

Supporting Information

Details of the mutational process

Since random mutations could have a bias towards increasing the requirement K , we assume that with probability $P_K^+(K_{j,i}) = b_K + (1 - b_K) \exp(-K_{j,i} / \sigma_K)$, $K_{j,i}$ is sampled uniformly from $[K_{j,i}, a_K K_{j,i}]$ and with probability $1 - P_K^+$ from $[K_{j,i} / a_K, K_{j,i}]$. Here $a_K > 1$, $\sigma_K > 0$, and $0 \leq b_K \leq 1$ parameterize the magnitude of mutations, the range of typical values, and the bias in favor of degrading mutations, respectively. Similarly, with probability P_C^+ , $C_{j,i}$ is sampled uniformly from $[C_{j,i}, a_C C_{j,i}]$ and with probability $1 - P_C^+$ from $[C_{j,i} / a_C, C_{j,i}]$. The probability to increase the resource consumption parameters is chosen to be log-normal, $P_C^+(c_{j,i}) = C_0 / 2C_{j,i} \cdot \exp(-(\log(C_{j,i} / C_0))^2 / 2\sigma_C^2)$. The parameters here are $a_C > 1$, the amplitude of mutations, $C_0 > 0$, the value towards which mutations typically tend, and $\sigma_C > 0$, which determines how far from C_0 values of $C_{j,i}$ can stray. Drawing the mutations in this way prevents runaway in parameter space towards extreme values. This is both technically convenient, but also reflects the reality of physiological constraints that bound the range of possible organisms.

Sensitivity to parameter values

Different values of the six parameters of the mutational process can give rise to many processes – from highly constrained mutations of small amplitude to large and essentially random mutations. To determine the effect of the particular choice of the mutational

process on the evolution of biodiversity, we randomly sampled 100 combinations of mutational parameters and simulated evolution in an environment with 20 resources. In all the cases, the main results, as represented by Fig. 2, were reproduced (Fig. S1). For the rest of the numerical simulations, consisting of realizations with many more values of the number of resources, and 20 repetitions in each environment, were done with one choice of the mutational parameters such that

$$\begin{aligned} a_K &= 1.5, & b_K &= 0.97, & \sigma_K &= 0.1 \\ a_C &= 1.5, & C_0 &= 0.2, & \sigma_C &= 0.02. \end{aligned}$$

Analytical test for existence of ecological equilibrium for a given set of species parameters (Supporting Information for Fig. 3)

In this section we derive the conditions for n species competing for k resources to exist in equilibrium. This test, applied to all the subsets of species that include the new mutant lineage, is used to calculate the distribution and maximum possible species number in Fig. 3 of the main text.

Conditions for stability of a fixed point in this model were previously derived for 3 species and 3 resources (1). Here we extend these results to any number of species and resources.

Let $C_{ji}, K_{ji}, j = 1, \dots, k, i = 1, \dots, n$ be species parameters

governing the system of differential equations

$$(1) \quad \begin{aligned} \frac{dN_i}{dt} &= N_i(\mu_i(R_1, \dots, R_k) - m), & i = 1, \dots, n \\ \frac{dR_j}{dt} &= D(S_j - R_j) - \sum_{i=1}^n C_{ji} \mu_i(R_1, \dots, R_k) N_i, & j = 1, \dots, k \\ \mu_i(R_1, \dots, R_k) &= \min_j \mu_{ji} = \min_j \left\{ \frac{rR_j}{K_{ji} + R_j} \right\}. \end{aligned}$$

The parameters K_{ji} are called the *resource requirement* parameters, and C_{ji} the *resource consumption*. S_j are parameters for the supply of resources in the environment.

Fixed point conditions

A fixed point is defined as a point $(N_1^*, \dots, N_n^*, R_1^*, \dots, R_k^*)$ at which the time derivatives of all variables are zero. The fixed point requirement for the abundance of species i is given by

$$(2) \quad 0 = \frac{dN_i}{dt} \Big|_{N_i=N_i^*} = N_i^* (\mu_i(R_1^*, \dots, R_k^*) - m) \Rightarrow \min_j \left\{ \frac{rR_j^*}{K_{ji} + R_j^*} \right\} = m.$$

If j is the index of the resource which limits the growth (saturates the minimum growth rate) of species i in equilibrium, then

$$(3) \quad \frac{rR_j^*}{K_{ji} + R_j^*} = m \Rightarrow R_j^* = \alpha K_{ji}, \quad \alpha \equiv \frac{m}{r - m}.$$

Thus the equilibrium concentration of a limiting resource is determined by the parameters of the species it is limiting. It follows that for two or more species to be limited by the same resource it is necessary that they have exactly the same requirement parameter for this resource, which we assume is never the case. Since each species must be limited by a separate resource, the number of species that can coexist in equilibrium cannot exceed the number of resources.

The condition that j is the limiting resource for species i means that the growth rate of this species with respect to any other resource is greater:

$$(4) \quad \frac{rR_j^*}{K_{ji} + R_j^*} < \frac{rR_{j'}^*}{K_{j'i} + R_{j'}^*}, \quad \forall j' \neq j,$$

which can be rewritten as

$$(5) \quad \frac{R_j^*}{K_{ji}} = \alpha < \frac{R_{j'}^*}{K_{j'i}} \quad \forall j' \neq j.$$

For any other species i' that is limited by a resource j' , eq. (3) can be used to rewrite this condition as

$$(6) \quad \alpha < \frac{R_{j'}^*}{K_{j'i}} = \frac{\alpha K_{j'i'}}{K_{j'i}},$$

or

$$(7) \quad K_{j'i} < K_{j'i'} \quad \forall i \neq i'.$$

This means that for a resource j' which is limiting species i' in equilibrium, $K_{j'i'}$ is the largest element in the j' -th row of $\{K_{ji'}\}$. In other words, *if* a resource is a limiting resource for a species, then that species must be the one which has the largest requirement for the resource.

For each resource j , we denote by $\sigma(j)$ the index of the largest element in the row:

$$(8) \quad \sigma(j) : K_{j\sigma(j)} = \max_i K_{ji}.$$

A necessary condition for equilibrium with n species is that there are n resources that are each limiting one of the species. A subset of resources $\{j_1, j_2, \dots, j_n\}$ can be the set of limiting resources in equilibrium only if each of the species is represented:

$$(9) \quad \{\sigma(j_1), \sigma(j_2), \dots, \sigma(j_n)\} = \{1, \dots, n\}.$$

In particular, a necessary condition for the existence of such an equilibrium is that $\{1, \dots, n\} \subseteq \{\sigma(1), \sigma(2), \dots, \sigma(k)\}$.

Listing all possible equilibrium solutions with n species thus begins by finding all subsets of resources that satisfy eq. (9).

Given a subset of resources that satisfies eq. (9), we can relabel the resources so that, WLOG, the i -th species is limited in equilibrium by the i -th resource. The n equations in (2) are satisfied by setting

$$(10) \quad R_j^* = \alpha K_{jj}, \quad i = 1, \dots, n.$$

The rest fixed-point equations are

$$(11) \quad 0 = \left. \frac{dR_j}{dt} \right|_{R_j=R_j^*} = D(S_j - R_j^*) - \sum_{i=1}^n C_{ji} \mu_i(R_1^*, \dots, R_k^*) N_i^*, \quad j = 1, \dots, k.$$

For $j=1, \dots, n$, substituting the solutions (10) yields

$$(12) \quad 0 = D(S_j - \alpha K_{jj}) - \sum_{i=1}^n C_{ji} m N_i^*, \quad j = 1, \dots, n.$$

It is convenient at this point to introduce the following vector and matrix notation:

$$(13) \quad \mathbf{N} = \begin{pmatrix} N_1 \\ \vdots \\ N_n \end{pmatrix}, \quad \mathbf{K} = \begin{pmatrix} K_{11} \\ \vdots \\ K_{nn} \end{pmatrix},$$

$$\mathbf{R} = \begin{pmatrix} R_1 \\ \vdots \\ R_n \\ \hline R_{n+1} \\ \vdots \\ R_k \end{pmatrix} = \begin{pmatrix} \bar{\mathbf{R}} \\ \tilde{\mathbf{R}} \end{pmatrix}, \quad \mathbf{S} = \begin{pmatrix} S_1 \\ \vdots \\ S_n \\ \hline S_{n+1} \\ \vdots \\ S_k \end{pmatrix} = \begin{pmatrix} \bar{\mathbf{S}} \\ \tilde{\mathbf{S}} \end{pmatrix}, \quad \mathbf{C} = \begin{pmatrix} C_{11} & \cdots & C_{1n} \\ \vdots & \ddots & \vdots \\ C_{n1} & \cdots & C_{nn} \\ \hline C_{n+11} & \cdots & C_{n+1n} \\ \vdots & \ddots & \vdots \\ C_{k1} & \cdots & C_{kn} \end{pmatrix} = \begin{pmatrix} \bar{\mathbf{C}} \\ \tilde{\mathbf{C}} \end{pmatrix}.$$

Using this notation (and denoting fixed point variables with an asterix), eq. (12) can be solved by setting

$$(14) \quad \mathbf{N}^* = \frac{D}{m} \bar{\mathbf{C}}^{-1} (\bar{\mathbf{S}} - \alpha \mathbf{K}).$$

The remaining $k-n$ equations of (11) are

$$(15) \quad 0 = D(\tilde{\mathbf{S}} - \tilde{\mathbf{R}}^*) - m\tilde{\mathbf{C}}\mathbf{N}^*,$$

from which we obtain

$$(16) \quad \tilde{\mathbf{R}}^* = \tilde{\mathbf{S}} - \frac{m}{D} \tilde{\mathbf{C}}\mathbf{N}^* = \tilde{\mathbf{S}} - \tilde{\mathbf{C}}\bar{\mathbf{C}}^{-1}(\bar{\mathbf{S}} - \alpha \mathbf{K}).$$

Equations (10), ((14) and ((16) give the values of the variables at a fixed point in terms of the species parameters (K_{ji} , C_{ji} , r , and m) and the parameters of the environment (\mathbf{S} and D), provided that the limiting resources satisfy eq. (9) (before the index relabeling), and that the inequality (5) holds for $j'=n+1, \dots, k$. The conditions on the resources guarantee that they are all positive, but the positivity of the species abundances need to be checked for a biologically relevant solution.

Stability conditions

A point of equilibrium, or stable fixed point, is a fixed point that has the property that the system returns to it after a small perturbation. The precise formulation begins by writing the system of differential equations for a small perturbation around the fixed point and keeping only terms that are linear in the perturbation. Writing

$$(17) \quad \mathbf{N} = \mathbf{N}^* + \delta \mathbf{N}, \quad \bar{\mathbf{R}} = \bar{\mathbf{R}}^* + \delta \bar{\mathbf{R}}, \quad \text{and} \quad \tilde{\mathbf{R}} = \tilde{\mathbf{R}}^* + \delta \tilde{\mathbf{R}},$$

the linearized equations of motion take the form

$$(18) \quad \frac{d}{dt} \begin{pmatrix} \delta \mathbf{N} \\ \delta \bar{\mathbf{R}} \\ \delta \tilde{\mathbf{R}} \end{pmatrix} = \mathbf{J} \begin{pmatrix} \delta \mathbf{N} \\ \delta \bar{\mathbf{R}} \\ \delta \tilde{\mathbf{R}} \end{pmatrix},$$

with the Jacobian given by

$$(19) \quad \mathbf{J} = \begin{pmatrix} \mathbf{0} & \mathbf{A} & \mathbf{0} \\ -m\bar{\mathbf{C}} & -D\bar{\mathbf{I}} - \bar{\mathbf{F}} & \mathbf{0} \\ -m\tilde{\mathbf{C}} & -\tilde{\mathbf{F}} & -D\tilde{\mathbf{I}} \end{pmatrix},$$

and

$$(20) \quad \begin{aligned} \mathbf{A}_{n \times n} &= \{A_{ij}\}, & A_{ij} &= \frac{N_i^* r}{K_{ii}(1+\alpha)^2} \delta_{ij}, \quad i, j = 1, \dots, n \\ \bar{\mathbf{F}}_{n \times n} &= \{\bar{F}_{ji}\}, & \bar{F}_{ji} &= C_{ji} A_{ii}, \quad i, j = 1, \dots, n \\ \tilde{\mathbf{F}}_{(k-n) \times n} &= \{\tilde{F}_{ji}\}, & \tilde{F}_{ji} &= C_{ji} A_{ii}, \quad j = n+1, \dots, k, \quad i = 1, \dots, n \end{aligned}$$

$\bar{\mathbf{I}}_{n \times n}$ and $\bar{\mathbf{I}}_{(k-n) \times (k-n)}$ are identity matrices, and δ_{ij} is the Kronecker symbol which is equal to 1 when $i=j$ and zero otherwise.

The stability condition is that the (real part of the) eigenvalues of \mathbf{J} are all negative. The eigenvalues of the Jacobian are solutions of the equation

$$(21) \quad \begin{aligned} 0 &= \det(\mathbf{J} - \lambda \mathbf{I}_{(n+k) \times (n+k)}) \\ &= \det \begin{pmatrix} -\lambda \mathbf{I} & \mathbf{A} & \mathbf{0} \\ -m\bar{\mathbf{C}} & -(D+\lambda)\bar{\mathbf{I}} - \bar{\mathbf{F}} & \mathbf{0} \\ -m\tilde{\mathbf{C}} & -\tilde{\mathbf{F}} & -(D+\lambda)\tilde{\mathbf{I}} \end{pmatrix}. \end{aligned}$$

We use the following identity for the determinant of a matrix in terms of its blocks:

$$(22) \quad \text{If } \mathbf{X} = \begin{pmatrix} \mathbf{X}_{11} & \mathbf{X}_{12} \\ \mathbf{X}_{21} & \mathbf{X}_{22} \end{pmatrix} \text{ then } \det(\mathbf{X}) = \det(\mathbf{X}_{22}) \cdot \det(\mathbf{X}_{11} - \mathbf{X}_{12} \mathbf{X}_{22}^{-1} \mathbf{X}_{21}).$$

Applied to eq. (21), this gives

$$(23) \quad 0 = \det(-(D+\lambda)\tilde{\mathbf{I}}) \cdot \det \begin{pmatrix} -\lambda \mathbf{I} & \mathbf{A} \\ -m\bar{\mathbf{C}} & -(D+\lambda)\bar{\mathbf{I}} - \bar{\mathbf{F}} \end{pmatrix}.$$

The first factor of the right hand side of this equations shows that $k-n$ degenerate solutions of this equation are $\lambda = -D$, which is negative and therefore automatically satisfies the requirements of equilibrium. For any other solution, it is possible to divide by the first factor. The second factor can be simplified using an identity similar to eq. (22):

$$(24) \quad \text{If } \mathbf{X} = \begin{pmatrix} \mathbf{X}_{11} & \mathbf{X}_{12} \\ \mathbf{X}_{21} & \mathbf{X}_{22} \end{pmatrix} \text{ then } \det(\mathbf{X}) = \det(\mathbf{X}_{11}) \cdot \det(\mathbf{X}_{22} - \mathbf{X}_{21}\mathbf{X}_{11}^{-1}\mathbf{X}_{12}).$$

This identity can be applied only if \mathbf{X}_{11} is non singular, which here means for $\lambda \neq 0$. For $\lambda=0$ to satisfy eq. (23) it must hold that

$$(25) \quad \det \begin{pmatrix} 0 & \mathbf{A} \\ -m\bar{\mathbf{C}} & -D\bar{\mathbf{I}} - \bar{\mathbf{F}} \end{pmatrix} = 0,$$

which can happen only if the species parameters are tuned very precisely. For general parameter values we can assume that this is not the case, and can therefore use eq. (23) to get

$$(26) \quad 0 = \det(-\lambda\mathbf{I}) \cdot \det \left(-(D + \lambda)\bar{\mathbf{I}} - \bar{\mathbf{F}} - (-m\bar{\mathbf{C}})\left(-\frac{1}{\lambda}\mathbf{I}\right)\mathbf{A} \right).$$

Since $\lambda \neq 0$ it is possible to divide by the first factor, and realizing that $\bar{\mathbf{C}}\mathbf{A} = \bar{\mathbf{F}}$, the equation further simplifies to

$$(27) \quad 0 = \det \left(-(D + \lambda)\bar{\mathbf{I}} - \left(1 + \frac{m}{\lambda}\right)\bar{\mathbf{F}} \right).$$

If $D=m$ (as it actually is in our simulations) then $\lambda=-m$ is a possible solution to this equation, and it satisfies the stability condition. For any other solution, or when $D \neq m$, eq.

(27) can be divided by $\left(-1 - \frac{m}{\lambda}\right)^n$ to give

$$(28) \quad 0 = \det\left(\bar{\mathbf{F}} - \left(-\frac{\lambda(D+\lambda)}{m+\lambda}\right)\bar{\mathbf{I}}\right).$$

The last equation is the eigenvalue equation for the matrix $\bar{\mathbf{F}}$,

$$(29) \quad 0 = \det(\bar{\mathbf{F}} - x\bar{\mathbf{I}}),$$

with the identification

$$(30) \quad x = -\frac{\lambda(D+\lambda)}{(m+\lambda)}.$$

Solving eq. (30) for λ gives:

$$(31) \quad \lambda = \frac{-(x+D) \pm \sqrt{(x+D)^2 - 4mx}}{2}.$$

If λ is real, both solutions to λ are negative iff

$$(32) \quad \begin{aligned} & -(x+D) + \sqrt{(x+D)^2 - 4mx} < 0 \\ & \quad \Downarrow \\ & \sqrt{(x+D)^2 - 4mx} < x+D \\ & \quad \Downarrow \\ & (x+D)^2 - 4mx < (x+D)^2 \\ & \quad \Downarrow \\ & x > 0. \end{aligned}$$

λ can be complex only if

$$(33) \quad 4xm > (x+D)^2,$$

in which case x is positive and therefore the real part of λ is negative:

$$(34) \quad \begin{aligned} \operatorname{Re}(\lambda) &= \operatorname{Re}\left(-\frac{(x+D) \pm \sqrt{(x+D)^2 - 4xm}}{2}\right) \\ &= \operatorname{Re}\left(-\frac{(x+D)}{2}\right) \\ &= -\frac{(x+D)}{2} < 0 \end{aligned}$$

From (32) and (34) it follows that all the eigenvalues of the Jacobian are negative, $\lambda < 0$, if

and only if all the eigenvalues of $\bar{\mathbf{F}}$, with matrix elements $\bar{F}_{ji} = \frac{r}{(1+\alpha)^2} \frac{C_{ji} N_i^*}{K_{ii}}$,

$i, j = 1, \dots, n$, are all positive.

Community size is determined by species properties and not by dynamical constraints imposed by initial conditions

Fig. S2 shows data from 100 realizations of evolution in an environment with 20 essential resources (Data from one such realization is presented in Fig. 3). At each step in the course of evolution, after a beneficial mutation was drawn, we used the values of the species parameters to calculate the size of the largest subset of stably coexisting species that contains the new mutant lineage. For this, we used an exact analytic solution for equilibria of the ecological equations of motion. In addition, we recorded the number of species that actually remained after the system had settled to a new equilibrium. The shade of each square reflects the frequency of states with a given actual number of species (ordinate) normalized by the total number of instances sharing the same maximum possible number of species (abscissa). When the system exhibits persistent fluctuations, the actual number of species can exceed the maximal number possible at equilibrium.

Depletion of limiting resources during evolution

In this section we provide an analytical explanation for the effect demonstrated in Fig. 4c: limiting resources are depleting faster than non-limiting resource.

Without loss of generality, assume that species 1 is limited by resource 1 in equilibrium.

Eq. (10) provides the equilibrium value of the concentration of resource 1 as:

$$(35) \quad \bar{R}_1^* = \alpha K_{11}.$$

So long as resource 1 is the limiting resource for this species, its equilibrium concentration does not change. If, however, a mutation arises (denoted with index m) which is also limited by this resource (this will most likely be a mutation of species 1 itself), the requirement of the mutant species for resource 1 must be smaller than that of species 1:

$$(36) \quad K_{1m} < K_{11}.$$

Otherwise, the concentration of resource 1, given by eq. (35), will be below the minimum needed to sustain the mutant species, indicating that the mutation was not a beneficial one. Subsequently, the mutation will spread, and it will keep spreading until the resource concentration settles on a new, lower, value:

$$(37) \quad \bar{R}_1^* = \alpha K_{1m} < \alpha K_{11}.$$

(At this point species 1 can no longer persist and it becomes extinct.)

We conclude that the concentration of a limiting resource is reduced each time a new beneficial mutation appears which is limited by this resource.

Consider now the ratio of the equilibrium abundances of a resource which is limiting a species undergoing adaptation (\bar{R}_1^*) and a resource which is not limiting any existing species (\tilde{R}_{n+1}^*). From eqns. (16) and (35) we have

$$(38) \quad \frac{\bar{R}_1^*}{\tilde{R}_{n+1}^*} = \frac{\alpha K_{11}}{\tilde{S}_{n+1} - \sum_{i,j=1..n} \tilde{C}_{n+1i} C^{-1}_{ij} (S_j - \alpha K_{jj})}$$

$$= \frac{K_{11}}{A + \sum_{i=1..n} B_i K_{ii}},$$

Where A and B_i are functions of the supply parameters as well as the C 's. Since the fitness of a species does not depend on the C s at any time we can assume that due to drift these parameters are randomly fluctuating around some constant value. It follows that as the set of limiting resources is repeatedly depleted according to the result derived above and the denominator approaches zero, the numerator is bounded below and remains finite. In the limit that $K_{ii} \ll A/B_i$ as well as $K_{11} \ll A$ we have

$$(39) \quad \frac{\bar{R}_1^*}{\tilde{R}_{n+1}^*} \approx \frac{K_{11}}{A} \ll 1.$$

Depletion of limiting resources decreases the probability of speciation and increases the chance of extinction

While the actual growth rate of a given species is determined by the resource for which it grows most slowly, the ranking of its growth rates on other resources (μ_{ji} in eq. (1)) has consequences both for predicting the likely properties of a mutant formed from this species, and for the likelihood that the species goes extinct following a reduction in the concentration of a non-limiting resource. This can be seen by considering the normalized resource concentrations defined by the ratios R_j/K_{ji} for species i and resource j . Since the growth rates μ_{ji} are monotonically increasing functions of these ratios, the rank order of the former and the latter among resources (for a fixed species) is the same. We have already seen that at equilibrium the normalized concentration of the limiting resources is equal to α , and all other ratios must be larger.

Assume now that species 1 is limited by resource 1 etc., and consider the double ratio:

$$(40) \quad \frac{R_1^*/K_{12}}{R_4^*/K_{42}}.$$

This is an example of the relation between growth rates of a species (here species 2) with respect to limiting vs. non-limiting resources (1 and 4). K_{12} and K_{42} are under no selection and their ratio should approach a constant of order 1. On the other hand, since R_1 is the limiting resource for species 1 while R_4 does not limit any of the species, the conclusion eq. (39) can be applied. Putting these facts together we get

$$(41) \quad \frac{R_1^*/K_{12}}{R_4^*/K_{42}} \ll 1 \text{ or } \frac{R_1^*}{K_{12}} \ll \frac{R_4^*}{K_{42}}.$$

This argument demonstrates why the normalized concentration (and therefore the growth rate) of a limiting resource is expected to be smaller than that of a non-limiting one.

If we represent each of the ratios as a small circle on a vertical line, and use different lines for different species, a hypothetical situation for 3 species competing for 5 resources is shown in Fig. S3. The numbers inside the circles are the indices of the resources and the blue circles indicate resources which are most limiting for one of the present species. The accumulation of the blue circles in the lower positions of each line is a consequence of the argument made above.

At the instant of its occurrence, a mutation has a modified set of the normalized resource concentrations R_j/K_{ji} , compared to its ancestor, due to the change in the resource requirements. The resource for which the resource/requirement ratio is lowest is the limiting resource for the mutant, and the corresponding normalized resource concentration has to be larger than α for the mutation to be beneficial (=able to expand). Two examples of mutations on species 1 are shown in Figs. S4 and S5.

In Fig. S4 the mutant is limited by resource 1, the same as its ancestor. With the normalized resource concentrations as shown, the mutation is beneficial, and the mutant population starts out growing at a rate faster than m , the mortality rate. As it grows it causes the concentration of resource 1 to drop until it is at the equilibrium value for the mutant species. As resource 1 is being depleted in this way, the ratios R_1/K_{11} , R_1/K_{13} and R_1/K_{13} are decreasing as well (orange arrows). For species 1 this immediately brings the ratio below the minimal value of α which is necessary to sustain it and it is driven to extinction. This is the common process whereby a mutant substitutes its ancestor.

However species 1 is not the only species affected by the spread of the mutant lineage. Due to the relatively low initial concentration of resource 1 normalized by the requirement of species 3, the new equilibrium concentration of resource 1 will be too low for it as well and it will be driven to extinction along with species 1. This demonstrates how the low normalized resource concentrations for limiting resources, coupled with the fact that such resources are under selective pressure, can cause a spreading mutation to drive several other species to extinction.

The example in Fig. S5 is of a new mutation that can spread without eliminating other species. For a speciation event of this type to occur, the mutant species must be limited by a resource that is not limiting any of the pre-existing species. The accumulation of normalized concentrations of limiting resources at the bottom of the scales imply that a mutation of the type shown in the illustration must be “large” in the sense that it involves a significant rise in the requirement (and therefore a significant drop in the normalized concentration) for a non-limiting resource (4 in this case). There is also some fine-tuning involved to ensure that the requirement for the resource limiting the ancestor (1) drops sufficiently to prevent it from remaining most limiting. These considerations, which are based on the intensified depletion of limiting resource compared to non-limiting ones, suggest that the probability of speciation events, such as the one shown above, is small.*

* This reasoning assumes that mutations are small in the sense that the properties of the mutant are correlated with the properties of the ancestor. When this is not the case, it has already been shown² that it is unlikely that the parameters of a random collection of species satisfy the conditions for a stable equilibrium.

Speciation and extinction – comparison with a naïve niche-model

It is illuminating to contrast the balance between extinction and speciation in the complete model to expectations based on a simple model. We consider an intuitive, niche-based model, motivated by the work of MacArthur and Levins (2), that posits k resources accommodating k single-species niches. At each adaptive step the new spreading species either invades a previously occupied niche (replacement) with probability n/k (where n is the number of species present before mutation) or fills an unoccupied niche (speciation) with probability $p_{spe}(n) = 1 - n/k$ for $n \leq k$. Fig. S6 shows, for this model as well as for the full model (for species competing for 100 resources), the dependence of the change in the number of species over an adaptive step, Δn , on n itself. Such curves show the evolutionary stable number of species through their intercept with the horizontal axis, as well as provide insight into dynamical behavior away from these points. The line of $\Delta n(n)$ coincides with that of $p_{spe}(n)$ when there are only replacements and speciations ($\Delta n = 0$ or 1), as in the simplified model (dashed line). In that model, the evolutionary stable number of species is reached when all the niches are occupied and the probability of finding an unoccupied one vanishes. In the full model, the effect of a similar exhaustion of environmental opportunities can be seen by separating from $\Delta n(n)$ the contribution of $p_{spe}(n)$ (solid lines). Comparison to the simple model confirms the expectation that in the full model the probability of speciation is reduced. It is also clear, however, that the diminished speciation accounts for only part of the gap in the number of species between the simple and full models. Extinction makes up the difference.

The importance of extinctions in determining the number of species that are sustained in an environment is underscored by the shape of the distribution of Δn (Fig. S6, inset). While replacement events are most common, and speciation ($\Delta n = +1$) and double extinction ($\Delta n = -1$) nearly cancel each other, the balance is tipped by the more negative values. This example illustrates the importance of *mass* extinctions: it is not uncommon for more than half the species to be eliminated by the spread of a single new mutant lineage. In contrast with the naïve model, when species compete for essential resources, the evolutionarily stable number of coexisting species is regulated not only by saturation of the environmental niches and the decrease in the probability of speciation but also by the increased probability of catastrophe.

The role of superspecies

A superspecies is a species that is more adapted to the environment than all other present species and therefore drives all its competitors to extinction (3). A partial superspecies is superior to some of its competitors, driving only those species to extinction. We examine extinctions that follow the spread of a mutant lineage and ask whether the mutant species is a (partial) superspecies. The mutant species is considered superior to another species if in a one-on-one competition the mutant species is the only survivor. Considering such competitions between the mutant species and each of the species it drives to extinction, a degree of superiority can be defined as the fraction of head-to-head competitions won by the mutant species. Shown in Fig. S7 is the average degree of superiority as the number of resources changes from 2 to 100. We observe that while extinctions are largely triggered by superspecies when the number of resources is low, this is not the case at

higher dimensions, where the probability of a mutant species to be superior to one of the species it drives to extinction approaches 1/2.

Inclusion of explicit trade-offs

Trade-offs in resource utilization have been suggested as important in enabling multiple species to coexist. Their presence prevents the occurrence of superspecies that are superior to other species in all respects (3, 4). Our analysis suggests that, in the model discussed here, the triggering of extinctions by superspecies is not the primary mechanism that keeps biodiversity low during the course of evolution. We therefore expect that the introduction of explicit trade-offs between the requirements for different resources will not considerably affect the number of species sustained over evolutionary times. The results of simulations confirming this expectation are shown in Tab. 1.

Trade-offs were implemented by requiring that the mean over j of K_{ji} be constant (5). For each of the environments considered for Tab. 1, ten realizations of evolution were simulated, each consisting of 1500 steps. In each realization no explicit constraint were imposed on the K s for the first 1000 steps, and trade-offs were implemented for the last 500 steps. The number of species for the dynamics without constraints was averaged over 500 steps, from 501 to 1000, from all ten runs, while for the dynamics in the presence of trade-offs averages were calculated from the steps 1001 to 1500.

It should be noted that even without explicit constraints, the mutational process that we used contains a bias towards degradation of resource requirements which can be tuned by the parameter b_K , and that can effectively introduce trade-off: while the requirement for at least one of the resources must decrease for a beneficial mutation, the bias towards degradation (especially for values of b_K close to 1) causes the requirement for all other

resources to increase. The b_K panel of Fig. S1 indicates that, like the explicit trade-offs, the implicit constraints implied by the mutation bias have little effect on the biodiversity sustained by evolution.

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