FORMAÇÃO DE TEIAS TRÓFICAS E SUA RESISTÊNCIA À INTRODUÇÃO E EXCLUSÃO DE ESPÉCIES: PROPRIEDADES RESULTANTES DE UM MODELO COMPUTACIONAL BASEADO NO INDIVÍDUO

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Resumo

Um modelo baseado no indivíduo para história de vida e interações tróficas de peixes é proposto nesta tese. Ele integra teorias sobre fisiologia, crescimento, reprodução e alimentação num mesmo arcabouço dinâmico. As comunidades são formadas por um processo seqüencial de assembleamento que seleciona espécies com melhor ajuste às condições locais. No capítulo 1, experimentos computacionais foram feitos para avaliar a resposta seletiva de 10 características bionômicas em gradientes de produtividade, taxas de ataque por predadores, distribuição do tamanho corporal no conjunto regional de espécies, e a presença/ausência de assimetrias nas habilidades dos peixes em consumir presas e em evitar predação. Este último fator inclui conflitos funcionais entre a eficiência de captura versus generalidade de dieta e intensidade de forrageamento versus defesa contra predadores. As comunidades resultantes foram fortemente afetadas pelos gradientes. Picos de riqueza ocorrem em produtividades moderadamente baixas, associadas a baixas taxas de ataque, o que pode estar relacionado ao efeito estabilizador de respostas funcionais menos saturadas e às características emergentes das espécies. Com alta disponibilidade de recursos, espécies de rápido crescimento e tamanhos variados dominaram, promovendo rápida depleção dos recursos durante a formação das comunidades e ocasionando fortes efeitos de prioridade. As assimetrias de consumo aumentaram a coexistência onde ela tende a ser mais difícil, mas a diminuíram em seus pontos de pico. Mas seu principal efeito foi o de modificar a composição ao longo dos gradientes, modulando o formato das associações emergentes entre as características biológicas das espécies bem sucedidas. No capítulo 2 foram realizados experimentos de invasão e exclusão, para avaliar como as características das espécies e das comunidades estão relacionadas ao sucesso de invasão e à extinção de nativos. Invasores bem sucedidos possuem história de vida similar à da comunidade invadida, mas pouca sobreposição de dieta. Por outro lado, invasores distintos das espécies nativas têm maior chance de promover extinções, ressaltando um conflito entre estabelecimento e impacto. Os padrões gerais de invasões e exclusões indicam a predominância de interações competitivas. Esta tese evidencia que o estudo de gradientes e a inclusão dos múltiplos conflitos funcionais experimentados por organismos como peixes são de grande importância para a compreensão dos mecanismos que determinam a distribuição da diversidade biológica e sua suscetibilidade a perturbações em paisagens heterogêneas.

Palavras-chave: Modelo baseado no indivíduo. Peixes. História de vida. Predação. Gradientes ambientais. Invasões biológicas.

Abstract

An individual-based model for fish life history and trophic interactions is here proposed. It integrates theories for individual physiology, growth, reproduction, and feeding in the same dynamical framework. Communities are formed by a sequential assembly process which selects for species best adjusted to local conditions. Simulation experiments were carried out to evaluate the distribution of diversity and selective response of 10 bionomic features along gradients of resource productivity, predators maximum attack rates, body size distribution in species pool, and the presence/absence of asymmetries in both the abilities of fish to consume prey and to avoid being consumed. This last factor includes tradeoffs concerning capture efficiency versus diet generality and foraging intensity (associated to growth rate) versus defense against predators. The resulting communities were strongly affected by the gradients. Richness peaks are localized at moderately low productivities associated to low maximum attack rates, which might be related to the stabilizing effect of less saturated functional responses and to the emergent features of selected species. At high resource availability, fast growing species with variable sizes dominated, promoting early fast resource depletion during assembly and leading to strong priority effects. The hierarchical consumption asymmetries increased coexistence where it tends to be more difficult, but diminished it at its points of peak. But its main effect was modifying species trait composition along other gradients, modulating the shape of emergent associations among biological features of successful species. Additional invasion and deletion experiments were carried out to evaluate how species and community features are related invasion success and native extinctions. Successful invaders tend to possess similar life-history features to invaded community, but low diet overlap. On the other hand, invaders dissimilar from native species are more probable to cause extinctions, highlighting a conflict between establishment and impact. In agreement with the low contribution of piscivory to total biomass fluxes, the overall patterns of invasions and extinctions demonstrates the predominance of competitive interactions in simulated communities. This work emphasizes that studying gradients and properly including the multiple tradeoffs faced by organisms like fish is of great importance to understand the mechanisms determining the distribution of biological diversity and its susceptibility to perturbations in heterogeneous landscapes.

Keywords: Individual-based model. Fishes. Life history. Predation. Environmental gradientes. Biological invasions.

1. INTRODUÇÃO GERAL

A modelagem tem um papel essencial na compreensão de processos ecológicos (MAY, 1973; MAYNARD SMITH, 1974; JORGENSEN, 1994). Além de ser a maneira formal pela qual estabelecemos relações entre variáveis, os modelos matemáticos ou computacionais permitem investigar questões ainda fora do alcance da coleta empírica ou experimental de dados, servem como guia para o planejamento dessas coletas, e são ferramentas úteis para a predição de mudanças e a avaliação de manejo em sistemas naturais. A Ecologia engloba processos e padrões altamente complexos, em níveis de organização que vão desde genes até a biosfera, passando por entidades tão conhecidas quanto importantes como organismos, populações, comunidades, ecossistemas, paisagens, biomas e províncias biogeográficas (BEGON et al., 1996; BROWN & LOMOLINO, 1998). Como reflexo dessa complexidade, existe uma grande variedade de modelos, que se diferenciam em parte pelo grau de refinamento das entidades mais básicas representadas (GIACOMINI, 2010). No caso da Ecologia de Comunidades, os modelos mais tradicionais voltados para a dinâmica das espécies são também os mais simples, derivados do modelo de Lotka-Volterra (VOLTERRA, 1926). Eles representam o tamanho populacional de uma espécie por uma única variável, conhecida por variável de estado, e promovem interações entre espécies por coeficientes que determinam diretamente a magnitude e o sinal da interação (GOTTELI, 2007). Cada população flutua continuamente no tempo, e sua taxa de variação é diretamente influenciada pelos níveis das outras populações por meio dos coeficientes de interação. Por representarem a espécie como um único compartimento, esses modelos ignoram a influência de qualquer variabilidade intra-específica sobre a dinâmica. Uma opção intermediária para se incluir diferenças dentro de uma população é dividi-la em mais compartimentos, que podem ser definidos por características como idade, estágio de desenvolvimento, ou tamanho corporal. Têm-se assim os modelos estruturados por idade, estágio, ou por tamanho (CASWELL, 1989). Outra opção é representar a variação dessas características por distribuições contínuas de freqüência de indivíduos ao invés de incluí-los em compartimentos discretos, como nos modelos fisiologicamente estruturados (PERSSON et al., 1998). Os modelos estruturados têm a grande vantagem de levar em conta variações intra-especificas relevantes de uma forma ainda matematicamente tratável. Mas tornam-se impraticáveis se o número de espécies, de compartimentos por espécie, ou de características biológicas for demasiadamente grande.

No extremo de maior complexidade e refinamento biológico encontram-se os modelos baseados no indivíduo (MBI) (HUSTON et al., 1988;DEANGELIS & MOOIJ, 2005). De certa forma, os MBIs podem ser concebidos como extensões de modelos estruturados. Por exemplo, se a idade é usada como fator de variação intra-específica, diferenças de idade podem ser representadas em diferentes graus de refinamento usando-se diferentes quantidades de compartimentos populacionais, desde um caso mais simples com dois compartimentos (com apenas um divisor de idade entre indivíduos novos e indivíduos velhos), até um número indefinido de compartimentos. O fato é que, para um dado tamanho populacional, refinar as informações sobre idade criando-se novos compartimentos implica na redução do número de indivíduos por compartimento. Num limite onde o intervalo de idades definindo cada compartimento tende a zero, e o número de compartimentos tende a infinito, ter-se iam apenas um ou poucos indivíduos por compartimento. Neste caso, é muito mais viável representar os indivíduos separadamente, ao invés de modelar compartimentos. Essa é a grande característica dos MBI: o indivíduo é a unidade básica de representação, sendo modelado explicitamente (UCHMANSKI & GRIMM, 1996). Com isso, não apenas a idade, mas um número praticamente indefinido de outras características biológicas com variação contínua pode ser incluído num mesmo modelo dinâmico. Isso permite que um grande volume de informações sobre história natural e biologia básica de organismos, acumulado ao longo de décadas, seja usado para o estudo de níveis de organização maiores, como populações, comunidades e ecossistemas. Ou seja, padrões populacionais ou ecossistêmicos passam a ser interpretados pelas propriedades de seus elementos, os indivíduos. Por isso a modelagem baseada no indivíduo é vista por alguns autores não apenas como um extremo num contínuo de complexidade de modelos, mas como uma mudança de paradigma na representação teórica de sistemas ecológicos (JUDSON, 1994; UCHMANSKI & GRIMM, 1996; GIACOMINI, 2007), ou até como a possibilidade de unificação da teoria ecológica e de sua aproximação com a Ecologia de campo (HUSTON et al., 1988).

Por normalmente possuir muitas regras, variáveis e parâmetros, um MBI não é tratável analiticamente como um modelo puramente matemático. Ao invés disso, ele é tipicamente um modelo de simulação computacional. Em termos práticos, os dados sobre o estado da comunidade ecológica são representados num MBI por meio de uma matriz. Uma possibilidade é usar cada linha dessa matriz para representar um dado indivíduo, e cada coluna representaria uma informação sobre esse indivíduo (tal como espécie à qual ele pertence, idade, peso, ou estágio de desenvolvimento, dentre muitas outras possíveis). Por meio das regras impostas ao comportamento dos indivíduos, tais informações são atualizadas

de tempo em tempo, configurando a dinâmica da comunidade. Por exemplo, com a passagem de um intervalo temporal, todos os valores da coluna representando a idade são incrementados em uma unidade (como o dia); os valores na coluna representando peso corporal podem aumentar ou diminuir, dependendo da quantidade de alimento adicionado a cada indivíduo, e assim por diante. Sempre que um indivíduo morre, a linha que o representa é computacionalmente deletada da matriz. Nascimentos ocorrem pela inclusão explícita de novas linhas, e assim a matriz da comunidade muda constantemente de tamanho. Nesse processo, podem-se armazenar quaisquer informações que se acharem necessárias, desde a trajetória detalhada de cada característica de um indivíduo, ou a contagem do número total de linhas de cada espécie para ter-se acesso aos padrões de flutuação populacional, até a simples contagem do número de espécies para ter-se acesso à dinâmica de riqueza na comunidade.

Abordagens focadas nas características biológicas das espécies, ao invés da simples composição taxonômica das comunidades, têm ganhado cada vez mais força em estudos ecológicos (MCGILL et al., 2006). A análise da seleção de histórias de vida de peixes é um exemplo notável (MIMS et al., 2010). O reconhecimento da variedade de estratégias de história de vida e seu ajuste a diferentes tipos de ambiente é fundamental para se entender os padrões naturais de distribuição de peixes e predizer sua reação a perturbações como sobrepesca e alteração de habitat (WINEMILLER & ROSE, 1992; OLDEN et al., 2006). Embora análises teóricas tradicionais tenham fornecido regras úteis, elas normalmente ignoram a interdependência entre múltiplas características. Por exemplo, a resposta seletiva da idade e do tamanho de maturação a níveis variados de predação é normalmente analisada assumindo-se valores fixos da taxa de crescimento corporal (ROFF, 1992; STEARNS, 1992). Ao permitir-se aos organismos ajustarem a taxa de crescimento em resposta ao risco de predação, um fenômeno bem documentado na literatura (WERNER & ANHOLT, 1993; WELLBORN et al., 1996), os resultados tornam-se bem diferenciados do previsto anteriormente (ABRAMS & ROWE 1996). Estendendo-se o argumento, é bem provável que a seleção de algumas características dependa do conjunto de um grande número de outras, uma vez que é a sua ação combinada que determinará o valor adaptativo de seus portadores. O mesmo é válido para a susceptibilidade de espécies a perturbações como sobre-explotação e invasões biológicas, que depende da combinação de uma série de fatores ambientais e intrínsecos de sua bionomia. Por tornar a inclusão de muitas características mais praticável, os modelos baseados no indivíduo são uma alternativa apropriada para o estudo da resposta múltipla de características biológicas a mudanças ambientais.

A presente tese propõe e utiliza um MBI para investigar o padrão de seleção de história de vida de peixes e sua resposta a perturbações ao longo de gradientes ambientais. Peixes foram escolhidos como organismos-modelo por possuírem grande diversidade de estratégias tróficas, comportamentais e reprodutivas (GERKING, 1994; MIMS et al., 2010), além de sua importância prática como recurso pesqueiro e como elementos reguladores de ecossistemas aquáticos (HILBORN & WALTERS, 1992; JACKSON et al., 2001). Não é sem motivo que os peixes representam provavelmente o grupo mais estudado por meio de MBIs (GRIMM, 1999; DEANGELIS & MOOIJ, 2005). No presente caso, a atenção está voltada essencialmente para interações tróficas, que são os fatores que moldam o comportamento e a mortalidade dos peixes aqui modelados. Isso não quer dizer que outros fatores, como tolerâncias a condições abióticas, doenças, dispersão e resistência a distúrbios, associações simbióticas, dentre outros, não tenham importância como fatores limitantes das populações de peixes. Questões práticas impedem a inclusão sem fim de detalhes biológicos no modelo, do contrário ele seria demasiadamente complicado para ser útil. Dentro destas limitações, a escolha da predação como elemento chave tem apoio na literatura, que tem consistentemente ressaltado a sua importância na estruturação do comportamento de indivíduos, populações e comunidades principalmente de peixes (SIH et al., 1985; THORP, 1986; JACKSON et al., 2001; SHIN & CURY, 2001).

A tese está dividida em dois capítulos. O Capítulo 1 apresenta o modelo e avalia por meio de simulações computacionais como várias características bionômicas dos peixes respondem a quatro tipos de gradientes: (i) produtividade, medida pela capacidade suporte de recursos basais que são a fonte primária de alimento; (ii) taxas de ataque, que determinam a capacidade máxima dos peixes em capturar alimento (incluindo outros peixes), e implicitamente determinam a disponibilidade de refúgios contra predação (KOEN-ALONSO, 2007); (iii) distribuição do tamanho corporal máximo caracterizando as espécies do conjunto regional formador das comunidades; (iv) existência de conflitos funcionais gerando hierarquias entre espécies no que diz respeito à capacidade de captura de presas e defesa contra predadores. A seleção das características bionômicas se dá durante o processo de formação das comunidades, inspirado nos modelos dinâmicos de assembléia (GIACOMINI, 2010). Espécies de peixes com características diversas são geradas computacionalmente e introduzidas seqüencialmente em comunidades previamente compostas por recursos, sem peixes. Ao longo do tempo, apenas espécies de peixes com características apropriadas persistem numa comunidade local. O processo de assembléia funciona dessa forma como um

filtro dinâmico, permitindo que a estrutura das comunidades surja como fenômeno emergente, ao invés de ser imposto arbitrariamente (GIACOMINI, 2010).

O Capítulo 2 tem caráter mais aplicado. Ele utiliza uma parte das comunidades geradas no primeiro capítulo para fazer experimentos computacionais de invasão e exclusão de espécies, simulando dois grandes tipos de perturbações que normalmente assolam ecossistemas naturais (DUNNE & WILLIAMS, 2009; ROMANUK et al., 2009). Por meio de tais simulações, foi possível estabelecer quais são os efeitos das variáveis que caracterizam espécies e comunidades e quais delas são mais importantes na determinação do sucesso de invasão e da extinção de nativos.

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2. CAPÍTULO 1

Assembling multiple life history traits of fishes in gradients of productivity and predator attack rate: an individual-based modeling approach

2.1. Introduction

Ecological communities are not static structures; on the contrary, they change in composition along many time scales (HUBBELL, 2001). Still, most field studies aimed to reveal assembly rules rely only on current species composition (WEIHER & KEDDY, 1995). The usual procedure consists in calculating some index from observed data, which measures a pattern of co-occurrence, and comparing it to a null model expectation; e.g., assuming all species being randomly distributed among communities (GOTELLI & GRAVES, 1996). In such an approach, the analysis of patterns becomes more interesting when functional traits are explicitly included, assuming they are relevant to resource partitioning and could work as a signature of niche differentiation and structuring by competition (MCGILL *et al.*, 2006). Several empirical studies have succeeded in showing significant patterns, providing evidence for regular niche spacing among co-occurring species based on body size and a variety of other morphological characters (BOWERS & BROWN, 1982; TRAVIS & RICKLEFS, 1983; HOPF & BROWN, 1986; LOCKWOOD *et al.*, 1993; WEIHER & KEDDY, 1999). Indeed, if we are interested making ecological generalizations, we must concentrate on species features potentially common to all kinds of studied systems. Patterns based uniquely on taxonomic composition of a given region are not a proper subset for predicting what should happen in others (MCGILL *et al.*, 2006).

The advantage of theoretical assembly models is to allow the assessment of the entire community development process, using driving factors under the modeler control. It is possible to analyze in detail how the mechanisms underlying the assembly process are translated into patterns. The models traditionally used in community assembly studies are based on systems of simple differential equations, like the Lotka-Volterra (POST & PIMM, 1983; CASE, 1990; DRAKE, 1990; PIMM, 1991; LAW & MORTON, 1996; MORTON, *et al.*, 1996; LOCKWOOD *et al.*, 1997). These models represent population sizes as state variables, and are commonly restricted to more abstract demographic and community parameters such as population growth rates and coefficients of interaction. At most, they are amenable to the inclusion of just one bionomic feature as the determinant of interactions and species parameters, usually body size (YODZIS & INNES, 1992; JONSSON & EBENMAN, 1998; LOEUILLE & LOREAU, 2005). In order to link population dynamics and ecological interactions to organism bionomic traits, individual-based models (IBMs) represent a conceptually suitable approach (JUDSON, 1994; GRIMM & RAILSBACK, 2005;

DEANGELIS & MOOIJ, 2005; LOMNICKI, 1999; GIACOMINI, 2007). By modeling individuals explicitly and following them along their entire life cycles, the IBMs offer a great flexibility for implementing rules accounting for physiology, life history strategies and behavior in detail. Consequently, their parameters tend to have a clearer biological interpretation, closer to what can be measured in nature. Most important is the fact that population and community-level parameters, such as birth and death rates, carrying capacity or coefficients of interaction do not have to be imposed *a priori*. On the contrary, such parameters, together with the dynamics itself, are better viewed as emergent properties in an IBM, resulting from the rules imposed to individual organisms and the environment in which they develop (GRIMM & RAILSBACK, 2005).

IBMs have been extensively used to address fish population and community dynamics (DEANGELIS & GROSS, 1992; GRIMM, 1999; GRIMM & RAILSBACK, 2005; DEANGELIS & MOOIJ, 2005; GIACOMINI *et al.,* 2009). Some have been successfully applied to empirical data, aimed at describing and explaining the dynamics of particular systems (ROSE *et al.*, 1999; MCDERMOTT & ROSE, 2000; HUSE *et al.,* 2004). Others are mainly proposed as tools to analyze the effects of predation and/or fishing (Shin & CURY, 2001; VAN NES *et al.,* 2002), or to bring insights concerning the effects of ecosystem features and environmental changes on fish production and coexistence (DEANGELIS *et al.*, 1997; DEANGELIS *et al.,* 2005). They have the common feature of giving special attention to trophic interactions, but they include life history features as well. Two ubiquitous features of fishes that such models must deal with are the individual growth and ontogenetic diet shifts (MITTLEBACH & PERSSON, 1998; SHIN & CURY, 2001; VAN NES *et al.,* 2002). Growth provides a link between trophic ecology and life history, as both are strongly determined by body size (PETERS, 1983; WOODWARD *et al.,* 2005; BROSE *et al.,* 2006; BROSE, 2010). Fish diet, in particular, is much more dependent on size relations than on taxonomic identities (MITTLEBACH & PERSSON, 1998; JENNINGS *et al.,* 2001). The larger the individual is, the larger tends to be its mean prey size and its range of eligible prey, and the lower is the potential number of predators and predation pressure it experiences (SCHOENER, 1989; COHEN *et al.,* 1993; EMMERSON & RAFFAELLI, 2004; WOODWARD *ET AL.*, 2005; BARNES *et al.,* 2010). Larger fish tend also to have higher fecundity (BLUEWEISS *et al.,* 1978). But reaching larger sizes has costs, related mainly to delayed starting of reproductive life, which can increase the chances of mortality before producing any offspring (STEARNS, 1992; ABRAMS & ROWE, 1996). Such mortality might result from predation or starvation, among other factors. All these tradeoffs are

mediated by growth rate, which determines how long a fish takes to reach a size refuge from predation and how much energy production is available at a given time to be diverted between growth and reproductive effort (ROFF, 1992; ABRAMS & ROWE, 1996). But growth rate can also be involved in another tradeoff, as it tends to be associated with activity and foraging rates, which likely increases detection by predators and consequently the predation mortality (WERNER & ANHOLT, 1993; LIMA, 1998; ABRAMS, 2003). Thus a model addressing both life history assembly and emergent food web properties in fish communities must take in account these and other related tradeoffs.

Fish growth has been traditionally modeled by a von Bertalanffy growth model (VON BERTALANFFY, 1938). Although it provides a good fit to most observed data, it does not account mechanistically for the factors determining its asymptotic behavior, a characteristic of most organisms with indeterminate growth (CHARNOV, *ET AL.* 2001; LESTER, *ET AL.* 2004). Even so, the von Bertalanffy model is the basis for many important theoretical predictions concerning life history ecology and fisheries assessment (BEVERTON & HOLT, 1957; PAULY, 1980; HILBORN & WALTERS, 1992; CHARNOV, 1993). But as it ignores the role of reproductive investment, it does not allow for a direct link between growth and other life history traits (SHUTER *et al.* 2005). Recently, a biphasic growth model was proposed to take into account reproduction as an explicit constraint to fish growth (LESTER *ET AL.*, 2004; QUINCE ET AL., 2008). Besides predicting realistic growth curves, it allows for a thorough analysis of life history evolution by means of simple optimization techniques, providing some assumptions about mortality rates are made. If one assumes further that predation and starvation are the main sources of mortality in fish populations, this mortality can be treated rather mechanistically in a trophic oriented IBM, instead of being imposed. As suggested by structural models of food web and empirical data, the trophic relations among species can be simple functions of their traits, specially body size (WILLIAMS & MARTINEZ, 2000; JENNINGS *ET AL.*, 2001; STOUFFER *ET AL.*, 2006; PETCHEY *ET AL.*, 2008; WILLIAMS & MARTINEZ, 2008; BARNES *ET AL.*, 2010). If applied to individual organisms, such simple functions can also explain intraspecific variation and relevant ontogenetic diet changes (GIACOMINI *et al.*, 2009), which have important consequences for both life history and food web theory.

Two key gradients defining species diversity traits and overall assemblage structure are predation pressure and resource productivity (CONNELL & ORIAS, 1964; PAINE, 1966; REZNICK & ENDLER, 1982; SIH *ET AL.*, 1985; ANHOLT & WERNER, 1995; ROSENZWEIG, 1995; DAY *ET AL.*, 2002). These gradients are not independent, so that the

environmental features that enhance resource consumption by a given fish may also result in increasing predation pressure. In many freshwater communities, larger and productive sites are also those which concentrate higher trophic level species (WELLBORN *ET AL.*, 1996; DE ROOS *ET AL.*, 2002; POWELL & MCKANE, 2009), which are ultimately limited by the total amount of energy available from prey. Despite the many ecological, behavioral or phylogenetic factors affecting predator-prey interactions, the predation effect is manifested through functional and numerical responses (HOLLING, 1959; HOLT, 1977; ABRAMS, 1982). The first might be a direct function of prey density and some intrinsic attack rate, which depends on the interplay between the predator's capabilities and the prey's defenses, both mediated by environmental conditions (i.e. presence of spatial refuges, habitat complexity, etc.) (GOTCEITAS & COLGAN, 1989; KOEN-ALONSO, 2007). The second is a function of predator's own life history traits. Thus, assembly studies capable to vary both resource productivity and mean attack rates can bring valuable insights on the trophic ecology of co-occurring species and their associated life history features, besides possibly demonstrating how they can interact to define successful species.

Here we propose an individual-based approach to modeling the success of different life history traits and food web assembly along environmental gradients, taking into account many of the tradeoffs recognized by general theory but rarely analyzed together in the same dynamic framework. In particular, we introduce a method to generate a consumption ordering hierarchy among individuals based on two tradeoffs: (i) predation efficiency versus diet generality and (ii) foraging rate versus defense to predation. Such tradeoffs are well recognized and ought to be general, but they have not yet been properly accounted for by other IBMs. These rules promote asymmetries among species concerning both competitive and defensive abilities. We tested how this hierarchy may affect the resultant communities selected by the assembly process. As in any assembly model, the present IBM must make assumptions about the regional pool from which the species propagules come. We investigated the influence of regional processes by varying the distribution of maximum body size characterizing the species pool.

The assembly experiments resulted in strong responses of diversity and many individual species traits to all gradients tested. The presence of consumption ordering produced qualitatively different associations between bionomic features, stressing that the assessment of the tradeoffs inherent to predation events might be of paramount importance in interpreting empirical data and guiding theoretical community modeling.

2.2. Methods

Below we provide a brief description of the individual-based model and simulation procedures, stressing their major rules relevant to the interpretation of results. A detailed model description, following the ODD (Overview, Design concepts, and Details) protocol proposed by Grimm *et al.* (2006) is provided in the Appendix.

2.2.1. Model description

The description below has two parts: (a) Environment and resources, (b) Fishes, comprehending the basic model components. Fishes are the main organisms for which the model was designed, and are represented with considerable level of detail. On the other hand, the resources are represented as simple biomass compartments, just like in traditional state variable models (JUDSON, 1994; GIACOMINI, 2007), and provide a basal source of food to fish consumers. In another section, *Assembly experiments*, it is described how communities were formed in this study, which environmental conditions define the gradients, and which dependent variables were used to evaluate the selective response of species traits and the diversity patterns.

(a) Environment and resources

The environment is composed by a series of basal resources, whose state in a time step (week) is given by a continuous measure of biomass (g). The biomass of each resource grows independently according to a discrete logistic model (GOTELLI, 1998). So, the resource growth behavior is characterized by:

(i) resource carrying capacity K (g); and

(ii) intrinsic growth rate R (1/week).

The carrying capacity varies seasonally, following a sine function with a period of one year, or 52 weeks (A cosine function would have the same behavior; except that the resource fluctuations would follow opposite phases along the year, which is not a matter of concern since the temporal scale is arbitrarily defined). The carrying capacity then fluctuates around a mean carrying capacity μ_K (g). The amplitude of seasonal fluctuations is a fixed proportion of μ_K, given by φ. For the present simulations, we used $\varphi = 0.3$, which means that the carrying capacity fluctuates between $0.7\mu_K$ and $1.3\mu_K$. Values of μ_K and other parameters relevant to the experiments here carried out are presented in Table 1. For simplicity, we are using a common value of μ_K for all basal resources within a given simulation.

Each resource is also characterized by a size range, delimited by a minimum (l_{min}) and maximum (l_{max}) lengths (cm). This range is important to determine the resource vulnerability to predation, as predation interactions are size-structured.

The resource size also determines its intrinsic growth rate, by means of an alometric relationship, well described by a power function (FENCHEL, 1974). The power function is a pervasive rule found in many relationships among biological variables, especially those including body size (BROWN *et al.*, 2004). Examples of biological variables alometrically related to body mass are: almost every morphological variable, including body length or gape size, rates like metabolism, ingestion, production, development, mortality and intrinsic population growth, life spam, population density, among others (GOULD, 1966; PETERS, 1983; CALDER, 1984; BROWN ET AL., 2004; SAVAGE ET AL., 2004). In general terms, a given biological variable V is a power function of body mass M when:

$$V = z_1 M^{z_2}$$

where z_1 is a coefficient of proportionality and z_2 is an exponent defining the shape of the relationship. Empirical data and the metabolic theory predict that the exponent z_2 tends to be multiple of ¼ for many physiological and ecological features (SAVAGE et al., 2004). So we applied such general body of theory to conceptualize and parameterize most traits determining organism functions in our model.

For the simulations, we used 100 basal resources contiguously distributed in size spectrum, in a logarithimic scale (see Apendix for details). A contiguous distribution means that there is no gap between resources with adjacent sizes, from the minimum size of the smallest resource (0.01cm) to the maximum size of the largest resource (10cm). The logarithm scale implies that there are more resources with smaller sizes. As the alometric relationship between intrinsic growth rate and mean resource size is negative (z_2 = -0.25) (FENCHEL, 1974; SAVAGE et al., 2004), the rules above guarantee that the resources are more frequent and grow faster at smaller sizes.

(b) Fishes

Fish organisms (females only) are modeled explicitly. At each time step, the model updates the state of each individual concerning the following variables: age (T, years), developmental stage (egg/embryo, juvenile or adult), weight (W, grams), and the number of components (for the case of super-individuals, N). The individual's total weight is divided among three variables: the irreversible mass (X), the reversible mass (Y) (PERSSON *ET AL.*, 1998; CLAESSEN *et al.*, 2002), and the gonad mass (G). We assume here that the reversible

mass is composed predominantly by fat reserves, which can be used when the metabolic demands exceed the amount of ingested food. The irreversible mass is constituted of permanent tissue (mainly protein), which can either grow or stay constant in time. It represents a great proportion of organs like bones, the nervous system and all other minimum parts necessary to ensure the vital functions of the organism. The individual length (L), an important dimension for size structured interactions, depends entirely on the irreversible mass. The reversible mass and the gonad, being composed mainly by lipids, are assumed to have energetic value eight times higher than irreversible mass (WEATHERLEY & GILL, 1987; JOBLING, 1994). Each individual has also a species identity, which is linked to a unique and fixed combination of values of the parameters characterizing individual behavior and physiology.

To work with a number of individuals that is not too large to be computationally intractable, we use the super-individual concept, as proposed by Scheffer *et al.* (1995). A super-individual is a cohort of identical organisms, created at each time interval when the females of a given species spawn. It differs from a unitary individual just by having a number of components, or individuals represented within the superindividual (N) that is larger than 1. It is assumed that very similar individuals do not need to be modeled separately, as they do not differ markedly in their effects upon the environment. A factor in favor of grouping fish as super-individuals is that it is analogous to schooling, so common in fish (SHIN & CURY, 2001; HEMELRIJK & KUNZ, 2005).

The newborn fish has a characteristic total weight W_0. It is mostly composed by reversible mass (yolk), plus a tiny fraction of irreversible mass (embryo). It will feed on the yolk until the body condition (Y/X) drops below a threshold value qj, which is the maximum condition characterizing a juvenile. Thereafter, the fish reaches a juvenile stage and it will need to feed on external resources. It becomes adult as soon as its irreversible mass surpasses the species specific size at maturation X_{mat}. The adult fish is capable to spawn only during a period of the year devoted to gonad production (the reproductive period), instead of somatic tissue. The spawning schedule is governed by two species parameters:

(i) the uniformity parameter u, and

(ii) the timing parameter η.

The first defines a continuum of strategies, from a perfect fractional spawner, which never accumulates gonad content and immediately spawns every produced egg along the entire reproductive period, to an extreme batch spawner, which stores all produced eggs to liberate them only at the last time step of the reproductive period. The timing parameter

determines the position of reproductive period, in a cyclical manner. For instance, if $\eta = 0$ or $\eta = 1$, the species will finish its reproductive period at mid-spring (exactly when $K = \mu_K$); if $\eta = 0.25$, it will occur at peak summer; $\eta = 0.5$, at mid-autumn; $\eta = 0.75$, at peak winter. All co-specific individuals have coincident reproductive periods, so reproduction is synchronized within a species. Fecundity is not imposed *a priori*. It is instead an emergent feature depending on the realized amount of gonad production divided by egg size.

The fish growth is modeled by means of the biphasic growth model proposed by Quince et al. (2008). It states that the asymptotic growth pattern so commonly observed in fishes is caused by increasing investment in reproduction along a fish adult lifetime (LESTER *ET AL.*, 2004; QUINCE *et al.*, 2008). In our case, we constrain growth to be a function of a maximum irreversible mass X_{inf}, which is another species specific parameter. As the fish approaches this size, it decreases the proportion of the year devoted to growth of somatic mass (X + Y), increasing the length of reproductive period. The first proportion is given by $(X- X_{inf})/X_{inf}$, so that when $X = X_{inf}$, the production throughout the year is entirely devoted to the gonad, and the fish stop growing permanently. When growing in somatic tissue, the fish divides its production differently to the reversible and irreversible mass: the poorer is its body condition (Y/X), the more it will invest in the reversible component.

The biphasic model assumes that the production is an alometric function of body mass (QUINCE et al. 2008). In our case:

$$\mathscr{P} = \zeta X^{\beta} \qquad \text{Eq. (1)}$$

where $\mathscr{P}$ is the potential production (g/week) of a given fish individual in a given time step, ζ is a growth coefficient, which is a species specific parameter, and β is the alometric exponent. In relative terms, the growth coefficient determines how fast the individual grows, discounting the effect of body size. The potential production is simply the difference between potential food ingestion (*PIng*) and metabolic demands (*Loss*), both also alometric functions of irreversible mass, with the same exponent β. Following the general tenets of metabolic ecology, we are assuming $\beta = 0.75$ (Savage *et al.* 2004). So the large is the individual, the more it will be his demand for food, and the more biomass it will produce, but less than in a proportional fashion. The potential production is assumed here as a fixed proportion of potential ingestion, more specifically: $\mathscr{P} = 0.3PIng$ (BRETT & GROVES, 1979; WEATHERLEY & GILL, 1987). It is a simple constraint, which ensures that the advantages related to fast growth are obtained by the cost of high metabolic expenses (e.g. due to behavioral activities related to foraging, and to physiological activities related to assimilation

of larger amounts of food). The metabolic demand is fixed for an individual of a given species with a given irreversible mass. The realized ingestion can be nonetheless lower than the potential ingestion, depending on food availability.

More specifically, *PIng* is the asymptote of a type III functional response determining the amount of food ingested by a unitary fish. For a super-individual, this asymptote is multiplied by its number of components. For the general case:

$$F_{i,j} = \frac{PIng_i N_i \alpha_{i,j} B_j^{\,2}}{PIng_i N_i + \sum_k \alpha_{i,k} B_k^{\,2}} \qquad \text{Eq. (2)}$$

where $F_{i,j}$ is the biomass of resource j consumed by the (super)individual predator i; $PIng_i$ is the potential ingestion of each component of (super)individual i and N_i is the number of components; B_j is the biomass of eligible resource j (which can include fishes); k is the number of eligible resources; and $\alpha_{i,j}$ is the attack rate of predator i on resource j. The quadratic exponent defines the type III functional response, which can result from implicit spatial refuges for prey or prey switching (KOEN-ALONSO, 2007), and help stabilizing the dynamics, so it was preferred. Each fish species has a fixed attack rate for a given resource kind. The larger is $\alpha_{i,j}$, the more efficient is the consumer 'i'at catching prey 'j', which can be interpreted as lower effectiveness of spatial refugees for that prey. The relative differences among the attack rates on several resources can be interpreted as resulting from predator's preferences or differential defensive prey capacity. Each community is characterized by a maximum attack rate, α_{max}, which is the maximum attack rate of any consumer species on any resource kind.

The eligibility of resources, including fish, depends on predator/prey length ratios. Each consumer has a minimum and a maximum prey length, which defines its predation window (CLAESSEN *et al.*, 2002). Those limits are assumed here as constant proportions of consumer's own body length, which are given by the species specific parameters δ and ε, respectively. For instance, a given fish 10cm long and whose species is characterized by δ = 0.05 and ε = 0.4 will be capable to eat only food items with sizes lying within the range 0.5cm - 4cm. As the fish reaches 20cm long, this food size range – the predation window – will become both higher and larger, in this case: 0.1cm – 0.8cm. Individuals with the same length, but pertaining to species with different values of these parameters can have markedly different diets. Species with high δ and ε tend to include new large prey and to loose from diet small previous prey fast along growth. On the other hand, low values make the species keeping a similar diet based on small prey along the entire lifetime. The difference between ε and δ

gives a relative measure of the diet generality of a species. These size-based rules are the simplest way of creating differences in species trophic strategies, while including ontogenetic diet changes along growth, a widespread phenomenon observed in fish populations (MITTELBACH & PERSSON, 1998).

In a given time step, predation proceeds by choosing, one by one, (super)individuals to eat. The order in which the individuals are chosen is of key importance to determine relative competitive abilities, as the first consumers in the sequence will experience higher food availability. So we establish simple rules to associate competitiveness to proper bionomic features of species. We assume that individuals with higher chances to access food are those which:

(i) have higher foraging activity and consequently higher food intake rate and growth coefficient ζ;

(ii) have more specialized diet, in other words, a smaller difference between the upper and lower limits of predation window ($\varepsilon - \delta$).

The second feature depends on the assumption that specialization is accompanied by higher efficiency in prey search or capture. If the chosen consumer eats fish (which depends on fish availability and the attack rate $\alpha_{i,fish}$), the eligible fish prey must also be ordered in some manner. But now the first in the sequence will have a disadvantage, as they have more chances to be eaten before the consumer accomplishes its demand for fish prey (given by $F_{i,fish}$). In this case, we assume that more active prey have higher risks to be detected. As the activity level is assumed to be embedded in the growth coefficient ζ, it is used as the ordering factor for prey, in the same manner as for consumers, so that individuals that grow faster are also more vulnerable to be eaten first. This tradeoff is well documented by the literature, mainly for aquatic environments and visually oriented predators like fish (LIMA & DILL, 1990; WERNER & ANHOLT, 1993; WELLBORN ET AL., 1996; ABRAMS, 2003; BIRO et al., 2003). It expected to occur when either active or ambush predators are involved. The major difference between these two kinds of predators is that the first tend to have a larger detection field. The second, although being static most of time, depend even more on moving (active) prey to be able to detect and to catch them.

Another factor can be used to order prey if the consumer is cannibal: the chance of co-specific prey being eaten first is further multiplied by a cannibalism level *Cann* characterizing the consumer's species. *Cann* varies from 0 to 1: in the first case, the consumer cannot eat on any co-specific prey; in the second, the consumer is indifferent to whether the prey is of the

same species or not. Additionally, if a fish prey is in egg/embryo stage, it is considered less vulnerable, as it has no activity at all, appearing last in the sequence of eligible prey.

The rules for predation sequence described above configure the presence of a *consumption ordering hierarchy*. Alternatively, the sequences of consumers and prey can be purely random, configuring a null model where competitive ability and vulnerability to predation have no relation to species traits. It configures a complete absence of hierarchy, as all consumers have equal chances of accessing food when competing. In any case, a predation cycle in a given time step finishes when all (super)individuals have had the chance to eat and/or have been eaten. As the individual ordering process is stochastic (even if a hierarchy is imposed), the consumers and prey sequences within a predation cycle do not necessarily repeat exactly from one time step to another.

There are three sources of fish mortality:

(i) predation,

(ii) starvation, and

(iii) exceeding the species specific longevity.

All predated individuals are considered dead, even if only partially eaten. Fish starves to death whenever the energetic content of reversible mass is not enough to supply the metabolic demand in excess of ingested energy. Longevity is an alometric function of maximum size (X_{inf}) (Peters 1983). Immediately after achieving an age longer than the specified longevity, the (super)individual is considered computationally dead. Mortality in a super-individual by predation or starvation has the effect of decreasing accordingly its number of components, N.

In summary, by combining the several continuously varying biological parameters, the model rules allow a great variety of life history and trophic strategies to emerge, incorporating mechanistically some of the major tradeoffs recognized by ecological theory:

(i) growth *versus* reproduction

(ii) structural growth *versus* storing energy

(iii) offspring size and survivorship *versus* offspring number

(iv) growth rate *versus* survivorship at low resource levels

(v) diet breath *versus* capture efficiency

(vi) foraging *versus* defense against predation

2.2.2. Assembly experiments

Assembly experiments were carried out in order to select for life-history strategies, given gradients of resource mean carrying capacity (μ_K), maximum attack rates (α_{max}), and the shape of maximum body size (X_{inf}) distribution of species pool. The resource carrying capacity is treated here as a measure of ecosystem productivity. We also investigated how the presence of consumption ordering hierarchy influences the major patterns, by comparing it with a model version where predation sequences are purely random. In each simulation, the propagules were sampled by the Monte Carlo approach, until a specified maximum time (t = 50 years), following the protocol suggested by Giacomini *et al.* (2009). This protocol yields a total of 7803 species introduced in each community. After that, the introductions cease, and the dynamics proceeds for an additional sufficient time (50 years) in order to drive the community to a more stable composition, where only the well suited species can persist. The experiments followed a factorial design, using 5 values for each of the first two factors (Table 1), three for size distribution and two characterizing the presence/absence of consumption ordering, resulting in a total of 5^2x3x2 = 150 factorial combinations. Within each, we simulated 30 community replicates, totaling 4500 communities generated independently.

The attack rates for each consumer species 'i' were defined stochastically, as follows:

(i) first a potential piscivory level, $_i$, was determined from a uniform distribution within the interval [0,1]. Completely piscivorous species have $\phi = 1$, and species with $\phi = 0$ can never eat other fishes.

(ii) the attack rate of that species on fish prey, $\alpha_{i,fish}$, was then set to $\phi_i * \alpha_{max}$;

(iii) the values of attack rates on basal resources were drawn from a uniform distribution within the interval $[0,(1- \phi)*\alpha_{max}]$.

So fishes are considered here a very distinct kind of resource, and specialized piscivory constrains the maximum possible attack rates on all other resource kinds (basal resources).

The maximum body size (X_{inf}) characterizing the species pool was chosen to follow a power-law distribution:

$$p(X_{inf}) = \varpi X_{inf}^{\xi} \qquad \text{Eq. (3)}$$

where $p(X_{inf})$ is the probability density function of X_{inf}, ξ is an exponent defining the shape of the distribution and ϖ is a normalization constant chosen so that the Eq. (3) integrates to 1 between the limits imposed to X_{inf} (Table 1). Negative ξ values with high magnitudes produced distributions strongly skewed towards small body sizes. A null value of ξ corresponds to the uniform distribution.

Six life-history parameters, ζ, η, u, X_{mat}, W_0, and X_{inf}, and four trophic parameters, δ, ε, Cann, and ϕ, were under selection by the assembly process. We preferred to model X_{mat} by means of the dimensionless parameter $\theta = X_{mat}/X_{inf}$, which measures the relative size at maturity. Instead of X_{mat}, the parameter θ was chosen directly from an uniform distribution during the assembly proccess (Table 1). In order to perform the analyses, each of these bionomic parameters was transformed to an index of selective response, in order to facilitate the interpretation of the direction and magnitude of changes promoted by the assembly process as compared to original species pool. Suppose in a community 'i' the mean observed value of a parameter among successful species is given by O_i; then the selective response SR_i of this parameter in the community 'i' is calculated as:

$$SR_i = \begin{cases} (O_i - \mu_O)/(O_{\max} - \mu_O) & \text{if } O_i > \mu_O \\ (\mu_O - O_i)/(\mu_O - O_{\min}) & \text{if } O_i < \mu \end{cases} \qquad \text{Eq. (4)}$$

where μ_O is the expected value for parameter O in the species pool, and O_{max} and O_{min} are, respectively, its maximum and minimum values. SR varies from -1 (when all species in the community assume exactly the minimum possible value) to 1 (when all species assume the maximum value). SR = 0 means either no selection or a stabilizing selection towards the expected value μ_O.

The other fish parameters were kept constant or were functions of those cited above. The coefficient of allometric function for longevity is nearly to currently empirical estimates (FROESE & PAULY, 2006; GIACOMINI *et al.*, 2009), and allows for the slowest growing species to attain around 90% of their asymptotic size in ideal conditions. The energetic content ratio between irreversible mass and reversible mass (or gonad) is given by the parameter γ (QUINCE et al., 2008). To infer a value for γ, we considered that the irreversible mass was composed basically by protein and water, and the reversible mass by lipids. We opted to use wet weight because the weight-length relationship is generally estimated on this basis. As the energetic content of lipid is roughly double that of protein (WEATHERLEY & GILL, 1987; JOBLING, 1994), and the body deposition of 1g of protein can be associated with 3g of water deposition (JOBLING, 1994), we have a gross estimate of $\gamma = 1/2/4 = 0.125$. The maximum conditions qj and qa were assumed to have the same value. Although adults tend to have more lipid content, this excess is generally associated to reproduction. All those fat reserves associated to gonad production can be assumed to grow implicitly during the reproductive period, but going directly to the gonad compartment (G). So we assumed for simplicity that the fat reserves used only to repair metabolic losses were the same for juveniles and adults. Another simplifying assumption was that all individuals have the same

body shape, as the weight-length relationship is isometric and have the same coefficient for all species. It is not to say that body shape differences are not important in nature. Body shape can have important consequences mainly for habitat use (DOUGLAS & MATHEWS, 1992). But neither habitat differentiation was included in the model, nor did we include rules to link shape differences to species performance, so any variation in shape would be meaningless at this point.

For each final community we also calculated an index of functional diversity, adapted from the functional attribute diversity index (FAD) (WALKER *et al.*, 1999). It depends on the Euclidean distance among all species pairs in a community, considering all bionomic parameters subjected to variation. But different from FAD, we used the mean among such pairs, instead of the sum, in order to not include a richness confounding effect on its calculation, but just the overall distinctness of species in parameter space.

Together with bionomic parameters, each species has an identification number corresponding to the order in which it was introduced into the community. This number varied from 1 to 7803. If its mean value among the successful species is consistently low, we could say that some priority effect was preventing the establishment of later arriving species. On the other hand, high means would imply in a dependence of some facilitation mechanism. To evaluate how such tendencies were distributed along the gradients, we propose a priority effect index (PI), calculated as:

$$PI = 1 - ID/7803 \qquad \text{Eq. (5)}$$

where ID is the species identification. This index varies from 0 (the opposite of a priority effect, i.e. facilitation) to 1 (extreme priority effect).

Table 1. Model parameters whose variation was directly investigated by the present assembly experiments. For a complete list of parameters and constants, see Table A1 in Appendix.

Symbol	Unit	Values	Description
Cann		0 - 1	Level of cannibalism
δ		0 - 0.07	Coefficient for the lower limit of the predation window.
ε		0.01 – 0.7	Coefficient for the upper limit of the predation window.
ζ	$g^{(1-\beta)}$ /week	0.06 – 0.24	Coefficient of the function for potential growth rate
η		0 - 1	Reproductive timing
θ		0.1 – 0.8	Relative size at maturation = X_{mat}/X_{inf}
u		10^{-10} - 1	Uniformity of spawning along time

ϕ		0 - 1	Piscivory level
W_0	g	0.001 - 0.1	Egg size
X_{inf}	g	5 - 1000	Asymptotic irreversible mass
μ_K	g	$\{10^2, 10^3, 10^4, 10^5, 10^6\}$	Mean carrying capacity of a resource
α_{max}	$g^{(-2)}$/week	$\{10^{-7}, 10^{-6}, 10^{-5}, 10^{-4}, 10^{-3}\}$	Maximum attack rate allowed by the environment
ξ		{-2, -1, 0}	Exponent shaping the power-law distribution of X_{inf}

2.3. Results

A total of 19776 species persisted to the end of assembly experiments. They were unevenly distributed along the gradients, as shown by Figure 1. The richest communities were found at moderately less productive communities ($\mu_K = 10^3$) with the lowest attack rate ($\alpha_{max} = 10^{-7}$). At the lowest productivity, the richness peaks at intermediate attack rate (10^{-5}). All simulations with the lowest productivity combined with the two lowest attack rates resulted in the complete extinction of consumer assemblages. The effect of increasing mean body size of species pool is an overall decrease of richness. On the other hand, the presence of consumption ordering tends to slightly decrease richness in the most species-rich points of the gradient, but increases richness in the vast majority of cases, especially at the most productive communities.

This last effect is better viewed by means of the functional diversity index (FD), presented in Figure 2. The greatest difference between the presence and absence of consumption ordering concerning FD occurs at the highest productivity value, but particularly when the largest attack rate also occurs. In great part, this difference can be explained by a much higher proportion of communities containing two or more coexisting species with consumption ordering in such gradient position. Although not producing richness peaks as high, the consumption ordering process enhanced the coexistence along the greatest part of the gradient space. It was not only the within-community functional diversity which was affected, but also the composition, as will become clear below with a closer inspection of bionomic traits of successful species. Given such remarkable differences between the resultant communities with and without consumption ordering, it is surprising that they produced nearly the same total number of species; 9939 (50.26%) versus 9837 (49.74%), respectively.

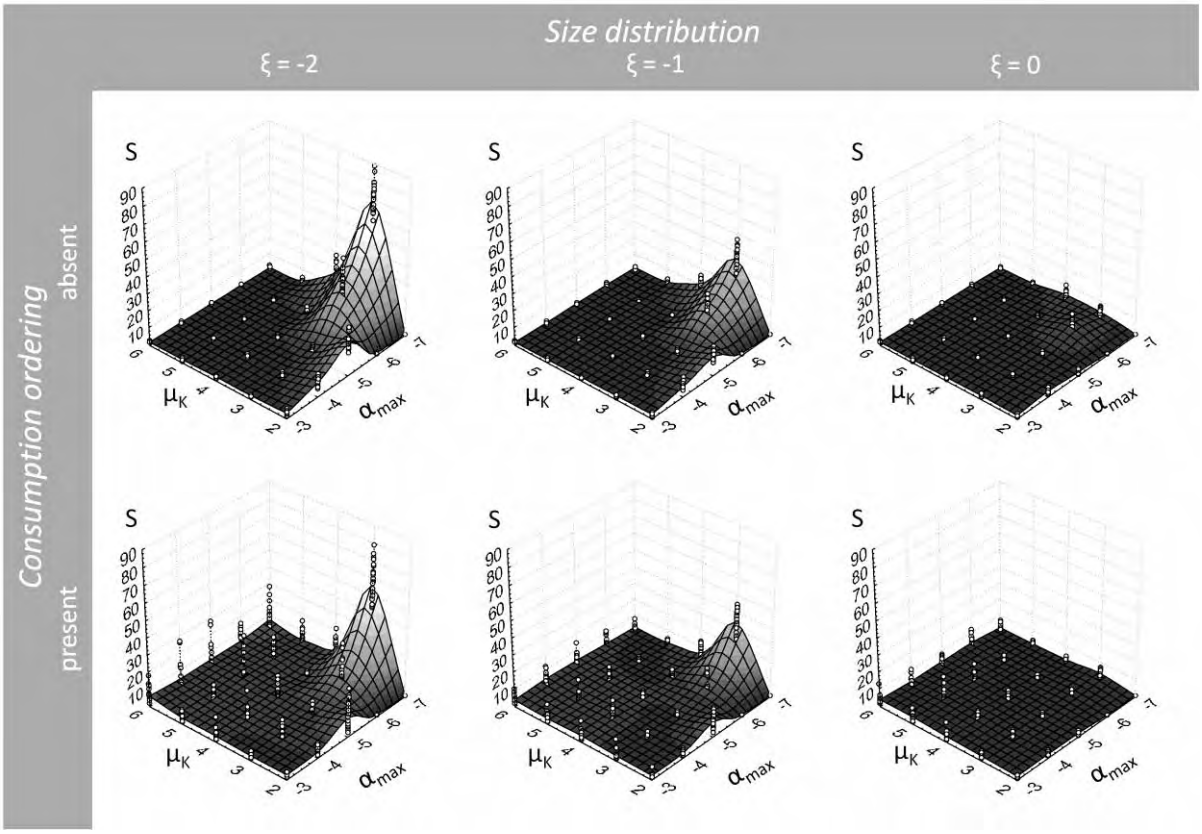


Figure 1. Final species richness at each community (scatter points) and corresponding distance-weighted least-squares surfaces along gradients of $\log_{10}$ of mean resource carrying capacity (μ_K), $\log_{10}$ of maximum attack rates (α_{max}), exponent (ξ) shaping size distribution of species pool and the presence/absence of consumption ordering hierarchy during predation sequences.

The pattern of population variability along time is shown here by the mean coefficient of variation (CV) of consumers' biomass (Figure 3). It was presented in a logarithm scale, to facilitate viewing differences along the gradient. We can see that the lowest coefficients of variation are found where the richest communities tend to occur. Indeed, there is a significant negative correlation between richness and log(CV) ($r = -0.35$, $p < 0.001$). An illustrative contrast between patterns of population dynamics can be seen by comparing communities on opposite positions of productivity gradient (Figure 4). Besides presenting larger fluctuations throughout time, the populations living on most productive sites explode at the very beginning of assembly process, leading to a fast depletion in resource levels (Figure 4a), which is followed by a crash in consumers' population level. The biomass accumulation in the least productive communities is much slower (Figure 4b), preventing a severe resource depletion. Accordingly, the priority effects tend to be higher at more productive sites and/or at sites with larger attack rates (Figure 5), although they are alleviated by consumption ordering hierarchy, mainly on these parts of the gradient. Such patterns together demonstrate that population variability, invasibility along the assembly process and final species richness are clearly linked.

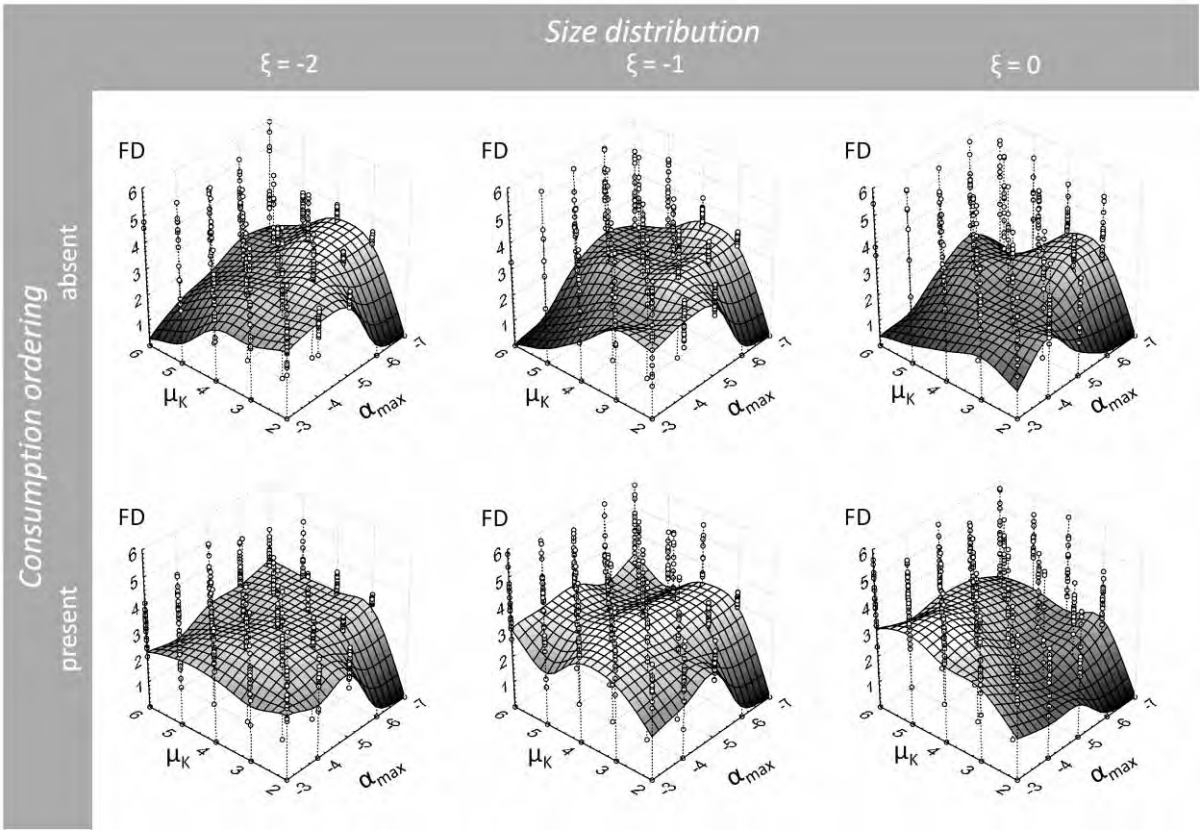


Figure 2. Functional diversity index (FD) at each community (scatter points) and corresponding distance-weighted least-squares surfaces along gradients of $\log_{10}$ of mean resource carrying capacity (μ_K), $\log_{10}$ of maximum attack rates (α_{max}), exponent (ξ) shaping size distribution of species pool and the presence/absence of consumption ordering hierarchy during predation sequences.

A closer inspection of how attack rate and resource biomass are related to determine the type III functional response can bring insight on its potential stabilizing role, which have implications for the observed diversity patterns. Considering that in the present simulations each consumer species interacted with a mean of 74 resources, and assuming equal contribution of resources to diet, the maximal functional response can be simplified to the following equation if we make the potential ingestion of a unitary individual, *PIng*, equal to 1 (100%),:

$$F = 74\left(\frac{\alpha_{\max} B^2}{1+74\alpha_{\max} B^2}\right) \qquad \text{Eq.(6)}$$

where B is the common value of resource biomass, α_{max} is the maximum attack rate and F is the proportion of *PIng* which is realized (F = Ing/PIng). Figure 6 plots this relationship for the five values of $\alpha_{max.}$ When each resource biomass is around the order of magnitude of 10^2g (corresponding to the lowest mean carrying capacity), the two lowest attack rates do not suffice to result in more than 70% of the species potential ingestion, which would correspond to zero-growth ingestion level (remembering that this percentage is the fixed metabolic

requirement). The minimum α_{max} allowing growth is 10^{-5}, which is exactly where the richness peak occurs for that carrying capacity (Figure 1). Among the three suitable options, this is also the attack rate for which the functional response is less saturated (more accelerating) at such a resource level. If the carrying capacity is increased by one order of magnitude (i.e. B = 10^3), an identical situation occurs but with the attack rate two orders of magnitude smaller ($\alpha_{max} = 10^{-7}$). If using an attack rate one order of magnitude lower (10^{-8}), the functional response would probably no longer be sufficient to supply the metabolic requirement, as Ing/PIng < 0.7. So it seems that the richness peak occurs, for each productivity level, at the minimum α_{max} value that still allows species to grow.

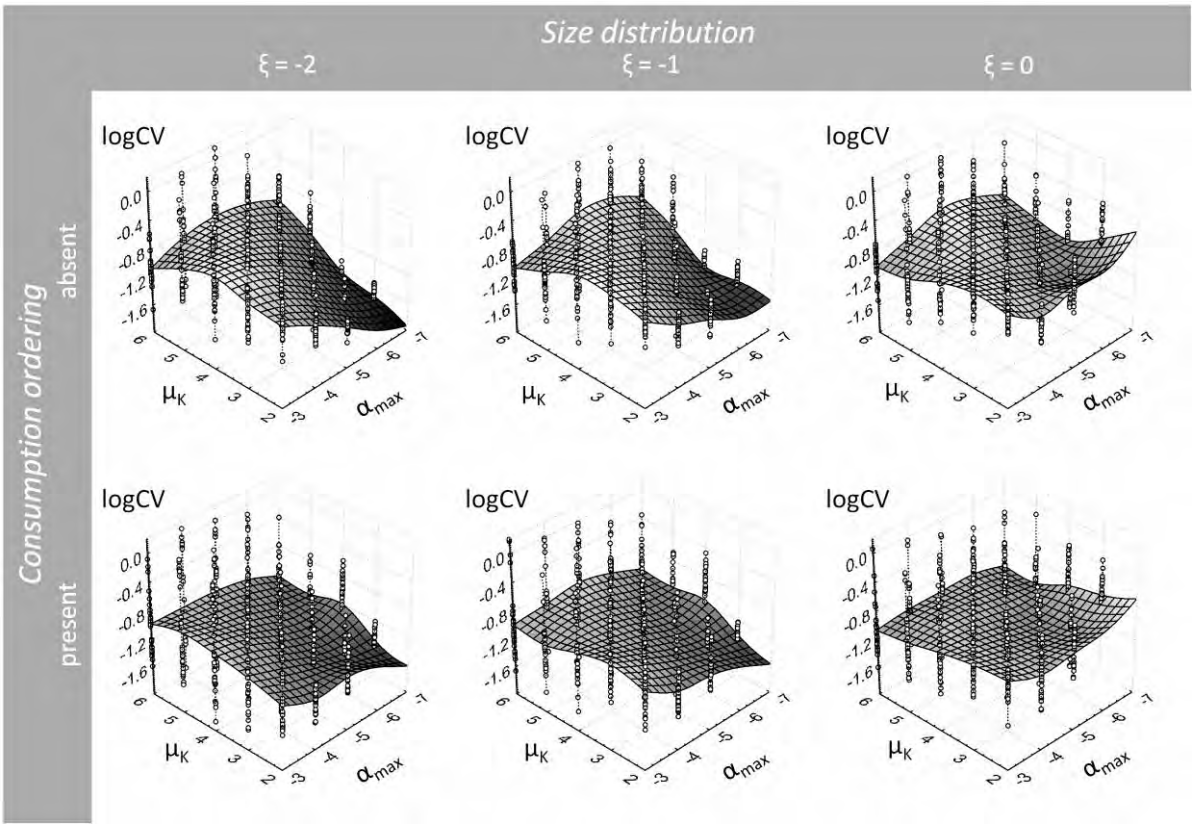


Figure 3. Log_{10} of the coefficient of variation (CV) of consumer biomass at each community (scatter points) and corresponding distance-weighted least-squares surfaces along gradients of log_{10} of mean resource carrying capacity (μ_K), log_{10} of maximum attack rates (α_{max}), exponent (ξ) shaping size distribution of species pool and the presence/absence of consumption ordering hierarchy during predation sequences. The CV was calculated from the last 30 years of simulation in each community, considering the annual censuses of total biomass of consumer assemblage.

All the resultant trait distributions deviated from the original species pool distributions, which emphasize the filtering effect of the assembly process. There were some strong associations between traits, which is also an emergent pattern, as the traits were generated independently during species creations. The kind of association depended mostly

on the presence/absence of consumption ordering. Figure 7 exemplifies the associations that can arise after we take into account all successful species. It includes only the parameters more directly involved with the consumption ordering (and specially the upper limit of predation window). Without consumption ordering, the successful species concentrate at lower δ and higher ε values, denoting an almost absolute advantage of more generalized diet. The consumption ordering still produces a peak of species concentration in this parameter region, but the main peak has now moved to lower values of ε, meaning a specialization towards smaller-sized resources. The growth rate in both cases was concentrated towards extreme values. But we observe no strong association between ζ and ε in the absence of consumption ordering, while in its presence a dichotomy emerges: successful species tend to have either high predation windows and low growth rates, or low predation windows and high growth rates.

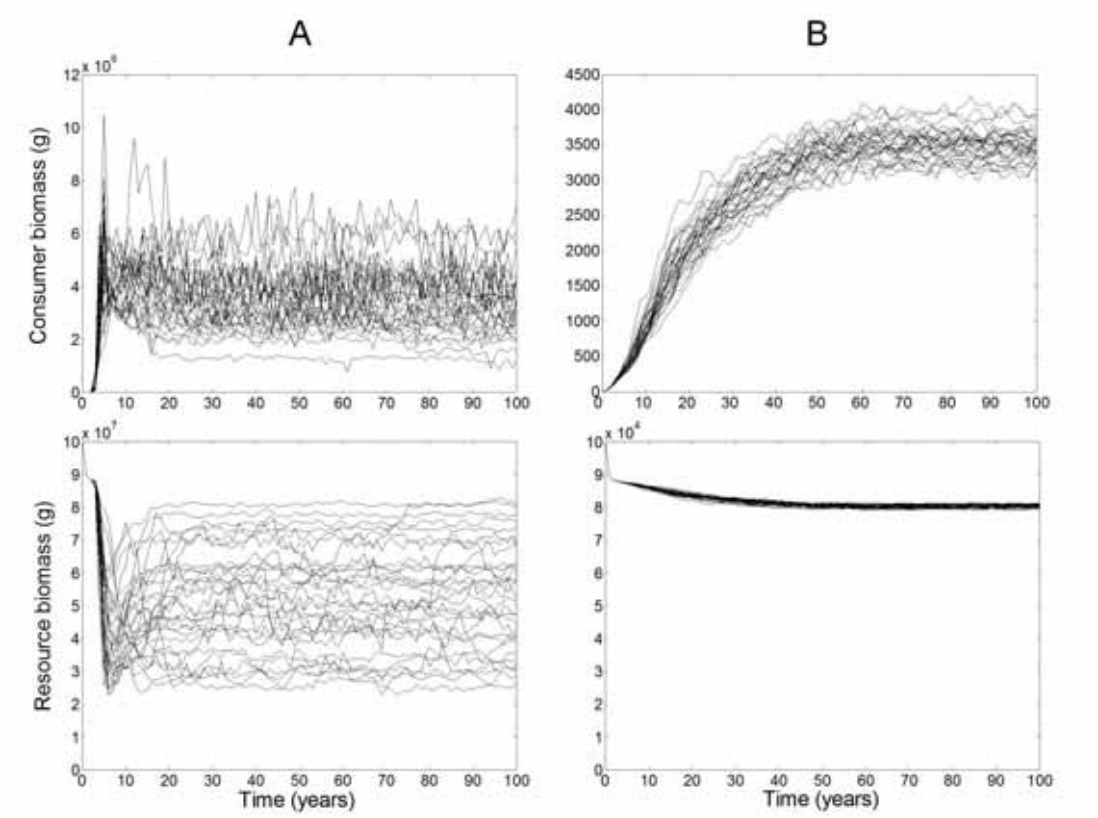


Figure 4. Annual censuses of total biomass of consumers and resources. The curves of 30 community replicates are superimposed in each graph. (A) mean carrying capacity of each resource $\mu_K = 10^6$; (B) $\mu_K = 10^3$. Other parameters are: $\alpha_{max} = 10^{-7}$; $\xi = -2$; consumption ordering absent.

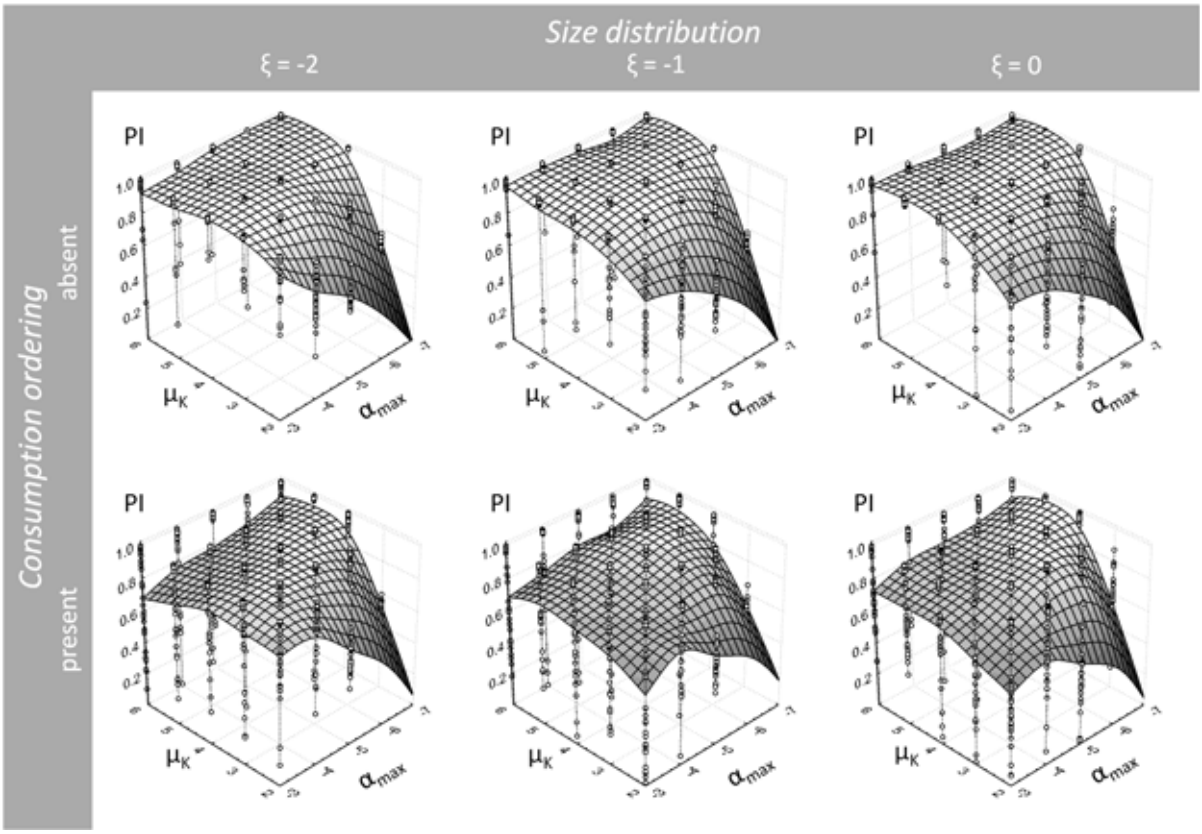


Figure 5. Priority effect index (PI) at each community (scatter points) and corresponding distance-weighted least-squares surfaces along gradients of $\log_{10}$ of mean resource carrying capacity (μ_K), $\log_{10}$ of maximum attack rates (α_{max}), exponent (ξ) shaping size distribution of species pool and the presence/absence of consumption ordering hierarchy during predation sequences.

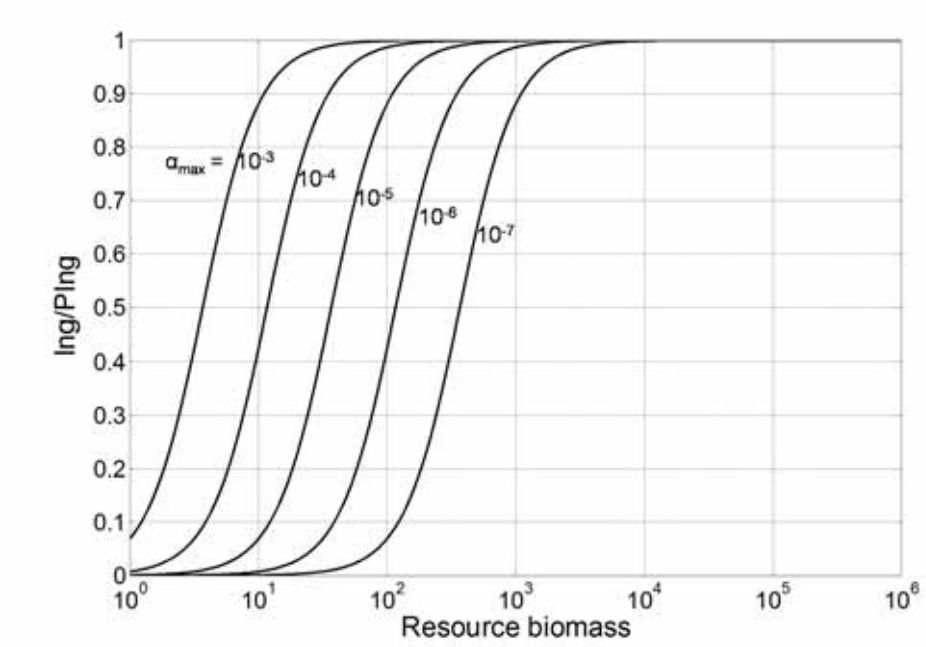


Figure 6. Relative functional responses as functions of resource biomass and attack rates (α_{max}, represented by each curve).

The cannibalism presented a diverse response. Without consumption ordering, we see no apparent association between Cann and ε, although for larger predation windows, there is a larger concentration of non-cannibalistic species. As expected, the positive Cann values for this case presented no trend, following the same uniform pattern from original species pool. This is because random predation sequences did not take in account quantitative differences within this parameter, but only the categorical classification between cannibals (Cann > 0) and non-cannibals (Cann = 0). On the other hand, the presence of consumption ordering leads to both qualitative and quantitative trends of cannibalism to emerge. For the largest predation windows, there is still a tendency (although not so strong) for non-cannibals to dominate, and little differences among positive Cann values. But, as we decrease the predation window, the proportion of non-cannibals decreases rapidly until the complete domination by cannibals. The interesting point here is that the highest Cann values are not favored, so that the majority of species is composed of cannibals with low preferences for co-specific prey. This leads to a rather simple conclusion that, as long as a consumption ordering hierarchy is imposed to predation, the possibility of preying on co-specifics constitutes an advantageous feature, but it is better to prefer prey of other species whenever they are available.

The analysis above ignores the influence of other gradients, however. Some of the relationships among traits can be better understood if looked in more detail. Below we show a series of figures allowing a close inspection at each trait for each gradient combination. Firstly, Figure 8 presents the maximum body size response. In general, there was a tendency towards smaller body sizes. Nevertheless, contrary to expectation, the species pool distribution did not affect substantially the selection pattern. We were expecting a stronger filtering effect at uniform body size distribution, producing species much smaller than in original pool. But there is no such sort of absolute optimum favoring small fishes: the resulting communities were reasonably neutral to the original distribution. It means also that communities formed by species pools with larger mean body sizes tend to contain larger surviving species. Nonetheless, there were some very strong selective responses, localized mainly at the lowest productivities combined with the lowest attack rates, in which only extremely small species were able to survive.

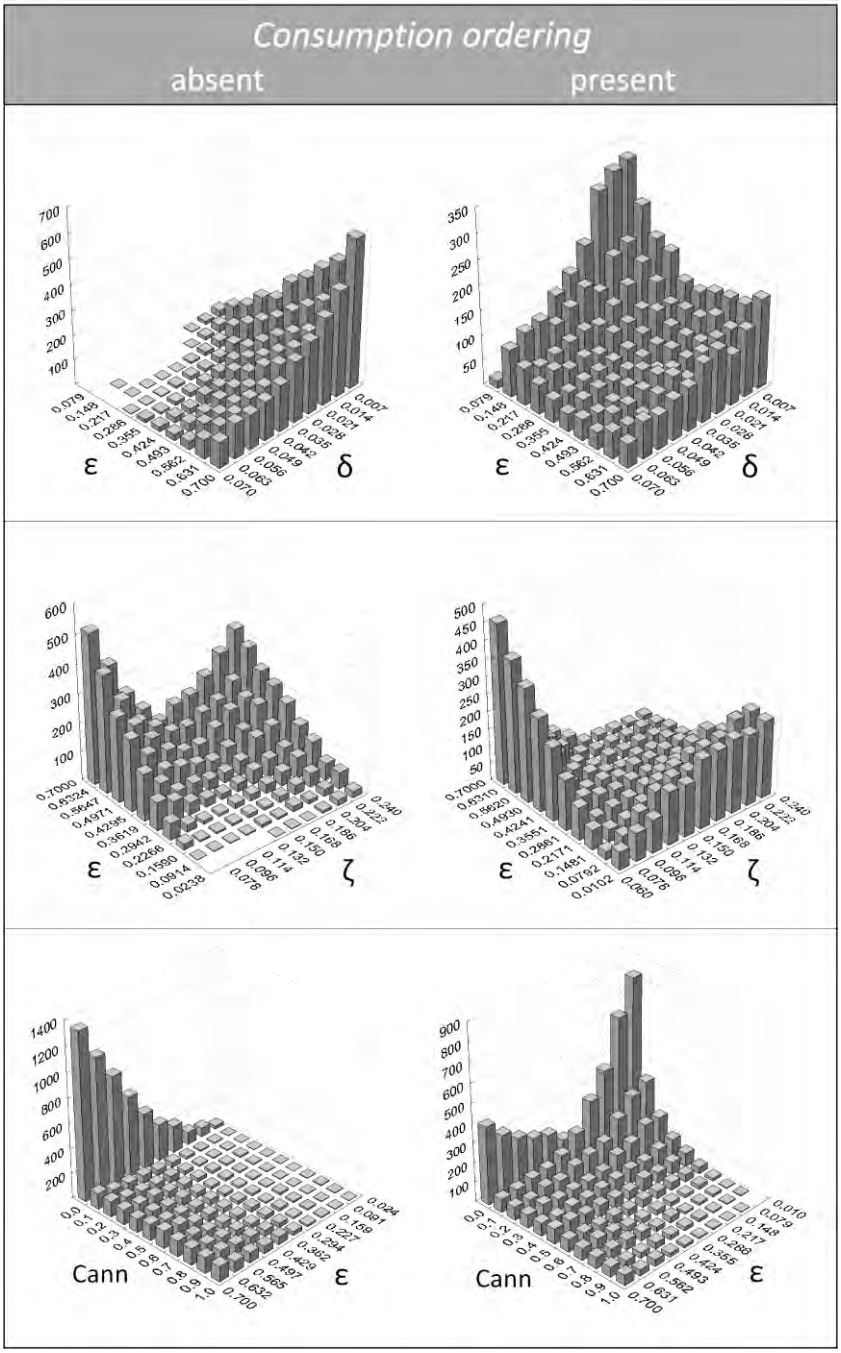


Figure 7. Bivariate histograms relating the upper and lower limits of predation window (ε and δ), the growth rate (ζ) and the level of cannibalism (Cann), on the presence or absence of consumption ordering. The frequencies are numbers of successful species.

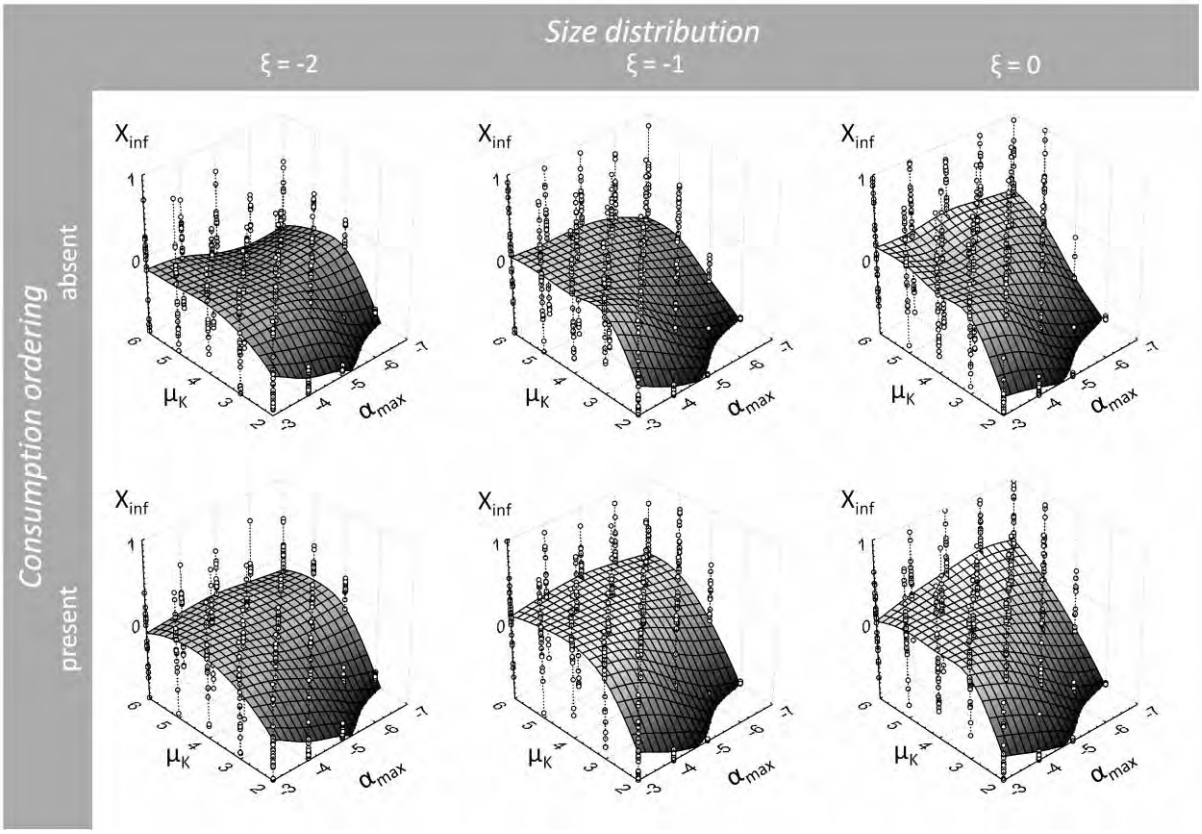


Figure 8. Selective response of mean maximum irreversible mass (X_{inf}) at each community (scatter points) and corresponding distance-weighted least-squares surfaces along gradients of $\log_{10}$ of mean resource carrying capacity (μ_K), $\log_{10}$ of maximum attack rates (α_{max}), exponent (ξ) shaping size distribution of species pool and the presence/absence of consumption ordering hierarchy during predation sequences.

The main gradient responsible for changes in size is the productivity (μ_K): communities with more available resource biomass allow the persistence of larger fishes. Increasing attack rates tended to increase mean size only at lower productivities, while at higher productivities, there were no effect at all or even the opposite effect was observed (i.e. when $\xi = 0$ and consumption ordering is present). The general effect of consumption ordering seems to be a slight increase in mean body size in most parts of the gradient, mainly at $\mu_K = 10^6$ and $\alpha_{max} = 10^{-7}$.

Two other life history features, the growth rate (ζ) and the relative size at maturation (θ), also had lower values at the least productive communities with lowest attack rates (Figure 9 and Figure 10). Nonetheless, while θ was almost unresponsive over most of gradient, ζ increased rapidly from negatively selected values, stabilizing with very large, positively selected values on intermediate and more productive portions of the gradient. It explains the scarcity of species with intermediate growth rates (Figure 7). Despite the general positive selection characterizing fast growing species at the plateau, the growth rates tended to be consistently decreased by the presence of consumption ordering.

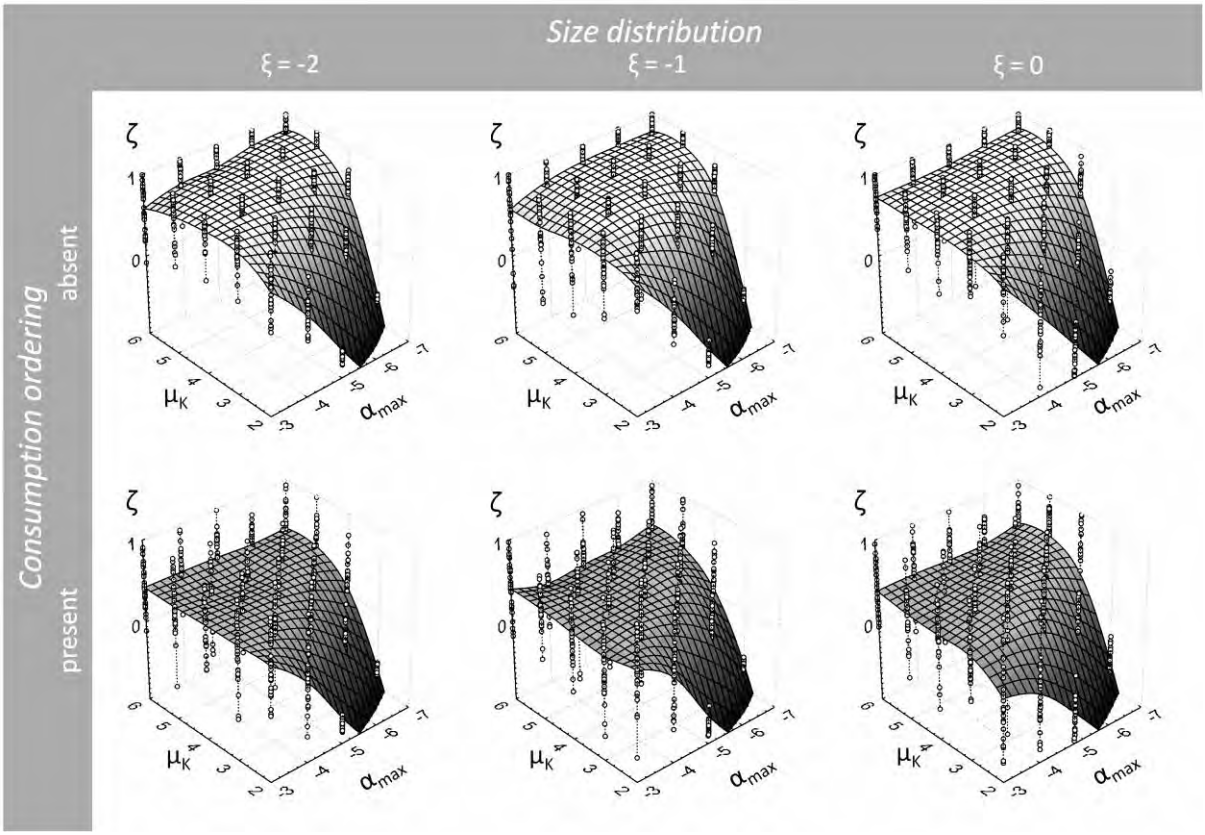


Figure 9. Selective response of mean coefficient of growth rate (ζ) at each community (scatter points) and corresponding distance-weighted least-squares surfaces along gradients of $\log_{10}$ of mean resource carrying capacity (μ_K), $\log_{10}$ of maximum attack rates (α_{max}), exponent (ξ) shaping size distribution of species pool and the presence/absence of consumption ordering hierarchy during predation sequences.

The consumption ordering produced highly contrasting patterns for the egg size, W_0: in its absence, there was a general tendency for larger eggs positively along almost all the gradients, while in its presence the selection favored very small egg sizes (Figure 11). The differences are greater on more productive communities. Although not entering directly in the predation ordering functions, the egg size selection was indirectly influenced by the fact that individuals in the first stage of development do not forage, thus showing no activity at first, and then appearing as the last available fish prey when there is an ordering hierarchy. Larger eggs take longer to develop into juveniles, being somewhat protected during this phase if predators choose more active prey. They also tend to reach larger initial juvenile sizes, shortening the time spam during which they are more vulnerable to predation until the first reproduction. Lower encounter rates among predators and prey in early life stages due to low visibility or mobility are likely to occur with fish (BROWNWELL, 1985; FOLKVORD & HUNTER, 1986), especially if the predators adopt ambush foraging tactics (GREENE, 1986). Without consumption ordering, none of these factors makes difference, as the eggs have the same chances to be predated as other eligible prey. In this case, the egg size was smaller at

higher productivities, probably reflecting an advantage of higher fecundities under this condition, especially because it is associated to larger body sizes (Figure 8) and higher growth rates (Figure 9).

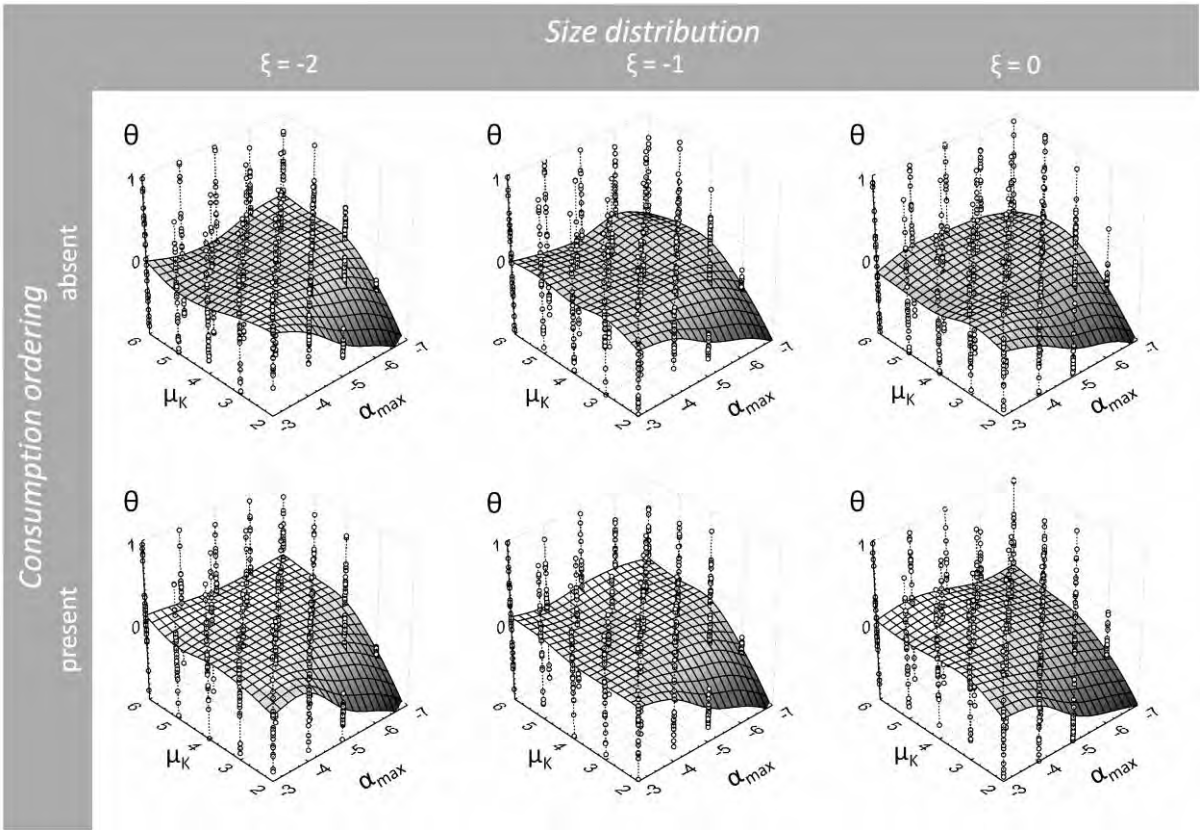


Figure 10. Selective response of mean relative size at maturation (θ) at each community (scatter points) and corresponding distance-weighted least-squares surfaces along gradients of $\log_{10}$ of mean resource carrying capacity (μ_K), $\log_{10}$ of maximum attack rates (α_{max}), exponent (ξ) shaping size distribution of species pool and the presence/absence of consumption ordering hierarchy during predation sequences.

The parameters related to spawning uniformity (u) and reproductive timing (η) did not respond substantially to gradients, if at all (Figure 12 and Figure 13). They may be rather more responsive to gradients of seasonality and/or disturbance regimes, which have more to do with reproductive timing constraints, but those gradients were not included in the present simulations. Nevertheless, there was some selection concerning the totality of successful species, which can be observed more easily by univariate histograms (Figure 14). Higher uniformity and intermediate timing seems to be advantageous at the simulated conditions. But these patterns are mainly due to the more restrictive conditions imposed by low productivities and low attack rates, where the richest communities were produced. With $\mu_K > 10^3$ and $\alpha_{max} > 10^{-5}$, the two parameters already assume a roughly uniform distribution, just like that expected from the original species pool (not shown). The peak of η occurs between 0.6 and 0.7. It means that the fish would finish spawning during the second half of autumn. In the

circumstances described above, we have very small and slow growing fishes, which start adult life soon and prefer to distribute spawning more uniformly along the reproductive season. By simulating individuals under such conditions, we saw that the first spawning interval tends to begin in summer, and the second already in spring. So the newborn offspring tend to experience a more suitable period, while the adult growth season is more restricted to lower resource levels during winter. Combined with egg sizes near the predicted mean (0.0505g, Figure 11), we conclude that fishes living under very poor resource levels have very low fecundities, in most cases producing only one offspring per week.

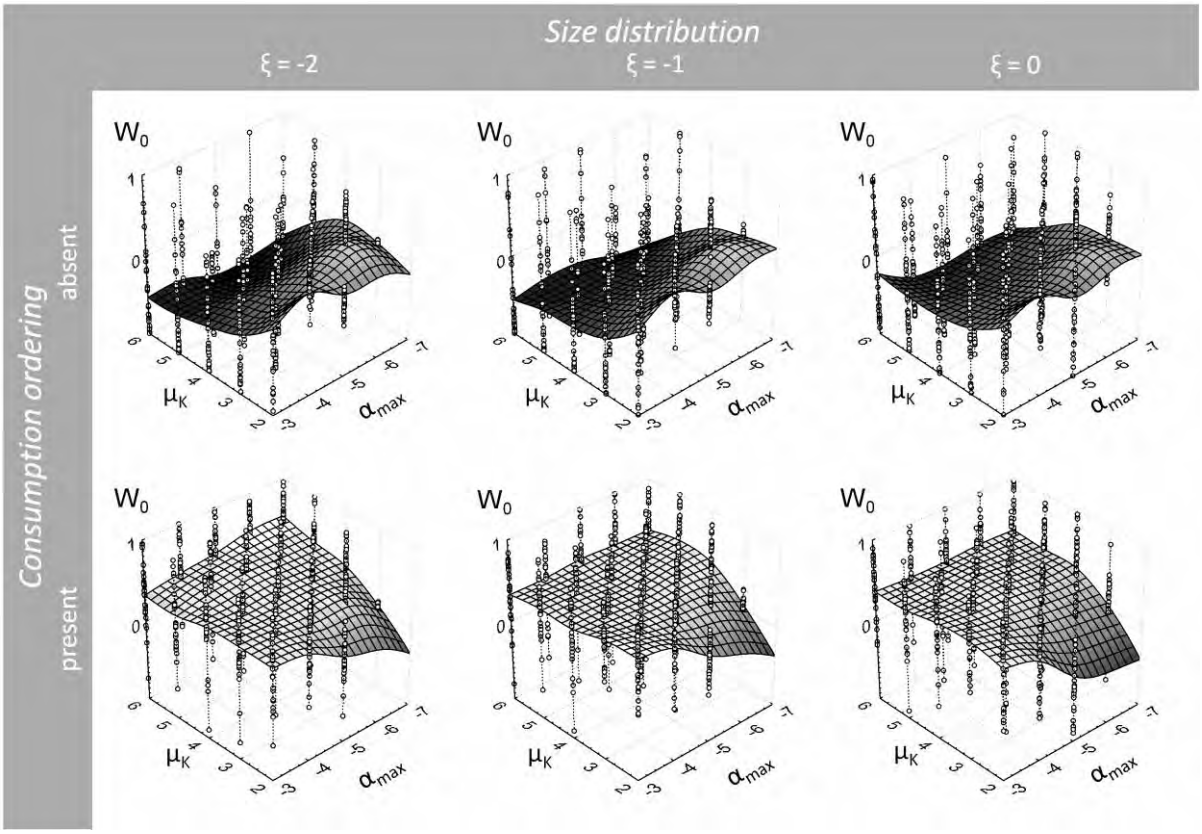


Figure 11. Selective response of mean egg size (W_0) at each community (scatter points) and corresponding distance-weighted least-squares surfaces along gradients of $\log_{10}$ of mean resource carrying capacity (μ_K), $\log_{10}$ of maximum attack rates (α_{max}), exponent (ξ) shaping size distribution of species pool and the presence/absence of consumption ordering hierarchy during predation sequences.

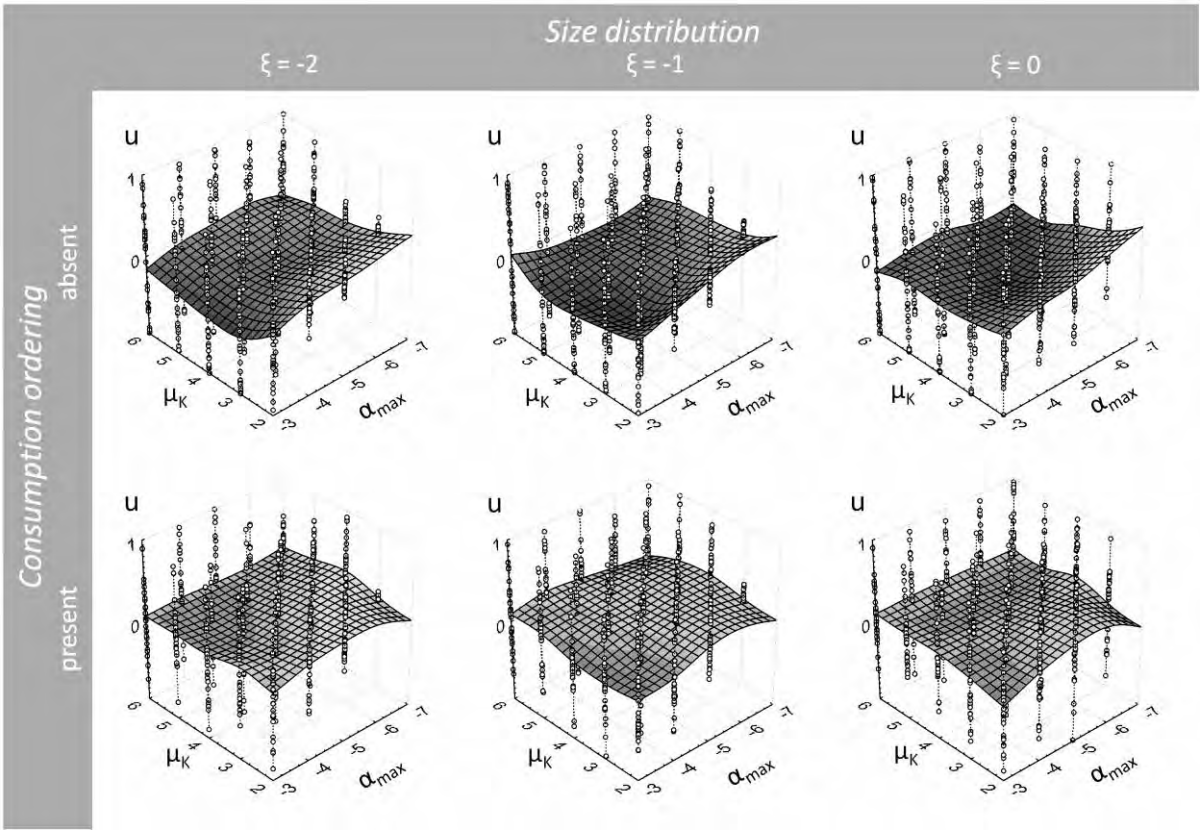


Figure 12. Selective response of mean uniformity of spawning (u) at each community (scatter points) and corresponding distance-weighted least-squares surfaces along gradients of $\log_{10}$ of mean resource carrying capacity (μ_K), $\log_{10}$ of maximum attack rates (α_{max}), exponent (ξ) shaping size distribution of species pool and the presence/absence of consumption ordering hierarchy during predation sequences.

Trophic traits also showed interesting responses. Without consumption ordering, wider predation windows (i.e. more generalist species) tend to dominate (Figure 7), but it occurs in different ways along the gradients. At lower resource availability (low μ_K and low α_{max}), the predation window enlarges predominantly by increasing its upper limit ε (Figure 15), while the lower limit δ is less responsive to selection (Figure 16). On the other hand, at higher resource availability (high μ_K and/or high α_{max}), the predation window increases mainly by decreasing its lower limit δ (Figure 16). This pattern is more prominent for the uniform species pool's body size distribution ($\xi = 0$). Because in the first situation the fishes tend to be very small (Figure 8), it makes sense that they must diversify their diet only by including food items higher in the size spectrum. The opposite occurs with larger fishes, living essentially in more productive communities. As they grow large, even moderately high values of δ are sufficient to exclude many of the smallest basal resources from diet (remembering that resource lengths follow a logarithmic scale, so the biomass is concentrated lower in the size spectrum). Large consumers must avoid this by having low δ values.

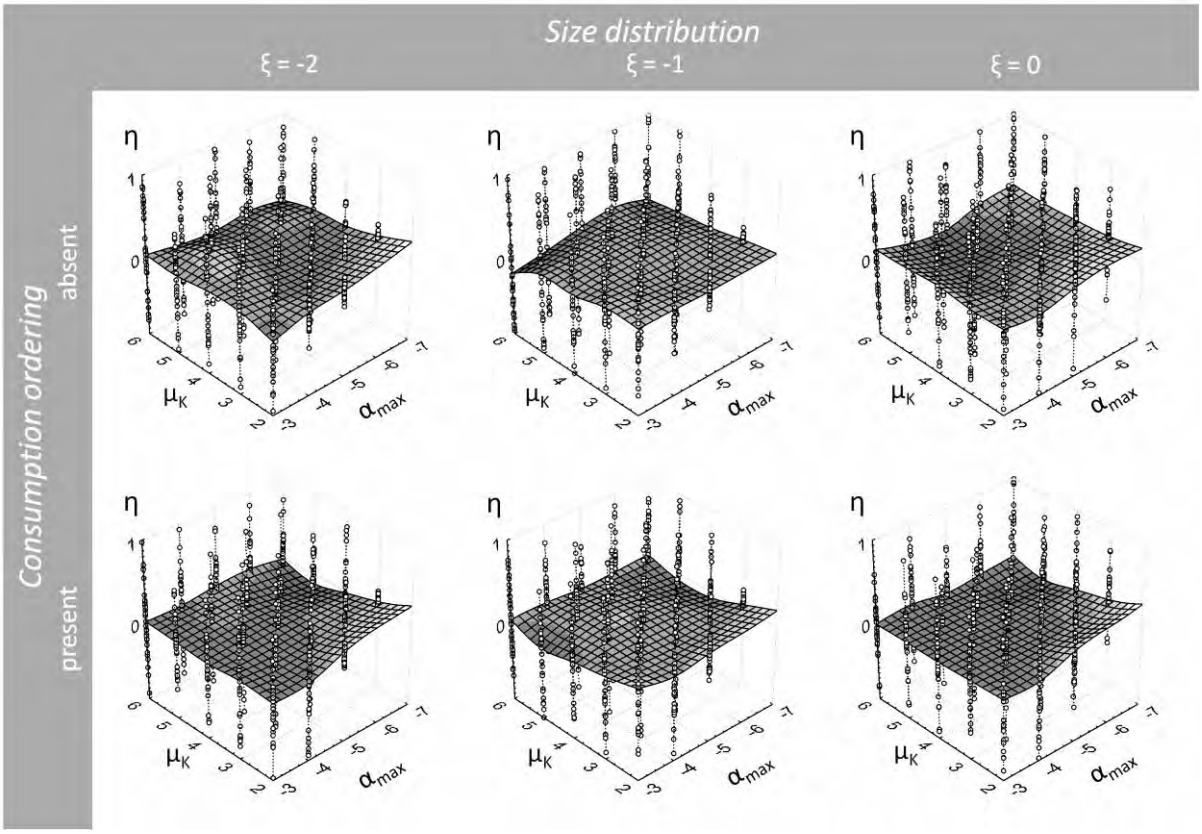


Figure 13. Selective response of mean reproductive timing parameter (η) at each community (scatter points) and corresponding distance-weighted least-squares surfaces along gradients of $\log_{10}$ of mean resource carrying capacity (μ_K), $\log_{10}$ of maximum attack rates (α_{max}), exponent (ξ) shaping size distribution of species pool and the presence/absence of consumption ordering hierarchy during predation sequences.

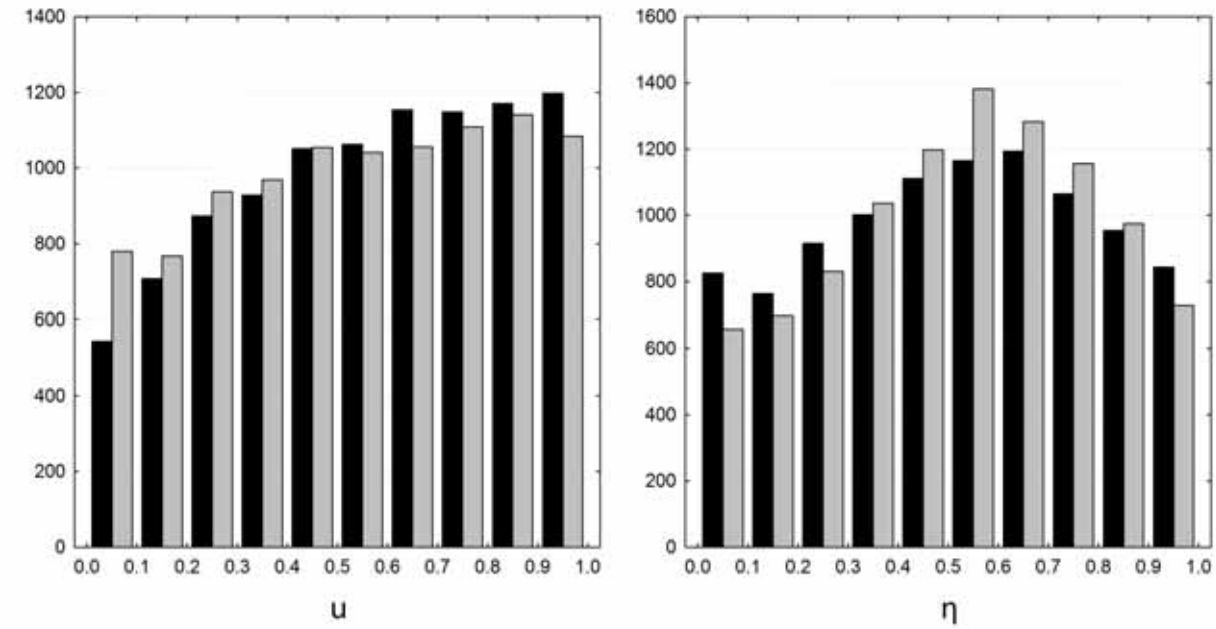


Figure 14. Histograms of the uniformity of spawning (u) and the reproductive timing parameter (η), with and without consumption ordering (black and gray bars, respectively). The frequencies are the numbers of successful species.

With consumption ordering we have a quite different picture. Although at lower resource availability the pattern does not change, slight increases in both μ_K or α_{max} turns the advantage toward species with lower than expected ε, but not as much toward lower δ when compared to cases without consumption ordering (Figure 15 and Figure 16). So, the preponderance of species with specialized diets, as shown by Figure 7, depends on the occurrence of sufficiently high resource availability. At very low resource availability, the necessity to include as many food items as possible overcomes the hierarchy imposed by the consumption ordering procedure.

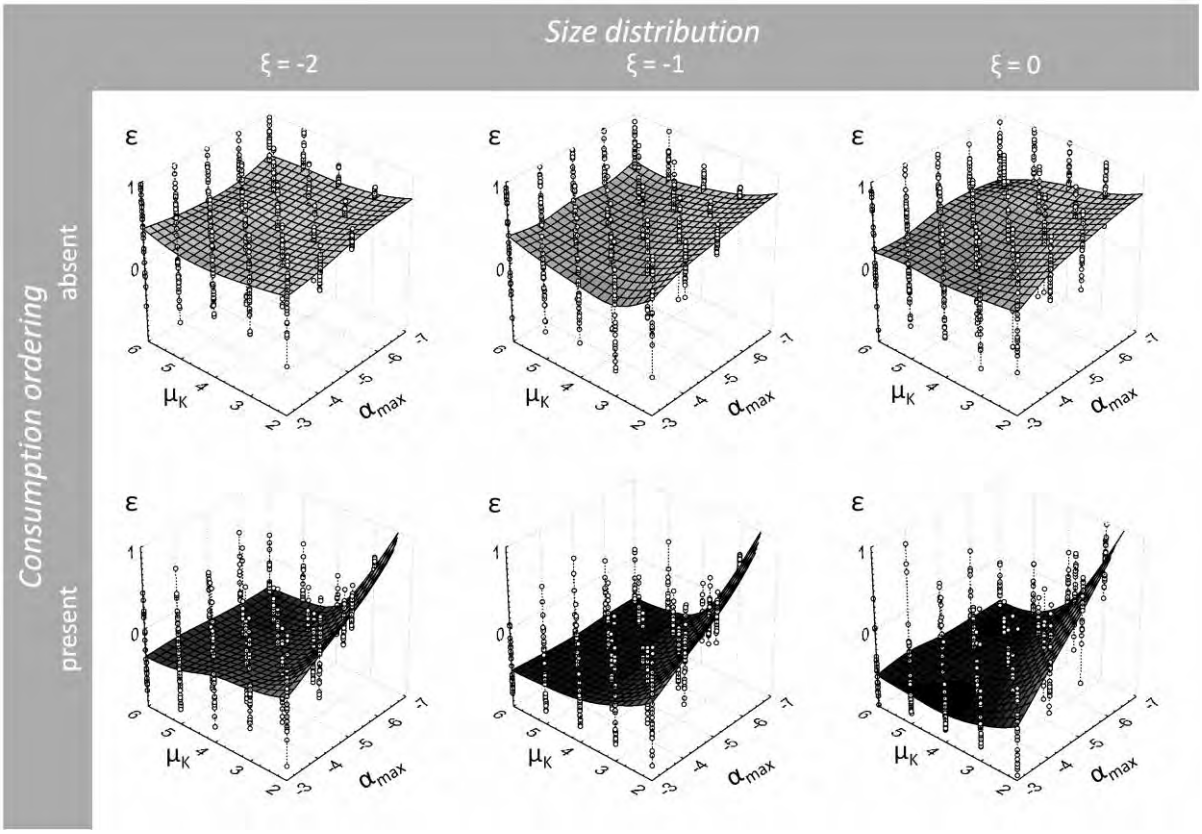


Figure 15. Selective response of mean upper limit of predation window (ε) at each community (scatter points) and corresponding distance-weighted least-squares surfaces along gradients of $\log_{10}$ of mean resource carrying capacity (μ_K), $\log_{10}$ of maximum attack rates (α_{max}), exponent (ξ) shaping size distribution of species pool and the presence/absence of consumption ordering hierarchy during predation sequences.

Cannibalism followed a more complex pattern. In order to assess its qualitative and quantitative features properly, we analyzed separately the proportion of cannibals (species with Cann > 0, Figure 17), and we took in account the selective trends of only positive Cann values ($Cann^+$, Figure 18). One striking pattern is the nearly absolute dominance of cannibals at the highest productivity and attack rate, irrespective of other gradient components (Figure 17). Without consumption ordering, the proportion of cannibals decreases rapidly to levels near those expected from the original species pool distribution (50% of cannibals), as we

decrease resource availability. For uniform body size distribution the response is rather more complicated. As expected, among cannibals there is no apparent response of Cann values (Figure 18). With consumption ordering, cannibals dominate along most of the gradient. By increasing body size distribution uniformity, there is a stronger decrease in the proportion of cannibals at the lowest resource availability. Among cannibals, we observe a marked tendency for lower cannibalism levels to dominate, except at the lowest resource availability conditions (Figure 18).

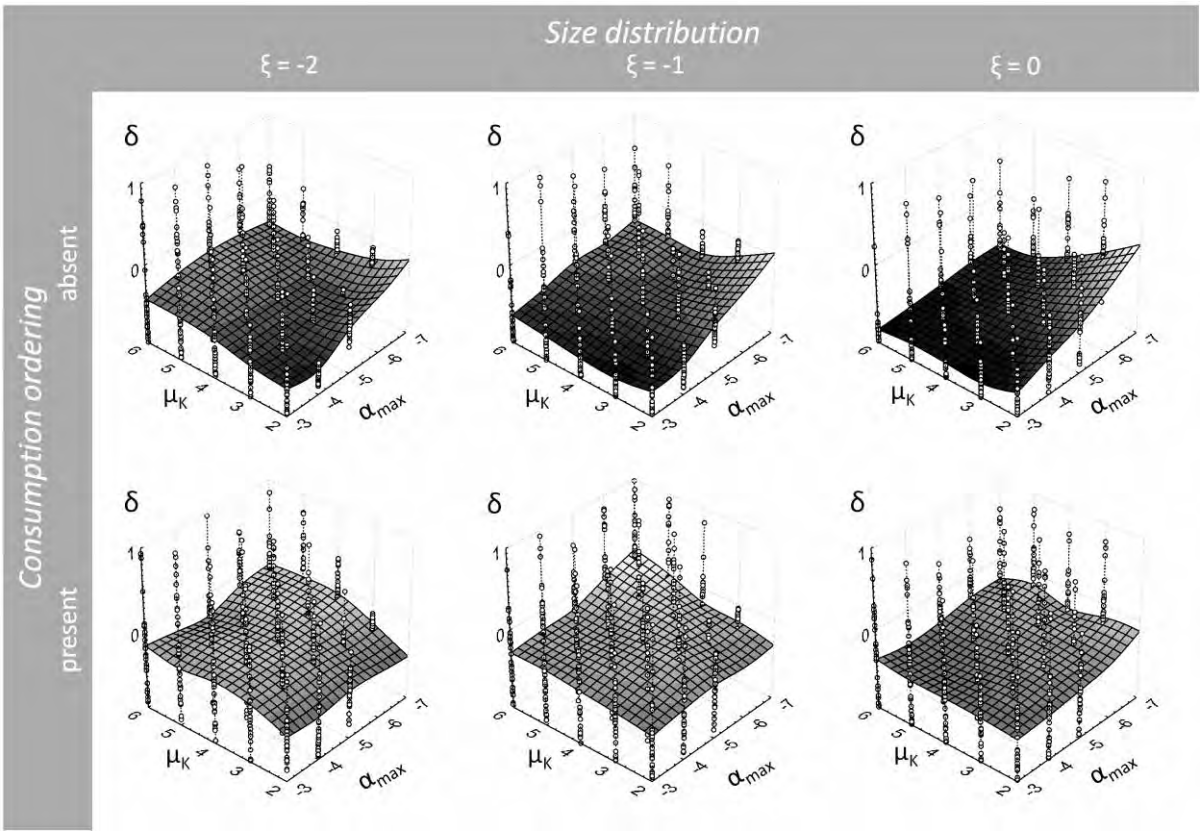


Figure 16. Selective response of mean lower limit of predation window (δ) at each community (scatter points) and corresponding distance-weighted least-squares surfaces along gradients of $\log_{10}$ of mean resource carrying capacity (μ_K), $\log_{10}$ of maximum attack rates (α_{max}), exponent (ξ) shaping size distribution of species pool and the presence/absence of consumption ordering hierarchy during predation sequences.

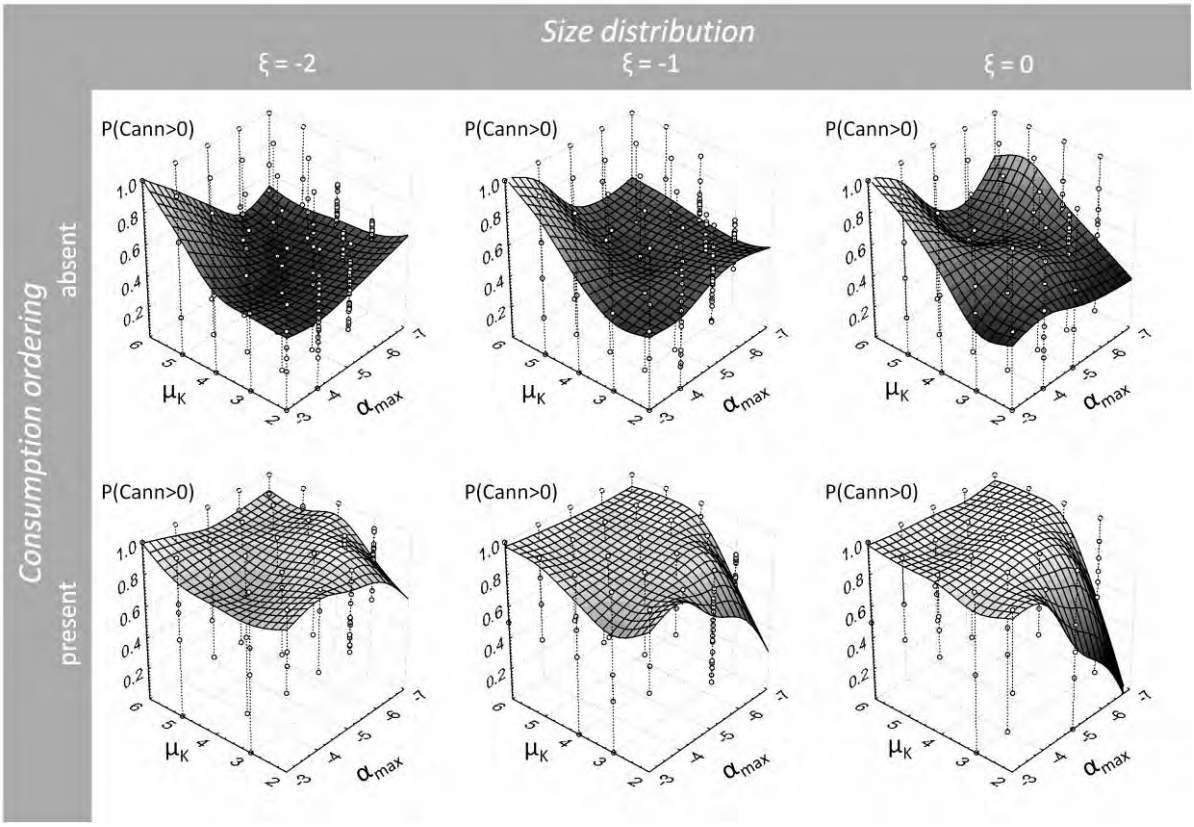


Figure 17. Proportion of cannibals (species with Cann > 0) at each community (scatter points) and corresponding distance-weighted least-squares surfaces along gradients of $\log_{10}$ of mean resource carrying capacity (μ_K), $\log_{10}$ of maximum attack rates (α_{max}), exponent (ξ) shaping size distribution of species pool and the presence/absence of consumption ordering hierarchy during predation sequences.

The piscivory level was mostly affected by resource productivity, although a slight positive correlation was also observed with attack rates at lower productivities (Figure 19). Nevertheless, there was a general negative selection, leading to communities with lower piscivory than expected from the original species pool. Given the constraining role of piscivory, imposing limits to attack rates on all other resources, it makes sense for there to be some level of negative selection against it. It also makes sense that the selection is stronger at lower productivities and attack rates, where consumers are already more limited in the amount of available food provided by basal resources.

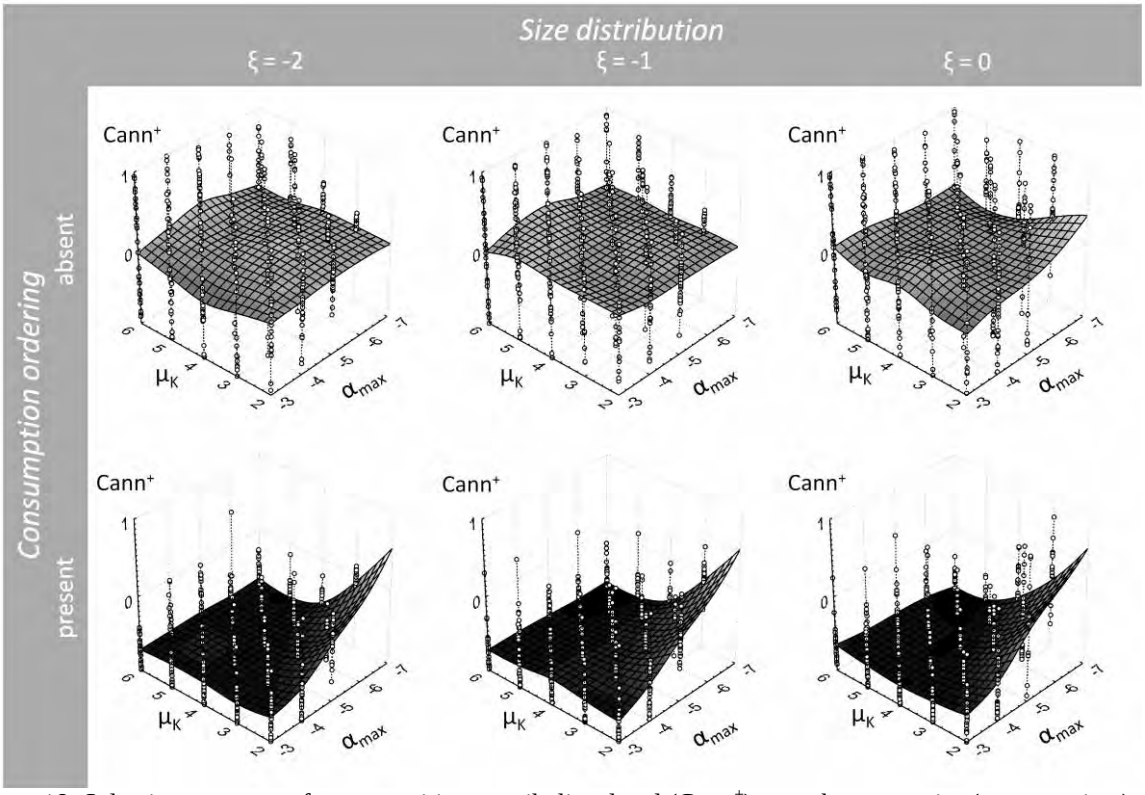


Figure 18. Selective response of mean positive cannibalism level ($Cann^{+}$) at each community (scatter points) and corresponding distance-weighted least-squares surfaces along gradients of $\log_{10}$ of mean resource carrying capacity (μ_K), $\log_{10}$ of maximum attack rates (α_{max}), exponent (ξ) shaping size distribution of species pool and the presence/absence of consumption ordering hierarchy during predation sequences.

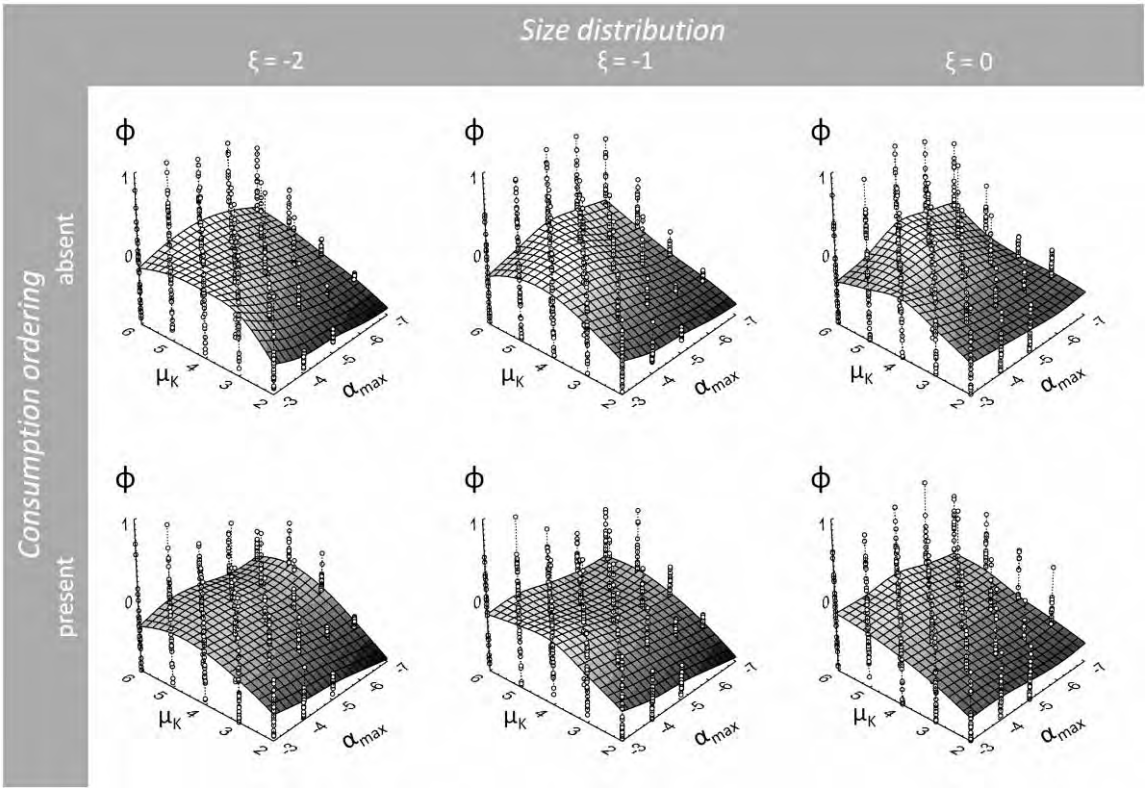


Figure 19. Selective response of mean piscivory level (ϕ) at each community (scatter points) and corresponding distance-weighted least-squares surfaces along gradients of $\log_{10}$ of mean resource carrying capacity (μ_K), $\log_{10}$ of maximum attack rates (α_{max}), exponent (ξ) shaping size distribution of species pool and the presence/absence of consumption ordering hierarchy during predation sequences.

2.4. Discussion

Despite great residual variability, the figures show consistent trends for most ecological variables along gradients. In natural instances, the trilateral model of Winemiller & Rose (1992) seems to be a good predictor for the adjustment of life history features to environmental conditions, at least in freshwater (MIMS *et al*., 2010). It conceptualizes three endpoint strategies, whose selection is related mainly to competition/predation level and habitat predictability: (i) opportunistic, species with small body size, early maturation and low juvenile survivorship (small eggs and/or absence of parental care), usually associated to unpredictable habitats with frequent disturbances; (ii) equilibrium strategists, small to medium sized species, moderate lengths at maturation, low fecundity but high investment per progeny, generally associated to stable environments with high competition and/or predation; (iii) periodic strategists, large sized species with late maturation, high fecundity and low investment per progeny, associated to highly seasonal environments and large spatial scales. As in Winemiller and Rose's scheme, the present model produced highly congruent life history traits distributions along gradients, concerning mainly maximum size, relative size at maturation, growth rate and egg size, as well as trophic characteristics like relative maximum prey size, cannibalism and piscivory degree. But, as the modeled environment was highly predictable, with only moderate seasonality, having competition and predation as the only ecological sources of mortality (absence of disturbances), and without large scale spatio-temporal variations, it adjusts better to what would be expected in an equilibrium strategy. In the trilateral model, species can be located continuously between any two or three strategies (MIMS et al. 2010). So the observed trends may be considered major variations closer to the equilibrium strategy endpoint, driven by differences in resource availability and predation level. At very low resource availability and predation, we observe a tendency towards opportunistic strategies (small size, earlier maturation, relative indifference to egg size). It is interesting because this trend did not require disturbance regimes, meaning that opportunistic strategies could arise also from sites with strong resource deprival, even if reasonably constant in time. As we increase resource availability and predation, two alternative possibilities emerge, depending on whether consumption ordering is present or not. Without consumption ordering, together with increasing maximum and maturation size we observe decreasing egg size, and consequently increasing fecundity. It characterizes a trend towards periodic strategy (WINEMILLER & ROSE, 1992; MIMS et al., 2010). On the other hand, with consumption ordering egg size follows the opposite pattern, slightly increasing with

higher productivity and predation, which configures a reinforcement of equilibrium strategy. The selection for higher piscivory and proportion of cannibals, together with relatively lower growth rates and larger eggs when consumption ordering is present highlights the importance of predation on more productive environments. An interesting point is that in absence of consumption ordering the model predicts that increasing fecundity may be selected in places with higher predation pressure. Probably high offspring numbers can overcome high egg mortality in this situation. But the simple existence on nature of many species with strong parental care and large eggs mainly in more constant and risky environments is an argument against complete absence of consumption ordering, which would never predict increasing egg sizes as they would present no advantage. Interesting also is the fact that consumption ordering generated more diverse assemblages exactly at more productive sites.

Among simulated gradients, productivity (resource carrying capacity) has the easiest interpretation. Nevertheless, as we did not model space explicitly, increasing carrying capacities may have two alternative meanings: (i) higher resource densities or (ii) larger areas. Which situation applies best would depend also on how we interpret attack rate variation. The attack rate determines ultimately the proportion of potential ingestion that can be realized, given current resource biomass. Many factors, either functional/taxonomic or environmentally driven, could alter the attack rate for a given resource-consumer pair. Functionally or taxonomically different species groups can have quite different attack rates on the same resource type. Such differences may arise from behavior, morphological adaptations, and physiological constraints, to cite just a few. But, as we are not concerned with comparisons among major taxonomic or functional groups (e.g. between endotherms and ectotherms), the variation in maximum attack rates may be better interpreted here as a feature of the environment. Space itself is one potential factor that might explain attack rate variability (Figure 20a). The type III functional response is commonly thought to arise as consequence of spatial constraints (KOEN-ALONSO, 2007). By having an initial accelerating phase, this functional response provides refugee for prey when they are at low densities, which can result from diffusion limitation of predators (DE ROOS *ET AL*. 1991; WILSON 1996). Decreasing the attack rate coefficient has a similar effect of limiting predator dispersal capacity (CUDDINGTON & YODZIS 2000). In other words, if the space is enlarged, the individual predators become less capable to access the entire prey population on a given time interval, which implies a lower attack rate. Thus, for a constant total productivity, decreasing α_{max} can be interpreted as increasing the spatial extent of the environment, having as a consequence decreasing resource density (Figure 20a). On the other hand, for constant α_{max}, increasing μ_K

would be the same as increasing resource density on a fixed area. In order for higher carrying capacity be interpreted as resulting solely from larger space, it must then be accompanied by decreasing maximum attack rate (a diagonal route along μ_K versus α_{max} coordinate plane).

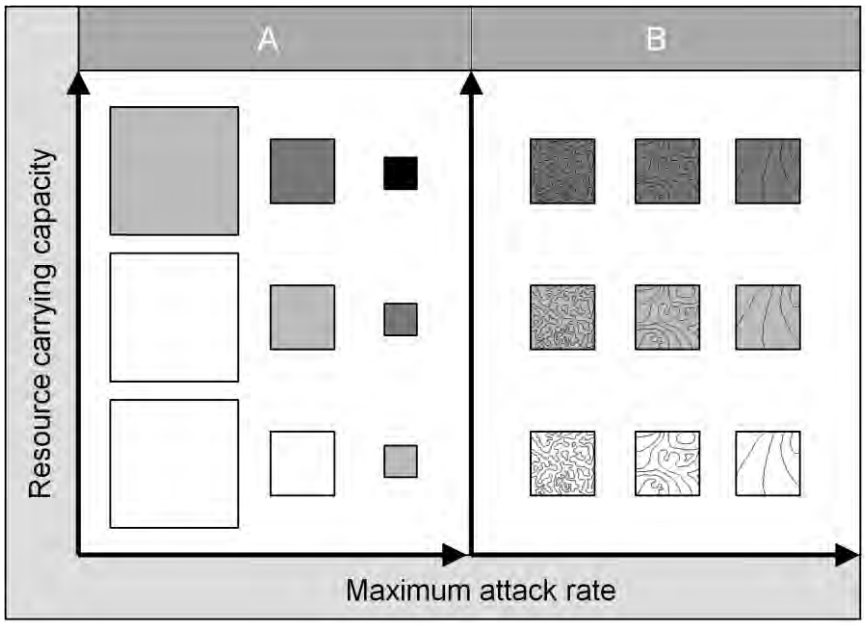


Figure 20. Two alternative hypotheses to interpret combined variation of resource carrying capacity and maximum attack rate. Each square represents an environment inhabited by a community. Its area corresponds to the spatial size, and its darkness, to the resource density. (A) Increasing space is the cause for decreasing attack rates, due to predator's diffusion limitation; (B) Increasing habitat complexity instead is what decreases attack rates.

But there is another important factor that could affect maximum attack rates: habitat structural complexity (Figure 20b). The presence of entangled vegetation or high dimensional fractal substrates can diminish prey capture efficiency, providing refugees and enhancing coexistence (GILLINSKY, 1984). In order to work, this hypothesis does not require changes in spatial extent, so that increasing resource carrying capacity can be thought of as essentially increasing resource density. Combining these two hypotheses, we have many possibilities of environment types that could fit to the gradients here studied. It emphasizes that modeling attack rates with such a type III functional response provides a very general framework to study systems dominated by consumer-resource dynamics. As long as space can be assumed implicitly, it can serve to compare habitat patches with different sizes but similar environmental characteristics, as well as equal sized patches differing in resource density, structural complexity or both.

The richness pattern along the gradients (Figure 1) is consistent with a unimodal productivity-diversity relationship, if we control for attack rate variation. For a given

maximum attack rate, there is a peak of richness at some resource carrying capacity. This peak is positioned at higher carrying capacities the lower is the maximum attack rate, suggesting the existence of optimal resource density (according to hypothesis A of Figure 20) or optimal density/complexity combination (according to hypothesis B). The peaks reach higher richness levels the further we increase carrying capacity and decrease attack rate, diagonally along the bivariate gradient. Therefore, if the effect of attack rate due to spatial constraint or habitat complexity is not taken into account, one might often observe only a rather monotonic productivity-diversity relationship. It all depends on how these gradient features are correlated in nature. In general, discussions concerning the effects of productivity on community dynamics should assume the area effect is controlled (ABRAMS, 1995). In this sense, hypothesis A is consistent only with a unimodal productivity-diversity relationship. Alternatively, if one is interested in varying areas, then the apparent diagonal monotonic increase in richness is consistent with both hypothesis A and the predictions of island biogeography/species-area theory (MACARTHUR & WILSON, 1967; ROSENZWEIG, 1995; HUBBELL, 2001). But if hypothesis B is the case, then a monotonic productivity/diversity relationship could arise as long as productivity (resource density) and habitat complexity are positively correlated. Such a correlation is quite possible, given that some complexity-increasing factors like aquatic vegetation tend to grow better at more productive sites.

Irrespective of which environmental factors determine the attack rates, it is worth trying to explain why the observed diversity pattern emerges. At sufficiently low productivity and attack rate, none species is able to survive to the end of assembly process, simply because the available resources are not enough for organisms to satisfy their metabolic demands and/or to reproduce successfully. This is the case here for communities with $\mu_K = 10^2$ and $\alpha_{max} = 10^{-7}$ or 10^{-6}. From this situation, any increase either in resource productivity or in maximum attack rate is expected to increase the probability of species survival and consequently diversity. At some point, however, the richness reaches an optimum and then starts to decrease. At first sight, it seems to be counterintuitive that higher resource availability could result in lower consumer diversity. But such a negative effect characterizing the second tail of a unimodal pattern has been suggested both empirically and theoretically (ROSENZWEIG & ABRAMSKY, 1993; TILMAN & PACALA, 1993). The explanations rely basically on competitive exclusion in very productive sites, although the theoretical basis for it has been criticized (ABRAMS, 1995). Furthermore, the usual competitive-exclusion arguments depend on spatial heterogeneity, which is not considered in the present model. Besides showing that

unimodal diversity-productivity relationship does not depend on spatial heterogeneity, we argue that the explanation must rely on the dynamical features of the modeled consumer-resource system.

It is well known that the type III functional response has a stabilizing effect on dynamics, especially in its more accelerating (less saturated) portion (MURDOCH & OATEN, 1975; ABRAMS & HOLT, 2002). Figure 6 showed that richness peaks occur at resource levels and attack rates corresponding to more accelerating portions of functional responses. For resource levels higher or equal to 10^4, all functional responses were almost completely saturated, which tends to generate less stable dynamics and could be responsible for the lower observed richness. It also can explain why much of variability in community attributes along the gradients is concentrated at the two lowest carrying capacities. Of course, that picture is just a simplification, as the resources' biomasses are not equal as assumed, and the attack rates, as well as the number of food items, can vary among species. But it can serve as a rough guide to understand the interplay between the roles of productivity and attack rates on dynamics. Additional simulations, including many lower values for α_{max}, could help fill the empty right side of Figure 6, and testing whether our hypothesis is true for this model system. If the community stability can be measured by the variability in biomass (WILMERS *et al.*, 2002), particularly by its coefficient of variation (CV), then the stability hypothesis finds another support, as richness is negatively associated to population variability (Figure 3).

The higher dominance in more productive sites is also related to species features. Large-sized and fast growing species are able to persist only when the resource biomass is high enough. In this situation, early colonists tend to deplete resource levels after a burst of high population growth (Figure 4a), and thereafter a few or even just one species dominates the assemblage, preventing the establishment of subsequent species establishment. This is reflected by the very high priority effects observed in more productive portion of gradient (Figure 5). This is on its own an important prediction of our model: the priority effects shall be stronger at more productive sites. It remains to be investigated by which specific mechanism(s) this priority effect takes place, whether by predation or any other factor which may be linked to population abundance and structure in the initial phases of assembly. Those early dominating species are characterized by having mainly high body growth rates (ζ, Figure 9), besides a relatively higher piscivory level (ϕ, Figure 19). Combined with the fact that their functional responses are more saturated, this can contribute to stronger interactions, which tend to prevent coexistence (MAY, 1973; MCCANN *ET AL.*, 1998; KOKKORIS *et al.*, 1999). On the other hand, at low productivity and low attack rate the consumers are not able

to supply their entire food demand (PIng) even when the resources are at their carrying capacities. The biomass curves along the assembly process are much smoother, tending to stabilize slowly (Figure 4b). Species can establish at any time during the assembly process, so that the mean priority effect index is near the null expectation (PI ≈ 0.5, Figure 5). There is strong selection for very small, slow growing, early reproducing and less fecund species. Nonetheless, they thrive in relatively great richness, even with low standing abundance and biomass. A remarkable example which could fit in this situation is found in the fish assemblages of Rio Negro and similar black water rivers, in the Amazon basin. The nutrient content and productivity in these rivers are very low, but the species richness is high when compared to the more productive counterparts in this same basin (GOULDING *et al.*, 1988). While the dominant forms in more productive rivers are young of medium and large species, in the black waters the assemblages are dominated by fishes having very small adult sizes (GOULDING *et al.*, 1988). Despite obvious evolutionary and biogeographic influences, the mechanisms embodied in our model can provide an entirely ecological explanation for such differences in species richness and composition.

To reach high richness levels, the local community also depends on the regional pool from which the propagules come. We saw that flatter (more uniform) body size distributions, despite being intrinsically more diverse, generate poorer communities, no matter what the productivity or maximum attack rate are. This is due to the scarcity of species kinds (small body size) more suited to potentially species-rich environments. Nonetheless, it is possible that a much larger assembly time would suffice for a uniform distribution to generate diverse communities, as long as priority effects do not interfere. But it is still clear that, in order for an assemblage to reach its potential diversity within a given time scale, it is necessary for there to be an adequate source of functional forms.

Trait variability in the present model is generated by immigration from an infinite species pool, so it ignores the ultimate source of variation, which is evolution. It must be assumed that trait diversity necessary to any adjustment between environment and species composition is not constrained by phylogeny or genetic variance. Although not strictly true, the assumption may not be so serious in the studied time scale, for which immigration represents the predominant process of species entry in most communities usually studied in natural world. Besides, this is a common assumption of many optimization models used to study life-history selection (STEARNS, 1992; ROFF, 1992). Assembly by evolution or immigration can produce different outcomes, as showed by Powell & McKane (2009). For instance, the positive relationship between species number and resource availability tend to be

steeper in communities generated exclusively by evolution, and also the proportion of top predators and other food web features are also differentially affect. But the most important distinction between evolution and immigration, besides the obvious differences in spatial and temporal scales, depends on the own process of trait selection. Trait change by evolution tends to be gradual and temporally autocorrelated. In a fitness landscape of trait values, natural selection always leads to "uphill" trait modification, trapping it at some local peak if the landscape is rugged enough (KAUFFMAN, 1993). On the other hand, using immigration from an already existing species pool allows many more strategies to be present in the same community simultaneously, providing a more efficient search in parameter space. Assembly by immigration is also much more repeatable, both in modeling terms and experimentally (POWELL & MCKANE, 2009). One disadvantage is that the pool must be defined arbitrarily, at least in the initial phase of community construction. But once constructed, such communities can be used as source and finite pools to generate posterior and more realistic assembly scenarios. Another possibility is to keep pools infinite, but to also adopt a more Bayesian perspective, by successively adjusting the source pool of trait distributions as the community develops and the cumulating persistent species (sampling units) depart from original (*a priori*) distributions.

The last alternative can be interpreted as an implicit mechanism of feedback among local and regional processes. If the regional landscape (in this case, a spatial landscape) is constituted of identical community patches, then a fixed source distribution of traits (such like the uniform distributions here used) differing from the total set of assembled communities could not be accepted as representing the regional species pool. This would be the case of our study, as in all points along the gradients we observed at least one trait that was subjected to substantial deviation from the original distribution. Over the long run, the successful variants would dominate all local communities, which together form the regional pool. But community patches do not need to be identical. On the contrary, habitat heterogeneity is a pervasive feature of natural landscapes. Then using fixed source trait distributions still makes some sense, just requiring assumptions about the relative contribution of the different kinds of environment. For instance, if the uniform body size distribution is to be accepted as representing the regional pool, then those low productivity and species-rich communities containing only small bodied species must be considered exceptions in a landscape dominated by high productivity sites containing a large variety of species body size. Differences in dispersal capacities could also help larger species to be better represented in the immigrant pool (ETIENNE & OLFF, 2004).

Depending on such relative contributions of environment kinds in a landscape mosaic, the differential responses of traits along the gradients we modeled could support a rich diversity of species. Disturbances, such as prolonged droughts, could reset highly productive communities to states invasible by alternative species, overcoming the restrictions for coexistence imposed by priority effects. This mechanism of turnover would depend on the availability of nearby dispersers and stochastically determined colonization success, or alternatively on a colonization-competition tradeoff (CALCAGNO *et al.*, 2006). In a metacommunity context, dispersal limitation can play a significant role (HOLYOAK *et al.*, 2005). Together with habitat heterogeneity, it modulates the capacity of a species pool to adjust local composition to environmental changes, like a complex adaptive system (LEVIN, 1998; LEIBOLD *et al.*, 2005). Mass effects of dispersal can contribute to increase even the local diversity levels by maintaining sink populations (DIAS, 1996; HOLYOAK *et al.*, 2005). It will be interesting to extend the present model to explicitly simulate networks of connected habitat patches, and evaluate how dispersal rates could influence the distribution of species traits along spatially structured gradients, the adaptive capacity of communities to adjust to local conditions, and the overall metacommunity diversity. Dispersal heterogeneities among species can also produce emergent scenarios not predicted by non-spatial models. For instance, allometrically determined dispersal rates can generate unimodal body size distributions, even if local conditions favor smaller species (ETIENNE & OLFF, 2004). Furthermore, additional gradients still not considered here, like seasonality, disturbance regimes or habitat predictability could greatly enhance the variety of species strategies (WINEMILLER & ROSE, 1992; MIMS et al., 2010), contributing to increase at least the potential regional diversity.

This view of a landscape mosaic connected by dispersal is necessary in order to consider that the model system is able to support diversity levels similar to those observed naturally. In terms of isolated local coexistence it is not so suitable, as in most simulated communities the richness was reasonably low (the median number of successful species was only 2). Maybe the low dimensional feature of trophic interactions, based almost entirely on body size, together with ontogeny was responsible for restricting coexistence. Ontogenetic diet shifts can enhance resource partitioning among individuals of a size structured population, thus alleviating intraspecific competition. On the other hand, it can exasperate interspecific competition, as the young of all species must eat nearly the same small-sized resources. These two phenomena are the basic ingredients for decreasing the chances of coexistence (CHESSON, 2000). But additional niche dimensions, representing implicit

morphological, physiological and behavioral features, could be included in the future to define resource eligibilities and produce more diverse assemblages. Although body size is generally recognized as the major axis determining trophic interactions (WILLIAMS & MARTINEZ, 2000; WOODWARD *ET AL.*, 2005; PETCHEY *et al.*, 2008), recent analyses have pointed to a great contribution of additional dimensions to food web structuring (ROHR *et al.*, 2010).

In some manner, many implicit aspects of predation and niche partitioning are already encapsulated in attack rate values. Randomly attributed values among species can be interpreted as an indefinitely high number of dimensions (other than body size) defining resource preferences. Nevertheless, the body size is still the main factor in the model, as it alone defines eligibility (unless a given attack rate is equal to zero, which is a very improbable outcome). Alternatively, attack rates could be some explicit function of a limited number of species attributes. These can be traits already in the model or auxiliary abstract traits included just to serve this proposal. In this case, the match between traits of consumer and resource could determine how strong the attack rate and interaction between them should be, an approach similar to that used in the Webworld model (CALDARELLI *ET AL.*, 1998; DROSSELL *et al.*, 2001). Another possibility is to adaptively change attack rates, according to resource availability or some other measure of quality, which can further increase stability and coexistence (KONDOH, 2003). Such changes can be behavioral, at fast time scales, or evolutionary, from parent to offspring. In its current state, the model does not account for differences in resource quality. But differences can be included, especially concerning assimilation efficiencies, which could greatly enhance model realism. Adaptive changes can be applied to life-history as well. For instance, the coefficients of ingestion and loss function, and consequently the growth rate, can be made a behavioral function of resource availability, individual condition and/or predation risk. It is known that organisms like fish tend to diminish both ingestion rate and metabolism when they face food scarcity (WEATHERLEY & GILL, 1987; JOBLING, 1992). Many individuals of diverse taxa are also capable to become less active and grow slower when in the presence of potential predators (LIMA & DILL, 1990; LIMA, 1998; PEACOR & WERNER, 2004).

We showed that consumption ordering hierarchy and its inner tradeoffs can increase coexistence where it tends to be more difficult (in the case of highly productive sites). Besides influencing local diversity, it has large consequences for community composition along gradients. Without giving any advantage to specialized species, the assembly selection always favors increasing generalization. As we give some advantage to specialists, putting them first

in the consumption sequence, both strategies emerge along the gradients: increasing generalization when resource availability is too low, and increasing specialization at higher availabilities. Specialization was directed towards smaller resources, which represent the most abundant source of food. Examples which could fit this situation are medium sized fishes eating fine detritus, small invertebrates, eggs or plankton. The absence of piscivorous specialized at relatively large prey has probably to do with high priority effects. At the beginning of assembly process, early dominating species grew in an environment with abundant basal resources but still a scarce stock of fish prey. Maybe it would be possible for piscivores specialized in large prey to thrive if we introduce them on already assembled communities using large propagule numbers and suitable values for other parameters, but it would also depend on whether productivity and attack rates are high enough. Another parameter directly involved on consumption ordering, the growth rate ζ, was affected in a somewhat more subtle way. When consumption ordering was either present or absent we observed a similar pattern of increase of mean growth rate as we increased resource availability. But the plateau values obtained with consumption ordering were visibly lower, for the same values of productivity and attack rates. The first pattern clearly depends on another tradeoff included in this model, concerning growth and metabolism: faster growing species have higher metabolic demands. Without this tradeoff, probably no trend in growth rate would be observed, as fast growth and low metabolic demands would always be advantageous together. The second pattern results from the tradeoff between foraging gain and predation risk inherent to consumption ordering process. Probably the predation exerted early in community construction prevented the supremacy of very fast growing species at the presence of consumption ordering. As the species do not have such high growth rates, the first drastic resource depletion event takes a little longer to occur, and consequently the priority effects tend to be lower with consumption ordering. The cannibalism was shown to be a beneficial feature for species involved in communities with consumption ordering, but only as the last option, when prey of no other species is available. Finally, the egg size is a good example of an indirectly affected trait. The preponderance of larger eggs only when the ordering is present demonstrates that predation is an important driving force shaping species composition in the modeled communities.

Despite the conceptual importance of establishing a hierarchy of competition and predation vulnerability based on individual features, and now its confirmed influence on species composition and distribution along gradients, virtually no individual-based model of community dynamics that we were aware of before the early version of this model

(GIACOMINI *et al.,* 2009) has used such a procedure (e.g. MCCAULEY *ET AL.*, 1993; ROSE *ET AL.*, 1999; SHIN & CURY, 2001; MAMEDOV & UDALOV, 2002; PARROTT & KOK, 2002; VAN NES *ET AL.*, 2002; HUSE *ET AL.*, 2004; ARIM *et al.,* 2010). In general, modeled predation sequences are purely random. But random ordering assumes that species traits have no influence on predation events when competition takes place. Whenever competition is asymmetrical, it is the order in which individuals are sorted within a model that determines who shall eat more and who shall eat no food at all. Our rules to establish individual hierarchies were based on two simple tradeoffs concerning diet generality versus predation efficiency and foraging intensity versus defense against predators. But many other and more complex rules are possible. Whatever the rule, individual-based modeling can make it possible to infer which emergent patterns we can expect from it in a dynamical perspective, and to test the appropriateness of alternative mechanisms, as long as empirical data is available.

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3. CAPÍTULO 2

Deleting and introducing species in individual-based modeled fish assemblages

3.1. Introduction

Biodiversity loss due to human induced disturbances is a longstanding and well recognized phenomenon (PIMM *ET AL.*, 1995; MCKINNEY & LOCKWOOD, 1999; PIMM *ET AL.*, 2001). So are the myriad consequences for ecosystem functioning and services (CHAPIN *ET AL*, 2000; DE MARCO, JR. & COELHO, 2004; WOODWARD, 2009). There is already a reasonable body of knowledge about relative vulnerability of systems and species to direct human impacts, like overexploitation or habitat destruction. Some of the most notorious examples are large bodied species, more easily depleted or extinguished due to higher resource requirements and lower population return times, besides having larger appeal for poaching or fishing (PIMM *ET AL.*, 1988; MYERS & WORM, 2003; GALETTI *ET AL.*, 2009). Among communities, those more isolated like oceanic islands and some freshwater environments stand as the most endangered due to their unique sets of species with very restricted distribution (BROWN & LOMOLINO, 1998; NOGUEIRA *ET AL.*, 2010). But to properly understand the implications of changing diversity, we need a theory capable to predict the several secondary consequences of primary species loss, although our current knowledge in this area is still overly coarse (DUNNE & WILLIAMS, 2009). It is necessary an accurate appreciation of how interlinked species are to each other, and how the many indirect effects spread out within each community (STRAUSS, 1991; MONTOYA *ET AL.*, 2006). The great complexity of ecological networks, like food webs, brings high uncertainty concerning the fate of their components, especially because nonlinear dynamics is generally involved (MAY & OSTER, 1976; YODZIS, 1988; YODZIS, 2000).

The same complexity issues make it pretty hard to predict another widespread impact: the establishment of introduced species and its effects upon native communities (LODGE, 1993; MOYLE & LIGHT, 1996; ENSERINK, 1999). Different from the species loss case, predicting invasion success is even more difficult because in many instances we are dealing with species which have never been in contact before. Available data still do not allow for broad generalizations across taxa and geographic domains, except for a few rules concerning mainly propagule pressure, human affiliation or prior invasion success (JESCHKE & STRAYER, 2006; LOCKWOOD *ET AL.*, 2009). Although having practical importance to risk assessment and management, these rules do not inform much about the inner ecological process (e.g. species interactions) determining invasion success and impacts. But more ecological rules are emerging as proper data are catalogued and analyses on species traits bring new insights (KOLAR & LODGE, 2001; KOLAR & LODGE, 2002). For instance,

phylogenetic relatedness of exotic species with residents has been show to negatively affect invasiveness (STRAUSS *ET AL.*, 2006). It emphasizes that studying the match between features of invader and resident community may be a better approach than simply trying to seek for general predictors of either one, and is an explanation for the occurrence of heterogeneous effects of the same invader over different communities. As closely related species tend to have more similar characteristics, this kind of pattern alludes to classical theory of competition and limiting similarity (MACARTHUR & LEVINS, 1967; ABRAMS, 1983), and reinforces community ecology as a promising framework to study general process underlying invasions (SHEA & CHESSON, 2002). On the other hand, each environment has a set of particular constraints which can prevent the establishment of too different species. This is stressed by the fact that some studies have shown that successful fish invaders tend to have their native range closer to invaded watersheds or a suit of traits similar to species of invaded community (MARCHETTI *ET AL.*, 2004a; RIBEIRO *ET AL.*, 2008).

Although empirical data are the ultimate test for any proposed rule or theory, current data are still limited. Given the highly variable nature of ecosystems, the question of how species features determine their relative influence over cascading effects or their chance of invasion success demands a large number of community replicates. Experimentally extinguishing or introducing species in natural places and following dynamics at relevant temporal scales is generally unfeasible or unethical. Besides, available data on invasions is highly biased as most failed introductions are not perceived or reported, precluding statistical comparisons to find good predictors of invasion success (KOLAR & LODGE 2001), with a few exceptions (KOLAR & LODGE, 2002; MARCHETTI *ET AL.*, 2004a; 2004b; RUESINK, 2005; RIBEIRO *et al.*, 2008). Modeling is then a suitable alternative to address this sort of questions (PARKER *ET AL.*, 1999; ENSERINK, 1999; EBENMAN & JONSSON, 2005).

Amongst models investigating cascading effect of extinctions, the simplest ones rely purely on network properties of large empirical food webs (SOLE & MONTOYA, 2001; DUNNE *ET AL.*, 2002b). They revealed strong dependence of food web robustness on features like network connectance and link degree of deleted species (SOLE & MONTOYA, 2001; DUNNE *ET AL.*, 2002b). But as they did not model dynamics explicitly, they had to assume that species go extinct only after losing all prey. Consequently, excluding top predators would have never any effect. We know this is not true, both theoretically (LEVIN, 1970; ABRAMS, 1999) and empirically (PAINE, 1966). Explicit dynamical models had brought several insights on the consequences of primary extinctions. Former models were essentially based on Lotka-Volterra systems (PIMM, 1979; 1980; BORRVALL ET AL.,

2000; EBENMAN ET AL., 2004). Although not suffering from the problems of purely network analysis above, they were restricted to very simple and arbitrarily defined food web structures. But more recent approaches are intermediately located in this spectrum of topological realism. Instead of using empirical structures as templates, they rely on recently developed structural models (CATTIN *ET AL.*, 2004; WILLIAMS & MARTINEZ, 2008) or evolutionary assembly (CALDARELLI *et al.*, 1998) to generate large food webs which closely match some basic empirical properties, allowing for more general predictions concerning trophic roles of species and community fragility over wider range of richness and complexity (DUNNE & WILLIAMS, 2009).

There are also several models for invasions, generally requiring explicit dynamics (POST & PIMM, 1983; CASE, 1990; CASE, 1991; MOYLE & LIGHT, 1996; HEWITT & HUXEL, 2002). Invasion success and/or effects have been tested against community maturity (POST & PIMM, 1983), level of self organization (GILPIN, 1994), species richness (POST & PIMM, 1983; CASE, 1990), interaction strengths (CASE, 1990; KOKKORIS *ET AL.*, 1999), and propagule pressure (LOCKWOOD *ET AL.*, 1997; HEWITT & HUXEL, 2002). Most are based on Lotka-Volterra dynamics, restricting the analyzed variables mainly to gross or highly abstract community parameters, like richness, connectance or interaction coefficients. The work of Romanuk *et al*. (2009) is a first attempt to include individual species features to test for invasion success in a dynamical model. Using the structural niche model (WILLIAMS & MARTINEZ, 2000) to generate resident food webs and applying a nonlinear bioenergetic model for dynamics (BROSE *et al.*, 2005), they showed that both fundamental and realized features of species can increase their chances of establishment. The first comprise parameters of niche model, which determine species potential for interactions, not depending on the match with invaded community. One example of successful fundamental strategy is of species eating low in trophic niche axis while being relatively invulnerable to predation (ROMANUK *ET AL.*, 2009). This niche axis can be thought as an abstraction of major bionomic features like body size which together are assumed to determine feeding links in food webs (WILLIAMS & MARTINEZ, 2000). On the other hand, successful realized features depend on the matching pattern of invader with resident species, including high generality, herbivory or omnivory (ROMANUK *ET AL.*, 2009).

In this study, an individual-based model (IBM) was used to generate experimental communities. IBMs simulate individuals explicitly, allowing more refined biological features to be modeled in the same dynamical framework (UCHMANSKI & GRIMM, 1996; DEANGELIS & MOOIJ, 2005). These features need not be restricted to trophic ecology as in

previous models cited above, but may also include many life history traits, so important to population dynamics, species selection, coexistence and invasiveness (STEARNS, 1992; SAKAI *ET AL.*, 2001; CHESSON, 2003). There is increasing awareness about the importance of a trait based approach to ecology (MCGILL *ET AL.*, 2006; MESSIER *ET AL.*, 2010). Accordingly, we need models capable to address species parameters more easily measurable in nature, and this is one of the major advantages of IBMs (HUSTON *ET AL.*, 1988; JUDSON, 1994). Our model was designed for dynamics of fish assemblages (GIACOMINI *et al.*, 2009). Fishes are the most diverse vertebrate group (NELSON 2006), presenting a wide range of reproductive and feeding strategies (WINEMILLER & ROSE, 1992; GERKING, 1994; MIMS *et al.*, 2010). They are also matter of large concern for biological invasions and species endangerment (CASAL, 2006), which makes them good model organisms to test for trait based invasion and extinction rules. Included in the model are key characteristics like maximum body size, size at maturation, egg size, growth rate, and a continuum of spawning schedules. Growth and reproduction are integrated by means of recently proposed biphasic growth model (QUINCE *et al.*, 2008), and trophic interactions are size structured (EBENMAN & PERSSON, 1988; CLAESSEN *et al.*, 2002). Biological rates and times like metabolism, ingestion, longevity and resources' intrinsic growth rates are alometric functions of size, following the basic tenets of metabolic ecology (BROWN, 2004; SAVAGE *et al.*, 2004). All rules imposed to individuals were constrained by tradeoffs, so that no given strategy could do better in all kinds of environments. Indeed, the previous assembly experiments used to create the communities here studied produced consistent trends for most bionomic traits along gradients of productivity and predator attack rates (Chapter 1, see Methods below). Although allowing variability along several gradients, the model is not spatially explicit, dealing only with local community dynamics. It means that, among the series of steps an introduced species must pass since the transportation to spreading across the new landscape (SAKAI ET AL., 2001; LOCKWOOD et al., 2007), the model is restricted to the establishment phase and impacts on local community only. Also the model was not designed to deal with metapopulation or metacomunity dynamics explicitly, which means that dispersal effects on population persistence or extinction are not accounted for.

Taking advantage of the large number of biological variables included in the model, the present study confronts three major trait classifications generally used by the literature: (i) community *versus* species traits (CASE, 1990); (ii) fundamental *versus* realized traits (ROMANUK *et al.*, 2009); and (iii) individualistic traits *versus* traits depending on the match between the species and local community (STRAUSS *et al.*, 2006). Although one or another

classification appears recurrently in ecological studies, we still do not have knowledge of any published paper dealing with all these three classification schemes in the same analysis. By means of computer simulation experiments of species introductions and deletions, the present study evaluates how invasion (establishment) success and native extinction are related to dozens of biological variables and if any hierarchy concerning the relative influences of such variables can be imposed to the categories above.

3.2. Methods

Below is a brief description of the components characterizing studied communities and dynamics relevant to the interpretation of Results. The individual-based model and the procedures to generate the communities are detailed in the Appendix and Chapter 1 respectively.

3.2.1. Study communities

3.2.1.1. Environment

The environment is only implicit, represented by a hundred basal resources, which are primarily distinguished by their size ranges (length, cm). The smallest resource has a minimum size of 0.01cm, and the largest, a maximum size of 10cm. The size limits of resources are contiguous, meaning that the maximum size of one given resource coincides with the minimum size of the next larger resource. They are uniformly distributed in a logarithm scale of size, so that the size boundaries increase exponentially from the smallest to the largest resource. Each resource grows in biomass according to the discrete logistic model (GOTELLI, 1998), whose intrinsic growth rate has a negative alometric relation with resource's geometric mean size, following a power function with exponent -0.25 (FENCHEL, 1974; SAVAGE *et al.,* 2004), so that smaller resources grow faster, but less than in a proportional manner. All resources of a given community have the same mean carrying capacity μ_K, although the carrying capacity itself varies seasonally between the limits $0.7\mu_K$ (at peak winter) and $1.3\mu_K$ (at peak summer). The above rules make that the overall resource biomass and growth rate are more concentrated lower in the size spectrum (i.e. fishes eating smaller resources have a more abundant food supply).

3.2.1.2. Fishes

Fishes (females only) are modeled explicitly. The basic fish entity is the super-individual, which is analogous to a fish school cohort (SHIN & CURY, 2001; GIACOMINI *ET AL.*, 2009). Each super-individual is created as the collective offspring from a spawning event of a given fish species at a given time step (week), and is composed by identical

individual components, whose number is the same as the number of eggs produced in that spawning event. The life cycle is characterized by three stages: (i) egg/embryo, when the fish eats exclusively on yolk, (ii) juvenile, from which the fish needs to feed on external resources (potentially including other fishes) but still do not reproduce, and (ii) adult, when the fish is able to reproduce, investing an increasing proportion of time to egg production instead of just growing, according to the biphasic growth model of Quince *et al*. (2008). Fish body is divided in three components: (i) reversible or storage mass; (ii) irreversible or structural mass; (iii) gonads (in adults only). The fish length is entirely determined by irreversible mass according to a fixed weight-length relationship, following a power function ( ).

Direct interactions of individuals with each other and with basal resources are restricted to predation. The eligibility of food items is determined by size relations: each fish is able to feed only on prey (basal resources or other fishes) whose size lies within given maximum and minimum limits (the predation window) (CLAESSEN *et al*. 2002). Such limits are assumed as fixed proportions of consumer's own body length. For instance, if a fish is 10cm long, and if its predation window is determined by the minimum proportion of 0.01 and a maximum proportion of 0.5, it will be able to feed only on food items whose size is not smaller than 0.1cm or larger than 5cm. These proportions are species specific parameters, making it possible to create relevant interspecific differences in trophic strategies. Additionally, species preferences for each resource kind (including fishes as prey) are quantitatively tuned by attack rates, embedded in a type III multispecies functional response (Koen-Alonso 2007). The functional response defines how much of each available resource a given fish predator is able to consume. The attack rate defines how fast consumption increases with increasing resource levels. So it is a measure of predatory capacity, or conversely, of the lack of prey refugees (as small is the attack rate, more refugees will be available for prey).

When competing for food, fishes with higher growth rates and relatively narrower predation window (more specialized) have advantage. On the other hand, the same higher growth rates make them more vulnerable to predation among a list of eligible prey. The model assumes that fast growth is associated to high activity levels (e.g. foraging), and that this implicit activity mediates a tradeoff between foraging gain and mortality risk (LIMA & DILL, 1990; WERNER & ANHOLT, 1993; ABRAMS, 2003), which is a factor with important implications for life history selection (DAY *et al.*, 2002) and structuring of aquatic communities (WELLBORN *et al*., 1996). Species can also be cannibal in different degrees, depending on how they prefer fish prey of other species as compared to co-specifics, and vary in their level of piscivory, which is a measure of preference for fish prey as compared to other

resource kinds (basal resources). Mortality occurs by three ways: (i) predation; (ii) starvation; (iii) exceeding species specific longevity. A fish starves and dies whenever its storage mass is not enough to supply metabolic demands in excess of ingested energy.

Modeled fish reproduces by means of direct mass allocation from gonads to offspring (newly created super-individuals). Fecundity is highly dependent on circumstances, as it varies according to fish size, the amount of mass production devoted to gonads (which is dependent on growth parameters and food availability), and egg size. Each species has a characteristic reproductive timing, which determine the position of the reproductive period along a year. Within a reproductive period, the fish can distribute spawning equally throughout time or concentrate it in a few or just a unique event. It will depend on its species' uniformity of spawning parameter. Together, the reproductive timing and the uniformity parameter defines a wide range of spawning schedules characterizing fish reproduction.

3.2.1.3. Community assembly

The communities were formed by sequentially introducing species, adapting the protocol proposed by Giacomini *et al*. (2009). They started having only basal resources at their mean carrying capacity. Then three propagules, each of different species, were introduced each week during fifty years. Each introduced species was created by a Monte Carlo sampling approach, in which the values of biological parameters were drawn randomly and independently from fixed and continuous probability distributions. We assumed a primordial species pool with uniform distributions for all parameters, except for the maximum body size, which had a negative power law distribution. Thereafter, the dynamics proceeded without new introductions for fifty years more. A total of 1440 communities were generated this way, following a factorial design with varying resource's mean carrying capacity (four values), maximum attack rates (four values), skewness of body size distribution of primordial species pool (three values), and thirty community replicates for each factor combination. The resource carrying capacity is here assumed as a measure of system productivity. The maximum attack rate determines implicitly the amount of prey refuge: as large is the maximum attack rate, less refuge will be available in the modeled environment. The skewness of body size distribution is a factor of regional influence. It is determined by the exponent of a power function: as large (less negative) is the exponent, the more uniform will be the distribution from which potential colonizers come, and the larger will be the mean body size. Table 1 provides a complete list and description of relevant parameters.

At the end of these community assembly experiments, the total number of persisting species was 7804. Local species richness varied from zero (only basal resources present) to 79

fish species, with mean 5.42 and median 2. The richest communities were those with the lowest resource carrying capacity, the lowest attack rates and the most skewed body size distribution of primordial species pool (the distribution with largest frequency of smaller sizes) (see Chapter 1). Sites with highest productivity and attack rates were subjected to strong priority effects (earlier colonists tended to dominate the assemblage fast and preventing the establishment of later arrivers), which is hypothesized as the cause for their much lower richness (Chapter 1). There was a strong trend of species features along gradients: at lower productivities and lower maximum attack rates, selection favored species with smaller sizes, earlier maturation, slower growth, lower piscivory, and the potential for more generalized diet (i.e. relatively larger predation window). The proportion of cannibals was also relatively smaller, although the large proportion of cannibals attained at high productivities and attack rates was composed mainly by species with quantitatively low levels of cannibalism. Egg size was unresponsive to selection at low productivities and attack rates, but productive communities presented a tendency for larger eggs. Species of less productive sites exhibited a little tendency for more distributed spawning along year (larger uniformity parameter), and for reproductive period finishing at late autumn. The effect of regional body size distribution was mainly diminishing overall richness and producing communities with larger mean body size at more uniform size distribution of primordial species pool. In the final assembled communities, fishes were mostly primary consumers, as the contribution of piscivory to realized overall biomass fluxes was very small.

3.2.2. Invasion and deletion experiments

Each assembled community was subjected to both deletion and invasion experiments, which occurred alone or together. In an invasion experiment, a randomly selected species from the total assembled pool (7804 species) was introduced each week during ten years (the same species). Propagule pressure was modeled with a Poisson distribution, which determined the number of introduced individuals in each week. Two values were used for mean propagule number: 1 or 5 individuals/week. Each introduced individual was at the beginning of adult life, with maximal body condition (ratio between storage and structural masses = 0.1). After the initial ten years, introductions ceased and dynamics proceeded for forty years more.

In a deletion experiment, a randomly chosen species was completely excluded from the assemblage, and dynamics was simulated for fifty years. In order to evaluate the

synergistic effect of deletions and introductions, we also simulated them together, combining the same recipe outlined above for each one. Control simulations were done without any intentional deletion or introduction, in order to provide a baseline for comparison. So we had a factorial experimental design with two explanatory variables: (i) species introduction (INTROD), with three values (none, one propagule/week, and five propagules/week); and (ii) species deletion (DEL), with two values (none or one species deleted); giving six combinations. As all combinations were simulated for all 1440 communities, we had a total of 8640 simulations. The simulations were carried out in Matlab platform.

In the terminology we use hereby, a **resident community** is the community where introduction and deletion occurs; a **source community** is the community from where the introduced species come; and a **native or resident species** is a species original to the resident community. Species pool is of two kinds: (i) the **primordial species pool** represents the infinite pool composed by continuous distributions of bionomic parameters previously used to create species and assemble communities; (ii) **assembled species pool**, which we will refer thereafter as simply 'species pool', is the total collection of species which survived throughout the assembly process and constitute the resident communities used for invasion and deletion experiments.

3.2.3. Analysis

The dependent variables are invasion success (0 if introduced species is not able to persist until the end of simulation time, 1 otherwise), and occurrence of native species extinction. In the first case, a 50 years simulation of a community is the sampling unit, while in the second the unit is a species in a simulation, which can be either extinct (1) or not (0). As the dependent variables are binary, we used logistic regressions as statistical models for analysis.

We tested the influence of 35 variables on the invasion and extinction chances. They are described in Table 1. Two of them, DEL and INTROD, are the experimental perturbation (P) variables. The remaining variables can be classified according to three criteria:

(i) Firstly, a variable may be a community (C) or a species (S) feature. The species in this case are either deleted or introduced species. The community features are measures of environmental properties or community state, setting the conditions experienced by deleted/introduced species just prior to each simulation experiment. Examples are: mean resource carrying capacity, species richness, and community saturation.

(ii) Secondly, a variable may refer to a fundamental (F) or a realized (R) feature. Fundamental features are the model parameters, which does not change along a simulation and ultimately determine the dynamical behavior of modeled entities (i.e. individual fishes and basal resources). Realized features are emergent state variables measured at some point or period of time. They are comprised mainly by metrics of trophic structure: link density of resident community (DUNNE *et al.*, 2002a), skewness of distribution of interaction strengths (BERLOW *et al.*, 1999), generality and vulnerability (BERSIER *et al.*, 2002), proportion of fish in diet, among others (Table 1). The basic data to calculate all metrics of trophic structure is a food web matrix containing the biomass fluxes from prey (fish species and basal resources) to predators (fish species). Each biomass flux was calculated cumulatively throughout the last (100^{th}) year of simulation during the assembly phase of community (Chapter 1), just prior the start of invasion/deletion experiments.

(iii) Thirdly, a variable may be an individualistic feature (I) or it may depend on the match (M) between focal species (deleted or introduced) and resident community traits (i.e. distance or overlap indexes). Species matching traits measure the distance (standardized Euclidean distance concerning species fundamental traits) or diet overlap (using Pianka's index) between introduced or deleted species and resident community species. Community matching traits measure the absolute difference between features of resident and source community.

To assess the relative importance of these different kinds of explanatory variables in statistical models, we adopted an *a priori* model selection approach (MARCHETTI *et al.*, 2004a). It consists in previously defining the combinations of explanatory variables used to predict a given dependent variable, and deciding what have the best fit to available data. In our case, the variable categories above entirely define these combinations. For instance, the maximum fish size (X_{inf}), is a species-specific (S), individualistic (I), and fundamental (F) feature, so it enters in models S (a model containing every and only species-specific features), I (with individualistic features only), F, SI (a model with features that are both species-specific and individualistic), SF, IF, SIF, the global model (the model containing all possible variables), and finally a model with only X_{inf}. In other words, a given variable is included in a model if it has at least one category in common with that model. The perturbation variables DEL and INTROD are of special kind and were included in all models, whenever possible.

Models were compared by means of an information theoretic approach, using Akaike Information Criteria (AIC) (BURNHAM & ANDERSON, 2004; MARCHETTI *ET AL.*,

2004a). Better models have lower AIC values (BURNHAM & ANDERSON, 2004). For each question investigated, we present the AIC values along with respective Akaike weights, which sum to one along all models and give their relative likelihood of being the best model to explain analyzed data (WAGENMAKERS & FARRELL, 2004). The analysis of invasion success comprised 58 candidate models, the same number as that for influences of invasions on extinction chances. The effects of species deletion on extinction chances had fewer models (42), as there was no community-matching (CM) variable (which require the existence of a 'source' community, a situation applicable only to invasion instances). So all models with CM combination were not represented in this case, and consequently all models with CI combination had to be excluded (as they coincide with purely C models).

The relative importance of each explanatory variable can be assessed by summing the Akaike weights of all models containing the variable (WAGENMAKERS & FARRELL, 2004; MARCHETTI *ET AL.*, 2004a). It has the advantage of overcoming eventual multicolinearity problems, as the Akaike weights depends only on the overall model fit, which is not affected by correlations among explanatory variables (GRAHAM, 2003). Nevertheless, due to the overwhelm importance of global models, this procedure was not so useful to distinguish among variables. Then we had to use the traditional approach of comparing regression coefficients and significance levels to assess variable importance. In this situation, colinearity is a indeed an issue as it tends to inflate variance estimation, decreasing power and sometimes promoting sign reversals between coefficients of correlated variables (GRAHAM, 2003). As a solution, we used a Principal Components Regression approach (FEKEDULEGN et al., 2002). It consists in replacing original explanatory variables with the factors generated from a Principal Component Analysis (PCA) among them. These factors are linear combinations of original variables, and are orthogonal, which means that colinearity is completely eliminated. The coefficients giving the effects of original variables are back calculated by multiplying a matrix containing the PCA eigenvectors by the vector containing the regression coefficients of PCA factors (FEKEDULEGN et al., 2002).

In the analysis on invasion success, simulations with INTROD = 0 were ignored, as the result would be trivial in this case. We did the same to test for the influences of invader characteristics on extinction chances, as invader characteristics are not defined when there is no introduced species at all. Conversely, to test for the influences of deleted species characteristics, we excluded data with DEL = 0, and consequently this perturbation variable was not included in any model. The results of control simulations (DEL = 0 and INTROD = 0) were used in a separate analysis to test exclusively for the effects of perturbation variables

and their interaction on extinction chances. Another analysis with control simulations, using Principal Components (logistic) Regression, was carried out to assess the intrinsic influences of individualistic community variables (i.e. not depending on species deletion or introduction) on extinction chances.

The logistic regressions and AIC calculation were done in R platform. To adjust for overdispersion, scaled deviance was set to 1 in all analyses.

Table 1. List of explanatory variables. There are three major criteria for classifying variables: (i) whether they refer to community (C) or species (S) features; (ii) whether they refer to fundamental (F) or realized (R) features; (iii) whether they refer to individualistic features (I) or features depending on the match (M) between invader and resident community. The variables INTROD and DEL are the experimental perturbations (P).

Symbol	**Categories**	**Values**	**Description**
INTROD	P	{0,1,5}	Propagule pressure (mean number of introduced individuals/week).
DEL	P	{0,1}	Occurrence of species deletion.
$\log(\mu_K)$	C,I,F	{3,4,5,6}	Log_{10} of mean carrying capacity of a basal resource (g). It can be interpreted as a measure of system productivity.
$\log(\alpha_{max})$	C,I,F	{-7,-6,-5,-4}	Log_{10} of maximum attack rate allowed by the environment. The attack rate defines predators' capacity to catch prey, or, conversely, the implicit scarceness of prey refugee in the modeled environment.
ξ	C,I,F	{-2,-1,0}	Exponent shaping the power-law distribution of maximum sizes (X_{inf}) in primordial species pool. Larger exponents imply in more uniform size distributions.
S	C,I,R	5.419(9.940)	Resident species richness, just prior the start of invasion/deletion experiments. It is probably the most used variable in studies of invasions and community stability (MAY, 1973; SHEA & CHESSON, 2002; EBENMAN & JONSSON, 2005).
L/S	C,I,R	62.603(18.110)	Link density = total number of realized trophic interactions divided by species richness (VERMAAT *et al.*, 2009).
SK	C,I,R	2.427(1.553)	Skewness of the distribution of interaction strengths. Interaction strengths were measured as predator relative preferences for prey, as in McCann et al. (1998). Each one was calculated by dividing the biomass flux from a given prey to a given predator to the total biomass flux experienced by that predator. It is presumed to increase dynamical stability and coexistence in food webs (MCCANN *et al.*, 1998).
SAT	C,I,R	0.343(0.201)	Community saturation index, calculated as $1 - Btot/(100\ \mu_K)$, where Btot is the sum of resource biomasses in resident community, and $100\ \mu_K$ is the expected total biomass if all 100 basal resources were in their carrying capacity.
%PISCI	C,I,R	2.738(3.114)	Percentage contribution of fish prey to the overall diet of native species in resident community. It is calculated by summing all the biomass fluxes coming from fish and dividing it by the total biomass flux of the entire food web. It is used

			here as a surrogate measure for mean trophic level and for other food web metrics depending on the existence of third or higher trophic level, like mean omnivory and proportion of trophic loops (WILLIAMS & MARTINEZ, 2000; WILLIAMS & MARTINEZ, 2004).
$\Delta\mu_K$	C,M,F	1.337(1.045)	Absolute difference between $\log(\mu_K)$ of resident and source communities.
$\Delta\alpha_{max}$	C,M,F	1.336(1.031)	Absolute difference between $\log(\alpha_{max})$ of resident and source communities.
$\Delta\xi$	C,M,F	0.875(0.731)	Absolute difference between ξ of resident and source communities.
ΔS	C,M,R	21.724(22.054)	Absolute difference between S of resident and source communities.
ΔL/S	C,M,R	18.842(14.503)	Absolute difference between L/S of resident and source communities.
ΔSK	C,M,R	1.677(1.426)	Absolute difference between SK of resident and source communities.
ΔSAT	C,M,R	0.191(0.182)	Absolute difference between SAT of resident and source communities.
Δ%PISCI	C,M,R	2.856(2.937)	Absolute difference between %PISCI of resident and source communities.
Cann	S,I,F	introduced: 0.226(0.253) deleted: 0.154(0.180)	Level of cannibalism of introduced or deleted species.
δ	S,I,F	introduced: 0.028(0.020) deleted: 0.028(0.020)	Coefficient for the lower limit of the predation window of introduced or deleted species.
ε	S,I,F	introduced: 0.326(0.213) deleted: 0.244(0.168)	Coefficient for the upper limit of the predation window of introduced or deleted species.
ζ	S,I,F	introduced: 0.139(0.057) deleted: 0.174(0.047)	Coefficient of the function for potential growth rate of introduced or deleted species.
η	S,I,F	introduced: 0.512(0.275) deleted: 0.489(0.292)	Reproductive timing of introduced or deleted species.
θ	S,I,F	introduced: 0.370(0.199) deleted: 0.418(0.199)	Relative size at maturation = ratio between size at maturation and maximum size (X_{mat}/X_{inf}) of introduced or deleted species.
u	S,I,F	introduced: 0.567(0.271) deleted: 0.560(0.267)	Uniformity of spawning along time of introduced or deleted species.
ϕ	S,I,F	introduced: 0.263(0.229) deleted:	Piscivory level of introduced or deleted species.

		0.298(0.247)	
W_0	S,I,F	introduced: 0.063(0.026) deleted: 0.067(0.024)	Egg size of introduced or deleted species.
X_{inf}	S,I,F	introduced: 120.134(233.269) deleted: 253.617(299.901)	Asymptotic irreversible mass (maximum size) of introduced or deleted species.
MAHA	S,I,F	introduced: 10.945(6.693) deleted: 13.542(8.639)	Mahalanobis distance between a given species (introduced or deleted) and the entire species pool concerning the ten S,I,F variables above. The Mahalanobis distance was used because it takes in account correlations among variables. It is a measure of how peripherically the species is located in bionomic space, as related to other species. Previous empirical work has found that invasive species tend to occupy the periphery of bionomic space when compared to native species (OLDEN *et al.*, 2006).
relB	S,I,R	introduced: 0.184(0.277) deleted: 0.488(0.387)	Relative biomass of deleted or introduced species in original community, just prior the start of deletion/introduction experiment.
G	S,I,R	introduced: 38.584(17.086) deleted: 42.419(20.278)	Generality of a given predator species (introduced or deleted species). As we have quantitative data on biomass fluxes instead of just food web topology, the generality was calculated using a quantitative version based on information theoretic approach (BERSIER *et al.*, 2002). It is the exponential Shannon index of diversity of biomass fluxes going to the predator species: $G = e^{H'}$, where H' is the Shannon index; $H' = -\Sigma p_i(\ln p_i)$, where p_i is the proportion of biomass fluxes due to prey i (a fish species or a basal resource). G can be interpreted as the number of prey kinds a given predator would have if all biomass fluxes were equal, for the same diversity of fluxes H'.
V	S,I,R	introduced: 0.898(1.150) deleted: 1.000(0.502)	Vulnerability of a given prey species (introduced or deleted species). As we have quantitative data on biomass fluxes instead of just food web topology, the vulnerability was calculated using a quantitative version based on information theoretic approach (BERSIER *et al.*, 2002). It is the exponential Shannon index of diversity of biomass fluxes going out from the prey species: $V = e^{H'}$, where H' is the Shannon index; $H' = -\Sigma q_j(\ln q_j)$, where q_j is the proportion of biomass fluxes going to predator j (a fish species). V can be interpreted as the number of predator kinds a given prey would have if all biomass fluxes were equal, for the same diversity of fluxes H'.
%pisci	S,I,R	introduced: 1.878(3.060) deleted: 3.068(3.632)	Percentage contribution of fish prey to the diet of a given fish species (introduced or deleted species).
ED	S,M,F	introduced: 4.687(1.132) deleted: 4.172(1.094)	Weighted average of standardized Euclidean distance between introduced/deleted species and resident community concerning the S,I,F variables above (except MAHA). The distance between each native species and the introduced/deleted was weighted by the native's relative biomass in resident

			community just prior the invasion/deletion experiment.
O	S,M,R	introduced: 0.558(0.199) deleted: 0.500(0.213)	Pianka's index of overlap (PIANKA, 1973) between the diet of introduced species in its source community and the combined diet of native species in the resident community: $O_{jk} = \frac{\sum_i^n p_{ij} p_{ik}}{\sqrt{\sum_i^n p_{ij}^2 \sum_i^n p_{ik}^2}}$ where p_{ij} and p_{ik} are the proportions of the resource i in the diet of species j and resident community k (summing across all native species); n is the number of resources (including fishes as a whole, so n = 101).

3.3. Results

A total of 2670 (46.35%) species introduction attempts were successful. Invasion success was dependent on both propagule pressure (Wald X^2 = 11.139, p = 0.001) and species deletion (Wald = 715.244, p < 0.001), although the last effect was much stronger: while increasing propagule pressure had a rather subtle effect, the occurrence of species deletion before the invasion attempts more than doubled the chance of invader establishment (Figure 1). The effects are additive, as their interaction is not significant (Wald = 0.787, p = 0.375).

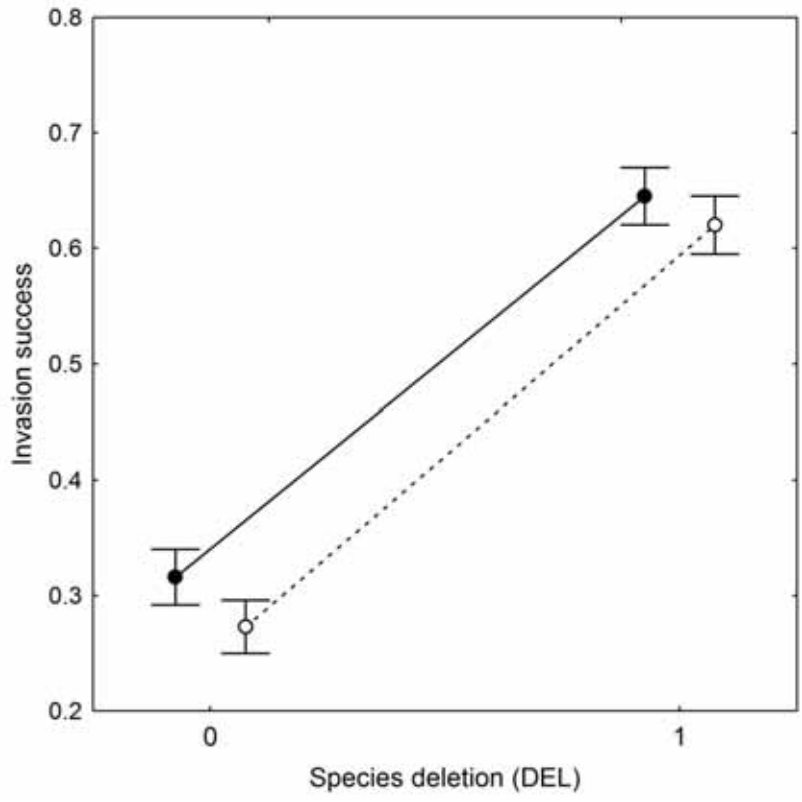


Figure 1. Mean invasion success (and standard errors) versus species deletion occurrence (x-axis) and propagule pressure (INTROD, marker and line patterns). Open circles-dotted line: INTROD = 1 propagule/week; solid circles-continuous line: INTROD = 5 propagules/week.

Among the 58 candidate models to explain invasion success, the global model provided by far the best fit. It is 25 orders of magnitude more probable to be the best model then the second in the list, according to the Akaike weights (Table 2). It means that there is no model comparable to the global, and that all categories of variables have virtually the same importance to determine invasion success in modeled communities.

Table 2. Ten best models for invasion success according to AIC selection. Presented are model names, AIC values and Akaike weights, w(AIC). The names give the combination of kinds of explanatory variables: C = fundamental features, S = species features, I = individual features, M = matching features, F = fundamental features, R = realized features. The global model contains all explanatory variables. The Akaike weights sum to 1 across all 58 models.

Model	***AIC***	***w(AIC)***
Global	6368.4	~1
F model	6480.5	4.548×10^{-25}
C model	6523.4	2.199×10^{-34}
M model	6687.4	5.371×10^{-70}
CM model	6749.2	2.043×10^{-83}
I model	6752.6	3.733×10^{-84}
CF model	6792.7	7.319×10^{-93}
R model	6839.9	4.122×10^{-103}
S model	6856.8	8.816×10^{-107}
CR model	6868	3.260×10^{-109}

A closer inspection of the global model reemphasizes the importance of previous species deletion to invasion success. It was the variable with largest effect and significance (Table 3). Nonetheless, as expected, several others had highly significant effects. In summary, the chance of invader establishment is higher when: (i) a native species is previously extirpated from resident community; (ii) the resident and source communities have similar productivity (μ_K), availability of refugees (α_{max}) and richness (S), but dissimilar link density (L/S); (iii) the resident community is more productive (higher μ_K), have lower availability of refugees (higher α_{max}), lower richness, higher link density, less skewed distribution of interaction strengths (SK), and higher proportion of fish prey in overall biomass fluxes (%PISCI) ; (iv) the introduced and resident species have similar fundamental traits (smaller ED), but small diet overlap (smaller O); (v) the invader is introduced at larger numbers (larger INTROD), have larger body size (X_{inf}), larger eggs (W_0), higher growth rate (ζ), later maturation (θ), more specialized and lower predation window (lower ε), lower piscivory (ϕ) and cannibalism level (Cann), but higher realized contribution of fish prey to the diet

(%pisci), higher dominance in source community (higher relB), and tends occupy a more peripherical position in bionomic space (larger MAHA). In the particular situation of our modeled communities, as after the assembly process many community and species parameters were correlated (see *Community assembly* section above and Chapter 1), the interpretation of this analysis can be further simplified: the invasion success is more probable when species inhabiting more productive communities with higher maximum attack rates are introduced in communities with these same characteristics. Several individual traits of successful invaders are exactly those found more frequently in such environmental conditions (i.e. large body and egg size, late maturation, high growth rate, low predation window and cannibalism level).

Table 3. Effects of explanatory variables in the global model for invasion success. The coefficients and standard errors (SE) were back calculated from a Principal Components Regression (except for DEL and INTROD). The variables are presented in decreasing order of the effect size, according to the test statistic (Wald X^2), and those with significant effects at 5% level are highlighted in bold.

Variables	*Coefficient*	*SE*	*Wald X^2*	*p*
DEL	**1.727**	**0.065**	**715.244**	**<0.001**
$\Delta\mu_K$	**-0.493**	**0.031**	**250.053**	**<0.001**
ΔS	**-0.295**	**0.031**	**88.632**	**<0.001**
log(α_{max})	**0.285**	**0.031**	**84.346**	**<0.001**
S	**-0.285**	**0.031**	**82.262**	**<0.001**
ED	**-0.272**	**0.031**	**76.420**	**<0.001**
W_0	**0.256**	**0.031**	**67.507**	**<0.001**
ε	**-0.235**	**0.031**	**56.483**	**<0.001**
$\Delta\alpha_{max}$	**-0.207**	**0.031**	**44.021**	**<0.001**
log(μ_K)	**0.191**	**0.031**	**37.417**	**<0.001**
ζ	**0.171**	**0.031**	**30.131**	**<0.001**
O	**-0.163**	**0.031**	**27.235**	**<0.001**
L/S	**0.154**	**0.031**	**24.297**	**<0.001**
ΔSK	**-0.150**	**0.031**	**23.139**	**<0.001**
Cann	**-0.147**	**0.031**	**22.205**	**<0.001**
relB	**0.145**	**0.031**	**21.598**	**<0.001**
ϕ	**-0.133**	**0.031**	**18.203**	**<0.001**
θ	**0.113**	**0.031**	**13.145**	**<0.001**
X_{inf}	**0.109**	**0.031**	**12.218**	**<0.001**
INTROD	**0.051**	**0.015**	**11.139**	**0.001**
MAHA	**0.091**	**0.031**	**8.441**	**0.004**
%PISCI	**0.088**	**0.031**	**8.042**	**0.005**
ΔL/S	**0.087**	**0.031**	**7.789**	**0.005**
%pisci	**0.077**	**0.031**	**6.030**	**0.014**
Δ%PISC	0.051	0.031	2.692	0.101
SK	-0.043	0.031	1.958	0.162
Δξ	0.040	0.031	1.629	0.202

ξ	-0.038	0.031	1.511	0.219
δ	-0.037	0.031	1.387	0.239
η	0.031	0.032	0.932	0.334
ΔSAT	-0.030	0.031	0.929	0.335
G	-0.028	0.031	0.806	0.369
SAT	0.023	0.031	0.549	0.459
V	-0.019	0.031	0.373	0.541
u	-0.005	0.031	0.021	0.885

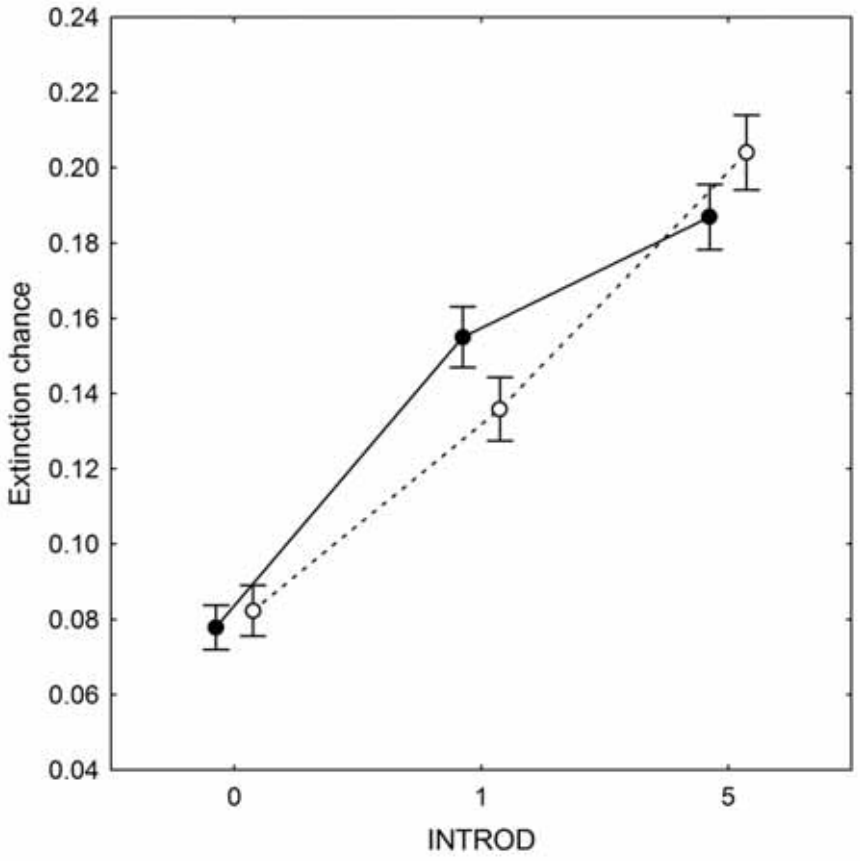


Figure 2. Mean extinction chance (and standard errors) versus propagule pressure (x-axis) and occurrence of species deletion (DEL, marker and line patterns). Open circles-dotted line: DEL = 1; solid circles-continuous line: DEL = 0.

From the total 42507 native species simulations, 5965 resulted in extinction. So the mean chance of extinction of a species in a 50 years simulation is 14%. Considering the analysis with perturbation variables only, the extinction chance of native species was strongly affected by propagule pressure (Wald $X^2 = 283.410$, $p < 0.001$), but not by species deletion (Wald $X^2 = 3.346$, $p = 0.067$). Their interaction was significant (Wald $X^2 = 7.061$, $p = 0.008$) (Figure 2). Although there is a little tendency for species deletion to increase extinction chance at extreme values of propagule pressure, the tendency is inverted at the intermediate value (INTROD = 1). Due to its significance, the interaction term was included in all models

for the effects of invasion on extinction chances. Invasion success increased considerably the extinction chance (Wald $X^2 = 352.637$, $p < 0.001$), from a mean of 14% to 23%.

The invasion effect on native extinctions was also best explained by the global model, which in this case is 15 orders of magnitude better than the second model (Table 4). Some characteristics are common to those allowing successful invasions (Table 5): (i) large invader body size (X_{inf}); (ii) large dominance in source community (relB); (iii) high growth rate (ζ); (iv) late maturation (θ); (v) large eggs (W_0); (vi) lower cannibalism; (vii) occupying the periphery of bionomic space (large MAHA); (viii) susceptible communities have productivity, richness and skewness of interaction strength distribution similar to source communities (low $\Delta\mu_K$, ΔS and ΔSK), but dissimilar link density (high $\Delta L/S$). But there are some important differences concerning the relative importance of variables and their effects when compared to invasion success (Table 5): (i) the invader's diet generality (G) has the most pronounced and positive effect on extinction; (ii) both the upper (ε) and the lower (δ) limits of predation window have also positive effects, which means that diet generality of harmful invaders is acquired by high diet turnover along ontogeny (i.e. fish tends to include larger resources and to loose smaller resources from diet fast along growth); (iii) piscivory level has now a positive effect; (iv) traits determining spawning schedule appears as important determinants, so that more harmful invaders have low uniformity of spawning, and reproductive year ending (last spawning event) near late spring or peak summer (low η); (v) harmful invaders are bionomically distinct from native species (high ED); (vi) opposite to the invasion success case, communities most susceptible to extinctions are the richest and the least productive; (vii) communities formed from primordial species pools with more skewed body size distribution are also more susceptible (negative effect of ξ), especially when receiving propagules from communities whose primordial pool has a less skewed distribution (positive effect of $\Delta\xi$).

Table 4. Ten best models for the effects of introduced species on native extinction chance, according to AIC selection. Presented are model names, AIC values and Akaike weights, w(AIC). The names give the combination of kinds of explanatory variables: C = fundamental features, S = species features, I = individual features, M = matching features, F = fundamental features, R = realized features. The global model contains all explanatory variables. The Akaike weights sum to 1 across all 58 models.

Model	***AIC***	***w(AIC)***
Global	22775	~1
I model	22843	1.714×10^{-15}
SI model	23035	3.481×10^{-57}
S model	23037	1.281×10^{-57}
F model	23355	1.134×10^{-126}

IF model	23373	$1.399x10^{-130}$
R model	23535	$9.292x10^{-166}$
SF model	23540	$7.627x10^{-167}$
SIF model	23541	$4.626x10^{-167}$
IR model	23700	$1.377x10^{-201}$

Table 5. Effects of explanatory variables of the global model for the effects of introduced species on native extinction chance. The coefficients and standard errors were back calculated from a Principal Components Regression (except for DEL and INTROD). The variables are presented in decreasing order of the effect size, according to the test statistic (Wald X^2), and those with significant effects at 5% level are highlighted in bold.

Variables	*Coefficient*	*SE*	*Wald* X^2	*p*
G	**0.406**	**0.017**	**597.076**	**<0.001**
relB	**0.355**	**0.017**	**448.581**	**<0.001**
X_{inf}	**0.317**	**0.016**	**405.311**	**<0.001**
θ	**0.317**	**0.016**	**389.472**	**<0.001**
log(μ_K)	**-0.226**	**0.017**	**179.023**	**<0.001**
MAHA	**0.146**	**0.016**	**81.569**	**<0.001**
ε	**0.145**	**0.016**	**79.141**	**<0.001**
S	**0.148**	**0.017**	**77.045**	**<0.001**
Cann	**-0.142**	**0.017**	**69.940**	**<0.001**
ζ	**0.126**	**0.017**	**56.621**	**<0.001**
u	**-0.100**	**0.017**	**35.415**	**<0.001**
ΔL/S	**0.094**	**0.017**	**31.646**	**<0.001**
Δξ	**0.088**	**0.017**	**27.810**	**<0.001**
ED	**0.082**	**0.017**	**23.907**	**<0.001**
INTROD*DEL	**0.071**	**0.016**	**20.888**	**<0.001**
ξ	**-0.074**	**0.017**	**18.989**	**<0.001**
INTROD	**0.041**	**0.010**	**15.408**	**<0.001**
ΔSK	**-0.060**	**0.017**	**12.283**	**0.001**
ϕ	**0.057**	**0.017**	**11.626**	**0.001**
δ	**0.054**	**0.017**	**9.907**	**0.002**
ΔS	**-0.049**	**0.017**	**8.384**	**0.004**
$\Delta\mu_K$	**-0.041**	**0.017**	**5.744**	**0.017**
η	**-0.040**	**0.017**	**5.631**	**0.018**
DEL	**-0.134**	**0.059**	**5.239**	**0.022**
W_0	**0.034**	**0.017**	**3.856**	**0.050**
%PISCI	0.029	0.017	2.989	0.084
log(α_{max})	0.028	0.017	2.725	0.099
%pisci	0.024	0.017	1.945	0.163
O	-0.020	0.017	1.399	0.237
V	-0.019	0.017	1.214	0.271
ΔSAT	-0.015	0.017	0.792	0.374
Δ%PISC	-0.015	0.017	0.751	0.386
$\Delta\alpha_{max}$	0.014	0.017	0.647	0.421
SK	0.010	0.017	0.370	0.543

SAT	0.006	0.017	0.133	0.716
L/S	0.005	0.017	0.089	0.765

The models explaining species deletion effects on extinction chances had a more uniform performance (Table 6). The model with the highest Akaike weight was the individualistic model (I), followed closely by the global model and the individualistic fundamental model (IF). The equivalence between the individualistic and the global model is mainly due to the scarceness of matching (M) variables, restricted to only ED and O, which in this particular analysis did not have detectable effects on extinction chance. There is also a preponderance of fundamental over realized features and of community over species features. It is partially explained by the large importance of productivity (μ_K), the only variable which appears alone in the list of ten best models.

Analyzing the individualistic model alone, we see that productivity has indeed a large effect on extinction chance, in the same direction as predicted by the analysis of invader effects, which makes sense as productivity is a characteristic of resident community only (Table 7). The same applies to species richness. But other community features arise as significant predictors of extinction: (i) the contribution of fish prey to overall biomass fluxes (%PISCI) tends to increase extinction chance; (ii) link density (L/S) also has a positive effect; and (iii) skewness of interaction strength decrease extinction chance. The deleted species' features with significant effects are the same characterizing invasive species, but with opposite signs, except for uniformity of spawning (u). The chance of secondary extinctions is higher when the deleted species has a lower relative abundance, is smaller, is more cannibal, concentrate spawning in a short time, is less piscivorous, grows slower, and has smaller eggs.

Table 6. Ten best models for the effects of deleted species on native extinction chance, according to AIC selection criteria. Presented are model names, AIC values and Akaike weights, w(AIC). The names give the combination of kinds of explanatory variables: C = fundamental features, S = species features, I = individual features, M = matching features, F = fundamental features, R = realized features. The global model contains all explanatory variables. The Akaike weights sum to 1 across all 42 models.

Model	***AIC***	***w(AIC)***
I model	15089	0.5162
Global	15090	0.3131
IF model	15092	0.1152
F model	15094	0.0424
IR model	15097	0.0095
R model	15099	0.0035
C model	15105	0.0002
CF model	15107	$6x10^{-5}$

$\log(\mu_K)$ model	15108	$4x10^{-5}$
SI model	15111	$9x10^{-6}$

Table 7. Effects of explanatory variables of the individualistic (I) model for the effects of deleted species on native extinction chance. The coefficients and standard errors were back calculated from a Principal Components Regression (except for INTROD). The variables are presented in decreasing order of the effect size, according to the test statistic (Wald X^2), and those with significant effects at 5% level are highlighted in bold.

Variables	*Coefficient*	*SE*	*Wald X^2*	*p*
INTROD	**0.179**	**0.008**	**451.975**	**<0.001**
$\log(\mu_K)$	**-0.121**	**0.020**	**38.257**	**<0.001**
relB	**-0.097**	**0.019**	**25.071**	**<0.001**
S	**0.079**	**0.019**	**16.910**	**<0.001**
%PISCI	**0.072**	**0.019**	**13.625**	**<0.001**
X_{inf}	**-0.072**	**0.020**	**12.969**	**<0.001**
Cann	**0.067**	**0.019**	**12.257**	**0.001**
u	**-0.053**	**0.019**	**7.932**	**0.005**
ϕ	**-0.050**	**0.019**	**6.514**	**0.011**
ζ	**-0.047**	**0.019**	**5.803**	**0.016**
W_0	**-0.043**	**0.019**	**5.024**	**0.025**
SK	**-0.043**	**0.020**	**4.763**	**0.029**
L/S	**0.042**	**0.020**	**4.645**	**0.031**
MAHA	-0.037	0.020	3.492	0.062
δ	-0.033	0.019	3.030	0.082
η	0.032	0.019	2.856	0.091
G	-0.032	0.020	2.708	0.100
ξ	-0.017	0.020	0.740	0.390
SAT	-0.012	0.020	0.378	0.539
θ	-0.012	0.020	0.356	0.551
V	0.006	0.019	0.114	0.736
$\log(\alpha_{max})$	0.007	0.020	0.111	0.739
%pisci	-0.004	0.019	0.047	0.828
ε	-0.004	0.020	0.039	0.844

Table 8 shows the results of the intrinsic community effects on extinction chance, considering only the control simulations (i.e. without any species introduction or deletion). Common to the two other analyses of extinction are the positive effect of richness and the negative effect of productivity (Table 5, Table 7), while the negative effect of interaction strength skewness (SK) is common to the analysis of species deletion effects only (Table 7). The percentage contribution of piscivory (%PISCI) and the shape of body size distribution of primordial species pool (ξ) presented opposite effects when compared to previous analysis where they were also significant. Community saturation (SAT) appears as a significant predictor, which did not occur in the previous analyses.

Table 8. Effects of community variables on native extinction chance, for control simulations only. The coefficients and standard errors were back calculated from a Principal Components Regression (except for INTROD). The variables are presented in decreasing order of the effect size, according to the test statistic (Wald X^2), and those with significant effects at 5% level are highlighted in bold.

Variables	*Coefficient*	*SE*	*Wald* X^2	*p*
S	**0.368**	**0.047**	**61.389**	**<0.001**
%PISCI	**-0.251**	**0.050**	**25.241**	**<0.001**
ξ	**0.180**	**0.050**	**13.003**	**<0.001**
log(μ_K)	**-0.171**	**0.048**	**12.758**	**<0.001**
SAT	**-0.132**	**0.048**	**7.610**	**0.006**
SK	**-0.104**	**0.048**	**4.667**	**0.031**
log(α_{max})	-0.068	0.049	1.927	0.165
L/S	0.054	0.049	1.206	0.272

3.4. Discussion

Although assembled from very diverse primordial species pools and along relevant gradients, the study communities do not present great trophic diversity. This is emphasized by the low contribution of piscivory (mean = 2.7%) to the overall biomass fluxes. As a consequence, irrespective of their topological structure, in quantitative terms the food webs here simulated have a more 'horizontal' structure, with most consumers standing on the second trophic level feeding almost exclusively on a linear array of basal resources, and a small proportion of interactions contributing to higher trophic levels. This kind of structure is more representative of freshwater environments, as opposed to marine environments where a more 'vertical' structure with longer food chains tend to be found (VERMAAT *et al.*, 2009).

The present simulation results reinforce the above interpretation. First, the previous deletion of a species drastically increased the chance of establishment of introduced species. This is expected in competitive assemblages, where the exclusion of one potential competitor liberates resources both for residents and future colonizers, enhancing their chance of population persistence. But this particular result is probably of general application, even for more complex food web structures (e.g. the exclusion of a potential predator could facilitate invasion), as long as previously extirpated species is not the unique potential food source for the invader. Second, species deletion decreased in many cases the chance of secondary native extinctions. It means that the communities without any perturbation had already an intrinsic potential for extinctions which was higher than in communities subjected to experimental species removal. After completely excluding a (competitor) species, even the effect of a posterior invader is alleviated due to more available resources. In other words, the 'vacant'

position provided by species exclusion both increase the chance of invasion and decrease the chance that this invasion affects remnant native species. This mechanism seems to work at least with intermediate level of propagule pressure, as demonstrated by Figure 2. Third, the chance of secondary extinctions was smaller when the relative biomass of deleted species was larger. It is consistent with a situation where interactions between species are predominantly negative (expected in competition), and the exclusion of most dominant species produces the most beneficial effects on other community members. It is also remarkable the congruence of several traits in their effects on extinction in deletion and invasion experiments: species with large body and egg size, low cannibalism, high piscivory and growth rates increase extinction when introduced and decrease when excluded, which means that fishes with these characteristics (together with large relative abundance) have a consistently large and negative impact on other species. Forth, invasion success was enhanced when the invader had lower diet overlap with resident community, in agreement with limiting similarity and species packing theories (MACARTHUR & LEVINS, 1967; MACARTHUR, 1970; ABRAMS, 1983), all of them based on competitive communities.

Although invader establishment had an important and significant contribution to extinctions, it was not a necessary condition. Quite the contrary, while increasing propagule pressure from 1 to 5 ind/week affected establishment only subtly, it promoted an almost linear increase in native extinction chance when compared to situations with no introductions. So the mere presence of invaders during the 10 years introduction period was enough to promote substantial native losses. This situation fits the ‘mass effect’ perspective of metacommunity theory (HOLYOAK et al., 2005). Mass effects occur when dispersal between nearby patches due to net differences in population sizes are high enough to change within-patch population dynamics (HOLYOAK et al., 2005). In the present case, the sources from where propagules come must be assumed implicitly. They can be nearby patches or very efficient transportation vectors in the case of long distance species introduction. There are remarkable instances in nature of very high propagule pressure (CARLTON & GELLER, 1993; HEWITT & HUXEL, 2002). Although the influence of propagule pressure on establishment success is already well recognized (LOCKWOOD *et al.*, 2005), the immediate impacts on native communities without depending on establishment have not been yet properly appreciated. Here, extremely high propagule pressure (5 ind/week) is responsible alone for a great part of observed extinction rates, overcoming even the beneficial effect of previous species deletion, which can also explain the significant interaction between the two perturbation variables (Figure 2).

Associated to high propagule pressure in determining extinctions are individual characteristics leading to high food consumption and predation: large body size (X_{inf}), high growth rate (ζ), high diet generality (G) and piscivory (ϕ), both characteristics associated to increased extinction chance in the present study. Interestingly, besides increasing generality, the high diet turnorver associated to harmful invaders (high δ) may be linked to good competitiveness, as the predation window may be narrow in this case (low difference between upper and lower limits), implying in high specialization and advantage in food contests within the model rules. So, it is not only propagule number or size (sensu LOCKWOOD *et al.,* 2005) which determine overall impact, but also propagule 'quality'. Together, they dictate the total resource demand (or 'metabolic' pressure) responsible for competition and predation on resident species, ultimately causing extinctions. They also determine invasion success, which correlates positively with extinction in this study. Nevertheless, the features enhancing invasion success are not exactly the same as those increasing extinction.

Several works have stressed that different invasion phases (e.g. transportation, establishment, integration, spreading) are ruled by different factors, so are the species characteristics necessary to complete each one of these phases successfully (KOLAR & LODGE, 2002; LOCKWOOD ET AL., 2007). This claim has found empirical support (KOLAR & LODGE, 2002; MARCHETTI *ET AL.,* 2004b; GARCIA-BERTHOU, 2007; RIBEIRO *et al.,* 2008). The same is valid for establishment success and impacts on native community, as demonstrated in the present study. Here, establishment probability is enhanced by increasing bionomic similarity between invader and resident community, while native extinction (impact) is increased by decreasing similarity. The first result is consistent with empirical findings (MARCHETTI *ET AL.,* 2004a; 2004b; RIBEIRO *et al.* 2008), where successful invaders tend to come from close areas, which presumably have similar environmental conditions to invaded community. In general, life history theory predicts the selection of an optimal set of traits at any given combination of environmental conditions (STEARNS, 1992). It then makes sense from this perspective that a successful invader must have life history traits in concordance with local conditions, and this is exactly what happened in the present simulations: besides having traits similar to resident species, successful invaders tend to come from closer portions of environmental gradient.

On the other hand, as establishment is not a necessary condition for introduced species to promote impacts (provided that mass effects are strong enough), the requisite of trait convergence is not so important in this case. One example of dangerous combination is that of large, fast growing, ontogenetic generalist but individually specialist, and piscivorous species

being introduced at species rich and unproductive assemblages (which generally supports only small sized, slow growing, less piscivorous and individually generalist species). Even not being capable to maintain a viable population in these local conditions due to high metabolic demands, the predatory capacity and high food consumption of some introduced individuals may be sufficient to deplete already depauperated native populations. Besides, piscivory itself may be a factor contributing to great damages, as frequently reported in the literature for fish invasions (ZARET & PAINE, 1973; FERNANDO, 1991; MOYLE & LIGHT, 1996; KITCHELL *et al.*, 1997). Although intentional introduction of a species like that in unsuitable places at large propagule pressure is a highly implausible picture, natural dispersal from more productive and suitable patches is a possible situation which could keep sink populations of invader at sufficient levels to cause impacts. It would depend of course on previous successful introduction in such productive environments, and on the capacity of invader to disperse across connected habitats.

The fact that extinction chance was determined by a mixture of characteristics common to invasion success and some with even opposite effects is an evidence for a conflict between establishment and impact. Although invasion success can increase extinction due to prolonged contact with invader, biotic resistance generally filter for colonizers with minimal interactions with resident species. This is in the core of limiting similarity hypothesis and niche theory (MACARTHUR & LEVINS, 1967; CHESSON, 1991; CHESSON, 2000). It has also been receiving support from assembly studies, which demonstrate that communities are built by selecting species with weaker interactions among them, as compared to the expected from species pool (KOKKORIS *ET AL.*, 1999; GIACOMINI *et al.*, 2009). In general terms, weak interspecific and strong intraspecific interactions are the basic recipe for community stability and species coexistence (MAY, 1973; CHESSON, 2000). By this theoretical perspective, it is not surprising that successful invaders in the present study were those more capable to partition diet with competing residents (lower O) even if converging in major bionomic features due to environmental constraints (lower ED). Accordingly, the lower predation window characterizing successful invaders magnify the intraespecific component of competition, as large sized adults have more chances to compete with smaller juveniles. The contrary is observed in more harmful invaders: higher predation windows and diet turnover along ontogeny, which diminish intraspecific competition between juvenile and adults. This is further alleviated by low levels of cannibalism. The conflict between establishment and impacts may explain the many cases in nature of successful invasions with negligible effects on native communities (WILLIAMSON & FITTER, 1996; JESCHKE & STRAYER, 2005).

One prediction of the present model is that such cases are more probable to consist of species eating low in food chains (e.g. detritivores, planctivores), while invasions with large impacts on fish assemblages are more associated to consumers specialized in large food items (e.g. large piscivores). This prediction has reasonable support in literature (FERNANDO, 1991; KITCHELL *ET AL.*, 1997; LATINI & PETRERE, JR., 2004; CAPOVA *et al.*, 2008).

The divergence in effects between establishment and impact concerning the community variables must be interpreted with caution. Species-rich and unproductive communities are less susceptible to invasions but their resident species are more prone to extinction. However, this propensity to extinction is more due to intrinsic properties of such communities than to experimental perturbations, as confirmed by control simulations. With more species and less resources available, population sizes tend to be low, so demographic stochasticity plays a crucial role in extinctions (PIMM, 1991). The same is worth for the skewness of interaction strength distribution (SK), which intrinsically decreased extinction chance even without the occurrence of any perturbation. It highlights further that many weak and few strong interactions (which produce left-skewed distributions) are stabilizing and tend to enhance coexistence and diversity, as predicted by previous theoretical works (MCCANN *ET AL.*, 1998; BERLOW, 1999). By contrast, the contribution of piscivory (%PISCI) affected extinction differentially after species deletion when compared to control simulations. While in the last case %PISCI decreased extinctions, in the first case it had a completely opposite effect. It is an interesting result, considering that cascading effects of species deletion leading to secondary extinctions generally require more complex food web structures, with more than two trophic levels (EBENMAN & JONSSON, 2005; DUNNE & WILLIAMS, 2009). For instance, a keystone predator is generally a species preying on second trophic level consumers, enhancing coexistence among them by eating preferentially on strong competitors (NAVARRETE & MENGE, 1996). Deleting it promotes the collapse of community structure and competitive exclusion of several species (PAINE, 1966). Cascading effects can occur also when important prey species is deleted, promoting the extinction of its specialized predators and other species depending on them (DUNNE, *et al.* 2002b). This situation would require also at least three well defined trophic levels. As a general picture, our results suggest that in more ‘horizontally’ structured fish food webs, as expected in freshwater communites (VERMAAT *et al.*, 2009), larger contribution of piscivorous interactions makes the community more susceptible to secondary extinctions after random species exclusion. It does not mean that the excluded species must be more piscivorous than others. Instead, fish prey

on which predators depend may be more important, as suggested by the negative influence of species piscivory level (ϕ) on extinctions in deletion experiments.

Our finding that species-richer and less productive communities are less invasible has support in general community theory (SHEA & CHESSON, 2002; BYERS & NOONBURG, 2003; BEISNER *ET AL.*, 2006). Simply stating, with more resources available and less species to share them, it becomes easier for a potential invader to establish. Maximum attack rates of consumers (α_{max}) also have influence: larger attack rates imply in more saturated functional responses and less stable dynamics (OATEN & MURDOCH, 1975). It contributed to higher priority effects, which are one of the main reasons for productive communities having lower richness just prior invasion experiments (Chapter 1). But the priority effects were really effective only during the prior formation of resident communities, when introduced species were introduced at very low number (one individual egg) and were created by a Monte Carlo procedure without guarantee that they would have viable combinations of bionomic parameters. In contrast, in invasion experiments only viable species selected throughout the assembly process constituted the species pool from which propagules came. Their high relative quality and higher propagule pressure were then sufficient to overcome previous priority effects.

Evidences in the invasion literature for the effects of several variables here studied lead to diverse conclusions. Maximum body size is one of the most studied species traits. As in the present study, it has been found to influence positively invader establishment by some authors (VILA-GISPERT *ET AL.*, 2005; DUGGAN *et al.*, 2006), but negatively by others (Ruesink 2005;Ribeiro *et al*. 2008) or even having no influence at all (JESCHKE & STRAYER, 2006). Features strongly correlated to body size, and expected to facilitate establishment in the present study are: life spam, with reported positive effects on establishment also in empirical studies (MARCHETTI *ET AL.*, 2004b; VILA-GISPERT *et al.*, 2005), and fecundity, to which have been attributed both positive (VILA-GISPERT *et al.*, 2005) and negative (JESCHKE & STRAYER, 2006) effects. Parental care is another commonly analyzed trait, with a consistently positive effect (MARCHETTI *ET AL.*, 2004b; JESCHKE & STRAYER, 2006). Although parental care was not explicitly accounted for in the present study, egg size can be interpreted as a surrogate measure for offspring survival, and it was also positively associated to establishment success here. Diet generality is generally associated to increased chance of invasion (KOLAR & LODGE, 2002; MARCHETTI *ET AL.*, 2004a; RUESINK, 2005), although in our simulations no significant effect was found. But having lower predation window is an indication of specialization in

small food items, so our model predicts more specialized invaders to be more successful, which nevertheless depends strongly on their introduction in more productive environments in order to succeed. Assuming that omnivory is positively correlated to the realized percentage of piscivory, our results are in agreement with empirical results of Ruesink (2005). The same applies to four other variables: (i) maturation as compared to Vila-Gispert et al. (2005), where late maturing fishes have more chances to establish; (ii) peripherical position of bionomic space (measured here by MAHA), as in Olden et al. (2006); (iii) growth rate, found to increase invasion success by Kolar & Lodge (2002); and (iv) distance to source community (measured here by distances in environmental gradient), which negatively affected success also in Californian (MARCHETTI *et al.*, 2004a) and Iberian (RIBEIRO *et al.*, 2008) watersheds. Propagule pressure has positive effect on invasion success both here and in several empirical studies (MARCHETTI *ET AL.*, 2004A; RUESINK, 2005; COLAUTTI, 2005; DUGGAN *et al.*, 2006).

Empirical assessments of impacts on native communities are much scarcer than of establishment. One result in common with present study is the negative influence of distance to source community on invader impact (in this case, invader integration measured as abundance in resident community) in Californian watersheds (MARCHETTI *ET AL.*, 2004a; 2004b). The meta-analysis of Ricciardi & Atkinson (2004) for several world's aquatic systems has also a result in congruence with ours: the impact on native species (reduction in abundance or extirpation) tends to increase with invader distinctness from resident community (assuming that taxonomic distinctness is directly related to bionomic distance, or ED), a result in agreement with (Strauss *et al.* 2006). In contrast, Olden et al. (2006) found that the native species with larger life history overlap with exotic species were those more impacted (in terms of distributional decline). Kolar & Lodge (2002) identified small eggs as characteristic of nuisance invaders in the Great Lakes, the opposite as found here. In our simulations, propagule pressure had a large effect on native extinctions, although Marchetti et al. (2004a), which explicitly tested the relationship between them, found a non-significant result. Our most influent variable, diet generality, has no parallel result in empirical surveys concerning impacts, although it is generally related to establishment or spreading phases. Omnivory of fishes introduced in Iberian watersheds decreased impact (invader abundance and distribution) (Ribeiro *et al.* 2008), differently from present study if we assume percentage piscivory as a surrogate for omnivory. They also tend to reproduce in a distinct season (Alcaraz *et al.* 2005). Considering that reproductive timing had a negative effect on

extinctions in our simulations, and that the most affected communities have a slightly larger value of this parameter, there is indication for a pattern similar to that in Alcaraz et al (2005).

The variety of effects outlined above is caused by a combination of intrinsic ecological and methodological factors. Contrasting trait effects can result from context dependence of invasions and different scales of investigation. Consider, for instance, a pool of invaders with reasonable diversity of body sizes. In our simulated communities, smaller species tend to do better in less productive sites while larger species do better at productive sites. If looked on the local scale of an unproductive site only, a regression relating body size of species pool with invasion success would find a negative effect (smaller species would establish more easily). The contrary would be found if the analysis was focused on a productive site instead, denoting the context dependence of trait effect. Opposite effects would be found also if we compare one local analysis of unproductive sites (whose expected effect is negative) with a more extensive analysis along a gradient of productivity, whenever productive sites tend to be more susceptible to invasion (due to their propensity to accept larger invaders, there would be a greater contribution of this species kind to cases of successful invasions), illustrating how different scales of investigation may generate opposite traits effects. The simulation results are indeed compatible with these situations. It may become clearer in future analyses by the inclusion of well chosen interaction terms in regression models. The empirical works cited above differ greatly in terms of chosen region, and scale, but also have serious biases concerning taxonomic group, controlling factors, and how variables are measured (VILA-GISPERT *ET AL.*, 2005; COLAUTTI, 2005; GARCIA-BERTHOU, 2007). The situation is even more complicated for the analyses on impacts, as very few works have used direct measures of impacts on natives (e.g. extinctions and abundance reductions after invasion) (RICCIARDI & ATKINSON, 2004; OLDEN *et al.*, 2006). Simulation models like the present one can be useful to indicate what kinds of effects we should expect from theory, and directing empirical research on gathering and compiling new data sets.

Finally, the prevalence of global models is a demonstration that all kinds of variables have crucial importance to determine invasion success and impacts. This situation was already found empirically by Marchetti et al. (2004a) for fish establishments in Californian watersheds, and is probably of general application, at least for data sets covering heterogeneous landscapes or extensive gradients. Predicting invasion would be certainly easiest by means of individualistic and realized features of either community susceptibility or invader capabilities. Matching variables, like similarities or distances, require more information as it depends on knowledge of both introduced species and resident community

receiving it. This information is not always readily available. But it is clear from the present study that in order to predict the fate of specific cases of introduction, it is necessary a proper assessment of the match between potential invader and community. On its turn, fundamental traits are fully tractable from a model perspective, but are difficult or sometimes even impossible to measure in nature. They can be though as the genetic potential in the case of introduced species. Although justifiable in practical terms, failure to account for genetic potential of introduced species may prevent the accurate prediction of species behavior in new environments (SAKAI *ET AL.*, 2001; LEE, 2002). Another group of variables not included in the present study is that of population-level variables. They consist in measures of within species variation, including age and size structure, and genetic diversity of both source population or propagules (SANDERS, 2010). For instance, recent experiments with plant species *Arabidopsis thaliana* point to genetic diversity of propagules as strong determinants of invasion success, being more important than even propagule size (CRAWFORD & WHITNEY, 2010). The present model did not include genetics explicitly, but future simulations can indeed help evaluating population-level variables by changing age and size structure of propagules, as well as their body condition (i.e. amount of storage versus structural mass). To deal with genetic variation, a promising approach is to make invasion experiments with recently proposed Eco-genetic models (DUNLOP *ET AL.*, 2007; DUNLOP *et al.* 2009).

Due to inherent complexity, individual-based models (IBMs) are generally applied to very particular systems and situations (DEANGELIS & GROSS, 1992; GRIMM, 1999). But they can serve as useful virtual laboratories to investigate more general questions, such as done here for predictors of species invasions, exclusions and associated impacts. More than simply identifying important variables, IBMs can shed light on the underlying mechanisms by putting several related theories (e.g. metabolic ecology, life history and predator-prey theory, community assembly) to work together in the same dynamical arena. On one hand, the present model allows studying the effects of a much larger number of variables than classical state variable models, getting closer to what may be expected in field situations. On the other hand, it suffers from many complexity problems common to natural ecosystems. For instance, correlations among explanatory variables such as found here is the rule in field studies, demanding the use of proper statistical techniques. But instead of viewing these correlations as just statistical obstacles, we must acknowledge that they are manifestations of the own ecological processes structuring communities (real or virtual ones). Using an assembly approach (GIACOMINI *et al.*, 2009), the model allows communities to be built sequentially

and their properties to emerge from dynamics instead of being imposed. If in some sense the prevalence of simple food webs in the present study restricts the application of results, it also stimulates future search for the conditions enabling more complex structures (e.g. longer food chains) to arise. These conditions may be hidden on the model itself, requiring just the adjustment of parameter values (e.g. increasing productivity and maximum body size in species pool), or they may be found by including new model rules for individual behavior and interactions (e.g. varying assimilation efficiencies, simulating space and movement explicitly). Finding such conditions and emerging structures is a valuable scientific endeavor on its own, besides expanding the scenery for the application of invasion and deletion experiments to a wide range of situations more compatible with the diversity of real world ecosystems.

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4. CONCLUSÕES GERAIS

- A modelagem baseada no indivíduo mostrou-se uma ferramenta eficiente para a investigação de questões teóricas que demandam um grande número de informações biológicas das espécies, como a seleção de múltiplas características da história de vida de peixes.
- O método de formação de comunidades pela introdução sistemática de espécies, embora artificial, foi bem sucedido na seleção de espécies ao longo de gradientes ambientais.
- O padrão de distribuição da riqueza de peixes é compatível com a hipótese da relação unimodal entre diversidade e produtividade: a riqueza é máxima em níveis intermediários de produtividade.
- Esse padrão é mediado pelas respostas funcionais dos predadores: repostas funcionais muito saturadas (alta disponibilidade de recursos e/ou altas taxas de ataque) promovem maiores flutuações populacionais e ocasionam efeitos de prioridade, que em conjunto tendem a diminuir a chance de coexistência e, por conseguinte, a riqueza. Diferenças nas taxas de ataque podem ser interpretadas como variação na extensão espacial (maiores áreas levariam a menores taxas de ataque) ou na disponibilidade de refúgios, que em geral depende da complexidade estrutural do habitat (maior complexidade levaria a menor taxa de ataque).
- A explicação anterior representa uma nova hipótese para explicar padrões unimodais de diversidade-produtividade, que independe da existência de heterogeneidade espacial dentro da comunidade.
- O padrão de riqueza não pode ser desvinculado da bionomia das espécies que compõem a comunidade: efeitos de prioridade só ocorrem em comunidades produtivas porque elas possibilitam o domínio prematuro por espécies com maior tamanho e com rápido crescimento corporal.
- Correlações entre diversas características biológicas emergiram como produto da seleção nas comunidades.
- As relações entre as características biológicas dependem fortemente da existência de assimetrias entre as espécies quanto ao consumo de presas e susceptibilidade à predação. A maior diferença ocorre em ambientes mais produtivos: com assimetria de consumo, as espécies apresentam uma tendência à estratégia de ‘equilíbrio’ (conforme

o modelo trilateral de história de vida de Winemiller & Rose, 1992), enquanto que na ausência de assimetria a estratégia favorecida está mais próxima da 'periódica'. Em ambientes menos produtivos, existe uma convergência para a estratégia do tipo 'oportunista'.

- Vinculadas à história de vida estão características tróficas dos peixes, definindo grau de canibalismo, piscivoria e especialização em itens alimentares de diferentes tamanhos, que responderam concomitantemente aos gradientes ambientais.
- Susceptibilidade à invasão e susceptibilidade aos impactos de invasores são influenciadas por poucas características em comum. Comunidades com mais recursos disponíveis e menor riqueza são mais suscetíveis à invasão. Por outro lado, suas espécies nativas têm menor chance de extinção. Invasores bem sucedidos tendem a possuir história de vida similar à da comunidade invadida, mas pouca sobreposição de dieta, maior especialização em itens alimentares de pequeno porte e menor grau de piscivoria. Por outro lado, invasores mais impactantes são mais diferenciados dos nativos, têm dieta generalista, preferência por itens alimentares de maior porte e maior grau de piscivoria.
- Uma comunidade previamente perturbada pela exclusão de uma espécie nativa tem chance duas vezes maior de ser invadida.
- A pressão de propágulos aumentou a chance de invasão e também de extinção de nativos. A influência da pressão de propágulos sobre os nativos deve-se em parte à sua relação com o sucesso da invasão, mas também ao efeito de massa exercido pelos indivíduos introduzidos.
- Espécies de peixe com maior demanda metabólica (maior tamanho e taxa de crescimento) e maior biomassa relativa são as que exercem maior influência sobre as demais na comunidade, aumentando a chance de extinção quando introduzidas e diminuindo-a quando excluídas.
- Deve-se ressaltar que estas conclusões são válidas para comunidades aquáticas de diversos níveis de produtividade, área e complexidade de habitat, embora devam se restringir a assembléias predominantemente competitivas de peixes, nas quais a influência de cadeias tróficas de três ou mais níveis seja pequena.

5. APÊNDICE

Model description

5.1. Model overview

5.1.1. Purpose

The objective of the model is to improve understanding about the assembly of species having different life-history strategies in communities of size-structured, trophically interacting species. Fishes are the group of organisms for which the rules are referenced, although the model is sufficiently general to be applied to other heterotrophic groups with indeterminate growth.

5.1.2. State variables and scales

Like many other assembly models, the present model assumes two spatial scales: a local scale, consisting of a community of co-occurring species whose dynamics is modeled explicitly; and a regional scale, which includes a pool of potential immigrant species. On the local scale, the model consists of two basic entities: (i) the environment, which comprises a defined number of basal resources and (ii) the assemblage of consumer species, whose individuals (or super-individuals – for description, see below) are explicitly represented. The state of a basal resource is given solely by its biomass. The consumer individuals are characterized by the following state variables: species identity (ID), age (T, years), developmental stage (egg/embryo, juvenile or adult), weight (W, grams), and the number of components (for the case of super-individuals, N). The individual's total weight is divided among three variables: the irreversible mass (X), the reversible mass (Y) (PERSSON *ET AL.* 1998; CLAESSEN *et al.* 2002), and the gonad mass (G). We assume here that the reversible mass is composed predominantly by fat reserves, which can be used when the metabolic demands exceed the amount of ingested food. The irreversible mass is constituted of permanent tissue, which can either grow or stay constant in time. It represents a great proportion of organs like bones, the nervous system and all other minimum parts necessary to guarantee the vital functions of the organism. The individual length (L), an important dimension for size structured interactions, depends entirely on the irreversible mass.

To work with a number of individuals that is not too large to be computationally intractable, we use the super-individual concept, as proposed by Scheffer *et al.* (1995). A super-individual is a cohort of identical organisms, created at each time interval when the females of a given species spawn. It differs from a unitary individual just by having a number of components, or individuals represented within the superindividual (N) that is larger than 1. It is assumed that very similar individuals do not need to be modeled separately, as they do not differ significantly in their effects upon the environment. A factor in favor of grouping

fish as super-individuals is that it is analogous to schooling, so common in fish (SHIN & CURY 2001; HEMELRIJK & KUNZ 2005). They can be dissociated after achieving a specified size limit X_N (based on the irreversible mass of each component), and then they start acting separately.

The environment space is only implicit. The existence of spatial refuges for individuals and resources are implicitly assumed by using a type III functional response for consumers (KOEN-ALONSO 2007).

5.1.3. Process overview and scheduling

Time (t, years) is assumed to be discrete, and proceeds by steps of size 1/D, where D is the number of time steps necessary to complete a year. We chose the week as the time step (D = 52 weeks/year), seeking for a compromise between fine-scale resolution and a reasonable speed for the simulations (GIACOMINI *et al.* 2009). During a time step, the main processes of the internal dynamics occur in the sequence specified by the Figure A1.

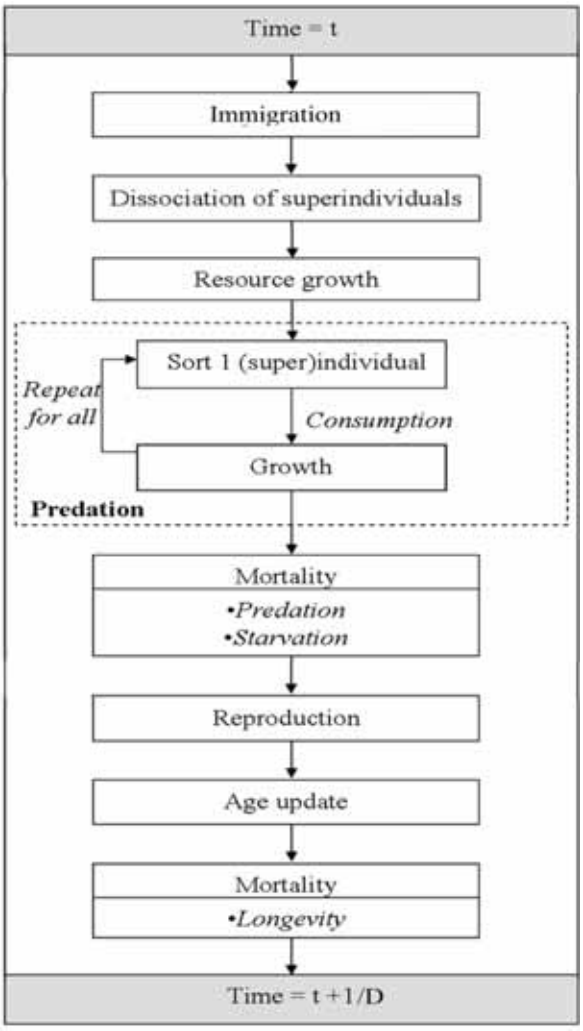


Figure A1 – Outline of the processes that promote community dynamics, during a time step. Modified from Giacomini *et al.* (2009)

During the execution of the predation module, the order in which the individuals will have access to the consumption is defined (Figure A1), which may be either completely random or follow a function of their bionomic features (see *Predation dynamics* bellow).

The life cycle comprises three phases: (i) the newborn individual (egg/embryo) is almost entirely composed by reversible mass (yolk/lipids), and it will feed only on the yolk; (ii) once being a juvenile, the individual will need to feed on external resources, used to metabolic demands and to growth, which is entirely devoted to its somatic component (X+Y); (ii) after reaching a given irreversible mass (X_{mat}), the individual becomes an adult, devoting an increasing proportion of time to the production of gonads instead of only somatic growth. Reproduction occurs periodically until death. Each species has a maximum longevity, which is an allometric function of its maximum asymptotic irreversible mass (X_{inf}). There is no recycling of dead biomass.

5.2. Design concepts

Emergence. The entire dynamics of the consumer populations (fishes) emerge from the rules imposed on the individuals and from their interactions with each other and with basal resources. The size-specific limit on longevity is the only imposed source of mortality. Resultant associations among species traits within a community and along environmental gradients are also emergent patterns from the model.

Sensing. The individuals are assumed capable of distinguishing: (i) resource types (including other fish); (ii) the size of the food items (basal resources or individuals); and (iii) the degree of activity of other individuals, when a bionomic-based consumption ordering takes place (see *Predation dynamics* bellow).

Interaction. The interactions in the model are restricted to predation, which occurs with an explicit weight transferral from prey (basal resource or individuals) to individual predators.

Stochasticity. It is included in two processes: (i) the immigration of individuals into the local community and (ii) the ordination of predation sequences.

Observation. At the end of each simulation, the following are stored: (i) the final community composition and related species traits; (ii) the food webs containing biomass fluxes among all consumer species and basal resources; and (iii) the annual census of biomass of total consumer assemblage and each basal resource.

5.3. Initialization

At the beginning of the assembly process, the community is composed only by the basal resources, at their mean carrying capacity μ_K. During a simulation, the consumer

assemblage builds up by the sequentially arriving of fish individuals introduced at an arbitrarily defined rate from a regional species pool, which is assumed here as infinite (see *Immigration* section below).

5.4. Input

There is a seasonal variation in the carrying capacity of basal resources, following a sine function with period of one year and amplitude arbitrarily specified. It is also possible to include stochastic disturbances in resource levels, with specified frequency and intensity. From these specified conditions, it is possible to study gradients of mean resource levels, amplitude of seasonal fluctuations, and the frequency and intensity of disturbances. Another source of external stochastic perturbation is the periodic introductions of fish individuals.

5.5. Submodels

5.5.1. *Basal resources.* The growth of each resource's biomass follows the discrete logistic model:

$$B_{i,t+1/D} = B_{i,t}\left[1 + R_i\left(1 - \frac{B_{i,t}}{K_t}\right)\right] - C_{i,t} \qquad \text{Eq. (A1)}$$

where $B_{i,t}$ is the biomass (in units of irreversible mass equivalents) of resource i at time t (years); D = 52 weeks/year; R_i is the intrinsic growth rate of resource i ($week^{-1}$); K_t is the seasonally varying carrying capacity at time t and $C_{i,t}$ is the amount of resource i consumed by fish from time step t to t+1/D. The number of resources is arbitrarily prescribed, according to the questions to be addressed.

The susceptibility to consumption is determined by a range of "particulate sizes" of the resource. Each resource 'i' is characterized by a size range (cm), whose lower and upper limits are given by the parameters $l_{min,i}$ and $l_{max,i}$, respectively. The resources are arranged in a linear array, contiguously and in ascending order along the size spectrum, so that the upper limit of a smaller resource coincides with the lower limit of the adjacent larger resource (i.e. $l_{max,1} = l_{min,2}$; $l_{max,2} = l_{min,3}$; or more generally, $l_{max,i} = l_{min,i+1}$). The distance between adjacent boundaries of resource sizes increases exponentially, which means that $\ln(l_{max,i} / l_{min,i})$ is constant. All resources are assumed to have the same carrying capacity at a given time. In this way, if the size spectrum is represented along an axis of the logarithm of length, the carrying capacity would be uniformly distributed, which is roughly compatible with general observations of biomass distribution along particulate sizes, at least for pelagic environments (SILVERT 1984). Although this contiguous size scale is in current use, it is possible to

generate any other arbitrary size distributions, including the possibility for overlaps or gaps in the size spectrum.

The temporal variation in K_t is deterministic, and given by a sinusoidal function:

$$K_t = sin(t2\pi)\varphi\mu_K + \mu_K \qquad \text{Eq. (A2)}$$

where φ is the proportional amplitude of resource oscillations (0 to 1), and μ_K is the mean carrying capacity.

The intrinsic growth rate depends on the geometric mean of resource size limits, according to the allometric function:

$$R_i = \nu\left(\sqrt{l_{\min,i} l_{\max,i}}\right)^{-0.75} \qquad \text{Eq. (A3)}$$

where *v* is a coefficient of proportionality and -0.75 is the product of 3 (denoting a cubic relation between length and weight) by -0.25, which is the exponent empirically observed and predicted by metabolic theory (FENCHEL 1974; BROWN *ET AL.* 2004; SAVAGE *ET AL.* 2004).

If completely depleted by consumers, each resource can immediately recolonize the community by a specified small amount of biomass (*recol*).

5.5.2. *Growth of individual fish.* The individual growth (ΔW, g/week) in a time step is determined by the difference between the assimilated food and the weight loss, all in irreversible weight equivalents (g). The weight loss, given by the power function Loss = cX^d (g/week), is fixed for a given size and species. The realized ingestion (Ing, g/week) may not be the same as the potential ingestion (PIng, g/week), specified by the power function PIng = aX^b (g/week), because it also depends on food availability. For simplicity, we are assuming 100% food assimilation efficiency. By making Loss and PIng functions of the irreversible weight only, we are assuming also that the reversible weight and the gonads do not interfere with metabolism or ingestion, as they are composed mainly by lipid reserves. In the case of a negative surplus (Loss > Ing) the energetic difference (in irreversible weight equivalents) is subtracted from the reversible weight. Each gram of reversible weight provides a total of $1/\gamma$ equivalent grams of irreversible weight, where γ is the ratio between the energetic contents of irreversible and reversible weights (QUINCE *et al.* 2008a). For example, if a fish eats nothing, and has metabolic expenses of 10g, it will lose only 5g of reversible weight if γ = 0.5. If the reversible weight fall below a threshold value, the individual dies of starvation. In the case of a positive surplus, it is allocated differentially to the components X, Y or G, depending on the individual stage and condition.

A newborn individual is composed mainly by yolk and a tiny fraction of irreversible mass representing the embryo (whose absolute weight, X_0, is assumed the same for all species). So the proportion of yolk will depend on the total egg weight, W_0, which is a species parameter. It is assumed that the irreversible mass already present in the egg grows by the same power functions characterizing juveniles and adults (Loss and PIng). In this case the assimilated food will not come from ingestion of external resources, but will be composed entirely by the yolk. In each week, the yolk will be consumed by the amount $(aX^b)\gamma$, and the irreversible weight will increase by the amount $(aX^b\text{-}cX^d)$ until the individual condition Y/X falls below the maximum condition characterizing a juvenile (Y/X = qj). Thereafter, the individual is a juvenile, and will need to ingest external food sources in order to grow. We assume, as in Persson *et al.* (1998), that the individual allocates the surplus production to reversible mass in the proportion (Xqj-Y)/Xqj where Xqj is the maximum Y for a given X of a juvenile. This rule works well for continuous time or when the temporal resolution is sufficiently fine. In the present time discrete model, which allows for reasonably gross time steps (such as a week), the surplus can be large enough to cause abnormal condition values, outside of the boundaries 0-qj. So we derive the following discrete time corrected rule for surplus allocation:

$$\kappa(X,Y,P)=\frac{1}{(1+qj)qj}\left[\frac{(X+Y)}{(X+Y+P)}\cdot\frac{Y}{X}+\frac{P}{(X+Y+P)}\cdot qj\right] \qquad \text{Eq. (A4)}$$

where κ is the fraction of the surplus production (P) allocated to irreversible mass (P = Ing - Loss, Ing > Loss). If not corrected, the term in the brackets would be just the current individual condition Y/X, as in Persson *et al.* (1998). Instead, we take a weighted average between the current individual condition and the maximum condition (qj), using as weighting factors the current somatic mass (X+Y) and the surplus production P, respectively, thus avoiding Y growing out of bounds if P is too large.

After reaching the adult size (X_{mat}), the individual will start allocating surplus production to reproduction during a given proportion of the year. When growing in somatic mass only, the adult will follow the same rules for the juvenile, except that its maximum condition is now set by qa, which can in theory be larger than qj (Persson *et al.* 1998). As there is a separate compartment devoted entirely to reproductive products (G), the adult reversible mass is assumed here to be composed only of those fat reserves not used for reproduction, but just to recover excess metabolic requirements.

In order to put growth and reproductive strategies in the same unifying framework, we are using the biphasic growth model of Quince *et al.* (2008a). Those authors assume that the exponents of weight loss and assimilation functions can be considered the same (b = d = β); therefore, the potential surplus production $\mathscr{P}$ will be also an allometric function of size:

$$\mathscr{P} = (a - c)X^{\beta} = \zeta X^{\beta} \qquad \text{Eq. (A5)}$$

where ζ is a growth coefficient. In this way, the individual will grow indefinitely, with increasing rate, but only if it does not reproduce. Nevertheless, after reaching maturity, the individual allocates an increasing proportion of time to gonad production, promoting decay in growth rate of somatic tissue and resulting in the asymptotic growth pattern so common in fishes. All surplus production is allocated to somatic growth during a proportion of the year equal to *p*. The remaining proportion (1-*p*) is devoted to gonad production only. The value of *p* decreases yearly according to a fixed rule, with an asymptotic value of zero, when the fish attains its maximum size (X_{inf}). The model allows using two alternative rules to determine *p* values. The first is a size-based rule, where:

$$p = \left(X - X_{\inf}\right)/X_{\inf} \qquad \text{Eq. (A6)}$$

so that *p* approaches zero as the irreversible mass approaches its asymptotic value. The advantage of this rule is to allow an easy determination of growth strategies when we are interested in analyzing the effects of maximum body size on species persistence during assembly. The other rule is more suitable to analyze the effects of reproductive investment, by assuming a fixed gonad-somatic index (g) for each species. This rule is based on the Quince *et al.* (2008a) FGO model. The total gonad production at the end of a reproductive period can be calculated as in (Lester *et al.* 2004):

$$G = \zeta X^{\beta}(1 - p)D\gamma \qquad \text{Eq. (A7)}$$

Using g = G/X, and the energetically weighted gonad-somatic index g' = g/γ (Quince *et al.* 2008a), we can rearrange the equation and get an expression for p:

$$p = 1 - \frac{g'}{\zeta X^{\beta-1} D} \qquad \text{Eq. (A8)}$$

The right hand side of Eq. (8) can take negative values if g' is too large or the growth coefficient is too small. This occurrence would just mean that, in such a combination of parameters, there would be no way to allocate sufficient surplus production in order to attain the specified g. If this happens, the *p* value is forced to be zero. The g can be thought of as a species parameter, but it is only an ideal measure of reproductive investment. The realized g will be lower as long as the mean realized ingestion is lower than the potential ingestion. By

means of Eq. (8), it is possible to calculate X_{inf} for a given fixed g, and the maximum g for a given X_{inf} by making $p = 0$.

The growth coefficient has a huge influence on the reproductive output. If it has to be used as part of a species strategy, it must also carry a cost. One possibility is to assume that faster growing individuals are also more demanding in terms of resource availability. This tradeoff has been observed in amphibian assemblages and seems to occur with invertebrates and plants (Schiesari *et al.* 2006), but we will consider it to be a general physiological constraint also applicable to fishes. Including it in the present model is straightforward, if we assume that the potential surplus production is a fixed proportion of the potential ingestion. In other words, $P = \omega PIng$, where ω is a constant, whose value is suggested to be around 0.3 by some authors (Weatherley & Gill 1987). As a consequence, $Loss = P(1-\omega)/\omega$, which means that the metabolic requirement increases with the growth potential. One expected consequence is that faster growing species do better at high resource availabilities, but are more prone to starve under poorer conditions.

The allometric exponent β is supposed to be constant among species. As an ideal baseline value, we are using $\beta = 0.75$, as it corresponds to the value predicted by optimization of energy flux in fractal-like distribution networks and exchange surfaces, common to all vertebrates (West *et al.* 1997; 1999; Savage *et al.* 2004).

5.5.3. *Diet.* An important concept included in the model is the predation window, which is the range of food sizes susceptible to being ingested by the individual (Claessen *et al.*, 2002). The lower and upper limits of the predation window are constant proportions of the predator's body length. These proportions are the bionomic parameters δ and ε, respectively. The length, calculated by the weight-length relationship $X = \Omega L^3$, was chosen instead of the weight because the ingestion of prey by fish predators is usually limited by their linear dimensions. The difference between ε and δ give us a relative measure of the diet generality of a species. As in the earlier model version (Giacomini *et al.* 2009), this predation window represents a discrete and sharp change in resource eligibility: if a resource size lies within the predation window (i.e. they have a non-empty intersection), it has 100% chance of being accessed by the predator (but not necessarily consumed, which will depend on the availability of other resources and on relative attack rates); if it lies completely outside the window, that chance drops to 0%. But more continuous functions for size-dependent eligibility can be easily incorporated by the model.

The amount of eligible biomass of each resource kind (including other fishes) consumed by an individual predator depends on the availability of the first and the functional

response of the second. We are using a multi-species type III functional response for generalist predators (Koen-Alonso 2007):

$$F_{i,j} = \frac{PIng_i N_i \alpha_{i,j} B_j^{\,2}}{PIng_i N_i + \sum_k \alpha_{i,k} B_k^{\,2}} \qquad \text{Eq. (A9)}$$

where $F_{i,j}$ is the biomass (in irreversible mass equivalents) of resource j consumed by the (super)individual predator i; $PIng_i$ is the potential ingestion of each component of (super)individual i and N_i is the number of components; B_j is the biomass of eligible resource j (which can include fishes); k is the number of eligible resources; and $\alpha_{i,j}$ is the attack rate of predator i on resource j. The exponent 2 defines the type III functional response, which can result from implicit spatial refuges for prey or prey switching (Koen-Alonso 2007), and help to stabilize the dynamics, so it was preferred.

5.5.4. *Predation dynamics.* Individuals compete asymmetrically. If the resource density at the beginning of a time unit is not enough to supply the whole assemblage demand, it will be distributed unevenly among the consumers. The process by which it takes place is the ordering of consumers during the predation cycle. The first individuals having access to food will experience higher resource availability. As consumption goes on, individual after individual, the resource density is depleted, and the last individuals in the sequence will have less chance to supply their demands. As a null model, this ordering could be completely random. But any other biologically more meaningful rule can be used, determining which kind of organisms should have competitive advantage. For example, the foraging activity level is supposed to influence positively the competitive ability (Wellborn *et al.* 1996). To incorporate such relation, the consumers with higher activity levels must assume former positions to access food along the predation sequence. The activity level is assumed here as proportional to the growth rate coefficient ζ, which could partially explain why faster growing species also have higher metabolic demands (i.e. due to more intense activity). Another component giving an advantage in resource capture is the degree of specialization. By including such a component, we introduce a tradeoff between diet generality and predation efficiency. Either the species is very good at exploiting a few resources, or it is able to consume a great variety of food, but at the expense of being less efficient. So a suitable ordering function to model all these tradeoffs is given by $\zeta/(\varepsilon - \delta)$. A given consumer individual has a chance proportional to this function (whose parameters are species-specific) to be drawn first during the predation sequence. So (super)individuals are drawn one by one

with relative chances determined by this ordering function. As the process is stochastic, the sequence may not necessarily be the same in the next time step.

If the consumer is piscivorous, the eligible fish prey must also be ordered in some manner, either randomly or biologically-based. The last prey in the sequence will have higher survival chances, as the predator has a limited demand (given by $F_{i,fish}$). The interesting point here is the possibility to include a tradeoff between competitive ability and vulnerability to predation, if the parameter used to order fish consumers is also used to order fish prey. This parameter is assumed to be ζ, due to its direct relation to activity level, so that more active prey are more prone to be detected by a given predator (Wellborn *et al.* 1996; Lima 1998). The ordering function used to sort potential fish prey for each individual consumer is then given just by ζ (i.e. each eligible prey will have a chance proportional to ζ to be consumed first) Potential prey in the egg/embryo life stage are assumed to have no activity at all, so their ordering function is multiplied by zero, making them less susceptible to predation (within a given list of eligible prey). If some potential prey are of the same species of the predator, their ordering function is further multiplied by an additional parameter *Cann* characterizing that predator. It measures the level of cannibalism, varying from 0 to 1, and is species-specific. Species with *Cann* = 0 never prey on co-specifics. On the other extreme, when Cann = 1, the predator is indifferent to whether the prey pertains or not to the same species.

A piscivorous fish feeds sequentially on fish individuals, until the energetically weighted consumed biomass exceeds $F_{i,fish}$. The last prey in this sequence (a unitary individual or a superindividual component), whose total weight exceeds the remaining predator demand, may or may not be consumed depending on how large this remaining demand is. Suppose the remaining demand is equal to f, and the weight of last prey is W, then a uniformly distributed random number between 0 and W is drawn. If this random number is lower than f, then that prey is consumed. But its consumption is partial; only an amount sufficient to complete the predator's demand for fish $F_{i,fish}$, is consumed. Even so, this last partially consumed individual is considered dead, and all its weight exceeding the predator demand (W – f) is lost from the system.

After having its chance to consume, the individual enters the growth module and will still be available to be preyed on by piscivorous fish thereafter. If the amount of food consumed by a super-individual is not sufficient for the survival of all its components, the food is uniformly distributed among them giving to each a minimum amount, in such a way to maximize the number of survivors. The predation cycle proceeds until all (super)individuals have had the chance to eat and/or have been eaten.

5.5.5. *Reproduction.* Each species has a characteristic timing parameter (η), which determines the position of its biological period in relation to the absolute annual period. As a consequence of the initial condition for resource carrying capacity, the season at time t = 0 is analogous to mid-spring. So, if η = 0, 0.25, 0.5 or 0.75, the last yearly spawning event would occur at the mid-spring, the summer peak, the mid-autumn and the winter peak, respectively. These strategies can have important influences on offspring survival in such seasonal environment. At the moment an individual becomes an adult, it will act immediately in synchronization with other adult co-specifics, following the calendar imposed by its timing parameter. The adult can spawn a given fraction of the gonad content in each time unit during the proportion of year it is able to reproduce (1 – p). This fraction is defined as a function of a spawning uniformity parameter (u):

$$f_t = \rho^{\left(\frac{1}{u}-1\right)}$$ Eq. (A10)

where ρ is the elapsed proportion (0-1) of the time interval in which the individual is able to reproduce, and f_t is the fraction of gonad contend (0-1) which must be spawned at time t. For u approaching zero, the species will tend to spawn only in the last time unit of the reproductive period, characterizing an extreme batch spawner (Figure A2a). For u = 1, the gonad content will always be completely used for spawning, and never stored, representing an extreme fractional spawner. In this last case, as the potential surplus production will be the same along the entire reproductive period, the number of eggs spawned can be completely uniform along this period (Figure A2c). Intermediate u values produce spawning peaks at intermediate times along the reproductive periods (Figure A2b). As we are modelling female individuals, the conversion efficiency from the spawned weight to hatchlings is 50%, assuming the rest of the offspring become males (Persson *et al.* 1998).

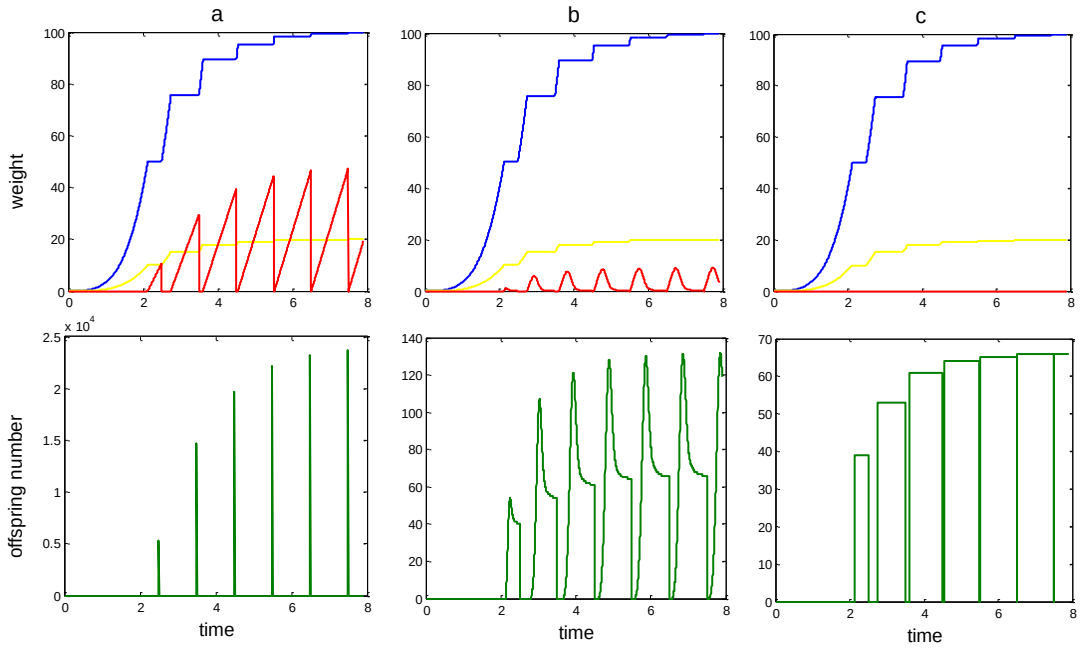


Figure A2. Examples of growth curves generated by the model, following a size-based determination of p (Eq. 8), and feeding *at libitum*. In the upper panels, the blue and yellow lines are X and Y mass and the red ones are G. In the lower panels, the green lines represents the number of offspring spawned in each day (D = 365). (a) u = 10^{-10}; (b) u = 0.25; (c) u = 1. Other parameters are: X_{inf} = 100; X_{mat} = 50; qj = qa = 0.2; W_0 = 0.001; X_0 = 0.0001; a = 0.1; c = 0.07; β = 0.75; η = 0.5; γ = 0,125; τ = 2.5.

Longevity. The longevity usually follows an allometric relationship with the body size, described by a power function (Calder 1984). In our case, the irreversible mass is the size reference, so that:

$$T_{max} = \tau X_{inf}^{0.25} \qquad \text{Eq. (A11)}$$

where T_{max} is the maximum life-spam (years), τ is a coefficient of proportionality and the exponent 0.25 the usually observed and predicted by metabolic theory (Savage *et al.* 2004). Whenever T = T_{max}, the individual is "deleted" from the community.

5.5.6. *Immigration*. In each time step, a given number of propagules (*propag*) are introduced into the community. Their identities are determined by a Monte Carlo approach. Each propagule pertains to a newly created species, with a unique combination of parameter values. The parameter values are drawn randomly and independently from uniform probability distributions (X_{inf} is a potential exception), whose limits are presented in Table A1 (*Bionomic parameters*). The maximum body size (X_{inf}) characterizing the species pool was chosen to follow a power-law distribution:

$$p(X_{inf}) = \varpi X_{inf}^{\xi} \qquad \text{Eq. (A12)}$$

where $p(X_{inf})$ is the probability density function of X_{inf}, ξ is an exponent defining the shape of the distribution and ϖ is a normalization constant chosen so that the Eq. (A12) integrates to 1

between the limits imposed to X_{inf} (Table A1). Negative ξ values with high magnitudes produce distributions strongly skewed towards small body sizes. A null value of ξ corresponds to the uniform distribution.

The value of *propag* was fixed at 3 ind/week (just one by species), and introductions occurred until an arbitrarily defined time span (t = 50 years) was reached. Each propagule is initialized in the same condition of a newborn egg of the species it represents.

Table A1. Parameters, variables and constants used in the model. The references are those that supplied information on the referred parameters, and also those that help estimating their values (although some values are not exactly the same from the original works).

Symbol	Unit	Values and functions	Description	References
Bionomic parameters				
$\alpha_{i,j}$	$g^{(-2)}$/week	0 - α_{max}	Attack rate of individual i on resource j	
a	$g^{(1-\beta)}$ /week	0.2 -0.8	Coefficient of the function for potential ingestion	
β		0.75	Common exponent of the functions for potential ingestion, weight loss, and growth rate	Savage *et al.* (2004)
c	$g^{(1-\beta)}$ /week	(1-ω)a	Coefficient of the function for weight loss	
Cann		0 - 1	Level of cannibalism	Giacomini *et al.* (2009)
δ		0 - 0.07	Coefficient for the lower limit of the predation window.	van de Wolfshaar *et al.* (2006); van Kooten *et al.* (2007)
ε		0.01 – 0.7	Coefficient for the upper limit of the predation window.	(van de Wolfshaar *et al.* (2006); van Kooten *et al.* (2007)
γ		0.125	Ratio of energetic content of irreversible mass to reversible mass or gonads	Weatherley & Gill (1987); Jobling (1994)
ζ	$g^{(1-\beta)}$ /week	ωa	Coefficient of the function for potential growth rate	
η		0 - 1	Reproductive timing	
propag	ind/week	3	Number of propagules introduced each time step	
qa		0.1	Maximum attainable condition (Y/X) of an adult.	Weatherley & Gill (1987); Jobling (1994)
qj		0.1	Maximum attainable condition (Y/X) of a juvenile.	Weatherley & Gill (1987); Jobling (1994)

θ		0.1 – 0.8	Relative size at maturation = X_{mat}/X_{inf}	
T_{max}	years	Eq(A11)	Longevity	Calder (1984)
τ	$year^{0.75}$	2.7	Coefficient of the allometric function of longevity	
u		10^{-10} - 1	Uniformity of spawning along time	
ϕ		0 - 1	Piscivory level	
ω		0.3	Proportion of ingested energy devoted to production	Brett & Groves, (1979); Weatherley & Gill (1987)
Ω	g/cm^3	0.01	Coefficient of weight-length relationship	Froese & Pauly (2005); Giacomini *et al.* (2009)
W_0	g	0.001 - 0.1	Egg size	
X_{inf}	g	5 - 1000	Asymptotic irreversible mass	
X_{mat}	g	θX_{inf}	Irreversible mass at maturity	
Resource parameters				
φ		0.3	Relative amplitude of seasonal carrying capacity oscillations	
k	number of resources	100	Number of basal resources	
K	g	Eq.(A2)	Carrying capacity of a resource, for a spatial cell	
l_{min}	cm	100 logarithmically equally spaced values from 0.01 to 9.74	Lower limit of a resource size interval.	
l_{max}	cm	100 logarithmically equally spaced values from 0.0345 to 10.00	Upper limit of a resource size interval.	
μ_K	g	$\{10^2, 10^3, 10^4, 10^5, 10^6\}$	Mean carrying capacity of a resource	
R	$week^{-1}$	Eq.(A3)	Intrinsic rate of increase of resource biomass.	Fenchel (1974); Savage *et al.* (2004)
Assembly parameters				
α_{max}	$g^{(-2)}$/week	$\{10^{-7}, 10^{-6}, 10^{-5}, 10^{-4}, 10^{-3}\}$	Maximum attack rate allowed by the environment	
ξ		{-2, -1, 0}	Exponent shaping the power-law distribution of X_{inf} in species pool	

5.6. References

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