Resonance-induced multimodal body-size distributions in ecosystems

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The size of an organism reflects its metabolic rate, growth rate, mortality, and other important characteristics; therefore, the distribution of body size is a major determinant of ecosystem structure and function. Body-size distributions often are multimodal, with several peaks of abundant sizes, and previous studies suggest that this is the outcome of niche separation: species from distinct peaks avoid competition by consuming different resources, which results in selection of different sizes in each niche. However, this cannot explain many ecosystems with several peaks competing over the same niche. Here, we suggest an alternative, generic mechanism underlying multimodal size distributions, by showing that the size-dependent tradeoff between reproduction and resource utilization entails an inherent resonance that may induce multiple peaks, all competing over the same niche. Our theory is well fitted to empirical data in various ecosystems, in which both model and measurements show a multimodal, periodically peaked distribution at larger sizes, followed by a smooth tail at smaller sizes. Moreover, we show a universal pattern of size distributions, manifested in the collapse of data from ecosystems of different scales: phytoplankton in a lake, metazoans in a stream, and arthropods in forests. The demonstrated resonance mechanism is generic, suggesting that multimodal distributions of numerous ecological characters emerge from the interplay between local competition and global migration.

Multimodal body-size distributions, in which a population exhibits several peaks of abundant sizes, characterize local ecosystems and have puzzled ecologists for many years (1–4). To resolve this puzzle, most previous studies concentrated on one important aspect of body size, namely resource partitioning or niche separation: larger individuals consume certain resources more efficiently than smaller ones, whereas smaller individuals have access to some resources that are unavailable to larger individuals. As a result, multimodal size distributions may originate from community-wide character displacement, in which natural selection pushes species to assort into packs, each of which fits to a particular niche (1, 4, 5).

Another aspect of size, however, relates to a growth-efficiency tradeoff (6, 7). Smaller individuals generally invest less effort in their development and have a higher maximal growth rate when the resource is abundant (8–12), whereas larger individuals have more efficient metabolism and are more successful in direct competitive interferences (Fig. 1A) (6, 13, 14). As a result, smaller individuals are more likely to be the first to populate newly formed patches, and the larger individuals follow only later. In this study, we show how this tradeoff may promote multimodal body-size distributions, and we identify several characteristics of the underlying dynamics.

Stochastic Subdivided Population Model
To examine how the growth-efficiency tradeoff leads to multimodal body-size distributions, we considered a population that is subdivided into several habitable resource patches. As in Levins’s classic metapopulation framework, we assume each patch is either empty or occupied by a single species (15–17). In our model, each species is specified by its maximal growth rate $q$, which is negatively correlated with its body size. The higher growth rate of smaller individuals results in more migrants sent to other patches. Larger individuals, on the other hand, are advantageous in interference and exclude the smaller individuals during within-patch competitions.

Specifically, we considered the following processes (Fig. 1): First, occupied patches are emptied at a rate $m$. This may occur because of mortality or because of path destruction and creation in which occupied patches vanish and new patches enter the system. Second, a patch occupied by a $q$-species spreads its offspring as migrants at a rate $q$. Each migrant arrives at a randomly picked patch. If the destination patch is empty, the migrant takes over. If it is occupied by a $q'$-species, the invasion probability is given by the sigmoidal function (Fig. 1C)

$$g_q(q', q') = \left[1 + e^{q-q'}\right]^{-1},$$

where $s > 0$ measures the selection strength. This function may be seen as a phenomenological rule reflecting stochastic competition in which a species with an inferior fitness (higher $q$) still may take over, but also may be derived from microscopic dynamics of competition between the resident and migrant subpopulations. In the deterministic limit, $s \to \infty$, the dynamics are reduced to the “colonization-competition” model of Hastings (16) and Tilman (17): the sigmoid ($g_q$) becomes a step-function and the larger species (lower $q$) always takes over.

To examine the possibility of multimodal distributions, we solve the long-term evolution of the entire size spectra. The hallmark of multimodal distributions is the emergence of discrete peaks within the continuous spectrum of possible $q$-values, $0 < q < \infty$. When the number of patches is large, the normalized distribution of patch occupancy (relative abundance), $\rho(q)$, evolves according to the dynamics:

$$\frac{d\rho(q)}{dt} = \rho(q) \left[ q - m - \int_0^\infty \rho(q') g_q(q, q') dq' \right] + \mu \frac{d^2\rho(q)}{dq^2},$$

where the term $q$ corresponds to colonization without competition, the term $m$ to mortality, the negative integral term to...
inhibition of colonization by competition, both due to the invasion of competing migrants and due to the inability to invade into already occupied patches, and the last term corresponds to mutations that slightly tune \( q \) at a rate \( \mu \) (SI Methods).

**Emergence of Multimodal Size Distributions**

In the long term, the distribution \( \rho(q) \) approaches a unique steady state that we examine for multimodality. The case in which competition over patches is deterministic \( (s \to \infty) \), i.e., a \( q \)- migrant invades a populated \( q' \) patch if and only if \( q < q' \) \((16, 17)\), exhibits a monotonous steady-state solution (Fig. 2A). For \( \mu = 0 \), this solution is \( \rho^*(q) = (\sqrt{m}/2)q^{-1/2} \) if \( q \geq m \), and \( \rho^*(q) = 0 \) otherwise \((18)\): species with \( q < m \) vanish whereas species with \( q > m \) distribute smoothly. (Evolution pushes species to differ, i.e., to become further away from their neighboring species along the \( q \)-axis.)

In contrast, when the competition becomes stochastic, as the selection strength \( s \) decreases below a certain threshold, peaks emerge and the steady-state distribution becomes multimodal (Fig. 2B–D). For \( s \) just below the transition, peaks are most prominent near the singularity at \( q = m \). As \( s \) decreases further, the peaks become significant even further away from the singularity. This implies species packing: evolution pushes species toward the peaks even when they already are populated by other species. Peaks are located at approximately equal distances that are of the order of the \( q \) range over which competition is stochastic, \( \delta q \sim 1/s \).

**Fig. 1.** Stochastic colonization-competition model. (A) Body size is associated with a tradeoff between maximal growth rate, \( q \), and competitiveness abilities such as direct interference. (B) Schematic illustration of the dynamic processes. Mortality (or patch destruction and creation): occupied patches are emptied at a rate \( m \). Migration: each species spreads migrants from its home patch to random patches at a rate proportional to its maximal growth rate \( q \). Competition: if the destination patch is empty, the migrant invades; if the patch is already occupied by a \( q' \)-species, the \( q \)-migrant takes over with a probability \( g(q, q') \) and is being eliminated otherwise. (C) The invasion probability \( g(q, q') \) has a sigmoidal shape with a width \( \sim 1/s \), which corresponds to stochasticity. Species with higher \( q \) have a smaller chance of taking over occupied patches. (D) Competition is much faster than migration, which implies that each patch is either empty \( (\varnothing) \) or occupied by a single species, entitled by its maximal growth rate \( q \). The resulting dynamics are that of a well-mixed population of patches subject to the illustrated rate equations for all \( q \) and \( q' \): exchange (up), colonization of empty patches (middle), and invasion into occupied patches (down). The corresponding mean-field equation is Eq. 2.

**Fig. 2.** Emergence of multimodal body-size distributions. Steady-state distributions of the model (Eqs. 1 and 2) are demonstrated when the selection strength \( (s) \) is varied. When competition is deterministic, the distribution is smooth (A). However, when competition is sufficiently stochastic, multimodal patterns emerge (B–D): peaks appear near the singularity at \( q = m \), followed by smooth tails on the right. The distance between consecutive peaks is of the order of \( 1/s \), and the width of the peaks is affected by the mutation rate \( (\mu = 5 \times 10^{-5}) \) (see also Fig. 51).
The width of the peaks and their abundance are affected by the mutation rate $\mu$ (Fig. S1): without mutations ($\mu = 0$), the distribution is discretized with many sharp zero-width peaks; whereas as $\mu$ increases, peaks are smeared and appear only near the singularity. This can be understood by dimensional analysis, which shows that the width of the first peak scales approximately are like $(\mu n)^{1/4}$ (see Supporting Information). This width becomes comparable to the interpeak distance $1/s$ at $\mu \sim 1/(ms^2)$, which is the critical mutation rate for the appearance of lumpiness. Equivalently, this determines the scaling of the critical selection strength $s_c \sim (\mu n)^{-1/4}$. To show generality, we also examined other sigmoidal invasion probabilities $q$, and very similar patterns emerged (Fig. S1).

**Comparison with Measurements**

To test the validity of our model, we first examined the empirical data by Janzen, who measured body lengths of thousands of randomly sampled arthropods from several forests (19). To estimate the maximal growth rate $q$, we used the well-established empirical relation $q \sim (\text{mass})^{-1/4}$ (8–12) and estimated mass $\sim (\text{length})^3$ (20, 21). The resulting distribution of biomass vs. maximal growth rate is multimodal, periodically peaked at larger sizes, and followed by a smooth tail at smaller sizes, just like the steady-state distributions exhibited by our model (Fig. 3A). Qualitative agreement was achieved by fitting the three model parameters, $m$, $s$, and $\mu$.

Our model also fits well to two other datasets: the time-averaged weight distributions of phytoplankton in Lake Kinneret and of metazoans in the Lone Oak stream (Fig. 3B) (22, 23). Moreover, we were able to universally fit all three distributions simultaneously by a single graph (Fig. 3B) via scaling all rates by the mortality $m$, as $q = q/m$, $s = ms$, and $\mu = \mu/m^3$ (SI Methods). The shape of this distribution is independent of $m$, which merely scales the $q$-axis by a value specific to each ecosystem. The scaled parameter $s = sm$ corresponds to the number of offspring an organism must renounce within a time window to guarantee taking over a patch within that time.

In addition to $s$ and $\mu$, which seem to be nearly the same for all three ecosystems, our model may predict via scaling the resource exchange rate $m$ of each ecosystem (see Methods): $\sim (2–3 \text{~mo}^{-1})$ for arthropods, $\sim (8 \text{~d}^{-1})$ for metazoans, and $\sim (1 \text{~d}^{-1})$ for phytoplankton. A careful empirical examination still is needed to verify these predictions, but the predicted exchange rates appear to be plausible. First, arthropods usually have an annual or seasonal life cycle, after which they lay eggs and sometimes migrate; moreover, their resources are plant products that often are also annual or seasonal (24). Second, the phytoplankton turnover rate is about $(2–6 \text{~d}^{-1})$ (25). The lower bound of this rate, which corresponds to small phytoplankton, may fairly estimate the resource exchange rate because of the relatively poor ability of small phytoplankton to persist without resources. This turnover rate also may approximate the resource exchange rate in the metazoans’ ecosystem, in which phytoplankton is a primary resource. More generally, our results are supported by the observation that turnover rates in plants also scale approximately like $(\text{mass})^{-1/4}$ (12).

**Resonance Mechanism for Multimodal Distributions**

The underlying “microscopic” dynamics of species competition has a natural effective frequency, which is exhibited at the “macroscopic” scale as the width over which the invasion probability $q$ varies (d$q \sim 1/s$, Fig. 1C). This frequency is inherent in the competition, and its resonance with colonization rates leads to a nearly periodic discrete pattern with a corresponding period $d_q \sim 1/s$ (see Supporting Information). Although competition in our model is fast, its characteristic frequency persists at the macroscopic scale because of its stochastic nature. Indeed, similar periodic patterns appear if we modify the model and assume that selection is deterministic but occurs over a nonnegligible period $s$, during which both competing species spread migrants from the same patch.

This resonance is evident in the dynamics (Fig. 4 and Movies S1 and S2). Assume that initially all individuals are “packed” and have the same maximal growth rate $q = q_1$ (Fig. 4A). As long as $q_1$ is sufficiently large, mutants with $q \leq q_1$ have a considerable competitive advantage and they invade the population, thereby pushing $q_1$ to lower values (Fig. 4A and B). As $q_1$ decreases, the fraction of occupied patches decreases (Fig. S2) and the competition with the $q_1$-pack becomes less important. Consequently,
the pack stops moving as \( q_1 \) approaches \( q_c \), where the competitive advantage of lower \( q \)-individuals is sufficiently low and is balanced by their reduced colonization rate. Meanwhile, species with sufficiently large \( q \) can proliferate by occupying the patches left unoccupied by the \( q_1 \) population (17), thereby creating new packs, which in turn also propagate to lower \( q \) (Fig. 4 B and C). Eventually, each pack stops at a \( q \)-value at which the benefit from the reduced inhibition of the pack itself is compensated by the cost of slower colonization (Fig. 4 C and D). Nevertheless, if competition is deterministic \((s \to \infty)\), then every mutant with \( q \leq q_1 \) invades \( q_1 \)-patches in every competition; hence, the population becomes more competitive and less fertile until it vanishes as \( q_1 \) approaches \( m \) [Fig. 4 E–G; “evolutionary suicide” (26)]. The succeeding packs undergo similar dynamics, which result in a series of evolutionary suicides, and no single pack is sustained. Eventually, newer packs catch the preceding ones, and a smooth distribution is obtained (Fig. 4H). Note that for stochastic competition, the transition from an initially smooth distribution into a lumpy one also is through a cascade of moving packs (Movie S3).

We derived an analytic steady-state solution of Eq. 2 for the multimodal distribution (see Supporting Information) assuming \( s \gg 1/m \) and the mutation rate is small enough to allow adiabatic adjustment of population abundance [adaptive dynamics (27)]. In this limit, the fraction of patches occupied by species from the first pack at \( q_1 > m \) (the area of the peak) is \( \Gamma(q_1) = (q_1 - m)/q_1 \) (Fig. S2). At steady state, this peak is located at \( q_s \approx m + 2/s \), and consequently, \( \Gamma(q_s) \approx 2/(ms) \). The few peaks are periodically located at distances of approximately \( \delta q \approx 4/s \) from one another, which supports the numerical solution (Fig. 2 and Fig. S1).

### Discussion

Our examination of body-size distributions of species competing over the same resources in a local environment, such as a forest or a lake, revealed a universal body-size distribution that holds for various taxa. We suggest that this is a natural consequence of the tradeoff between growth rate and competitiveness. We also found some characteristics of size distributions mediated by that tradeoff. First, multimodality appears at larger body sizes, whereas the distribution of smaller sizes is smooth. Second, evolution entails directional dynamics toward larger sizes, which is consistent with fossil records showing that species tend to increase in size during evolution (Cope’s rule) (14, 28). Our study suggests that examining biomass distributions plotted vs. \((mass)^{-1/4}\) may reveal features that are less apparent in the traditional \(log(mass)\) plot. On a \(log(mass)\) plot, peaks are still evident, but their periodicity may be masked and some extra peaks may appear at larger masses because of stochasticity. Hence, the \((mass)^{-1/4}\) transformation may enable meaningful comparison among several distributions.

Our model cannot fit all body-size distributions, particularly certain seemingly unimodal body-size distributions with a long tail at large sizes, which were found by several studies (29, 30). This may result from three possible effects. First, some of the analyzed ecosystems are much larger than a typical dispersal length, so large that the environmental conditions vary throughout the ecosystem. In contrast, our model assumes global connectivity and identical patches; therefore, it should be examined in relatively small, homogeneous regions. Indeed, Brown and Nicoletto (31) found that peaks become evident when the system size decreases. Second, our model disregards the possibility of resource partitioning within a niche or a patch, which is relevant in many ecosystems. Third, several studies examine the number of species (instead of the biomass) as a function of the mass (32, 33). Fitting to such available data of species size distributions requires...
**Supporting Information**

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### SI Methods

Here, we explain the derivation of Eq. 2 in the main text, and derive the rescaled equation Eq. S1. We assume infinitely many patches, and the resulting dynamics are that of a well-mixed population of patches with the following mean-field equation (Fig. 1D):

\[
\frac{dp(q)}{dt} = -mp(q) + gp(q) \left( 1 - \int_0^\infty p(q')dq' \right) + \int_0^\infty p(q')g_s(q,q')dq' - p(q) \int_0^\infty p(q')g_i(q',q)dq' + \mu \frac{d^2p(q)}{dq'^2},
\]

where the first term on the right-hand side of the first equality corresponds to mortality or resource exchange, the second term to invasion of q'-migrants into empty patches, the third term to invasion of q-migrants into already occupied patches, the fourth term to invasion of competing migrants into q-patches, and the fifth term to mutations that slightly tune q at a rate \(\mu\). Next, scaling all rates by the mortality \(m\), as \(q = q/m\), \(p = mp\), \(s = ms\), and \(\mu = \mu/m\), yields

\[
\frac{dp(q)}{dt} \approx \tilde{p}(q) \left[ \tilde{q} - 1 - \int_0^\infty \tilde{p}(q')(\tilde{q} + \tilde{q}')g_s(q',\tilde{q}')dq' \right] + \tilde{q} \frac{d^2\tilde{p}(q)}{dq'^2}.
\]

We used this equation to simultaneously fit data from different scales (Fig. 3B).

### SI Nearly Periodic, Stationary Pattern

In this section, we derive analytic steady-state solutions of our model. We use the following three simplifying assumptions: (i) mutation rate \(\mu\) is extremely small, hence the population abundance is adiabatically adjusted as the mutation process proceeds (adaptive dynamics) (1); (ii) selection is strong \((s \gg 1/m)\); and (iii) the invasion probability function \(g\) is given by a piecewise linear function (Eq. S6 below) instead of by Eq. 1. We conclude that the leftmost peaks along the q-axis are located at nearly equal distances from one another (this period is equal to the width over which \(g\) varies), and have nearly equal magnitudes. This implies a nearly periodic pattern starting at the right side of the singularity at \(q = m\).

**First Peak.** To find the location of the first, leftmost peak, assume that initially the entire population has the same maximal growth rate \(q = q_1\). Without mutations, it follows from Eq. 2 in the main text that the fraction of occupied patches, \(\Gamma(q_1)\), evolves according to

\[
\frac{d\Gamma(q_1)}{dt} = \Gamma(q_1)|q_1 - m - q_1\Gamma(q_1)|
\]

with the steady-state solution (Fig. S2)

\[
\Gamma(q_1) = \begin{cases} 
0 & \text{if } q_1 < m \\
q_1 - m & \text{otherwise.}
\end{cases}
\]

When rare mutants appear, they gradually invade the population if and only if their growth rate is positive (1). The growth rate of a \(q\)-mutant in a resident \(q_1\)-population is proportional to

\[
f(q'; q_1) = \left( \frac{1}{\rho(q')} \frac{dp(q')}{dt} \right)_{(\rho(q) - \Gamma(q_1)\delta(q-q_1)); \mu = 0)} = q' - m - \Gamma(q_1)(q_1 + q')g_s(q',q_1),
\]

where the term \(q'\) corresponds to colonization, the term \(m\) corresponds to mortality, and the last term is an inhibitory one resulting from competition. The direction toward which small mutations drive the population is determined by the sign of the selection gradient

\[
D(q_1) = \frac{bf(q'; q_1)/dq'}{q' - q_1} = 1 - \frac{1}{2}\Gamma(q_1)(1 + sq_1).
\]

When \(q_1\) is initially large, \(\Gamma(q_1)\) also is large and the inhibition via competition is the most prominent term \((D(q_1) < 0)\). Evolution then pushes the population toward lower \(q\) until \(q_1\) approaches \(q_c\), where \(D(q_c) = 0\) and the benefit from reduced inhibition by competition is compensated by the cost of slower colonization. For \(s \gg 1/m\), this implies

\[
q_c = m + \frac{2}{s} + O(s^2m^{-1}),
\]

\ [
\Gamma(q_c) = \frac{2}{sm} + O((sm)^{-2}).
\]

Note that \(q_c\) indeed locally maximizes \(f(q'; q_c)\) because

\[
\frac{d^2f(q'; q_c)}{dq'^2} \bigg|_{q'=q_c} > 0.
\]

**Following Peaks.** To derive the location of the second peak, we assume that \(g\) is given by a piecewise linear function that replaces Eq. 1:

\[
g(q,q') = \begin{cases} 
1 & \text{if } q < q' - \frac{2}{s} \\
\frac{1}{2} + \frac{s}{4}(q-q') & \text{if } q' - \frac{2}{s} \leq q \leq q' + \frac{2}{s} \\
0 & \text{if } q > q' + \frac{2}{s}
\end{cases}
\]

With this function, the steady-state location and magnitude of the first peak are still given by Eq. S5 because \(g(0)\) and \(g'(0)\) have the same values in Eq. S6 and in Eq. 1. Next, we state that the second peak does not influence the first, and later we will verify this statement, which allows us to use Eq. S5 in calculating the second peak.

The per capita growth rate of a \(q\)-species, given two populations at \(q_c\), and at \(q_2\) (i.e., \(\rho(q) = \Gamma(q_c)\delta(q-q_c) + \Gamma_2(q_2)\delta(q-q_2)\)), is given by

\[
\Gamma(q_1) = \begin{cases} 
0 & \text{if } q_1 < m \\
q_1 - m & \text{otherwise.}
\end{cases}
\]
\[ f(q', q_c, q_2) = q' - m - \Gamma_2(q_2)(q_2 + q')g(q_2, q') - \Gamma(q_c)(q_c + q')g(q_c, q'), \]

where \( \Gamma_2(q_2) \) is the fraction of patches occupied by the population from the second peak at \( q_2 \). If the population at \( q_2 \) is viable, then \( \Gamma_2(q_2) \) evolves until it saturates as the growth rate of the population at \( q_2 = 0 \), and then \( f(q_2; q_2, q_c) = 0 \), which implies

\[
\Gamma_2(q_2) = 1 - \frac{m}{q_2} \frac{\Gamma(q_c) q_2 + q'}{q_2} g(q_c, q_2) = 1 - \frac{m}{q_2} \frac{4}{sm} g(q_c, q_2) + O((sm)^{-2}).
\]

Therefore, in the first order of \( 1/sm \),

\[
\Gamma_2(q_2) = \begin{cases} 
0 & \text{if } q_2 < m + \frac{4}{s} \\
1 - \frac{m}{q_2} - \frac{4}{sm} & \text{otherwise}.
\end{cases}
\]

In line with our statement, the second peak does not affect the first, because \( q_2 \) is greater than \( q_c \) by at least \( 2/s \); therefore, \( g(q_c, q_2) = 1 \) and \( g(q_2; q_c) = 0 \) (Eq. 6).

The selection gradient for the second peak is given by

\[
D(q_2) = \frac{df(q'; q_c, q_2)}{dq'}_{q'=q_2} = 1 - \frac{1}{2} sm \Gamma_2(q_2) - \frac{1}{s} g'(q_c, q_2) + O((sm)^{-2}).
\]

Thus, \( D(q_2; q_c) = 0 \) implies

\[
0 = 1 - \frac{1}{2} sm \Gamma_2(q_2) - \frac{1}{s} g'(q_c, q_2) + O((sm)^{-2}),
\]

but \( g'(q_c, q_2) = 0 \); therefore, after substituting \( q_c = m + \frac{p}{s} \),

\[
2 = sm \Gamma_2(q_2) = sm \left( 1 - \frac{m}{m + \frac{p}{s} - \frac{4}{sm}} \right) \approx p - 4,
\]

which implies

\[
q_{c,2} = m + \frac{6}{s} + O(s^{-2}m^{-1}),
\]

\[
\Gamma_2(q_{c,2}) = \frac{2}{sm} + O((sm)^{-2}).
\]

The same method can be applied to derive the steady-state locations and magnitudes of the third peak, fourth peak, and so on. In the first order of \( 1/sm \), the first few peaks are periodically located at distances of approximately \( 6q \approx 4/s \) from one another, which implies a nearly periodic pattern.

**SI Dimensional Analysis**

**General Considerations.** Several insights may be gained by merely analyzing the dimensions of the observables and parameters of our model. First, note that \( q \) is a variable along the character axis, which consequentially has its own dimension \( (q \approx |q|) \). However, in our model, we also consider \( q \) as the migration rate, which seemingly implies \( q \approx 1/|t| \). Hence, a more appropriate claim for the sake of dimensional analysis is that the migration rate is \( \lambda q \), where \( \lambda \approx \frac{|t|}{|q|} \), and in our model we simply set \( \lambda = 1 \). Next, note that \( s \approx 1/|q| \) (Eq. 1), which implies \( sm/\lambda \approx 1 \). This explains our assumption \( s \gg 1/m \) in the previous section.

**Width of the Leftmost Peak.** To find the steady-state characteristic width of the leftmost peak, \( A \), note that it is determined by \( \mu \) and by the per capita growth rate, \( f(q_c) \). For sufficiently low \( \mu \), the peak is narrow, and because at steady state \( f(q_c) = f'(q_c) = 0 \), \( A \) depends solely on \( f''(q_c) \) and on \( \mu \). Because

\[
\mu \sim \frac{|q|^2}{|t|^2},
\]

\[
f''(q_c) \sim -\frac{1}{|t||q|^2},
\]

and

\[
A \sim |q|,
\]

it follows that

\[
A \sim \left( \frac{\mu}{f''(q_c)} \right)^{1/4}.
\]

Direct calculations yield

\[
f''(q_c) = -\frac{\lambda s}{2} \Gamma(q_c),
\]

and for \( s \gg \lambda/m \),

\[
\Gamma(q_c) \approx \frac{2}{sm};
\]

therefore,

\[
f''(q_c) \approx -\frac{\lambda^2}{m},
\]

which implies

\[
A \sim \left( \frac{\mu m}{\lambda^2} \right)^{1/4}.
\]

Setting \( \lambda = 1 \) yields

\[
A \sim (\mu m)^{1/4}.
\]

---

**Fig. S1.** Emergence of species packing. Steady-state distributions of the model (Eqs. 1 and 2) are demonstrated on logarithmic y-axes when parameters are varied. (Top) Various values of stochasticity, \( s^{-1} \). When competition is deterministic, the distribution is smooth (left), whereas when competition is sufficiently stochastic, lumpy patterns emerge. Peaks appear near the singularity at \( q = m \) and become more apparent with increased stochasticity. (Middle) Various mutation rates, \( \mu \). Without mutations, the entire distribution is quantized with sharp zero-width peaks, whereas as \( \mu \) increases, peaks become wider and are apparent only near the singularity. Peaks do not appear if \( \mu \) is sufficiently large (right). (Bottom) Various invasion probability functions, \( g \), all of which are sigmoidal, symmetric functions with the same variation width. (C1) \( g \) is given by Eq. 1 in the main text with \( s = 4 \). (C2) \( g \) is a piecewise linear function (Eq. S6 with \( s = 4 \)). (C3) \( g(q, q') = \frac{1}{2} \text{erf}(\sqrt{s}(q - q')) \). (C4) \( g(q, q') \) equals \( 1 - \frac{1}{2}e^{-\frac{(q-q')^2}{4s}} \) if \( q < q' \), and \( \frac{1}{2}e^{-\frac{(q-q')^2}{4s}} \) otherwise. In all four cases, the pattern is multimodal on the left, followed by a smooth tail on the right. Other parameters: \( \mu = 10^{-8} \) (Top), \( s = 8 \) (Middle), and \( \mu = 10^{-7} \) (Bottom).

**Fig. S2.** Demonstrated is the steady-state fraction of occupied patches, \( \Gamma(q_1) \), provided the entire population has the same maximal growth rate \( q_1 \) (Eq. S2).

\[ \Gamma(q_1) \]
Movie S1. Stochastic competition promotes multimodal distributions. The dynamics of the distribution \( \rho(q) \) (Eq. 2) is demonstrated for stochastic competition \((s = 8, \mu = 10^{-7})\). Packs emerge and propagate leftward to lower \( q \). The first few packs on the left approach stable positions, thus creating a steady-state multimodal pattern, whereas the packs that follow merge into a smooth tail.

Movie S1

Movie S2. Deterministic competition promotes smooth distribution. The dynamics of the distribution \( \rho(q) \) (Eq. 2) is demonstrated for deterministic competition \((s = \infty, \mu = 10^{-6})\). Packs propagate leftward to lower \( q \). The first few packs vanish at \( q = m \), leaving the packs that follow to create a smooth distribution.

Movie S2
Movie S3. From smooth to multimodal distribution. When competition is stochastic ($s = 32$, $\mu = 10^{-8}$) and $\rho(q)$ is initially smooth, a nearly periodic pattern of propagating packs emerges. Eventually, a stationary lumpy pattern remains near the singularity $q = m$, whereas on the right, the distribution becomes smooth again.

Movie S3