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# Food-web structure in low- and high-dimensional trophic niche spaces

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# Food-web intervality in low- and high-dimensional trophic niche spaces

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### Abstract

A question central to modeling and, ultimately, managing food webs concerns the dimensionality of trophic niche space, that is, the number of independent traits relevant for determining consumer-resource links. Food-web topologies can often be interpreted by assuming resource traits to be specified by points along a line and each consumer's diet to be given by resources contained in an interval on this line. This phenomenon, called intervality, is now known for 30 years and is widely acknowledged to indicate that trophic niche space is close to one-dimensional. We show that the degrees of intervality observed in nature can be reproduced in arbitrary-dimensional trophic niche spaces when phylogenetic correlations between resource traits are taken into account. Contrary to expectations, higher-dimensional niche spaces enhance intervality.

## 1 Introduction

Elton's[1] conception of a species' niche as "its place in the biotic environment, its relations to food and enemies", which was later formalized by Hutchinson[2] as a hyper-volume in a high-dimensional niche space, comprehensively relates to all ecologically relevant traits of a species. Cohen's trophic (feeding) niche space[3] specializes this concept to traits relevant for trophic interactions. In this view, food-web links result when a resource's traits characterizing its vulnerability to predation are located within the consumer's foraging niche[4], characterized by its foraging traits.

If, for example, a species' consumers were fully determined by its mean body size, the trophic structure of a community could be represented as in Fig. 1a, by resource body sizes and consumer foraging niches that extend across the body sizes of their resources. Standard representations of food webs, either as directed graphs (Fig. 1b), with arrows pointing from resources to consumers, or *adjacency matrices* (Fig. 1c), with the set of ones in each column indicating a consumer's diet, can then be derived. A *niche-overlap graph*[3] (Fig. 1d) is obtained by linking two consumers if they share a common resource. This obviously implies that their foraging niches (Fig. 1a) overlap. If the niche-overlap graph of a food web can be represented by the overlaps of foraging niches given by intervals along a line, the food web is called *interval*. If more than one trait determines trophic interactions, that is, in higher-dimensional niche spaces, this property is not generally satisfied. Specifically, the chance that a random food web is interval becomes vanishingly small as the dimensionality of niche space increases. As a second, stronger, characterization of interval food webs[5,6,7], a web's adjacency matrix web is said to have the *consecutive ones property* (COP) along the columns, if, with an appropriate ordering of species, the ones in each column are consecutive (Figs. 1c,2). A third, weaker, characterization of intervality used in some studies[8,9,6] is the *chordal* property[1] of the niche-overlap graph (essentially, graphs are chordal if each minimal cycle is a triangle; Fig. 1d).

The surprisingly high frequency of interval webs in empirical data[10] has been interpreted as an indication of an approximately one-dimensional trophic niche space. Several candidates for the trait corresponding to this dimension, most prominently body size[11], have been considered[10], but difficulties in establishing the association persist[10,7]. Yet, food webs are now regularly modeled as essentially structured by body size or some abstract trait variable[4,12,13,7,14,15,16,17]; which may have contributed to identifying community size structure as an ecological management objective[18]. Others have argued that evolutionary processes might cause intervality[8,4,6,19,20]. In fact, phylogenetic correlations in food webs are strong[6] and underlie the common practice of aggregating larger taxonomic groups in food webs to single compartments (e.g., Fig. 2). A prominent interpretation of food-web structure[6] invokes the tendency of phylogenetically related consumers to share resources as the structuring mechanism.

The purpose of our study here is to develop a coherent, unified theory of intervality, accounting for the combined effects of niche-space dimensionality and phylogenetic correlations, their relative strengths, and potential synergies. In contrast to previous work[8,6], our theory relies on the tendency of related resources to share consumers, i.e., on phylogenetic correlations between resource traits, which may be even stronger than those between foraging traits[21,22,23].

# 2 Intervality in evolving food webs

## 2.1 Model and variants studied

We studied model food webs resulting from interactions of a fixed number $S$ of species in a $D$-dimensional niche space. Associated with each species $i$ is a $D$-dimensional vector of resource (or vulnerability) traits $\vec{V}_i$ and a $D$-dimensional vector of foraging traits $\vec{F}_i$. Species $i$ consumes species $j$ if the distance $|\vec{F}_i - \vec{V}_j|$ between $\vec{F}_i$ and $\vec{V}_j$ is smaller than some fixed niche width $w$. For simplicity, complicating assumptions such as a trophic hierarchy or a distinction between consumers and producers were not included in the model, since these are not essential for our arguments and conclusions, as we shall explain below. We set $S = 50$ and chose $w$ such that the expected number of trophic links per species was 10 (Methods). These are typical values for recently published empirical food-web data sets[24]. Resource traits of species evolve independently through random walks (Methods) with a tendency to revert to a set of preferred traits[25,21] defined as $\vec{V}_i = 0$. Phylogenetic correlations between resource traits are generated by random branching events. These model the speciation of a species by adding an identical copy of it to the system, while randomly removing a third species (extinction) to keep $S$ fixed. We investigated model variants

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[1] If no pair of vertices that are non-adjacent in a cycle of a graph are connected by a link, the cycle is called *chordless*. A graph is called *chordal* if it has no chordless cycles of length larger than three.

without (variant I) and with (II) phylogenetic correlations. A special algorithm (Methods) allowed us to sample all model variants from the exact stochastic steady state of resource-trait evolution. As a simple way of modeling the adaptation of foraging traits to resource traits, we focused each species $i$ on some random resource $j$ by setting $\vec{F}_i = \vec{V}_j$. In another variant (III), we employed a simple model of adapting consumers (Methods) that seek to increase their fitness by adjusting their foraging traits, starting from a focused configuration with phylogenetically correlated resource traits.

## 2.2 Measures of intervality

To quantify intervality in the resultant food webs, we determined the probabilities $P_{\mathrm{COP}}$, $P_{\mathrm{interval}}$, $P_{\mathrm{chordal}}$ of obtaining food webs with the COP, or with interval or chordal niche-overlap graphs, respectively, and computed model averages of the following three quantitative measures of intervality known from the literature: the minimum number $N_{\mathrm{gap}}$ of additional links ("gaps", Fig. 2) required to obtain the COP[7], the fraction $D_{\mathrm{diet}}$ of triplets of consumers with more than one resource that do not have the COP[6], and the number $Cy_4$ of cycles of length four in the niche-overlap graph that violate the chordal property[9,6]. Logical relations[5,8,6,7] between these characterizations of intervality are illustrated in Fig. 3.

## 2.3 Results

We analyzed trophic niche spaces with $D = 1$ to 20 dimensions, as well as with $D = 200$ and $D = 2000$. As expected, all model variants exhibited perfect intervality for a one-dimensional niche space. In the absence of phylogenetic correlations (variant I, dotted lines in Fig. 4), deviations from intervality rapidly increased with $D$ and remained large for $D$ up to 2000. Deviations in terms of niche-overlap graphs ($1 - P_{\mathrm{interval}}$, $1 - P_{\mathrm{chordal}}$, $Cy_4$) slightly relaxed with increasing $D$, but the three measures based directly on the adjacency matrix ($1 - P_{\mathrm{COP}}$, $D_{\mathrm{diet}}$, $N_{\mathrm{gap}}$) increased monotonically. These results corresponds to the standard interpretation[3] of intervality as being indicative of $D \approx 1$. By contrast, with phylogenetic correlations (variant II, continuous lines), deviations from intervality were maximal at $D = 2$ or $D = 3$ and then decreased with increasing $D$, approaching perfect intervality for large $D$. Adaptation (variant III, dashed lines) of foraging traits enhanced intervality further. (As a result of this adaptation, the average number of links per species increased slightly to between 11 and 13. By increasing the niche width $w$ and thus the number of links per species, we easily verified that this increase alone would worsen intervality, rather than improving it.)

# 3 Discussion

## 3.1 Mechanism for intervality in high dimensions

We can offer the following quantitative explanation of why phylogenetic correlations among resource traits enhance intervality. In our model, the expected value of the squared distance between the $\vec{V}_i$ vectors of two species increases with the time since separation of their lineages and, up to a constant factor, follows a

$\chi^2$-distribution with $D$ degrees of freedom (Methods). Thus, this distribution's coefficient of variation decreases as $D^{-1/2}$ with niche-space dimensionality. For sufficiently large $D$, distance hence becomes a strictly increasing function of time since separation. As shown in Fig. 5, this implies intervality: intervals correspond to branches of the phylogenetic tree. This explanation applies also to model variants in which (IV) some species (producers) do not forage, (V) niche width varies between consumers, (VI) size affects the selection of a consumer's focal resource, or where (VII) a trophic hierarchy constrains consumer-resource interactions (results not shown). A general, rigorous statement and proof of these results will be published elsewhere.

The effect of dynamic adaptation to enhance intervality can also be understood. Seeking to increase its fitness, a species will typically adapt its foraging traits $\vec{F}_i$ so as to center them within the cluster of the resource traits of its prey: this improves the correspondence between resource sets and branches of the phylogenetic tree in comparison to the case with focused consumers.

## 3.2 Weaker intervality in empirical data

Large empirical food webs typically exhibit less pronounced intervality than shown in Fig. 4 [26,6,7]. For example, Cattin *et al.*[6] find values of $D_{\text{diet}}$ ranging from 0.004 to 0.35, with a mean of 0.18, for a set of seven food webs ranging in size from $S = 25$ to 94. When relaxing idealizations of our model, intervality is readily brought into alignment with these empirical values. For example, when increasing the tendency of resource traits to revert to the origin, so as to reduce phylogenetic correlations[21], the maximum of $D_{\text{diet}}$ shifts to increasingly larger dimensions $D$ (continuous line in Fig. 6). For smaller $D$, the value of $D_{\text{diet}}$ then approaches the uncorrelated case. As another example, to account for aspects of ecology not captured by our simple model, we randomly removed a fraction $x$ of the trophic links in food webs generated by model variant II, and randomly added the same number of links at other positions, thus generating webs with small-world topologies. With only 10% of links rewired, $D_{\text{diet}}$ again reaches typical empirical values (dashed lines in Fig. 6). This strong sensitivity of quantitative departures from intervality cautions against deducing niche-space dimensionality from intervality alone.

## 3.3 Conclusion and outlook

Phylogenetic clustering might explain the observed block structure of adjacency matrices[5], the abundance of specific network motives[27], the absence of holes in resource graphs[8], and the particular distribution of the number of a consumer's resources[12,28,19]. When intervality is no longer interpreted as constraining the dimensionality of trophic niche space, the importance of evolutionary processes for structuring communities is re-asserted.

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# A Appendix A

## A.1 Chordal graphs

If no pair of vertices that are non-adjacent in a cycle of a graph are connected by a link, the cycle is called *chordless.* A graph is called *chordal* if it has no chordless cycles of length larger than three.

## A.2 Branching random walks

Between speciation events, resource traits in the model evolve through independent, multidimensional Ornstein-Uhlenbeck processes,

$$d\vec{V}_i(t) = -r\,\vec{V}_i(t)\,dt + \sigma\,d\vec{W}_i.$$

The reversion rate $r$ characterizes environmental and physiological limitations to realizable traits, $\sigma$ is the rate of (neutral) evolution, and $\vec{W}_i$ denotes a $D$-dimensional Wiener process. At a rate $s$ per species, speciation events occur, with a copy of the branching species replacing a third, randomly chosen species (Moran process).

We choose units of time and distance in niche space such that $s = \sigma = 1$ without loss of generality. Then $r^{-1}$ corresponds to the time over which a species "remembers" its phylogenetic origin in units of speciation times. We set $r = 0.01$ to reflect the observed pattern of largely divergent, but occasionally convergent, evolution.

## A.3 Generation of steady-state food-web samples

We show how exact steady-state samples of our simple food-web model are computed without having to simulate the underlying stochastic dynamics. First, we recall that for a one-dimensional Ornstein-Uhlenbeck (OU) process,

$$dx = -r\,x\,dt + \sigma\,dW, \tag{1}$$

the variance at $t = 0$ for a process $x$ starting from a deterministic initial condition at $t = -T$ is

$$\operatorname{Var} x|_{t=0} = \frac{\sigma^2}{2r}\left[1 - \exp(-2\,r\,T)\right]. \tag{2}$$

We denote by $V_k^{(i)}$ the $i$th component ($1 \le i \le D$) of the vulnerability vector $\vec{V}_k$ of species $k$ at $t = 0$. By the linearity of the OU process and Eq. (2), we obtain for model variants II and III (which include phylogenetic correlations)

$$\mathrm{Var}\,(V_k^{(i)} - V_l^{(i)}) = \frac{\sigma^2}{r}\,\left[1 - \exp(-2\,r\,T_{kl})\right], \tag{3}$$

where $T_{kl}$ is the time since separation of the lineages of $k$ and $l$. We define the function relating times $T$ to variances $v$ as

$$v(T) := \frac{\sigma^2}{r}\,\left[1 - \exp(-2\,r\,T)\right]. \tag{4}$$

Model variant I (which excludes phylogenetic correlations) corresponds to the limit $T \to \infty$, $v(T) \to \sigma^2/r$.

Now, we choose an arbitrary species $m$ as a reference point. In order to obtain the covariance matrix of the vulnerability vectors of the other species relative to $m$, we observe that

$$\begin{aligned}\mathrm{Var}\,(V_k^{(i)} - V_l^{(i)}) &= \mathrm{Var}\,\left[(V_k^{(i)} - V_m^{(i)}) - (V_l^{(i)} - V_m^{(i)})\right]\\ &= \mathrm{Var}\,(V_k^{(i)} - V_m^{(i)}) - 2\,\mathrm{Var}\,(V_k^{(i)} - V_m^{(i)}, V_l^{(i)} - V_m^{(i)})\\ &\qquad + \mathrm{Var}\,(V_l^{(i)} - V_m^{(i)}).\end{aligned} \tag{5}$$

Thus

$$\mathrm{Var}\,(V_k^{(i)} - V_m^{(i)}, V_l^{(i)} - V_m^{(i)}) = \frac{v(T_{km}) + v(T_{lm}) - v(T_{kl})}{2}, \tag{6}$$

which can be evaluated using Eq. (4), provided the phylogenetic matrix $(T_{kl})$ is given. Since the solutions of the OU equation are normally distributed, the covariance fully determines the distribution of the resource traits relative to $\vec{V}_m$. The standard method for drawing samples from this distribution is to multiply the lower-triangular factor of the Cholesky decomposition of the covariance matrix with a vector of independent standard normally distributed random numbers. The focused foraging traits are obtained by randomly drawing from the set of $S$ species, with replacement, for each consumer one species as its focal species.

Phylogenetic matrices $(T_{kl})$, or coalescence times, of Moran processes can be sampled efficiently by simulating the coalescence of the $S$ lineages backwards in time until all lineages are connected[29]. Since speciation events are assumed to occur spontaneously and independently, the Gillespie algorithm[30] can be used: times between subsequent coalescence events are drawn from an exponential distribution with mean $\tau$ given by

$$\tau^{-1} = s\,M\,\frac{M-1}{S-1}, \tag{7}$$

where $s$ is the speciation rate and $M$ is the number of lineages remaining to be connected. To understand Eq. (7), it is useful to randomly label the two species emerging from a speciation as ancestral and child species. The probability for a species to coalesce with any child species going backwards in time by a short step $\Delta t$ is $s\Delta t$, the probability for any of the $M$ unconnected species to do so is $s\,M\,\Delta t$, accounting for the first two factors in Eq. (7). The last factor in Eq. (7) represents the probability that the child species is from one of the other $M-1$ unconnected lineages present at $t = 0$, rather than from a lineage that dies out before $t = 0$.

## A.4 Choice of niche width to obtain a given number of links per consumer

To compute the expectation value of the number $Z_c$ of links per consumer for model variants I and II, first notice that in our simple model each consumer has one focal resource species $l$ to which it is linked. The probability to have any other species $k$ as its resource is the probability that $|\vec{V}_k - \vec{V}_l|^2 < w^2$. Since the differences between vulnerabilities are normally distributed, $|\vec{V}_k - \vec{V}_l|^2 \sim v(T_{kl})\chi^2_D$, with $v$ as defined in Eq. (3) and the last factor following a $\chi^2$-distribution with $D$ degrees of freedom. The probability of linking a consumer focused on $l$ to a resource $k \neq l$, given the coalescence time $T$, is therefore given by the cumulative $\chi^2$-distribution

$$p(T) = \frac{\gamma\left(\frac{D}{2}, \frac{w^2}{2\,v(T)}\right)}{\Gamma(D/2)}, \tag{8}$$

where $\gamma(x, y) = \int_0^y e^{-t}t^{x-1}dt$ is the incomplete $\gamma$ function and $\Gamma(x) = \gamma(x, \infty)$ the standard $\Gamma$ function.

For model variant II, the coalescence time has an exponential distribution with mean[29] $\tau_c = (S-1)/2s$, i.e., the value of $\tau$ given Eq. (7) with $M = 2$. The probability for a consumer focused on $l$ to forage also on $k \neq l$ can thus be obtained as

$$P_{\text{link}} = \frac{1}{\tau_c}\int_0^\infty \exp(-T/\tau_c)p(T)dT. \tag{9}$$

This integral needs to be evaluated numerically. For model variant I, we obtain $P_{\text{link}} = \lim_{T\to\infty} p(T)$. For both variants I and II, the expected number of links per consumer is given by

$$\mathbb{E}(Z_c) = 1 + (S-1)P_{\text{link}}. \tag{10}$$

We numerically solved this equation for $w$ to obtain the niche width that yields the desired expected number of links per consumer.

## A.5 Adaptation of foraging traits

The fitness $f_j$ of each species $j$ combines positive effects from adaptation to resources with negative effects from interference competition with consumers with similar foraging traits[13],

$$f_j = \sum_i \exp\left(-\tfrac{1}{2}|\vec{V}_i - \vec{F}_j|^2/w_V^2\right) - a\sum_i \exp\left(-\tfrac{1}{2}|\vec{F}_i - \vec{F}_j|^2/w_F^2\right). \tag{11}$$

Parameters $a$ and $w_F$ are chosen to describe weak interference competition ($a = 0.2$) over a narrow range in niche space ($w_F = w/6$, where $w$ is the niche width used for model variant II); we set $w_V = w/3$, to interpret the niche width $w$ as the cut-off radius at which the trophic interaction strength drops to $\exp(-\frac{1}{2}w^2/w_V^2) \approx 1\%$ of its maximum possible value. Starting from model variant II, foraging traits are evolved according to

$$\frac{d\vec{F}_j}{dt} = \frac{\partial f_j}{\partial \vec{F}_j} \tag{12}$$

until a fixed point is reached.

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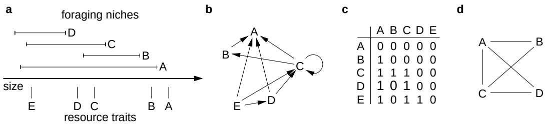
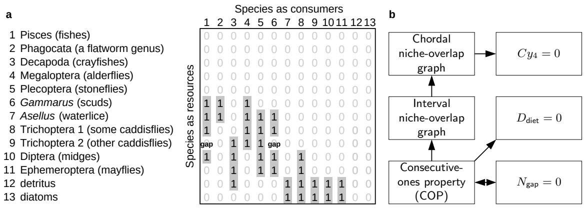


|   | A | B | C | D | E |
|---|---|---|---|---|---|
| A | 0 | 0 | 0 | 0 | 0 |
| B | 1 | 0 | 0 | 0 | 0 |
| C | 1 | 1 | 1 | 0 | 0 |
| D | 1 | 0 | 1 | 0 | 0 |
| E | 1 | 0 | 1 | 1 | 0 |

Fig. 1: Representations of food webs. **a** Resource traits and foraging niches in a one-dimensional niche space. **b** Food-web graph displaying the resulting resource-consumer links. **c** Adjacency matrix of the food-web graph. **d** Niche-overlap graph indicating which consumers share resources.



|    | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 |
|----|---|---|---|---|---|---|---|---|---|----|----|----|----|
| 1  | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2  | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 3  | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 4  | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 5  | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 6  | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 7  | 1 | 1 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 8  | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 9  | gap | 0 | 1 | 1 | 1 | gap | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 10 | 1 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 11 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 0 |
| 12 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |
| 13 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 1 | 1 | 1 | 0 | 0 |

Fig. 2: Adjacency matrix of the food web "Morgan's Creek" [10,31]. Indices of columns and rows refer to the same food-web vertices. Each '1' in the matrix specifies a diet item of a consumer. The label "gap" indicates additional diet items that would need to be added to give the matrix the consecutive-ones property (COP) along the columns.

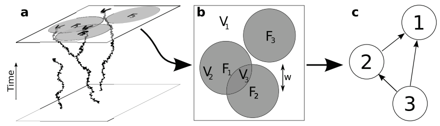


Fig. 3: Relations between qualitative and quantitative characterisations of intervality. Arrows indicate logical implications. The consecutive-ones property, explained by our theory, implies intervality by all other criteria.

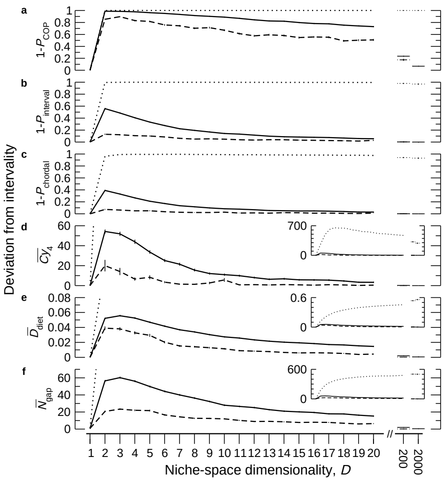


Fig. 4: Deviations from perfect intervality in dependence on niche-space dimensionality. $P_{\mathrm{COP}}$ (a), $P_{\mathrm{interval}}$ (b), and $P_{\mathrm{chordal}}$ (c) denote the probabilities of obtaining food webs with consecutive-ones property, and webs with interval and chordal niche-overlap graphs, respectively. $\overline{Cy_4}$ (d), $\overline{D}_{\mathrm{diet}}$ (e), and $\overline{N}_{\mathrm{gap}}$ (f) denote the averages of the quantitative measures for deviations from intervality explained in the text. Dotted lines (model variant I) and continuous lines (variant II) correspond to focused consumers without and with phylogenetic correlations, respectively ($10,000$ sample webs per point; for $\overline{N}_{\mathrm{gap}}$ only $1,000$), dashed lines to adapted consumers (variant III; $1,000$ sample webs per point, $D = 2,000$ excluded for computational reasons). Insets expand vertical axes. Vertical bars, where visible, indicate standard errors.

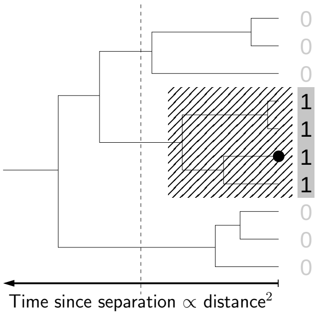


Fig. 5: Phylogenetic theory of intervality. Our model implies that for high-dimensional niche spaces the distance between the resource traits of two species strictly increases with the time since separation of their lineages (tree diagram). The diet of a focused consumer is given by all species with resource traits closer than some niche width to its focal species (filled circle), that is, by those lineages that separated from the focal species less than a given time ago (dashed line). This diet set corresponds to a branch (hatched area) of the phylogenetic tree and to a set of consecutive ones along the tree's tips.

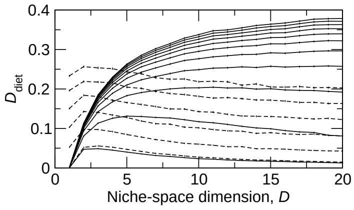


Fig. 6: Intervality in non-ideal model food webs. Intervality is weakened, and $D_{\text{diet}}$ thus is raised, by increasing the reversion rate $r$ (continuous lines, $r = 0$, $0.1$, ..., $1$ in units of the speciation rate; Methods) and also by randomly rewiring a fraction $x$ of a food web's trophic links (dashed lines, $x = 0$, $0.02$, ..., $0.1$). Notice that all continuous lines approach $0$ for sufficiently high $D$.