

Supporting Information

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SI Text

In this supporting information (SI), we present results on the facilitation among four stage-specific predators that specialize on four different life-history stages of the same prey species and on the consequences of environmental stochasticity for the emergent facilitation between the two stage-specific predators that are considered in the main text of the paper. In addition, we discuss in more detail examples of published results, both experimental and empirical, that can be explained by the emergent facilitation or can be interpreted as evidence for its occurrence.

Facilitation Among Four Stage-specific Predators. To illustrate the generality of the emergent facilitation discussed in the main text and some of its further consequences for community structure, we consider a prey population that is subdivided into four distinct life-history stages, representing small- and large-sized juveniles and small- and large-sized adults, respectively. Each of these four prey stages is potentially attacked by its own specialist predator. An exhaustive analysis of the dynamics of the model presented in the following text and its dependence on parameter values goes far beyond the scope of this SI. We will, therefore, only highlight some of its predictions to illustrate that emergent facilitation also occurs in prey species with more extended stage structure. In addition, the results presented illustrate the higher order form of emergent facilitation in which a stage-specific predator that itself persists only in the presence of a second stage-specific predator facilitates the persistence of a third stage-specific predator. These results are only presented as “proof-of-principle” to show that certain phenomena may occur without providing a detailed study of the likelihood of their occurrence in terms of model parameters.

Model Formulation and Parameterization. Prey-stage biomass dynamics are modeled with the same, stage-based biomass model as discussed in the main text but extended to four prey stages (1). The biomass densities of small-juvenile, large-juvenile, small-adult, and large-adult consumer stages we refer to as C_1 , C_2 , C_3 , and C_4 , respectively, and the densities of the corresponding specialist predators as P_1 , P_2 , P_3 , and P_4 . Dynamics are described by the following system of ODEs:

$$\begin{aligned} \frac{dR}{dt} &= \delta(R_{\max} - R) - \Omega(R, C_1, C_2, C_3, C_4) \\ \frac{dC_1}{dt} &= (1 - k_3)v_3(I_3)C_3 + v_4(I_4)C_4 + v_1(I_1)C_1 - \gamma_1(v_1(I_1), \mu_1)C_1 \\ &\quad - \mu_1(C_1, P_1)C_1 \\ \frac{dC_2}{dt} &= \gamma_1(v_1(I_1), \mu_1)C_1 + v_2(I_2)C_2 - \gamma_2(v_2(I_2), \mu_2)C_2 \\ &\quad - \mu_2(C_2, P_2)C_2 \\ \frac{dC_3}{dt} &= \gamma_2(v_2(I_2), \mu_2)C_2 + k_3v_3(I_3)C_3 - \gamma_3(k_3v_3(I_3), \mu_3)C_3 \\ &\quad - \mu_3(C_3, P_3)C_3 \\ \frac{dC_4}{dt} &= \gamma_3(k_3v_3(I_3), \mu_3)C_3 - \mu_4(C_4, P_4)C_4 \end{aligned}$$

$$\frac{dP_i}{dt} = (v_{P_i}(C_i) - d_{P_i})P_i \quad \text{for } i = 1, \dots, 4$$

As before, resource R follows semichemostat dynamics in absence of consumers. Mass-specific, net biomass production of consumer stage i and its specialist predator equals the balance between mass-specific assimilation and maintenance requirements, defined as $v_i(I_i) = \sigma I_i - T_C$ and $v_{P_i}(C_i) = \sigma M_{P_i} C_i / (C_i + 1) - T_{P_i}$, respectively. Here T_C and T_{P_i} represent the mass-specific maintenance requirements for consumers and for specialist predator species i , respectively, whereas σ equals the conversion efficiency. I_i represents mass-specific ingestion by consumers in stage i . In the following text we consider a scenario with only juveniles competing for limiting resource and adults having an unlimited food supply in which case juvenile and adult ingestion are defined as $I_1 = I_2 = M_C R / (R + 1)$ and $I_3 = I_4 = M_C$, respectively, whereas total resource foraging by consumers equals $\Omega(R, C_1, C_2, C_3, C_4) = M_C R (C_1 + C_2) / (R + 1)$. Similarly, in the contrasting scenario that we consider with adult consumers competing for limiting resource and unlimited juvenile consumer food supply, juvenile and adult consumer ingestion follows $I_1 = I_2 = M_C$ and $I_3 = I_4 = M_C R / (R + 1)$, respectively, and total resource foraging is defined as $\Omega(R, C_1, C_2, C_3, C_4) = M_C R (C_3 + C_4) / (R + 1)$. Hence, both consumer and predator foraging follows a type-II functional response of the resource the individuals compete for with maximum ingestion rate M_C and M_{P_i} for consumers and for predator species i , respectively.

Biomass of all consumer stages decreases through stage-specific mortality, which is the sum of consumer background mortality $d_c C_i$ and predation mortality: $\mu_i(C_i, P_i) C_i = d_c C_i + M_{P_i} P_i C_i / (C_i + 1)$. Biomass of both juvenile consumer stages also decreases through maturation $\gamma_i(v_i(I_i), \mu_i) C_i$ and increases through net-biomass production $v_i(I_i) C_i$. Small-adult individuals invest a fraction, $k_3 = 0.5$, of their net-biomass production into somatic growth whereas the remainder is invested into reproduction. Small-adult biomass increased through somatic growth therefore equals $k_3 v_3(I_3) C_3$, whereas its decrease through maturation is defined as $\gamma_3(k_3 v_3(I_3), \mu_3) C_3$ (1). Biomass of all but the smallest consumer stage increases through maturation from the preceding stage. Large-adult consumers invest all their net-biomass production into reproduction and their biomass density therefore only changes through maturation from the small-adult consumer stage and through mortality. Biomass in the small-juvenile consumer stage increases through reproduction by both small- and large-adult consumers, described by $(1 - k_3) v_3(I_3) C_3$ and $v_4(I_4) C_4$, respectively. As discussed in the main text, the maturation function $\gamma_i(v, \mu) = (v - \mu) / (1 - z_i^{1 - \mu/v})$ depends on the mass-specific investment of net-biomass production into somatic growth v , which equals $v_i(I_i)$ for both juvenile stages and $k_3 v_3(I_3)$ for small-sized adult consumers, the stage-specific mortality μ_i , and the ratio z_i of the smallest and largest value in the body size interval encompassed by consumer stage i . The specific form of the maturation function guarantees the full correspondence between the equilibria of the stage-based biomass model and those of a fully size-structured model with a continuous consumer size distribution (1). Dynamics of the biomass densities of the specialist predators reflect the balance between mass-specific net-biomass production $v_{P_i}(C_i)$ and constant predator mortality d_{P_i} .

All biomass densities are expressed in gram per unit volume whereas time is expressed in days. The choice of the unit volume is arbitrary and represents a scaling factor of all densities.

Consumers are assumed to reach a maximum size as large adults equal to 2 g. The ratio between the smallest and largest size of small-juvenile, large-juvenile, and small-adult consumers we assumed to be equal to $z_1 = 0.2$, $z_2 = 0.5$, and $z_3 = 0.2$, respectively. Consumer maturation therefore occurs at a body size of 0.4 g and consumers can increase by a factor of 5 in body size after maturation. Representative body masses for the 4 specialist, stage-specific predator species are taken equal to 30, 80, 140, and 200 g, respectively, reflecting a predator-prey body size ratio of 2 orders of magnitude. Mass-specific maximum ingestion and maintenance rate, as well as background mortality rate of consumers, and the 4 species of specialist predator species follow quarter power scaling laws of their respective adult-body sizes with proportionality constant 0.1, 0.01, and 0.001, respectively (see *Materials and Methods* section of the main text). Predator mortality values are expressed as multiples of their default background mortality, which equal $d_{P_1} = 0.00043$, $d_{P_2} = 0.00033$, $d_{P_3} = 0.00029$, and $d_{P_4} = 0.00027$. Values for assimilation efficiency, maximum resource density, and resource turnover rate are taken as equal to the values used in the main text: $\sigma = 0.3$, $R_{max} = 2$, and $\delta = 0.1$, respectively.

Unlimited Juvenile Food Supply. In case all adult consumers compete with each other for limiting resources although juvenile consumers have access to an unlimited food supply, the consumer population is in absence of predators dominated by small-adult individuals (Fig. S1, compare with consumer population structure at high predator death rate). Biomass densities of the three other consumer size classes are low. As a consequence, only prey availability for the specialist predator on small-adult consumer is high enough for it to invade a consumer-resource equilibrium, provided its death rate is sufficiently low (<15 times its background mortality level). Following establishment of the specialist predator on small-adult consumers in a consumer-resource community, biomass densities in all but the small-adult consumer stage will increase. However, only biomass in the two juvenile consumer stages increases above the level that is needed for specialist predators on these stages to persist (Fig. S1). The biomass increase of large-adult consumers is very small in absolute terms. Establishment of the specialist predator on small-adult consumers can hence change the stage composition of the consumer population to such an extent that specialist predators on either of the two juvenile stages can invade. The specialist predator on small-adult consumers thereby facilitates the invasion and persistence of both specialists on juvenile consumers. If both these predator species invade, they will compete with each other for juvenile consumer prey (data not shown). The specialist predator on small-juvenile consumers captures prey before they can reach the large-juvenile consumer stage and therefore decreases prey availability for the specialist on larger juveniles. As a consequence, the latter predator species tends to become competitively excluded by the former.

The results shown in Fig. S1 are qualitatively similar to the results shown in Fig. 2 (*Right Image*) of the main text. These results illustrate that emergent facilitation also occurs when prey populations have a more complicated stage structure. Furthermore, comparison of Fig. S1 with Fig. 2 emphasizes that it does not matter whether all or only part of the adult consumers are targeted by the specialist predator. However, occurrence of emergent facilitation crucially depends on the factor that the facilitating predator forages on the most abundant prey-size class. As an extension to the results presented in the main text, Fig. S1 makes clear that a specialist predator on the dominant-prey stage may facilitate more than one other predator species, to such an extent that even competition can arise between the species that are being facilitated. In other words, the specialist predator on the dominant-prey stage allows two other predator species to compete with each other.

Unlimited Adult Food Supply. In the case that all juvenile consumers compete with each other for limiting resources although adult consumers have access to an unlimited food supply, the consumer population is, in the absence of predators, dominated by small-juvenile individuals (Fig. S2, compare with consumer population structure at high predator death rate), especially if the biomass densities of the two adult-consumer size classes are low. Provided its death rate is not too high (<15 times its background mortality level), the specialist predator on small-juvenile consumers can invade the consumer-resource community. Establishment of this specialist predator will lead to a decrease in large-juvenile consumer biomass and to increases of both small- and large-adult consumer biomass. Only the increase in large-adult consumer biomass is sufficient to lift its density above the minimal subsistence level of its specialist predator (Fig. S2). The specialist predator on small-juvenile consumers therefore facilitates the invasion of the specialist predator on large-adult consumers.

As in the previous section, the results of the four-stage consumer model with four specialist predators presented in Fig. S2 show qualitatively the same pattern as the results for the simpler, two-stage consumer model with two specialist predators (Fig. 2 *Left*). We can therefore conclude that in the case in which density dependence among juvenile consumers is stronger than among adult consumers, a specialist predator on part or all of these juveniles will facilitate specialist predators on adult consumers as long as the facilitating species includes the most abundant (and hence dominant) juvenile-consumer size class in its diet.

Analogous to the results presented in Fig. 3 *Left*, the facilitating predator species allows the specialist predator on large-adult consumers to persist under a substantial range of mortality conditions in which it cannot persist on its own (Fig. S3). Fig. S3 also illustrates an additional, higher-order form of emergent facilitation. The specialist predator on small-juvenile consumers on its own cannot increase biomass densities of small-adult consumers to such an extent that the specialist predator on these small adults can invade (Fig. S2). However, small-adult consumer biomass increases even further through the combined action of the specialist predators on small-juvenile and large-adult consumers. As a consequence, the specialist predator on small-adult consumers can invade under a range of mortality conditions when both other specialists are present (Fig. S3). Ultimately, it is the change in consumer stage distribution brought about by the specialist predator on large-adult consumers that allows for the invasion and persistence of the specialist on small-adult consumers. In other words, the facilitated species turns facilitator.

Fig. 4 in the main text illustrates this higher-order emergent facilitation by presenting a time series of invasion events by specialist predators into a consumer-resource community at equilibrium. Invasion of the specialist predator on small adult-consumers (Fig. 4, $t = 1,000$) into the consumer-resource equilibrium is unsuccessful; it can also not invade a community at equilibrium consisting of resource, consumer, and specialist predator on small-juvenile consumers (Fig. 4, $t = 14,000$). Invasion of specialist predators on small-juvenile consumers (Fig. 4, $t = 6,000$) is successful and changes the consumer stage-distribution such that biomass of large-adult consumers increases significantly. This allows for a subsequent, successful invasion and persistence of the specialist predator of these large-adult consumers (Fig. 4, $t = 17,000$). Establishment of the latter predator species leads to a substantial increase in the biomass density of small-adult consumers, which is sufficient to allow for subsequent invasion and persistence of the specialist predator on these small-adult consumers (Fig. 4, $t = 25,000$). Persistence of this specialist predator therefore crucially depends on the presence of the specialist predator on large-adult

consumers, which itself relies for its persistence on the presence of the predator that targets the small-juvenile consumers. If the specialist predator on large-adult consumers would be driven to extinction, for example, because of over-exploitation, the predator on small adults would die out as well and both these predator species would go extinct irrespective of their mortality level if the specialist predator on small-juvenile consumers disappears from the community. Communities consisting of resource, consumers, and either one of the specialist predators on adult consumers are therefore not persistent under conditions that allow for stable persistence of a five-species community, including resource, consumers, and three specialist predators. This reinforces our conclusion in the main text that emergent facilitation promotes stable persistence of complex, multispecies communities under conditions that simpler communities cannot despite the fact that the community food web only consists of negative interactions such as predation and competition.

Influence of Environmental Stochasticity on Emergent Facilitation. In both the main text and the previous section, we presented results showing emergent facilitation among predators based on deterministic population models. To assess to what extent environmental stochasticity would affect the occurrence of the facilitation, we investigated the dynamics of an extended version of the model presented in the main text of the paper, including stochastic, daily variation in the productivity of the resource. Stochastic variation in the maximum resource biomass density (R_{\max}) was generated by using the spectral synthesis and spectral mimicry methods as described in detail by Vasseur (2), yielding a noisy time-series of R_{\max} values with a power spectrum that scales as $1/f^\beta$. Independent of the color of the noise, which is determined by the parameter β , the mean value of the generated time-series in R_{\max} was kept equal to 2.0, the default value as used in the main text. We used a value of 0.5 for the standard deviation in R_{\max} . Model dynamics were investigated by using numerical integration of the equations presented in Table 2 of the main text in which the actual value of R_{\max} changed discretely at 1 time unit (day) intervals according to the noisy time-series generated for this parameter. We only considered the scenario in which adult consumers have unlimited access to food while juveniles compete for limiting resources.

Fig. S4 shows that when competition among juveniles limits the consumer population in equilibrium adult-specialized predators cannot increase from low densities in a community which only consists of juvenile and adult consumers. The dynamics presented in Fig. S4 resemble the results for the analogous, deterministic model shown in Fig. 1 of the main text except for the fact that in Fig. S4, we artificially enforced the density of adult-specialized predators to remain above a threshold of 0.003 even when population growth rates were negative. A predator's incapacity to invade such a community therefore is independent of stochastic variation in R_{\max} . Also independent of stochastic variation in R_{\max} , the adult-specialized predator does manage to grow and reach positive equilibrium densities after successful establishment of the juvenile-specialized predator. We therefore conclude that stochastic variation in resource productivity does not qualitatively change the emergent facilitation between two stage-specific predators, specializing on juvenile and adult consumers, respectively. Fig. S4 reveals that environmental noise has a larger quantitative influence on population dynamics if it is dominated by fluctuations with larger wavelengths (i.e., if the noise is more reddish in color, Fig. S4 Right, $\beta = 1.5$). Environmental variability, which is closer to white noise variation in R_{\max} (Fig. S4 Left, $\beta = 0.5$), tends to be dampened much more quickly and therefore does not significantly affect biomass dynamics.

We also analyzed how average biomass densities of juvenile and adult consumers and their specialized predators vary as a function of the death rate of the adult-specialized predator for

different types of environmental stochasticity in R_{\max} (Fig. S5). We assumed a death rate of juvenile-specialized predators equal to $d_{P_j} = 10$ and otherwise to default parameters. For all values of $d_{P_A} = 0, 0.01, 0.02, \dots, 6$, we constructed a stochastic time-series of R_{\max} with a mean value of 2.0 and a standard deviation of 0.5 using either $\beta = 0.5$ or $\beta = 1.5$ and subsequently used this time-series in the integration of the model equations. Average biomass densities of all populations were measured over an interval of 50,000 time units after transient dynamics had disappeared.

For $d_{P_j} = 10$ the deterministic model predicts that adult-specialized predators cannot survive on their own but can persist in the presence of juvenile-specialized predators up to mortality levels that are 3.5 times their background mortality rate (compare Fig. 3 Left, in the main text at $d_{P_j} = 10$ with the solid line in Fig. S5 Lower). Stochastic variation in R_{\max} introduces variation in biomass density of adult-specialized predators especially in case of environmental noise that is more reddish in color (Fig. S5 Right, $\beta = 1.5$). Overall, however, the stochastic variation tends to increase the average density of the adult-specialized predator above the value predicted by the deterministic model. As a consequence, stochastic variation in R_{\max} also increases the range of death rate values for which adult-specialized predators can persist in the presence of the juvenile-specialized predator. In the case that environmental stochasticity is more reddish in color (Fig. S5 Right, $\beta = 1.5$), the pattern is less clear-cut than in the case of stochasticity, which is closer to white noise as a consequence of the much larger variation in average biomass density. In general, however, we conclude that stochastic environmental variability in resource productivity does not qualitatively change the occurrence of the emergent facilitation discussed in the main text of the paper and quantitatively can tend to increase the ranges of parameters over which the facilitation occurs.

Experimental Evidence for the Occurrence of Emergent Facilitation.

Correlated density responses of macroinvertebrate predators and planktivorous fish. Nielsen and coworkers (3, 4) investigated competition between macroinvertebrates and planktivorous fish in experimentally constructed enclosures, so-called artificial billabongs, on the floodplain of the River Murray, New South Wales, Australia. Each billabong was divided into two equal parts and common carp-gudgeons (*Hypseleotris* spp.)—a native planktivorous fish known to forage on large cladocerans and adult copepods (5)—were added to one-half of each billabong. Experiments ran for 2 years. The addition of planktivorous fish significantly increased densities of microcrustaceans (4), particularly juveniles. Both cladocerans and copepods, especially nauplii and cyclopoid copepodites, were found in greater densities in the presence of fish. Eight of fourteen predatory macroinvertebrate species also increased in the presence of fish (3). The six species of macroinvertebrates that decreased after introduction of planktivorous fish include notonectids and odonates that exhibit significant diet overlap with fish (3). Macroinvertebrate species that increased following fish introduction include acarine, coleopteran, hemipteran, and dipteran predators. For acarine predators, it has been shown experimentally that they forage on cladocerans with a preference for smaller-sized individuals (6). We have not found any data on diet and especially size-selectivity of the other macroinvertebrate predators that increased in the presence of fish.

Without providing any evidence, Nielsen and coworkers argued that the increases in macroinvertebrate densities may have resulted from the decreases in density of the notonectids and odonates (3). In contrast, however, they argued that these notonectids and odonates decreased because they forage on microcrustaceans and therefore overlap in diet with the planktivorous fish. Alternatively and perhaps more parsimoniously

than the postulated top-down explanation, the increase in eight of the fourteen macroinvertebrate species can also be explained as a bottom-up effect: The larger densities of small, especially juvenile, cladocerans and copepods (nauplii and copepodites) promote population growth and therefore densities of macroinvertebrates that forage on them. If true, the presence of positively size-selective fish benefits the negatively size-selective macroinvertebrate predators through emergent facilitation, in particular, the type in which competition is more intense among adult rather than juvenile prey and the adult-specialized predator facilitates persistence of juvenile-specialized predators (see Fig. 3 Left).

Correlation in Density of Size-selective Invertebrate and Fish Predators. Leibold and Tessier (7) investigated body-size patterns of coexisting *Daphnia* species in seven lakes that represent a gradient of predation risk. Predators included *Chaoborus* that selectively forage on small cladocerans and bluegill that select large individuals as their prey. The range of lakes represented a gradient of predation intensity in which *Chaoborus* density was positively associated with bluegill density. Leibold and Tessier (7) do not discuss explanations for the positive association between *Chaoborus* and bluegill, which is, however, in line with predictions based on the emergent facilitation effects discussed in this paper, in particular the type in which competition is more

intense among adult rather than juvenile prey and the adult-specialized predator promotes persistence of juvenile-specialized predators (see Fig. 3 Right).

Nested Distribution Patterns of Positively and Negatively Size-selective Predators. Zimmerman (8) analyzed the predator communities preying on the brook stickleback (*Culaea inconstans*) occurring at 26 sites across Michigan's upper peninsula. Two groups of predators were distinguished. Small predators that were shown to be gape-limited capable of consuming small sticklebacks only, and large predators capable of consuming all sizes of sticklebacks but with a presumed bias toward longer sticklebacks (8). Small predators were widely distributed in contrast to large predators. However, large predators always occurred only if small predators were also present. The nested distribution of the large predator group may have resulted from facilitation by small predators, as negatively size-selective predators have been shown to increase densities of large individuals in prey populations (9). In accordance with this explanation, sticklebacks were larger at sites where they coexisted only with small-predator communities than at sites where large predators also occurred. This type of emergent facilitation could occur if competition is more intense among juvenile than adult prey and the juvenile-specialized predator promotes persistence of adult-specialized predators (see Fig. 3 Right).

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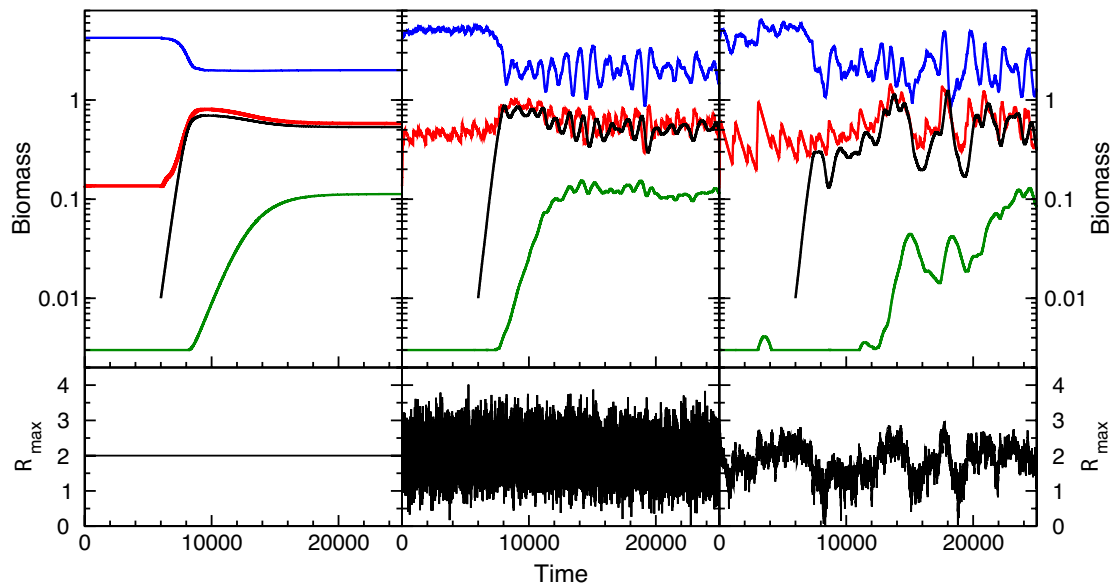


Fig. S4. Biomass dynamics of juvenile and adult consumers and their specialist predators (*Upper Image*) for different time-series of the maximum resource biomass density R_{\max} (*Lower Image*). Initially, the community consists of juvenile (*blue*), adult consumers (*red*), and adult-specialized predators (*green*). The density of these predators is forced to remain at a minimum threshold level >0.003 . Adult-specialized predators only increase significantly in density after the introduction of juvenile-specialized predators (*black*) at $t = 6,000$. (*Left*) In the absence of stochastic variation; (*Center*) stochastic variation in R_{\max} with a mean value of 2.0 and a standard deviation of 0.5 and $\beta = 0.5$; (*Right*) idem stochastic variation for $\beta = 1.5$. Adult consumers have unlimited food supply whereas juveniles compete for limiting resource. Death rates of juvenile- and adult-specialized predators equal $d_{P_J} = 10$ and $d_{P_A} = 1$, respectively (cf. Fig. 3, *Left Image*, in the main text), otherwise default parameter values.

