dispersal juvenile and an adult is

$$R_{JA} = \frac{1}{N} + \left(\frac{N-1}{N}\right) R,$$

where the first term is when the target adult is the parent (reproduction is clonal so relatedness to parents is 1), and the second term is when a different individual is the parent. R_{JA} is also equal to R_R so

$$R_t = (1-m)^t R_R. \tag{SI A.7}$$

Inclusive fitness effect

Following Lehmann and Rousset (2010), the inclusive fitness effect is calculated

$$S_{IF} = \frac{\partial w}{\partial z_\bullet} + \frac{\partial w}{\partial z_R} R_R + \sum_{t=1}^{\infty} \frac{\partial w}{\partial z_t} R_t. \tag{SI A.8}$$

The invasion fitness of the mutant strategy is found by evaluating S_{IF} at the resident steady-state, which is the strategy of sustainable resource use, $z_\bullet = z_R = z_t = y = y_t = 0$. The partial derivative terms are

$$\left.\frac{\partial w}{\partial z_{\bullet}}\right|_{0} = B, \quad \left.\frac{\partial w}{\partial z_{R}}\right|_{0} = -B(1-m)^2, \quad \left.\frac{\partial w}{\partial z_{t}}\right|_{0} = -(1-(m-1)^2)C_t. \tag{SI A.9}$$

Substituting into Eq. SI A.8

$$S_{IF} = B - BR_R(1-m)^2 - \sum_{t=1}^{\infty}(1-(1-m)^2)\,C_tR_t. \tag{SI A.10}$$

Substituting in expressions for R_R (Eq. SI A.5), R (Eq. SI A.6), and R_t (Eq. SI A.7), and rearranging,

$$S_{IF} = (1-R)\left(B - \sum_{t=1}^{\infty}\frac{C_t(1-m)^t}{N}\right). \tag{SI A.11}$$

Following Lehmann (2007), we assume that the effects of over-exploitation decay at a constant rate with time

$$C_t = \lambda^t C. \tag{SI A.12}$$

Substituting into Eq. SI A.8

$$S_{IF} = (1-R)\left(B - \frac{C}{N}\sum_{t=1}^{\infty}(\lambda(1-m))^t\right), \tag{SI A.13}$$

which gives the following condition for the invasion of over-exploitation:

$$\frac{B}{C} > \frac{1}{N}\sum_{t=1}^{\infty}(\lambda(1-m))^t. \tag{SI A.14}$$

Given that $\lambda(1-m) < 1$, then Eq. SI A.14 can be simplified

$$\frac{B}{C} > \frac{\lambda(1-m)}{N(1-\lambda(1-m))}. \tag{SI A.15}$$

Interpretation

From Eq. SI A.15, over-exploitation of the common-pool resource is promoted by: high individual benefits to over-exploitation (high B), a low impact on the pool (low C) that is short-lasting (low λ), a low probability that one's own offspring will inherit the pool (high m), and a large number of individuals sharing the pool (high N).

References

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