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## Effects of productivity, disturbance, and ecosystem size on food-chain length: insights from a metacommunity model of intraguild predation

Received: 2 October 2011 / Accepted: 24 January 2012 / Published online: 26 February 2012  
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**Abstract** Traditionally, productivity and disturbance have been hypothesized as important determinants of food-chain length. More recently, growing empirical evidence suggests a strong role of ecosystem size. To theoretically explore the effects of basal productivity, disturbance, and ecosystem size on food-chain length, we develop and analyze a metacommunity model of intraguild predation (IGP). The model finds that, when local IGP is weak, increasing basal productivity, weakening disturbance, and increasing ecosystem size will generally increase food-chain length. When local IGP is strong, by contrast, increasing basal productivity or weakening disturbance favors intraguild predators and hinders the coexistence of intraguild predators and intraguild prey, limiting food-chain length. In contrast, increasing ecosystem size can promote coexistence even when local IGP is strong, increasing food-chain length through inserting intraguild prey and changing the degree of omnivory by intraguild predators. Intraguild

prey needs to be the superior colonizer to intraguild predators for this to occur. We discuss that these theoretical predictions appear consistent with empirical patterns.

**Keywords** Disturbance · Ecosystem size · Food-chain length · Intraguild predation · Metacommunity · Productivity

### Introduction

Food-chain length is a central property of ecological communities that affects many of their functional aspects, such as primary and secondary production (Pace et al. 1999), population and community stability (Pimm and Lawton 1977), material cycling (DeAngelis et al. 1989), and concentration of contaminants in top predators (Kidd et al. 1998). Since Elton (1927) first noted variation in food-chain length among natural communities, many factors have been proposed to explain this variation, including basal productivity, disturbance, ecosystem size (area or volume), habitat heterogeneity, species richness, design and size constraints, optimal foraging, and the history of community organization (Pimm 1982; Post 2002).

The role of basal productivity, disturbance, and ecosystem size in determining food-chain length have received the most attention, and a number of distinct theories have been developed to explore ultimate mechanisms by which each potential determinant affects food-chain length (Pimm 1982; Lawton 1989; Persson et al. 1996; Post 2002). The effect of basal productivity is usually assumed to arise from incomplete energy transfer between trophic levels—a form of the second law of thermodynamics. The low efficiency of energy transfer per trophic level, around 10% but ranging from 2 to 50% (Pauly and Christensen 1995), implies that energy availability will inevitably decline with increasing trophic position, to a point where additional trophic levels cannot be sustained. Food chains are thus expected to be

**Electronic supplementary material** The online version of this article (doi:10.1007/s11284-012-0929-5) contains supplementary material, which is available to authorized users.

Gaku Takimoto is the recipient of the 15th Denzaburo Miyadi Award.

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longer where productivity at the base of food chains is higher (Elton 1927; Hutchinson 1959; Slobodkin 1961; Oksanen et al. 1981), and where energy-use efficiency of consumers is higher (Yodzis 1984). The effect of disturbance emerges from theoretical models that showed that longer food chains were less resilient to perturbations at the model equilibrium (Pimm and Lawton 1977). Such low resilience due to biotic interactions contained in long food chains is called dynamic constraints to food-chain length. Because dynamic constraints prevent long food chains from persisting in habitats with frequent or severe disturbance, food chains are expected to be shorter in more disturbed habitats (Pimm and Lawton 1977; Pimm 1982; but see Sterner et al. 1997). Effects of ecosystem size may arise through multiple mechanisms (Post et al. 2000; Holt 2002, 2010). Food chains are expected to be longer in larger ecosystems, because larger space provides greater total basal resources (Schoener 1989), contain more species and thus often higher-order predators (Cohen and Newman 1991), foster metapopulation dynamics (Holt 1993, 1996, 1997), and weaken dynamic constraints and stabilize predator–prey interactions (Spencer and Warren 1996; Wilson et al. 1998; Holt 2002).

Recently, an increasing number of empirical studies have tested and compared the effects of productivity, disturbance, and ecosystem size on food-chain length (e.g., Post et al. 2000; Takimoto et al. 2008; Sabo et al. 2010; references in Takimoto and Post, in preparation). A recent meta-analysis summarizing these findings suggests that, on average, the effects of productivity and ecosystem size are comparably strong, and the disturbance effect is the weakest (Takimoto and Post, in preparation). Despite these advances in empirical research, there are currently few theoretical attempts to examine and compare the effects of productivity, disturbance, and ecosystem size within a single framework.

Moreover, most theoretical studies to date have assumed that communities are organized into neat trophic levels, in the simplest case represented as simple, linear unbranched food chains. For such communities, food-chain length varies via the sequential addition or subtraction of species on distinct trophic levels. However, food webs are more complex than this, because of omnivory, where species' trophic roles in effect straddle multiple levels. A richer array of possible factors influencing food-chain length arises with omnivory. Intraguild predation (IGP) involving three species is the simplest food-web module with trophic omnivory. This module includes an intraguild predator (denoted IG-predator) which prey upon an intraguild prey species (denoted IG-prey), with both species feeding as well upon a basal resource (and hence potentially competing for this resource (Polis et al. 1989; Holt and Polis 1997)). Unlike linear food chains without trophic omnivory, the IGP module can embody three fundamentally distinct structural causes of variation in food-chain length: (1) addition (or removal) of top predators (an “additive mechanism”, comparable to what happens in linear food chains), (2) insertion (or removal) of intermediate predators (an

“insertion mechanism”), and (3) change in the degree of omnivory (an “omnivory mechanism”) (Post and Takimoto 2007). During community assembly, the additive mechanism occurs when the basal resource establishes first itself in a system without any species, the IG-prey then enters the system having the basal resource, and finally the IG-predator joins the system having the basal resource; this also occurs when the IG-predator arrives without the IG-prey being present. The insertion mechanism by contrast occurs when the IG-prey enters a system already consisting of the IG-predator and the basal resource. Finally, the omnivory mechanism occurs when species composition remains unchanged, but the IG-predator changes its dietary proportions between the IG-prey and the basal resource due for instance to changes in environmental conditions. Addition of top predators has been a widely recognized mechanism that changes food-chain length (e.g., Holt et al. 1999; Calcagno et al. 2011); however, recent empirical evidence suggests that the insertion and omnivory mechanisms can also explain substantial variation of food-chain length among communities (Post et al. 2000; Takimoto et al. 2008; McHugh et al. 2010).

Here we develop a metacommunity model of IGP to theoretically examine the simultaneous and interacting effects of basal productivity, disturbance, and ecosystem size on food-chain length. Drawing upon previous work, we hypothesize that increasing basal productivity, weakening disturbance, and increasing ecosystem size could increase food-chain length, even with omnivory. However, the potential for strong top-down effects of IG-predators on IG-prey could potentially constrain or alter these effects. More specifically, we address the following questions to gain insights about ultimate and proximate mechanisms by which environmental variables affect food-chain length: (1) is there any difference in strength among the effects of basal productivity, disturbance, and ecosystem size on food-chain length? (2) How do environmental determinants and the strength of local biotic interactions (i.e., dynamic constraints) interact to affect food-chain length? (3) What structural mechanisms (i.e., additive, insertion, and omnivory mechanisms) drive responses of food-chain length along environmental gradients? (4) Is there any interaction among the effects of these multiple determinants of food-chain length? Many ecologists have come to appreciate that explanations of ecological patterns often require invocation of multiple, complementary mechanisms, and we suspect that the same is true for determinants of food-chain length. By using a single mathematical model, our approach will offer a more unifying perspective about the effects of basal productivity, disturbance, and ecosystem size on food-chain length.

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## Model

### Formulation

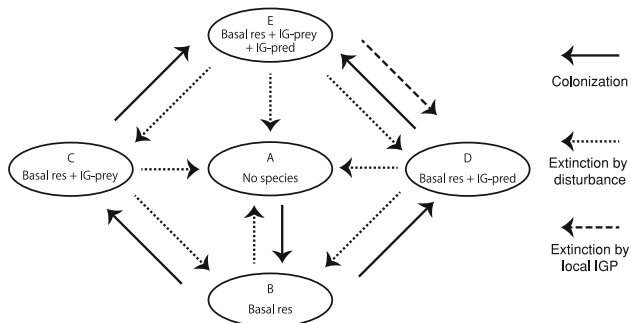
The metacommunity model that we develop extends the patch-dynamic framework of the Levins metapopulation

model (Levins 1969; Levins and Culver 1971) to consider multiple species interacting in an array of patches, coupled by dispersal (Leibold et al. 2004). To build up the model, we first need to specify the states that each patch can display. We then have to characterize the transitions among these states in terms of rates of colonization and extinction.

Given omnivory, a single patch can contain various combinations of local populations of the basal resource, the IG-prey, and/or the IG-predator. Thus, a patch can take either one of five possible states (for convenience denoted A, B, C, D, and E), depending on which species occur in the patch (Fig. 1). State A is an empty patch without any local population of any of these three species. State B is a patch with only the basal resource population. State C is a patch that has populations of the basal resource and the IG-prey. State D is a patch containing populations of the basal resource and the IG-predator. Finally, state E is a patch with populations of all three species.

State transitions among each of these can occur via colonization and extinction of local populations (Fig. 1). We first consider extinction dynamics. We assume that extinction of a local population is caused either by an extrinsic factor—disturbance—or by a deterministic factor intrinsic to the community module itself—the top-down force of IGP. Note that our assumption about extinctions differs from many metapopulation scenarios, where extinctions arise in small populations due to demographic stochasticity, even in constant environments. When disturbance hits a local population, the population goes extinct with a certain probability. If we assume that these disturbances are continually occurring at a local level, over enough patches, but not spatially or temporally auto-correlated, we can characterize the extinction dynamics as a constant extinction rate, amounting to an exponential distribution of waiting times to extinction.

The extinction of the basal resource necessarily causes extinction of the consumers that depend upon it, and in addition the consumers may go extinct on their own, leaving behind the basal resource, or maybe the IG-prey with the basal resource (if the local patch contained the



**Fig. 1** Transition between patch states. A patch can take either one of six states A–E. Species occurring at different patch states are shown in ellipses. Patch transition occurs via colonization, extinction due to disturbance, or extinction due to local IGP

full module to start with). A key assumption of our model is thus that local extinction of the basal resource causes simultaneous local extinction of the IG-prey and/or the IG-predator, because the IG-prey and the IG-predator cannot persist in patches without the basal resource. A patch in state B can experience just one kind of extinction transition:  $B \rightarrow A$ . We assume this can be represented by an extinction rate of  $e$ .

Now consider a patch in state C. It can experience two possible extinction events:  $C \rightarrow A$  (basal resource goes extinct, dragging along the IG-prey), or  $C \rightarrow B$  (the IG-prey alone goes extinct). These are mutually exclusive possibilities, so we can add the probabilities that they occur in a small amount of time  $dt$ , and thus add the rates of occurrence of these extinction events. For simplicity, we will assume that both these possibilities occur at the same rates, which in effect means that both species have the same sensitivity to perturbation by a disturbance, and the consumer has no effect on the extinction rate of the basal resource. So the total rate of transition out of this state via extinction should be  $2e$ . In like manner, the total rate of transition of state D (to A, or B), should also be  $2e$ . Finally, if we assume that it is vanishingly unlikely that a given disturbance will eliminate both the IG-predator and the IG-prey from a patch, the transitions are  $E \rightarrow A$  (basal resource disappears, as do both consumers), and  $E \rightarrow D$  and  $E \rightarrow C$ ; the net rate of these disturbance-driven extinctions should be  $3e$ . In addition, for patches in state E, the IG-prey experiences an elevated risk of extinction, due to IGP, which adds an amount  $a$  to the transition from E to D. We assume that increasing the strength of local IGP increases the magnitude of  $a$ , which is added to  $e$ , the extinction rate of a local population due to disturbance. The magnitude of  $e$  is our measure of disturbance rate. Likewise,  $a$  is the extinction rate of the IG-prey due to IGP.

We now turn to transitions among states via colonization. Colonization of a local population occurs when propagules reach a patch unoccupied by a given species, and successfully establish a new local population there. (Here we call a group of individuals colonizing a patch a “propagule.”) One can break down the rate constant of colonization for species  $i$ ,  $c_i$  (e.g., as used in Holt 1997), into two components:  $m_i$  is the realized number of propagules of species  $i$  originating from a local parental population per unit time (see below) which reach a given empty patch, and  $s_i$  is the probability that a propagule of species  $i$  establishes a local population upon arrival to a patch unoccupied by this species. Hence,  $c_i = m_i s_i$ .

We assume that the propensity of a patch occupied by a given species to colonize empty patches is unaffected by the presence of the other species occupying this patch (a limiting case of the more complex scenarios explored in Holt 1997). So for instance the rate of transition from A to B is determined by multiplying the availability of patches in state A, times the simple unweighted, summed abundance of patches in states B, C, D, and E (all of which have the IG-prey). A similar

assumption applies to the other transitions via colonization.

With these assumptions in hand, we can now write down the formal model. Letting  $p_X$  denote the frequencies of patches of state X (X = A, B, ..., E), the dynamic equations of patch frequencies are

$$\begin{aligned} \frac{dp_B}{dt} = & s_1 m_1 (p_B + p_C + p_D + p_E) p_A + e p_C + e p_D \\ & - s_2 m_2 (p_C + p_E) p_B - s_3 m_3 (p_D + p_E) p_B - e p_B, \end{aligned} \quad (1a)$$

$$\begin{aligned} \frac{dp_C}{dt} = & s_2 m_2 (p_C + p_E) p_B + e p_E - s_3 m_3 (p_D + p_E) p_C \\ & - 2e p_C, \end{aligned} \quad (1b)$$

$$\begin{aligned} \frac{dp_D}{dt} = & s_3 m_3 (p_D + p_E) p_B + (e + a) p_E - s_2 m_2 (p_C + p_E) p_D \\ & - 2e p_D, \end{aligned} \quad (1c)$$

$$\begin{aligned} \frac{dp_E}{dt} = & s_2 m_2 (p_C + p_E) p_D + s_3 m_3 (p_D + p_E) p_C \\ & - (3e + a) p_E, \end{aligned} \quad (1d)$$

where the subscripts  $i = 1, 2,$  and  $3$  represent the basal resource, the IG-prey, and the IG-predator, respectively.

To reiterate, the above model assumes that the realized numbers of propagules emanating from patches, and the establishment probabilities within patches, depend only on species identity, but not on patch states, and moreover that all species share a common and quantitatively equivalent susceptibility to disturbance, irrespective of patch states. A more general model without these assumptions was presented in online supplement. The model moreover does not consider complications such as the rescue effect (Gotelli 1991; Harding and McNamara 2002). However, importantly, we do consider an effect of changing total number of patches,  $T$ . Imagine that the arena of the metacommunity occupies an area  $A$ . If there are few patches present, at random across this arena, distances will be large, and many potential colonists will be lost, prior to reaching potential sites of colonization. Changes in the density of patches should thus influence the likelihood of successfully colonization. Specifically, we assume that the realized number of propagules,  $m_i$ , depends on  $T$ , and reach a maximum number,  $M_i$ , when  $T$  is sufficiently large. Formally,

$$m_i = m_i(T) = \begin{cases} T & (T \leq M_i) \\ M_i & (T > M_i) \end{cases}. \quad (2)$$

We present detailed derivation of this formulation in the online supplement. Put simply, this formulation assumes that a local population produces a fixed number,  $M_i$ , of propagules, but only a part of it can find target patches when  $T$  is small.

To facilitate model analysis, we conduct variable transformation:  $p_1 = p_B + p_C + p_D + p_E$ ,  $p_2 = p_C + p_E$ , and  $p_3 = p_D + p_E$ . New variables,  $p_i$  ( $i = 1,$

$2,$  and  $3$ ), represent the total frequencies of patches having the basal resource, the IG-prey, or the IG-predator, respectively. The transformed model is

$$\frac{dp_1}{dt} = s_1 m_1 (1 - p_1) p_1 - e p_1, \quad (3a)$$

$$\frac{dp_2}{dt} = s_2 m_2 (p_1 - p_2) p_2 - 2e p_2 - a p_E, \quad (3b)$$

$$\frac{dp_3}{dt} = s_3 m_3 (p_1 - p_3) p_3 - 2e p_3, \quad (3c)$$

$$\frac{dp_E}{dt} = s_2 m_2 (p_3 - p_E) p_2 + s_3 m_3 (p_2 - p_E) p_3 - (3e + a) p_E. \quad (3d)$$

The following analysis is based on this transformed model. When necessary, we calculate  $p_B$ ,  $p_C$ , and  $p_D$  from  $p_1$ ,  $p_2$ ,  $p_3$ , and  $p_E$  by using the above relationships.

### Environmental gradients

To examine how food-chain length responds to basal productivity, disturbance, and ecosystem size, we define these environmental variables in terms of model parameters. The gradient of basal productivity is expressed as changes in the establishment probability ( $s_1$ ) or the rate of propagule production ( $M_1$ ) by a basal-resource population. This definition is based on the idea that the increase of basal productivity will enhance the local establishment of basal-resource populations, and/or increase the production of propagule populations by the basal resource. The disturbance gradient is modeled as changes in the disturbance rate ( $e$ ). The ecosystem-size gradient is expressed as changes in the total patch number ( $T$ ). We note that increasing  $T$ , while fixing other parameters, will also increase the total basal productivity of the ecosystem. Since most empirical tests of the ecosystem-size effect examine the ecosystem-size gradients without controlling for the increase of total basal productivity, we use the increase of  $T$  without changing other parameters as the ecosystem-size gradient in our model. Additionally, we provide supplementary analysis about the effect of increasing  $T$  while keeping total basal productivity constant, to examine genuine effects of ecosystem size without the effect of total basal productivity. In this case, we will consider  $s_1 M_1 T$  as a measure of total basal productivity.

### Definition of food-chain length

We define food-chain length in our model as the trophic position of the top species in the ecosystem. This reflects three primary structural mechanisms causing changes in food-chain length: additive, insertion, and omnivory mechanisms (Post and Takimoto 2007). The top species is the one not eaten by any other species in the ecosystem. Depending on which species occur in the ecosystem, the top species can be either the IG-predator, the

IG-prey, or the basal resource. The IG-predator is the top species whenever it occurs in the ecosystem. In this case, food-chain length is defined as the trophic position of the IG-predator averaged across all of its occupying patches. Thus, the food-chain length in this case is  $(2p_D + 2.5p_E)/(p_D + p_E)$ , in which we assume that the IG-predator in patches of state E has the trophic position of 2.5. This value means that IG-predator individuals consume on average the same amount of the IG-prey and the basal resource in patches of state E. Choosing other values does not qualitatively alter our conclusions. Depending on the relative frequencies of  $p_D$  and  $p_E$ , the food-chain length can vary from 2 to 2.5. We consider the change of food-chain length due to changes in relative frequencies of  $p_D$  and  $p_E$  as the omnivory mechanism, because changing the relative frequencies of  $p_D$  and  $p_E$  results in different proportions of energy derived directly from the basal resource or from the IG-prey contributing to the whole IG-predator populations in the ecosystem. When the ecosystem has only the IG-prey and the basal resource, the top species is the IG-prey and the food-chain length is two (i.e., IG-prey's trophic position). When only the basal resource occurs in the ecosystem, the top species is the basal resource and the food-chain length is one (i.e., basal resource's trophic position). When no species occurs in the ecosystem, the food-chain length is zero.

**Model equilibria**

Before we analyze how food-chain length changes along environmental gradients, we examine the equilibria of model (3a–3d) and conditions for their existence (see online supplement for details). The model has five equilibria (I, II, III, IV, and V; Table 1). At equilibrium I, no species has positive frequency. Equilibrium II has only the basal resource. Equilibrium III has the basal resource and the IG-prey, and equilibrium IV has the basal resource and the IG-predator. Equilibrium V is a unique internal equilibrium with all species present.

The condition for equilibrium II to be feasible is

$$1 > \frac{e}{s_1 m_1}. \tag{4}$$

This condition means that sufficiently small  $e$  or sufficiently large  $s_1$  and  $m_1$  are necessary for the basal

resource to occur in the ecosystem. For equilibrium III to be feasible, the condition,

$$1 > \frac{e}{s_1 m_1} + \frac{2e}{s_2 m_2}, \tag{5}$$

should be satisfied. This condition is more stringent than condition (4), because the IG-prey can occur only if the basal resource is present (see, e.g., Holt 1997). Similarly, the condition

$$1 > \frac{e}{s_1 m_1} + \frac{2e}{s_3 m_3}, \tag{6}$$

is necessary for equilibrium IV to be feasible. This condition is also more stringent than condition (4), because the IG-predator cannot occur without the basal resource. Finally, equilibrium V is feasible when conditions (4–6) are satisfied, and either

$$1 < \frac{e}{s_1 m_1} + \frac{2e}{s_2 m_2} \left( \frac{s_2 m_2}{s_3 m_3} \right)^2 = \frac{e}{s_1 m_1} + \frac{2e}{s_3 m_3} \left( \frac{s_2 m_2}{s_3 m_3} \right), \tag{7a}$$

or

$$a < \frac{s_2 m_2 \left( 1 - \frac{e}{s_1 m_1} - \frac{2e}{s_2 m_2} \right) \left( 1 - \frac{e}{s_1 m_1} + \frac{e}{s_3 m_3} \right)}{1 - \frac{e}{s_1 m_1} - \frac{2s_2 m_2 e}{(s_3 m_3)^2}}, \tag{7b}$$

is satisfied. Under conditions (5) and (6), condition (7a) can be satisfied only if  $(s_2 m_2)/(s_3 m_3)$  is sufficiently larger than one. One interesting conclusion from (7a) is that an IG-prey can persist for any level of top down influence of the IG-predator in local communities, provided it can disperse sufficiently faster than the IG-predator and occupy sites opened by disturbance. Conditions (7a) and (7b) imply that, for the IG-prey and the IG-predator to coexist at equilibrium, the strength of local IGP ( $a$ ) must be sufficiently small unless the colonization rate of the IG-prey ( $s_2 m_2$ ) is sufficiently larger than that of the IG-predator ( $s_3 m_3$ ).

**Food-chain length along environmental gradients**

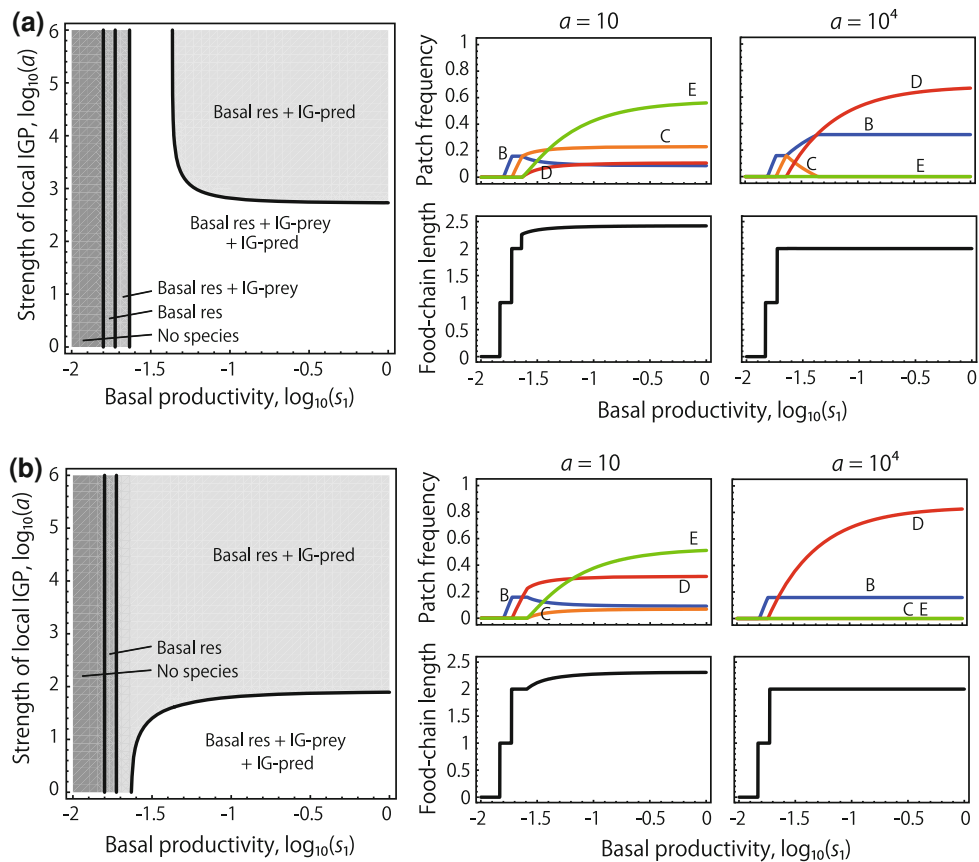
**Basal productivity**

We examine the effects of basal productivity by changing the parameters  $s_1$  and  $M_1$ . In either case, we find that the

**Table 1** Equilibrium of the model (3a–3d)

Equilibrium	$\bar{p}_1$	$\bar{p}_2$	$\bar{p}_3$	$\bar{p}_E$
I	0	0	0	0
II	$1 - \frac{e}{s_1 m_1}$	0	0	0
III	$1 - \frac{e}{s_1 m_1}$	$1 - \frac{e}{s_1 m_1} - \frac{2e}{s_2 m_2}$	0	0
IV	$1 - \frac{e}{s_1 m_1}$	0	$1 - \frac{e}{s_1 m_1} - \frac{2e}{s_3 m_3}$	0
V	$1 - \frac{e}{s_1 m_1}$	$\bar{p}_{2,V}$ <sup>a</sup>	$1 - \frac{e}{s_1 m_1} - \frac{2e}{s_3 m_3}$	$\frac{\bar{p}_{2,V}}{a} \left\{ s_2 m_2 \left( 1 - \frac{e}{s_1 m_1} - \bar{p}_{2,V} \right) - 2e \right\}$

<sup>a</sup>  $\bar{p}_{2,V}$  is the larger solution of the quadratic equation,  $(\bar{p}_2 - A)(\bar{p}_2 + B) = C$ , where  $A = \{s_1 s_2 m_1 m_2 - e s_2 m_2 - e(a + 2)s_1 m_1\}/s_1 s_2 m_1 m_2$ ,  $B = \{s_1 s_3 m_1 m_3 - e s_3 m_3 + e s_1 m_1\}/s_1 s_2 m_1 m_2$ , and  $C = e^2 a (2s_2 m_2 + s_3 m_3)/s_2^2 s_3 m_2^2 m_3$



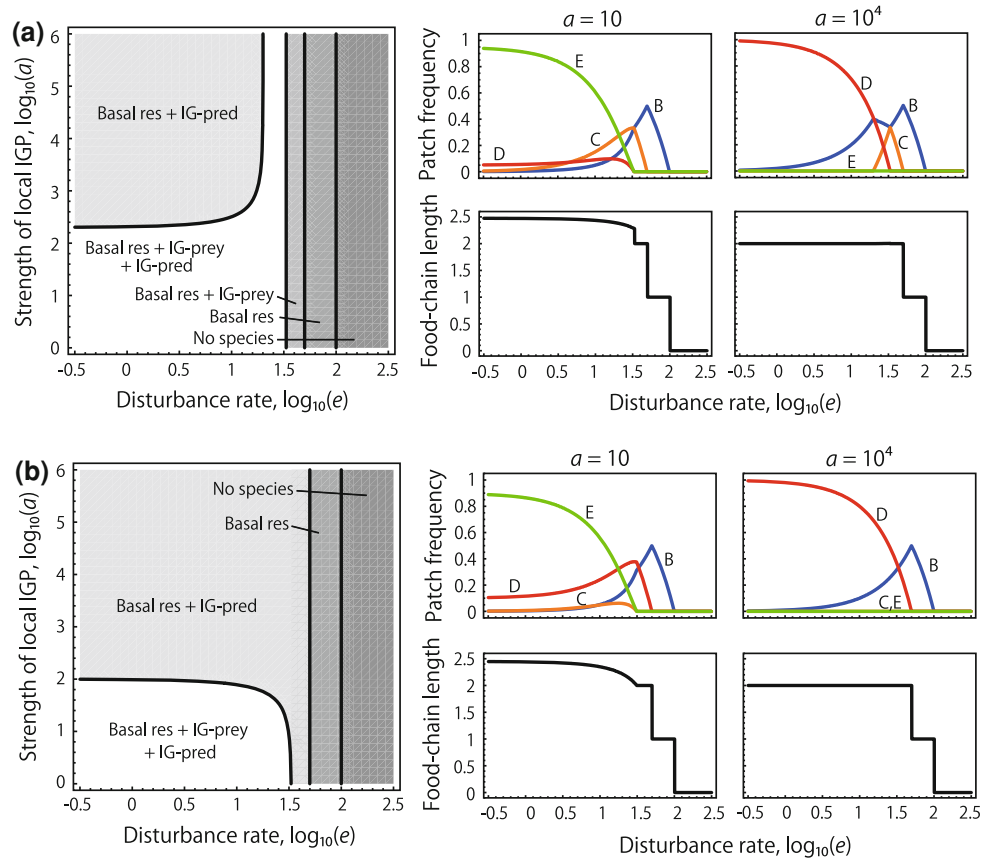
**Fig. 2** Equilibrium and food-chain length along the basal-productivity gradient with different strength of local IGP. **a, b** Left panels show the equilibrium attained with different basal productivity and strength of local IGP. Different equilibria realized in respective regions (equilibrium I–V; see text and Table 1) are termed as “No species”, “Basal res”, “Basal res + IG-prey”, “Basal res + IG-pred”, and

“Basal res + IG-prey + IG-pred”. Four right panels show responses of the frequencies of patches of different states (B–E) and food-chain length along the basal productivity gradient when  $a = 10$  and  $10^4$ . Specific parameter values used are **a**  $s_2 = 0.2$ ,  $s_3 = 0.1$ , and **b**  $s_2 = 0.1$ ,  $s_3 = 0.2$ . For other parameters, common values are used:  $M_1 = 10^6$ ,  $M_2 = 10^5$ ,  $M_3 = 10^4$ ,  $e = 10^{1.2}$ , and  $T = 10^3$ .

strength of local IGP has large influences. That is, strong local IGP tends to hinder the coexistence of the IG-prey and the IG-predator and to prevent a food chain from becoming longer than 2, as basal productivity becomes high. We illustrate this along the gradient of  $s_1$  (Fig. 2). The order of species that become able to invade the ecosystem depends on whether the colonization rate of the IG-prey, ( $s_2m_2$ ) is greater or smaller than that of the IG-predator ( $s_3m_3$ ) (online supplement). When  $s_2m_2 > s_3m_3$  (Fig. 2a), no species can persist in the ecosystem with very small  $s_1$ , with food-chain length being zero. An increase in  $s_1$  then allows the basal resource to enter the ecosystem, elevating food-chain length to 1 by the additive mechanism. A further increase in  $s_1$  permits the entrance of the IG-prey causing an increase of food-chain length to 2 (by the additive mechanism), and an even further increase allows the entrance of the IG-predator with food-chain length becoming greater than 2 (the additive mechanism). As  $s_1$  becomes even larger, the strength of local IGP ( $a$ ) starts to affect food-chain length. When

$a$  is relatively small, larger  $s_1$  promotes the IG-predator–IG-prey coexistence, causing monotonic increases in food-chain length (by the omnivory mechanism). When  $a$  is large, larger  $s_1$  augments the IG-predator, which in turn causes the extinction of the IG-prey. This leaves only the IG-predator and the basal resource in the ecosystem, reducing food-chain length to 2 (by the insertion mechanism). Further increases in  $s_1$  do not recover the IG-predator–IG-prey coexistence, and food-chain length remains at 2.

When  $s_2m_2 < s_3m_3$  (Fig. 2b), on the other hand, the entrance of the basal resource is followed by the entrance of the IG-predator as  $s_1$  increases, with sequential increases in food-chain length by the additive mechanism. When  $a$  is relatively small, further increases in  $s_1$  allows the entrance of the IG-prey (by the insertion mechanism), with subsequent increases in  $s_1$  gradually elevating food-chain length (by the omnivory mechanism). When  $a$  is relatively large, the IG-prey cannot enter the ecosystem with further increases in  $s_1$ , and food-chain length remains at 2.



**Fig. 3** Equilibrium and food-chain length along the disturbance gradient with different strength of local IGP. **a, b** *Left panels* show the equilibrium attained with different disturbance rate and strength of local IGP. Different equilibria realized in respective regions (equilibrium I–V; see text and Table 1) are termed as “No species”, “Basal res”, “Basal res + IG-prey”, “Basal res + IG-pred”, and “Basal res + IG-prey + IG-pred”. Four *right panels*

show responses of the frequencies of patches of different states (B–E) and food-chain length along the basal productivity gradient when  $a = 10$  and  $10^4$ . Specific parameter values used are **a**  $s_2 = 0.2$ ,  $s_3 = 0.1$ , and **b**  $s_2 = 0.1$ ,  $s_3 = 0.2$ . For other parameters, common values are used:  $s_1 = 0.1$ ,  $M_1 = 10^6$ ,  $M_2 = 10^5$ ,  $M_3 = 10^4$ , and  $T = 10^3$

Responses of food-chain length along the gradient of  $M_1$  are similar to those along the  $s_1$  gradient. A difference arises that the effect of increasing  $M_1$  is expressed only when  $M_1 \leq T$ , because  $m_1$  becomes independent of  $M_1$  when  $M_1 > T$ .

### Disturbance

As with basal productivity, we find that local IGP restricts strongly the coexistence and food-chain length along the disturbance gradient. We illustrate this along the decreasing gradient of  $e$  (Fig. 3). The order of species that become able to invade the ecosystem with decreasing  $e$  depends on the relative sizes of the colonization rates of the IG-prey ( $s_2 m_2$ ) and the IG-predator ( $s_3 m_3$ ) (online supplement). When  $s_2 m_2 > s_3 m_3$  (Fig. 3a), at very large  $e$ , no species can persist in the ecosystem with food-chain length being zero. Decreases in  $e$  then allow the basal resource to enter the ecosystem, elevating food-chain length to 1 by the additive

mechanism. Further decreases in  $e$  enable the IG-prey to enter the ecosystem, increasing food-chain length to 2 (by the additive mechanism). Even further decreases in  $e$  permit the entrance of the IG-predator and its coexistence with the IG-prey, with increases in food-chain length (by the additive and then the omnivory mechanisms). Where  $e$  is even smaller, the strength of local IGP ( $a$ ) becomes important. The coexistence, and a food chain longer than 2, are possible only when  $a$  is sufficiently small; otherwise the IG-predator excludes the IG-prey, reducing food-chain length to 2 (by the insertion mechanism).

When  $s_2 m_2 < s_3 m_3$  (Fig. 3b), as  $e$  decreases, the entrance of the basal resource is followed by the entrance of the IG-predator, with sequential increases in food-chain length to 2 through the additive mechanism. Where  $e$  is even smaller, the IG-prey can enter the ecosystem and coexist with the IG-predator, increasing food-chain length beyond 2 (by the insertion and then the omnivory mechanisms). Yet, for this to occur, the strength of local IGP needs to be small enough.

## Ecosystem size

The model shows that, in contrast to increasing basal productivity or weakening disturbance, sufficiently large ecosystem size can permit the coexistence and food chains longer than 2, no matter how strong local IGP is. When ecosystem size is large enough (i.e.,  $T > M_1, M_2,$  and  $M_3$ , and thus  $m_1 = M_1, m_2 = M_2,$  and  $m_3 = M_3$ ), condition (7a) becomes

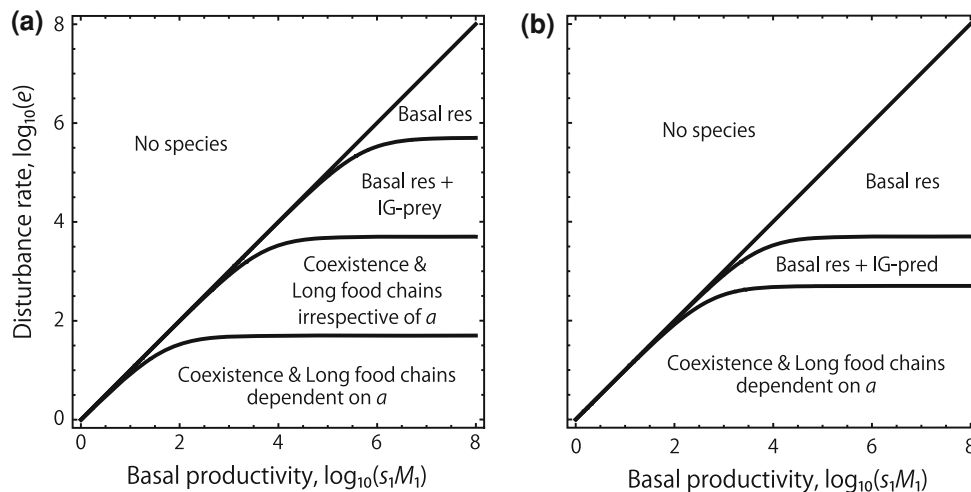
$$s_2M_2 > s_3M_3 \left\{ \frac{s_3M_3}{2e} \left( 1 - \frac{e}{s_1M_1} \right) \right\}. \quad (8)$$

Noting that  $(s_3M_3/2e)(1 - e/s_1M_1) > 1$  from (6), condition (8) means that the potential colonization rate of the IG-prey ( $s_2M_2$ ) needs to be sufficiently larger than that of the IG-predator ( $s_3M_3$ ). When this condition is satisfied, it assures that increasing ecosystem size will eventually permit the coexistence. Thus, when the IG-prey has colonization ability sufficiently superior to that of the IG-predator, large enough ecosystems will enable the coexistence and long food chains, regardless of the strength of local IGP.

Importantly, condition (8) reveals the interacting effects of basal productivity and disturbance on the effect of ecosystem size. Figure 4 visualizes condition (8), together with conditions (4–6), when the ecosystem is sufficiently large (i.e.,  $T > M_1, M_2,$  and  $M_3$ , and thus  $m_1 = M_1, m_2 = M_2,$  and  $m_3 = M_3$ ). When the potential colonization rate of the IG-prey is larger than IG-predator's ( $s_2M_2 > s_3M_3$ ), the coexistence and long food chains (longer than 2) are possible irrespective of the strength of local IGP ( $a$ ) in large enough ecosystems, if basal productivity ( $s_1M_1$ ) is beyond a certain

threshold (or within an intermediate range when disturbance is low) and if the disturbance rate ( $e$ ) is within a certain intermediate range (Fig. 4a). When the IG-predator is the potentially better colonizer ( $s_2M_2 < s_3M_3$ ), whether coexistence and long food chains are possible in large enough ecosystems depend always on  $a$  (Fig. 4b). Thus, the conditions required for strong ecosystem-size effects despite strong local IGP are threefold: (1) basal productivity exceeds certain levels, (2) disturbance is intermediate, and (3) the IG-prey is the better colonizer.

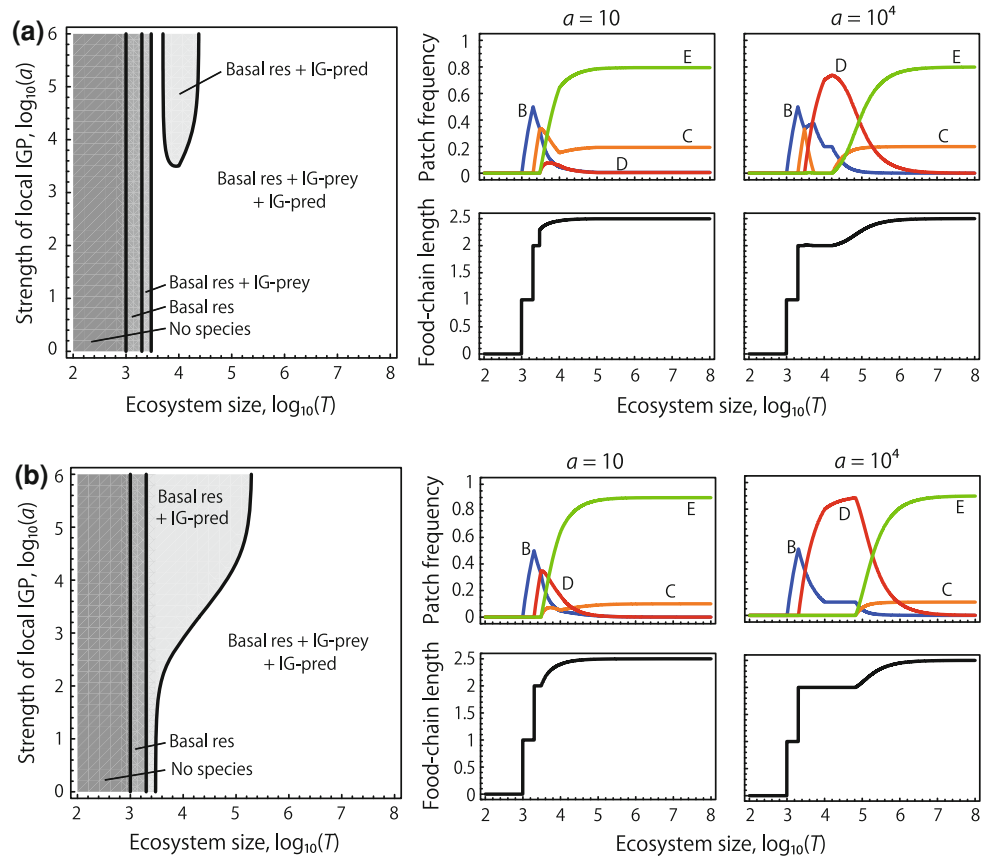
An example of this is illustrated in Fig. 5. When  $T$  is very small, no species can persist in the ecosystem with food-chain length being zero. Increasing  $T$  first enables the basal resource to enter the ecosystem, elevating food-chain length to 1 by the additive mechanism. When the establishment provability of the IG-prey is greater than IG-predator's ( $s_2 \geq s_3$ ; Fig. 5a), a further increase in  $T$  enables the IG-prey to enter the ecosystem, increasing food-chain length to 2 (by the additive mechanism). An even further increase in  $T$  permits the IG-predator, with food-chain length exceeding 2 (by the additive mechanism). When  $a$  is small, additional increases in  $T$  increase the frequency of patches of state E, steadily increasing food-chain length (by the omnivory mechanism). When  $a$  is large, more complex responses can occur. Additional increases in  $T$  initially act to drive the IG-prey away from the ecosystem, with food-chain length reduced back to 2 (by the omnivory and then the insertion mechanisms; although changes in food-chain length tend to be small). However, much further increases in  $T$  act in turn to promote the IG-prey, increasing the frequency of state-E patches and gradually increasing food-chain length (by the insertion



**Fig. 4** Interacting effects of basal productivity and disturbance on the effect of ecosystem size. Different parameter regions represent the ranges of basal productivity and disturbance where different equilibria are realized when ecosystem size is sufficiently large (i.e.,  $T > M_1, M_2,$  and  $M_3$ ). **a** When  $s_2M_2 > s_3M_3$ , the IG-predator–IG-prey coexistence and long food chains (longer than 2) can be realized irrespective of the strength of local IGP ( $a$ ) in large enough

ecosystems if basal productivity is beyond some limits and if disturbance is intermediate (parameter values are  $s_2M_2 = 10^6$ ,  $s_3M_3 = 10^4$ ). **b** When  $s_2M_2 < s_3M_3$ , the coexistence and long food chains (longer than 2) always depend on  $a$ , and when they are not realized the IG-predator co-occur with the basal resource with food-chain length being 2 (parameter values are  $s_2M_2 = 10^3$ ,  $s_3M_3 = 10^4$ )





**Fig. 5** Equilibrium and food-chain length along the ecosystem size gradient with different strength of local IGP. Condition (7a) is satisfied in this figure. **a, b** *Left panels* show the equilibrium attained with different ecosystem size and strength of local IGP. Different equilibria realized in respective regions (equilibrium I–V; see text and Table 1) are termed as “No species”, “Basal res”, “Basal res + IG-prey”, “Basal res + IG-pred”, and “Basal

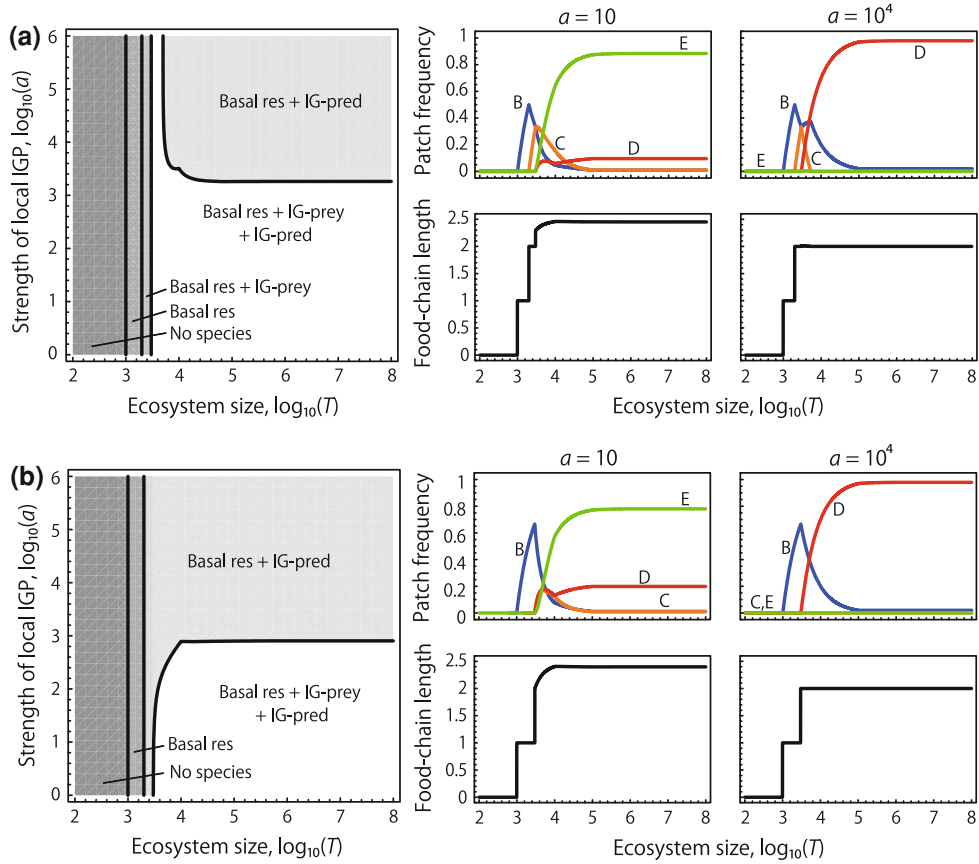
res + IG-prey + IG-pred”. Four *right panels* show responses of the frequencies of patches of different states (B–E) and food-chain length along the basal productivity gradient when  $a = 10$  and  $10^4$ . Specific parameter values used are **a**  $s_2 = 0.2$ ,  $s_3 = 0.1$ , and **b**  $s_2 = 0.1$ ,  $s_3 = 0.2$ . For other parameters, common values are used:  $s_1 = 0.1$ ,  $M_1 = 10^6$ ,  $M_2 = 10^8$ ,  $M_3 = 10^4$ , and  $e = 10^2$

and then the omnivory mechanism). When  $s_2 < s_3$  (Fig. 5b), increases in  $T$  first make the IG-predator to enter the ecosystem having only the basal resource, elevating food-chain length to 2 (by the additive mechanism). Further increases in  $T$  then allow the IG-prey to join the ecosystem, followed by gradual increases in food-chain length beyond 2 (by the insertion and then the omnivory mechanisms).

When condition (8) is not satisfied, on the other hand, local IGP has stronger influences on the possibility of the coexistence and long food chains. Whether the establishment probability of the IG-prey is greater or smaller than IG-predator’s (i.e.,  $s_2 \geq s_3$  or  $s_2 < s_3$ ), increasing ecosystem size can allow the coexistence and long food chains only if the strength of local IGP ( $a$ ) is sufficiently low (Fig. 6a, b). When local IGP is strong enough, the coexistence and long food chains will not be attained however large the ecosystem is. The threshold of  $a$  above which the coexistence and long food chains become impossible is given by the right-hand side of the condition (7b) with  $m_1 = M_1$ ,  $m_2 = M_2$ , and  $m_3 = M_3$  (i.e., when  $T > M_1$ ,  $M_2$ , and  $M_3$ ).

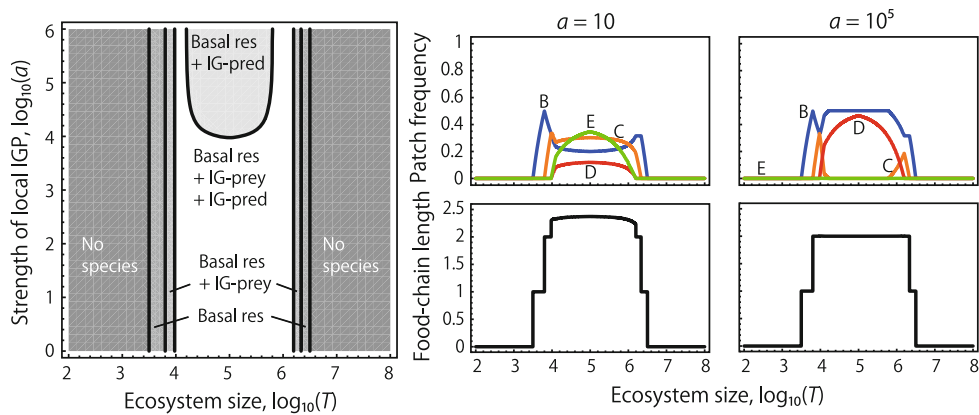
Depending on the relative sizes of  $M_1$ ,  $M_2$ , and  $M_3$  and other parameters, there are many possible cases differing in terms of the middle ranges of ecosystem size (i.e.,  $T < M_1$ ,  $M_2$ , or  $M_3$ ) at which local IGP does or does not limit the coexistence and long food chains. We list all cases in online supplement. Condition (8) determines whether the coexistence and long food chains are attained in large enough ecosystems regardless of the strength of local IGP.

Increasing ecosystem size without changing basal productivity necessarily increases total basal productivity. To examine the effect of increasing ecosystem size while removing the effect of increasing total basal productivity, we test the effect of  $T$  with  $s_1 M_1 T$  fixed at a constant level. When  $s_1 M_1 T$  is fixed, increases in  $T$  causes decreases in basal productivity ( $s_1$  or  $M_1$ ). We find that the increase of  $T$ , when it is small enough, still lengthens food chains, but too much increases in  $T$  shrink food-chain length (Fig. 7). This is because too much increases of  $T$  make basal productivity too low to keep long food chains. In other words, there is a limit to the effect of ecosystem size in increasing food-chain



**Fig. 6** Equilibrium and food-chain length along the ecosystem size gradient with different strength of local IGP. The condition (7a) is not satisfied in this figure. **a, b** *Left panels* show the equilibrium attained with different ecosystem size and strength of local IGP. Different equilibria realized in respective regions (equilibrium I–V; see text and Table 1) are termed as “No species”, “Basal res”, “Basal res + IG-prey”, “Basal res + IG-pred”, and “Basal

res + IG-prey + IG-pred”. Four *right panels* show responses of the frequencies of patches of different states (B–E) and food-chain length along the basal productivity gradient when  $a = 10$  and  $10^4$ . Specific parameter values used are **a**  $s_2 = 0.2$ ,  $s_3 = 0.1$ , and **b**  $s_2 = 0.1$ ,  $s_3 = 0.2$ . For other parameters, common values are used:  $s_1 = 0.1$ ,  $M_1 = 10^6$ ,  $M_2 = 10^4$ ,  $M_3 = 10^5$ , and  $e = 10^2$



**Fig. 7** Equilibrium and food-chain length along the ecosystem size gradient with different strength of local IGP. Total basal resource availability,  $s_1 M_1 T$ , is fixed constant by changing  $M_1$  along with the changes of  $T$  ( $\log_{10}(M_1) = 10 - \log_{10}(T)$ ). *Left panel* shows the equilibrium attained with different ecosystem size and strength of local IGP. Different equilibria realized in respective regions (equilibrium I–V; see text and Table 1) are termed as “No species”,

“Basal res”, “Basal res + IG-prey”, “Basal res + IG-pred”, and “Basal res + IG-prey + IG-pred”. Two *right panels* show responses of the frequencies of patches of different states (B–E) and food-chain length along the basal productivity gradient when  $a = 10$  and  $10^5$ . Parameter values used are:  $s_1 = 0.1$ ,  $s_2 = 0.2$ ,  $s_3 = 0.1$ ,  $M_2 = 10^4$ ,  $M_3 = 10^{4.1}$ , and  $e = 10^{2.5}$

length when total basal productivity is held constant. This indicates that the effect of ecosystem size on total basal productivity is one important effect of ecosystem size on food-chain length.

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## Discussion

We developed and analyzed a mathematical model of metacommunity IGP dynamics. The model has at least three unique features useful for addressing the ultimate and proximate mechanisms by which productivity, disturbance, and ecosystem size affect food-chain length. First, the metacommunity framework allows us to explore and compare the ultimate mechanisms by which productivity, disturbance, and ecosystem size affect directly or interactively food-chain length in a unified setting. Second, another merit of the metacommunity framework is that we can study how strength of local species interactions (i.e., IGP in our case) interacts with environmental variables to influence food-chain length. Third, the model expresses IGP dynamics, which allows us to explore what proximate structural mechanisms (i.e., additive, insertion, and omnivory mechanisms; Post and Takimoto 2007) causes responses of food-chain length along environmental gradients. With this model, we found that, if local IGP is weak, increasing basal productivity favors IG-predator–IG-prey coexistence and increases food-chain length. However, if local IGP is strong, increasing basal productivity ultimately hampers coexistence, limiting food-chain length. Similarly, weakening disturbance leads to the coexistence and increases food-chain length if local IGP is weak. If IGP is strong, too weak disturbance destroys coexistence and impedes the increase of food-chain length. In contrast, increasing ecosystem size can promote coexistence and increase food-chain length, even if local IGP is strong. Three conditions are required for this: (1) basal productivity is sufficiently large, (2) disturbance is intermediate, and (3) colonization ability of the IG-prey is sufficiently superior to that of the IG-predator. Regarding proximate structural mechanisms, basal productivity, disturbance, and ecosystem size can affect food-chain length through all the three structural mechanisms when local IGP is sufficiently weak. Strong local IGP, on the other hand, prevents the insertion and omnivory mechanisms through which increasing basal productivity or decreasing disturbance increase food-chain length, because strong IGP hampers the IG-predator–IG-prey coexistence. In contrast, increasing ecosystem size can invoke the insertion and omnivory mechanisms to increase food-chain length under strong local IGP. Taken together, these results suggest that strength of biotic interactions mediate responses of food-chain length along environmental gradients, affecting relative strength in the effects of different environmental variables on food-chain length. Below we discuss this in more detail and examine corresponding empirical examples.

Our metacommunity model shows that strong local IGP prevents food-chain length from increasing in response to increasing basal productivity. This is because increased basal productivity enhances the IG-predator and promotes strong local IGP to destroy the IG-predator–IG-prey coexistence. Previous theoretical studies also suggest that increasing productivity does not necessarily lead to longer food chains. Population dynamic models of IGP in local communities indicate that food-chain length is maximized at intermediate levels of productivity (Holt and Polis 1997, Diehl and Feissel 2001). The paradox of enrichment (Rosenzweig 1971) suggests that increasing productivity destabilizes and collapses simple predator–prey interactions, shortening food-chain length. These theoretical findings indicate that too high basal productivity intensifies predation and hampers predator–prey coexistence in food webs, potentially shortening food chains (Persson et al. 1996).

Our results also demonstrate that the strength of the local IGP interaction strongly influences the relationship between disturbance and FCL. When local IGP interactions are strong, food-chain length does not increase with weakened disturbance. This is because, as with increasing basal productivity, weakening disturbance enhances the IG-predator, and promotes strong local IGP, which acts to shorten food-chain length. Power et al. (1996) made a related empirical observation. In this example, the length of river food chains receiving periodic scouring floods was maximized at an intermediate flooding frequency. This occurred because weakening disturbance favored predation-resistant intermediate species, which indirectly suppressed disturbance-resilient and predation-prone species; this diminished energy to higher trophic levels, shortening food-chain length. A similar conclusion was recently reached for a metacommunity model of food-chain dynamics (Calcagno et al. 2011). These findings (including ours) suggest that disturbance may interact with local biotic interactions to determine food-chain length.

In contrast to increasing basal productivity and weakening disturbance, increasing ecosystem size can lengthen food chains regardless of the strength of local IGP interactions. When IGP is strong, the IG-prey needs to have high colonization ability for this to occur. Based on these findings, we predict that the ecosystem-size effect is more pronounced than the effects of basal productivity or disturbance in food webs where top-down forces by predators are strong and their prey has high colonization ability. This prediction matches an empirical example from terrestrial food chains on oceanic islands (Takimoto et al. 2008). In this example, ecosystem size (island area) determined food-chain length on islands, while disturbance affected only the identity of top predators with little influence on food-chain length. Disturbance had little influence, possibly because predation by *Anolis* lizards (IG-predator) on spiders (IG-prey) was strong (Schoener and Spiller 1996). Weakened disturbance favored lizards, but their strong predation eliminated spiders (Schoener and

Spiller 1996), which in turn lowers the trophic position of lizards. The lizard's trophic position on less disturbed islands was comparable to spider's trophic position on more disturbed islands without lizards (Takimoto et al. 2008), indicating that lizards on less disturbed habitats used food items similar to those utilized by spiders in more disturbed islands. On larger islands, spiders coexisted with lizards, and lizards attained higher trophic position (Takimoto et al. 2008).

In addition to mediating the strength of local species interactions, ecosystem size also influences total basal resource availability (Schoener 1989). When we separated these effects by fixing total basal productivity, we still observed the ecosystem size effect of mediating strong local interactions to increase food-chain length. However, this effect required that per-unit-size basal productivity was not too low. A well-designed microcosm experiment by Spencer and Warren (1996) found such genuine effect of ecosystem size by changing ecosystem size while keeping total basal-resource availability constant.

Overall, our model finds that increasing basal productivity, decreasing disturbance, and increasing ecosystem size all generally increase food-chain length, when local IGP is weak. Increasing ecosystem size can lengthen food chains even when local IGP is strong, if the IG-prey has sufficiently high colonization ability. These findings indicate that the interplay between biotic interactions and environmental variables is important to determine the length of food chains. A recent meta-analysis of empirical studies on environmental determinants of food-chain length found that productivity and ecosystem size has similar mean effect sizes, while the mean effect of disturbance is not significant (Takimoto and Post, in preparation). This result apparently matches the findings from our model. Moreover, this meta-analysis found that effects of ecosystem size are highly heterogeneous among individual empirical studies. This pattern might be explained, at least partially, by our model predictions that strong ecosystem size effects under strong IGP interactions require high enough basal productivity, intermediate disturbance, and high colonization ability of the IG-prey. Food-chain length is an important characteristic of ecological communities that affects many functional properties of ecosystems. Although current theory and empirical evidence suggest a strong role of ecosystem size, we need more empirical and theoretical works to better understand causes of natural and anthropogenic variation in food-chain length.

**Acknowledgments** This research was supported by the Japan Society for the Promotion of Science (21770091 and 23710285 to GT), and by the National Science Foundation (DEB-0516431 to DS).

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