



COMPETITION, TROPHIC INTERACTIONS AND THE IMPACT OF HABITAT FRAGMENTATION ON SPECIES RICHNESS

MASTER'S THESIS

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Photo on front page: *"On the way to Blenheim and Picton, South Island"*, 21-02-2006

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SUMMARY

The world is experiencing a rate of species extinction that is unprecedented in human history. The most important driving force of this global biodiversity loss is considered to be human induced alteration of ecosystems, leading to the destruction of species habitats. Quite some modeling studies have been done in order to gain insight in the impact of habitat fragmentation on the abundance of species that follow a trade-off between competitive strength and colonizing ability. Others have studied the impact of habitat fragmentation on species that interact with each other trophically. Almost no research has however been done that includes both a trade-off and trophic interactions. This is surprising because both concepts are highly compatible.

It is probable that trophic interactions and competitive coexistence made possible via a trade-off, co-occurs within many ecosystems. Such systems will probably respond in a different way to habitat fragmentation than is predicted by models that include only a trade-off or only trophic interactions. In this thesis results are presented and discussed of models that incorporate a group of resource and a group of consumer species. The species within both groups compete and coexist via a trade-off between competitive strength and colonizing ability. Resource and consumer species influence each other by trophic interactions, i.e. donor control and top-down control.

Among other things, the results of these models show that the impact of habitat fragmentation on resource species depends strongly on the strength of trophic interactions. When trophic interactions are strong, habitat fragmentation may lead to an increased species richness of resource species and favors competitively strong resource species, that are poor colonizers. When trophic interactions are weak, the impact of habitat fragmentation on resource species is opposite. Also the impact of the degree wherein areas of different size are isolated may have a very different impact on resource species richness, depending on the strength of trophic interactions. An increased migration between areas of different size will lead to the loss of resource species when trophic interactions are strong. Again the opposite is true when trophic interactions are weak.

Conventional conservation policies that try to deal with habitat fragmentation, are often based on a theoretical view of ecosystems that does not include competition nor trophic interactions. If the theoretical description of ecosystems presented in the thesis is correct, other conservation policies than the conventional would probably be the most effective.

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PREFACE

Johann Sebastian Bach's, *Die Kunst der Fuge*, shows how musical themes, that already sound beautiful when listened to independently can, when played simultaneously, make up a complex, but even more beautiful whole. A full understanding and recognition of all the different elements hidden within this masterpiece will require years of listening, but will eventually be impossible for most people. Only the analysis of its score and understanding of the sometimes strict rules where contrapuntal compositions are subjected to, may provide the insight necessary to fully enjoy all details hidden within this masterpiece. Studying the score of *Die Kunst der Fuge* may not seem to be an attractive activity, but provides the one who has done it with the big reward of an increased understanding and an even more inspiring event when listening to *Die Kunst der Fuge* again.

Studying the complex nature of ecosystems is like studying *Die Kunst der Fuge*, only this time a score is not available. Also the rules that determine the interactions between species are still largely unknown, although scientist have been able to come up with intriguing and plausible hypothesis. In this thesis some of these hypothesis are used in an attempt to write a draft score, only a caricature of real ecosystems, trying to fetch the essential processes occurring within them. Maybe it will inspire people to observe and describe ecosystems in a new, different, way.

1. Introduction

1.1 HABITAT FRAGMENTATION, SPECIES RICHNESS AND THE THEORY OF ISLAND BIOGEOGRAPHY

The world is experiencing a rate of species extinction that is unprecedented in human history. The most important driving force of this global biodiversity loss is considered to be human induced alteration of ecosystems, leading to the destruction of species habitats. (Saunders *et al.*, 1991; Fahrig & Marriam, 1994; Lawton and May, 1996; Brooks *et al.*, 2002; Reed, 2004; Millennium Ecosystem Assessment, 2005; United Nations Environment Programme, 2006). Current rates of habitat destruction are high. At present, between one-third and one-half of the land surface and more than half of all accessible surface water is estimated to be transformed by humans (Vitousek *et al.* 1997). Another 10-20% of grassland and forestland is projected to be converted between 2000 and 2050 (Millennium Ecosystem Assessment, 2005). Not only the direct loss of habitat is however supposed to lead to the extinction of species. Especially the isolation of remaining fragments is considered to provide a major contribution to species loss. Once a population is divided over different habitat fragments, a species is much more vulnerable to extinction, because its small sub-populations are more easily affected by environmental fluctuations.

The notion that not only the destruction, but also, and especially, the fragmentation of habitat is one of the most important drivers of biodiversity loss, is apparent since the theory of island biogeography of MacArthur and Wilson (1967) became generally accepted in the seventies (Powledge, 2003; Laurance, 2008). According to this theory, species richness of an island increases with its size and decreases with its degree of isolation. Following this line of reasoning, small and/or more isolated habitat fragments are expected to contain fewer species than larger and/or less isolated habitat fragments.

The mechanisms proposed in the theory of island biogeography have shaped conservation policies in the seventies (Diamond, 1975; Wilson and Willis, 1975; Terborgh, 1976) and continue to be the foundation of many present day conservation policies (Powledge, 2003; Watling and Donnelley, 2006; Laurance, 2008). Among these policies are the positing and size of nature reserves and the development of ecosystem networks that aim to reduce isolation of separate ecosystems. Also predictions of future human impact on biodiversity are highly influenced by the theory (Reid, 1997; United Nations Environment Programme, 2006).

Field measurements and field experiments studying the effect of habitat fragmentation on species richness however show conflicting results (see review of Debrinski and Holt, 2000), fueling a debate on the accuracy of the theory of island biogeography. A debate welcomed by the authors of the theory. Wilson (1999) states that he and MacArthur failed to appreciate the major impact of the theory of island biogeography on conservation biology. According to Wilson (1999), many flaws of the theory of island biogeography lay in its oversimplification and incompleteness. Still, the basic processes pointed out by the theory of island biogeography are sound and provide a good basis for the further development of our understanding of ecosystems.

1.2 THE IMPACT OF HABITAT FRAGMENTATION ON TROPHIC INTERACTIONS

One of the simplifications included in the theory of island biogeography is the assumption that the presence of one species in an area has no influence on the presence of another species. In practice species however highly influence each other's chance of survival via trophic interactions. Key mechanisms determining species richness are not only colonization and extinction of an area by species, as proposed by the theory of island biogeography (MacArthur & Wilson, 1967). The interactions between species play a central role in the species richness that is eventually achieved within an area too.

Field observations indicate that trophic interactions may have a great influence on the species present within fragmented landscapes. Small areas often lack the presence of species on a relatively high trophic level such as predators, insect parasitoids or herbivores. This causes a greatly different composition and often increased species richness of the trophic level they consume or prey upon (Hawkins and Gross, 1992; Hawkins *et al.* 1993; Kruess and Tscharntke, 1994; Roland and Taylor, 1997; Cappuccino *et al.* 1998; Zabel and Tschantke, 1998; Holt *et al.*, 1999; Maron *et al.*, 2001; Terborgh *et al.*, 2001; Scheffer *et al.* 2006). Habitat fragmentation thus seems to affect species on a high trophic level more than species on a low trophic level. The absence of species on a high trophic level in turn positively influences the abundance and biodiversity of the trophic level it consumes.

The assumption that habitat size directly influences trophic interactions and the composition of species has great influence on the presumed effect of habitat fragmentation on biodiversity. At a global scale biodiversity will be highest with a variation in habitat fragmentation. Highly fragmented landscapes will then namely provide safe Heaven for species on a low trophic level, where low fragmented landscapes provide habitat for species on a high trophic level. At landscape level, it is, following this assumption, very probable that several small areas varying in size and degree of isolation together contain a higher biodiversity than one big habitat of the same size.

1.3 COMPETING SPECIES AND TRADE-OFFS BETWEEN SPECIES TRAITS

In order to gain insight in the impact of habitat fragmentation on biodiversity while taking trophic interactions into account, assumptions have to be made about the structure of the networks made up by the interactions between species and the mechanisms that determine the coexistence of competing species within an ecosystem. Simple concepts have been brought forward that have shaped our view on the nature of species within an ecosystem and the structure of networks consisting of the interactions between them. Apart from the idea that different 'trophic levels' can be distinguished within one ecosystem, one of these concepts is the idea that species competing for the same resource must experience a trade-off between at least two traits relevant for their survival. The concept of trade-offs between species characteristics is generally accepted and often brought forward as one of the most suitable explanations for species coexistence (but see Hubbell, 2001). Would there not be any trade-off between species characteristics relevant for survival, a single species should have evolved outcompeting all other species.

Quite some trade-offs have been proposed as an explanation for the coexistence of competing species, most of them related with life-history traits of species (see review of Kneitel and Chase, 2003). Also the description of trade-offs differs. It is both common to describe trade-offs at the level of an individual (e.g. a trade-off between longevity and reproduction) and common to describe trade-offs at the level of populations (e.g. a trade-off between the growth rate and the carrying capacity of a population, *r/K* selected species; MacArthur and Wilson, 1967). However it remains so that in any case a trade-off is a negative relationship between the presence of two characteristics within a species.

A trade-off between the ability of species to colonize new sites and their competitive strength seems to explain coexistence of species in many animal and plant communities (Werner & Platt, 1976; Doherty & Fowler, 1994; Tilman *et al.* 1994; Stone, 1996; Hanski and Ovaskainen, 2000) and is one of the most often studied mechanisms allowing species coexistence between competing species. As one species cannot be both competitively strong and a good colonizer, coexistence is possible for a potentially unlimited number of species.

1.4 Modeling studies that include competitive coexistence and trophic interactions

Quite some modeling studies have been done in order to gain insight in the impact of habitat fragmentation on the abundance of species that follow a trade-off between competitive strength and colonizing ability (Nee & May, 1992; May, 1994; Tilman, *et al.* 1994; Moilanen & Hanski 1995; Banks, 1997; Morozov and Li, 2008). Others have studied the impact of habitat fragmentation on species that interact with each other trophically (May, 1994; Kareiva and Wennergren, 1995; Nee *et al.*, 1997; Bascompte and Solé, 1998; Holt *et al.*, 1999; Swihart *et al.*, 2001). Almost no research has however been done that includes both a trade-off and trophic interactions other than including predation resistance as a trait that is subject to a trade-off (e.g. Uriarte *et al.*, 2002). This is surprising because both concepts are highly compatible. As trade-offs are proposed for species that compete for the same resource, they, by definition, belong to the same trophic level. Furthermore it is unlikely that the groups of species where trade-offs usually are proposed for are not subject to trophic pressure from other taxa. Thorough analysis of food webs indicate that many species within an ecosystem are trophically equivalent, hence they share the same predator and prey (Sugihara *et al.*, 1989; Cohen and Palka, 1990; Martinez, 1991). There is thus some basis for the idea that trophic levels can be distinguished within an ecosystem wherein different competing species coexist. At the same time the number of remaining groups of species that is trophically different is still substantial (between 10 and 90; Sugihara *et al.*, 1989).

When studying the influence of habitat fragmentation on species following a trade-off, the simplification of including only one trophic level might thus not always be justified. When the type of species present within a trophic level changes, it can be expected that the influence trophic levels have on each other will also change. An external factor, such as habitat fragmentation, that has an influence on more than one trophic level at once, can thus be expected to have a much more complex influence on species richness than the outcome of models that include only one trophic level predict.

1.5 RESEARCH QUESTIONS AND HYPOTHESIS

As pointed out in the former paragraph, it is probable that trophic interactions and competitive coexistence made possible via a trade-off between competitive strength and colonizing ability, co-occur within ecosystems. Such systems will probably respond in a different way to habitat fragmentation than is predicted by models that include only a trade-off or only trophic interactions. Several relevant questions may arise about the impact of habitat fragmentation on such systems, among which are the following:

Research question 1

What is the effect of habitat fragmentation on species richness when the effect of habitat fragmentation on trophic interactions is taken into account?

Hypothesis 1

With increasing habitat fragmentation, species richness will decline until the highest trophic level can no longer be sustained. Loss of the highest trophic level alters the structure of the community and causes species richness to increase abruptly. Species richness of this newly formed community will then start to decline again with increasing habitat fragmentation until the next trophic level is lost.

Research question 2

What is the effect of habitat fragmentation on species type?

Hypothesis 2

Assuming a trade-off between competitive and colonizing ability, species types will shift from highly competitive to low competitive with increasing habitat fragmentation. Loss of the highest trophic level alters the type of species present in the trophic level it consumes. Competitive ability of the consumed trophic level will increase abruptly when the highest trophic level is lost. Competitive ability of this trophic level will then start to decline again until the trophic level is lost itself.

Research question 3

What is the effect of migration between areas of different size on the species richness within these areas?

Hypothesis 3

Increasing migration between areas of different size will be beneficial for species on a high trophic level, because the amount of resources available for them increases. It will however reduce the species richness of species on a lower trophic level, because there are more consumers present that consume them.

Gaining more insight in the answers to these questions is the intend of this research.

2. Model and Methodology

2.1 COLONIZATION AND EXTINCTION

The two basic mechanisms of the theory of island biogeography, colonization and extinction of species within habitat fragments, are also included in the basic meta-population model developed by Levins (1969). Although the used mechanisms are the same, the context wherein these mechanisms are applied is different. The theory of island biogeography seeks an explanation for the number of species found within a habitat fragment, where Levins model describes the proportion of all habitat fragments occupied by one single species. A great amount of researchers developed Levins model further in order to study the impact of habitat fragmentation on the abundance of species, among which are Bascompte and Solé (1998) and Tilman *et al.* (1994, 1997). Bascompte and Solé added an extra trophic level to Levins model and Tilman *et al.* incorporated competition between different species, following a trade-off between competitive and colonization ability. For this study, adapted versions of these models will be used in order to develop a new model that contains both trophic levels and species following the aforementioned trade-off.

Levins model can be expressed in the following way:

$$\frac{dR}{dt} = cR(1 - R) - eR$$

Where R is the fraction of sites or habitat fragments, that is occupied by a species, c is the colonization rate of empty sites and e is the extinction rate of occupied sites. Colonization depends on both the fraction of sites that is occupied (R) and the fraction of sites that is empty ($1-R$). Extinction solely depends on the fraction of sites that is occupied.

2.2 TROPHIC INTERACTIONS

The adapted version of the model of Bascompte and Solé (1998), used in this model as a building block for a new model, is made by Swihart *et al.* (2001). As Bascompte and Solé's (1998) model, the model of Swihart *et al.* (2001) describes the interaction between two species belonging to different trophic levels.

The model of Swihart *et al.* (2001) reads as follows:

$$\begin{aligned}\frac{dR}{dt} &= c_R R(1 - R - D) - e_R R - \mu RC \\ \frac{dC}{dt} &= c_C C(1 - C - D) - e_C C - \psi C(1 - R)\end{aligned}$$

Where R is the fraction of sites occupied by resource species, C is the fraction of sites occupied by consumers, c_R is the colonization rate of sites by resource species, c_C the colonization rate of sites by consumers, e_R is the extinction rate of resource species and e_C is the extinction rate of consumers. Consumers affect resource species by increasing its death rate. The strength of this 'top-down control' is determined by parameter μ . The absence of resource species increases the death rate of consumer species. The strength of this 'donor control' is determined by parameter ψ . Habitat destruction is incorporated with variable D , which indicates the fraction of sites destroyed.

2.3 TRADE-OFF BETWEEN COMPETITION AND COLONIZATION

Within the new model each trophic level can contain a potentially unlimited number of species, that follow a trade-off between competitive strength and the ability to colonize new habitat. When trophic interactions are not included, the equation for the i th species, follows the model of Tilman *et al.* (1994), which reads as follows:

$$\frac{dS_i}{dt} = c_i S_i (1 - \sum_{j=1}^i S_j - D) - e S_i - \sum_{j=1}^{i-1} c_j S_i S_j$$

The competitive ability of a species in this model manifests itself in the ability of a species to colonize a site that is occupied by another species. Species can only occupy sites that are empty or occupied by species that are lower in competitive rank. Sites occupied by the same species, or species higher in competitive rank cannot be colonized. Species are ordered from highest competitive ability (species 1) to lowest competitive ability (species N).

S_i is the fraction of sites occupied by species i , $\sum S_j$ represents the fraction of sites occupied by species higher in competitive rank together with the fraction of sites occupied by species i itself and $\sum c_j S_i S_j$ represents the fraction of sites lost to colonization by superior competitors. c_i represents the colonization rate of species i and e represents the extinction rate. Habitat destruction is also in this model incorporated with variable D , which indicates the fraction of sites destroyed.

Tilman *et al.* (1997) proposes several mathematical relationships in order to describe the trade-off between competitive rank and colonization rate. Their trade-offs are not based on a mechanistic explanation of the trade-off, but derived in order to obtain a specific distribution in the abundances of species when $D=0$. Obtaining the same distributions in a model that contains more than one trophic level would require a very complex relation between competitive rank and colonization rate. In practice the outcome of a model with one of these very complex relationships will be similar to the outcome of a model where a very simple relation between competitive rank and colonization rate is assumed. For this study a simple, linear, trade-off between competitive rank and species specific colonization rate c_i is thus assumed, following:

$$c_i = c_{\max} \frac{i}{N}$$

Where c_i is the colonization rate of species i , i is the competitive rank or species number of the species, c_{\max} is the maximum colonizing ability, or the colonizing ability of the weakest competitor and N is the total number of species included in the model. The total number of species included N , is the number of species that can *potentially* establish within the model, it is not sure however that they indeed will establish. Please note that the total number of species included N thus is different from the number of species with an abundance higher than zero, later on in this study defined as $NBG0$.

2.4 MEAN FIELD MODEL

Combining the two models presented above results in a new model that includes both trophic levels and unlimited number of species per trophic level. This model reads:

$$\begin{aligned}\frac{dR_i}{dt} &= c_{Ri}R_i(1 - \sum_{j=1}^i R_j - D) - e_R R_i - \mu R_i \sum_{h=1}^{NC} C_h - \sum_{j=1}^{i-1} c_j R_i R_j \\ \frac{dC_i}{dt} &= c_{Ci}C_i(1 - \sum_{j=1}^i C_j - D) - e_C C_i - \psi C_i(1 - \sum_{h=1}^{NR} R_h) - \sum_{j=1}^{i-1} c_j C_i C_j\end{aligned}$$

Where R_i is the fraction of sites occupied by resource species i and C_i is the fraction of sites occupied by consumer species i . The total number of species included at initialization is expressed with the term N_R for resource species and N_C for consumers. The other variables and parameters are the same as the variables and parameters used in the models above (see Appendix 1 for an overview of all variables and parameters).

In the above presented model, species might go extinct in the early stage of a model run depending on their initial values. In a latter phase this species however, might would have been very well capable to maintain itself in the model. In the below presented model it is assumed that there is always a small possibility for an extinct species to migrate from sites outside of the sites included in the model, giving species the possibility of reestablishing themselves after they may have gone extinct. Incorporating this external influx in the model gives the model the following appearance:

$$\begin{aligned}\frac{dR_i}{dt} &= c_{Ri}R_i(1 - \sum_{j=1}^i R_j - D) + f_R(1 - \sum_{j=1}^i R_j - D) - e_R R_i - \mu R_i \sum_{h=1}^{NC} C_h - \sum_{j=1}^{i-1} c_{Rj} R_i R_j - \sum_{j=1}^{i-1} f_R R_i \\ \frac{dC_i}{dt} &= c_{Ci}C_i(1 - \sum_{j=1}^i C_j - D) + f_C(1 - \sum_{j=1}^i C_j - D) - e_C C_i - \psi C_i(1 - \sum_{h=1}^{NR} R_h) - \sum_{j=1}^{i-1} c_{Cj} C_i C_j - \sum_{j=1}^{i-1} f_C C_i\end{aligned}$$

Where f represents the external influx of species. The value of f is taken very low. The abundance of species therefore remains almost zero when circumstances are not favorable for a certain species type. A species can thus only truly re-establish if circumstances have become better during increasing running time. Competitive rank and colonizing ability remain the key factors determining the abundance of species. Individuals that make an attempt to establish via the external influx can only colonize sites that are not occupied by better competitors.

The in this paragraph lastly presented model will, together with the spatially explicit model presented in the next paragraph, be used in order to find an answer to research question 1 and 2.

2.5 SPATIALLY EXPLICIT MODEL

Results of the mean field model are compared with results of a spatially explicit model, namely a cellular automaton. The cellular automaton will consist of a lattice with $m*m$ cells. Habitat fragmentation is included in this model by randomly selecting a fraction (D) of cells in the lattice that is destroyed. These cells cannot be occupied by any species and remain destroyed (-) during all time steps. The remaining cells are empty (0), contain resource species i (R_i), contain solely consumer species i (C_i) or contain resource species i and consumers species i (R_iC_i). Only one species per trophic level can be present in a cell.

The spatially explicit model follows rules that are similar to the mean field model. The probability of resource species to go extinct within a cell is determined by e_R when no consumer species are present and by $e_R + \mu$ when consumer species are present. The probability of consumer species to go extinct within a cell is determined by e_C when resource species are present and by $e_C + \psi$ when resource species are not present in the same cell. The main difference between the mean-field and the spatially explicit model is the way wherein colonization is derived. Colonization of sites (cells) in the spatially explicit model is determined by the species present in the four cells neighboring a cell. The probability that an empty site gets colonized by species i in the spatially explicit model becomes:

$$\omega_{0 \rightarrow i} = 1 - (1 - c_i)^{ni} + f$$

Where c_i is the colonizing ability of species i and ni is the number of neighboring cells wherein species i is present. Presence of species in cells further away than the four neighboring cells does not influence the chance a cell gets colonized. Replacement of species i by better competitor j is also possible and follows the same principal. As in the mean field model, replacement by poorer competitors is not possible. If two different species of the same trophic level will try to colonize the same site, the best competitor will win.

Since the mean field model is a, non-stochastic, continuous time model and the spatially explicit model is a discrete stochastic model, rates are converted into probabilities. The original rates of events occurring in an amount of time T within the mean field model are furthermore converted into the probability of that event happening within a cell during the length of one timestep after which the whole lattice is updated synchronously. As the length of timestep dT decreases, the probability of the occurrence of an event, such as colonization or extinction, also decreases. The relation between the length of timestep dT and the probability of an event happening is derived with the Poisson distribution:

$$probability = 1 - e^{(-rate*dT)}$$

The length of timestep dT and lattice size $m*m$ are chosen in such a way that decreasing the length of the timesteps and increasing lattice size has no impact on the outcome of the model.

The in this paragraph presented spatially explicit model will be used in order to find an answer to research question 1 and 2, together with the mean field model described in the former paragraph.

2.6 MIGRATION BETWEEN AREAS OF DIFFERENT SIZE

Apart from adapting the original mean field model into a spatially explicit model, it is also possible to re-write the original mean field model into a model that derives the impact of the ‘size of an area’ P , instead of habitat fragmentation D , on the abundance of species. ‘area size’ is here defined as the number of sites that are available for colonization within an area. The rewritten model is as follows:

$$\begin{aligned}\frac{dR_i}{dt} &= c_{Ri} R_i (P - \sum_{j=1}^i R_j) + f_R (P - \sum_{j=1}^i R_j) - e_R R_i - \mu R_i (\sum_{h=1}^{NC} C_c / P) - \sum_{j=1}^{i-1} c_{Rj} R_i R_j - \sum_{j=1}^{i-1} f_R R_i \\ \frac{dC_i}{dt} &= c_{Ci} C_i (P - \sum_{j=1}^i C_j) + f_C (P - \sum_{j=1}^i C_j) - e_C C_i - \psi (1 - \sum_{c=1}^{NR} R_c / P) C_i - \sum_{j=1}^{i-1} c_{Cj} C_i C_j - \sum_{j=1}^{i-1} f_C C_i\end{aligned}$$

The appearance of this model is similar to the original mean field model, only here a new variable P is incorporated, representing area size. P is included at the same place where the original habitat fragmentation variable D was incorporated, and at an extra position namely in the parts of the model that describe bottom-up and top-down control. The impact of ‘area size’ on the abundance of species thus is similar to the original impact of habitat fragmentation D , but somewhat different due to the different impact area size P has on top-down and donor control.

Once the model is converted from a model that describes the habitat fragmentation D into a model that describes the impact of area size P on the abundance of species, migration between areas of different size can be modeled in the subsequent way (following Mouquet & Loreau, 2003):

$$\begin{aligned}\frac{dR_{qi}}{dt} &= (1-d)c_{Ri} R_{qi} (P_q - \sum_{j=1}^i R_{qj}) + \theta \frac{d}{NP-1} \sum_{q \neq s}^{NP} c_{Ri} R_{si} (P_q - \sum_{j=1}^i R_{qj}) + f_R (P_q - \sum_{j=1}^i R_{qj}) \dots \\ &\dots - e_R R_{qi} - \mu (\sum_{h=1}^{NC} C_{qc} / P_q) R_{qi} - \sum_{j=1}^{i-1} (1-d)c_{Rj} R_{qj} R_{qi} - \sum_{j=1}^{i-1} \theta \frac{d}{NP-1} \sum_{q \neq s}^{NP} c_{Rj} R_{sj} R_{qi} - \sum_{j=1}^{i-1} f_R R_{qj} R_{qi} \\ \frac{dC_{qi}}{dt} &= (1-d)c_{Ci} C_{qi} (P_q - \sum_{j=1}^i C_{qj}) + \theta \frac{d}{NP-1} \sum_{q \neq s}^{NP} c_{Ci} C_{si} (P_q - \sum_{j=1}^i C_{qj}) + f_C (P_q - \sum_{j=1}^i C_{qj}) \dots \\ &\dots - e_C C_{qi} - \psi ((1 - \sum_{h=1}^{NR} R_{qc}) / P_q) C_{qi} - \sum_{j=1}^{i-1} (1-d)c_{Cj} C_{qj} C_{qi} - \sum_{j=1}^{i-1} \theta \frac{d}{NP-1} \sum_{q \neq s}^{NP} c_{Cj} C_{sj} C_{qi} - \sum_{j=1}^{i-1} f_C C_{qj} C_{qi}\end{aligned}$$

Where R_{qi} represents the abundance of resource species i within area q and C_{qi} represents the abundance of consumer species i within area q . Two new parameter are included, namely d , the proportion of colonizers that attempts to migrate to a new area and θ , the fraction of migrants that successfully establishes within a new area. A potentially unlimited number of area's N_p differing in size P can be modeled with this model. The other variables and parameters are the same as the variables and parameters used in the models above (see Appendix 1 for an overview of all variables and parameters).

The in this paragraph presented model will be used to answer research question 3, by studying the impact of migration success θ on species richness. Migration success θ is considered to be influenced by external factors, such as the realization of corridors between different areas. The proportion of colonizers that attempt to migrate d , is considered to be an intrinsic property of a species.

3. Results

3.1 EQUILIBRIAL ABUNDANCE OF SPECIES IN THE MEAN FIELD MODEL

The equilibrium abundance of resource species i and consumer species i can be found by solving $dR_i/dt=0$ and $dC_i/dt=0$ for respectively \hat{R}_i and \hat{C}_i . Assuming that f is so small that it can be neglected, the following solutions are obtained:

$$\hat{R}_i = 1 - D - \frac{e_R}{c_{Ri}} - \frac{\mu}{c_{Ri}} \sum_{h=1}^{NC} C_h - \sum_{j=1}^{i-1} R_j \left(1 + \frac{c_{Rj}}{c_{Ri}}\right)$$

$$\hat{C}_i = 1 - D - \frac{e_C}{c_{Ci}} - \frac{\psi}{c_{Ci}} \sum_{h=1}^{NR} (1 - R_h) - \sum_{j=1}^{i-1} C_j \left(1 + \frac{c_{Cj}}{c_{Ci}}\right)$$

The above presented formulas can be applied by first deriving the abundance of species 1, followed by species 2, until species i is reached. Further simplification of these formulas is possible, but requires a division between odd and even numbered species. A species is considered to be odd- or even-numbered when its number is odd relative to species bc , the best competitor whereof \hat{R}_i is bigger than zero. If $i-bc+1$ is odd, species i is considered to be 'odd-numbered', if $i-bc+1$ is even, species i is considered to be 'even-numbered'. The number of resource species bc can be found by finding the best competitor wherefore the statement $c_{Rbc} > e_R + \mu \hat{C}_{tot}$ is valid. The number of consumer species bc can be found by finding the best competitor wherefore the statement $c_{Cbc} > e_C + \psi(1 - \hat{R}_{tot})$ is valid. \hat{R}_{tot} and \hat{C}_{tot} refer to the sum of the abundance of all resource, respectively all consumer species.

$$\hat{R}_{i,(i-bc+1)odd} = \frac{c_{Rbc} c_{Rbc+2}}{c_{Rbc+1} c_{Rbc+3}} \dots \frac{c_{i-2}}{c_{i-1}} (1 - D) - \frac{c_{Rbc+1} c_{Rbc+3}}{c_{Rbc} c_{Rbc+2}} \dots \frac{1}{c_i} e - \frac{c_{Rbc+1} c_{Rbc+3}}{c_{Rbc} c_{Rbc+2}} \dots \frac{1}{c_i} \mu \sum_{h=1}^{NC} C_h$$

$$\hat{R}_{i,(i-bc+1)even} = \frac{c_{Rbc} c_{Rbc+2}}{c_{Rbc+1} c_{Rbc+3}} \dots \frac{1}{c_i} (D - 1) + \frac{c_{Rbc+1} c_{Rbc+3}}{c_{Rbc} c_{Rbc+2}} \dots \frac{c_{i-2}}{c_{i-1}} e + \frac{c_{Rbc+1} c_{Rbc+3}}{c_{Rbc} c_{Rbc+2}} \dots \frac{c_{i-2}}{c_{i-1}} \mu \sum_{h=1}^{NC} C_h$$

$$\hat{C}_{i,(i-bc+1)odd} = \frac{c_{Cbc} c_{Cbc+2}}{c_{Cbc+1} c_{Cbc+3}} \dots \frac{c_{i-2}}{c_{i-1}} (1 - D) - \frac{c_{Cbc+1} c_{Cbc+3}}{c_{Cbc} c_{Cbc+2}} \dots \frac{1}{c_i} (e + \psi) + \frac{c_{Cbc+1} c_{Cbc+3}}{c_{Cbc} c_{Cbc+2}} \dots \frac{1}{c_i} \psi \sum_{h=1}^{NR} R_h$$

$$\hat{C}_{i,(i-bc+1)even} = \frac{c_{Cbc} c_{Cbc+2}}{c_{Cbc+1} c_{Cbc+3}} \dots \frac{1}{c_i} (D - 1) + \frac{c_{Cbc+1} c_{Cbc+3}}{c_{Cbc} c_{Cbc+2}} \dots \frac{c_{i-2}}{c_{i-1}} (e + \psi) - \frac{c_{Cbc+1} c_{Cbc+3}}{c_{Cbc} c_{Cbc+2}} \dots \frac{c_{i-2}}{c_{i-1}} \psi \sum_{h=1}^{NR} R_h$$

Rewriting the model in this way provides the insight that habitat fragmentation (D) has a negative impact on the abundance of odd-numbered species, including species bc , but has positive impact on even-numbered species, as long as the impact of top-down control μ remains small or zero.

The careful reader has noticed that an important part of the solution for $d\hat{R}_i/dt=0$ and $d\hat{C}_i/dt=0$ remained unsolved in the above presented formulas, namely the total abundance of all resource species \hat{R}_{tot} and the total abundance of all consumer species \hat{C}_{tot} . Those abundances are important because they determine the impact of top-down control μ and donor control ψ .

$$\hat{R}_{tot} = \sum_{h=1}^{NR} \hat{R}_h$$

$$\hat{C}_{tot} = \sum_{h=1}^{NC} \hat{C}_h$$

A further solution of these total abundances is possible, but requires determination of $NBG0_R$ the total number of resource species whereof $\hat{R} > 0$ and $NBG0_C$ the total number of consumer species whereof $\hat{C} > 0$. Because the solution for $d\hat{R}/dt$ and $d\hat{C}/dt$ is different for odd- and even-numbered species, the solution of $d\hat{R}_{tot}/dt$ and $d\hat{C}_{tot}/dt$ is likewise different for an even or odd $NBG0_R$, respectively $NBG0_C$. The solutions for $d\hat{R}_{tot}/dt$ and $d\hat{C}_{tot}/dt$ are as follows (see Appendix 2 for a derivation of these solutions):

$$\begin{aligned} \hat{R}_{tot, NBG0Rodd, NBG0Codd} &= 1 - \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{1}{c_{Rbc}} e \dots \\ &\dots - \frac{(c_{NR}c_{NR-2} \dots c_{Rbc})(c_{NC}c_{NC-2} \dots c_{Cbc}) - (c_{NR-1}c_{NR-3} \dots c_{Rbc})(c_{NC}c_{NC-1} \dots c_{Cbc})\mu}{(c_{NR}c_{NR-2} \dots c_{Rbc})(c_{NC}c_{NC-2} \dots c_{Cbc}) + (c_{NR-1}c_{NR-3} \dots c_{Rbc+1})(c_{NC-1}c_{NC-3} \dots c_{Cbc+1})\mu\psi} D \\ \hat{R}_{tot, NBG0Rodd, NBG0Ceven} &= 1 - \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{1}{c_{Rbc}} e \dots \\ &\dots - (1 - \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{\mu}{c_{Rbc}} + (\frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{\mu}{c_{Rbc}})(\frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{c_{Cbc}}{c_{Cbc+1}}))D \\ \hat{R}_{tot, NBG0Reven} &= 1 - \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{c_{Rbc}}{c_{Rbc+1}} - (1 - \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{c_{Rbc}}{c_{Rbc+1}})D \\ \hat{C}_{tot, NBG0Rodd, NBG0Codd} &= 1 - \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{1}{c_{Cbc}} (e + \psi) \dots \\ &\dots - \frac{(c_{NR}c_{NR-2} \dots c_{Rbc})(c_{NC}c_{NC-2} \dots c_{Cbc}) + (c_{NR}c_{NR-2} \dots c_{Rbc})(c_{NC-1}c_{NC-3} \dots c_{Cbc+1})\psi}{(c_{NR}c_{NR-2} \dots c_{Rbc})(c_{NC}c_{NC-2} \dots c_{Cbc}) + (c_{NR-1}c_{NR-3} \dots c_{Rbc+1})(c_{NC-1}c_{NC-3} \dots c_{Cbc+1})\mu\psi} D \\ \hat{C}_{tot, NBG0Reven, NBG0Codd} &= 1 - \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{1}{c_{Cbc}} (e + \psi) \dots \\ &\dots - (1 + \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{\psi}{c_{Cbc}} - (\frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{\psi}{c_{Cbc}})(\frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{c_{Rbc}}{c_{Rbc+1}}))D \\ \hat{C}_{tot, NBG0Ceven} &= 1 - \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{c_{Cbc}}{c_{Cbc+1}} - (1 - \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{c_{Cbc}}{c_{Cbc+1}})D \end{aligned}$$

When studying the solutions of $d\hat{R}_{tot}/dt=0$ and $d\hat{C}_{tot}/dt=0$, several aspects of importance come to notice. If top-down control μ and donor control ψ are zero, the slopes of the total abundances $d\hat{R}_{tot,NBGO_{Rodd}}/dD$ and $d\hat{C}_{tot,NBGO_{Codd}}/dD$ are -1. Effectively this means that the amount of resource and consumer species lost with increasing habitat fragmentation, is equal to the amount of habitat destroyed. An increase in top-down control μ will lead to a decrease in the slope of $\hat{R}_{tot,NBGO_{Rodd}}$, while an increase in donor control ψ leads to an increased slope of $\hat{C}_{tot,NBGO_{Codd}}$. Top-down control thus reduces the impact of habitat fragmentation D on the total abundance of resource species, while donor control increases the impact of habitat fragmentation on the total abundance of consumer species if $NBGO$ is odd.

$$\frac{R_{tot,NBGO_{Rodd}}}{dD} \geq -1$$

$$\frac{C_{tot,NBGO_{Codd}}}{dD} \leq -1$$

Surprisingly top-down control μ and donor control ψ have no influence on the total abundance of resource and consumer species when $NBGO$ is even. Top-down μ leads to a decreased abundance of odd-numbered species, but this loss is compensated by an increase in abundance of species even-numbered species. The same principle, only the other way around, goes for donor control ψ when $NBGO$ is even.

Habitat fragmentation will thus always have a negative impact on the total abundance of consumer species, and on resource species when $NBGO_R$ is even. If $NBGO_R$ is odd, habitat fragmentation may have a positive impact on the total abundance of resource species in a scenario where donor control ψ is weak and top-down control μ is strong.

As can be seen in figure 1, abrupt changes can be observed in the impact of habitat fragmentation on the total abundance of resource and consumer species. Every time a species goes extinct, or when a new species establishes, the value of $NBGO$ changes. This leads to abrupt changes in the value of $d\hat{C}_{tot}/dD$ and $d\hat{R}_{tot}/dD$. If the total number of species included N goes to infinity, $d\hat{C}_{tot}/dD$ and $d\hat{R}_{tot}/dD$ however becomes seemingly constant. In this case the establishment or extinction of new species with increasing habitat fragmentation occurs so often that the shifts in the value of $d\hat{C}_{tot}/dD$ and $d\hat{R}_{tot}/dD$ are no longer visible.

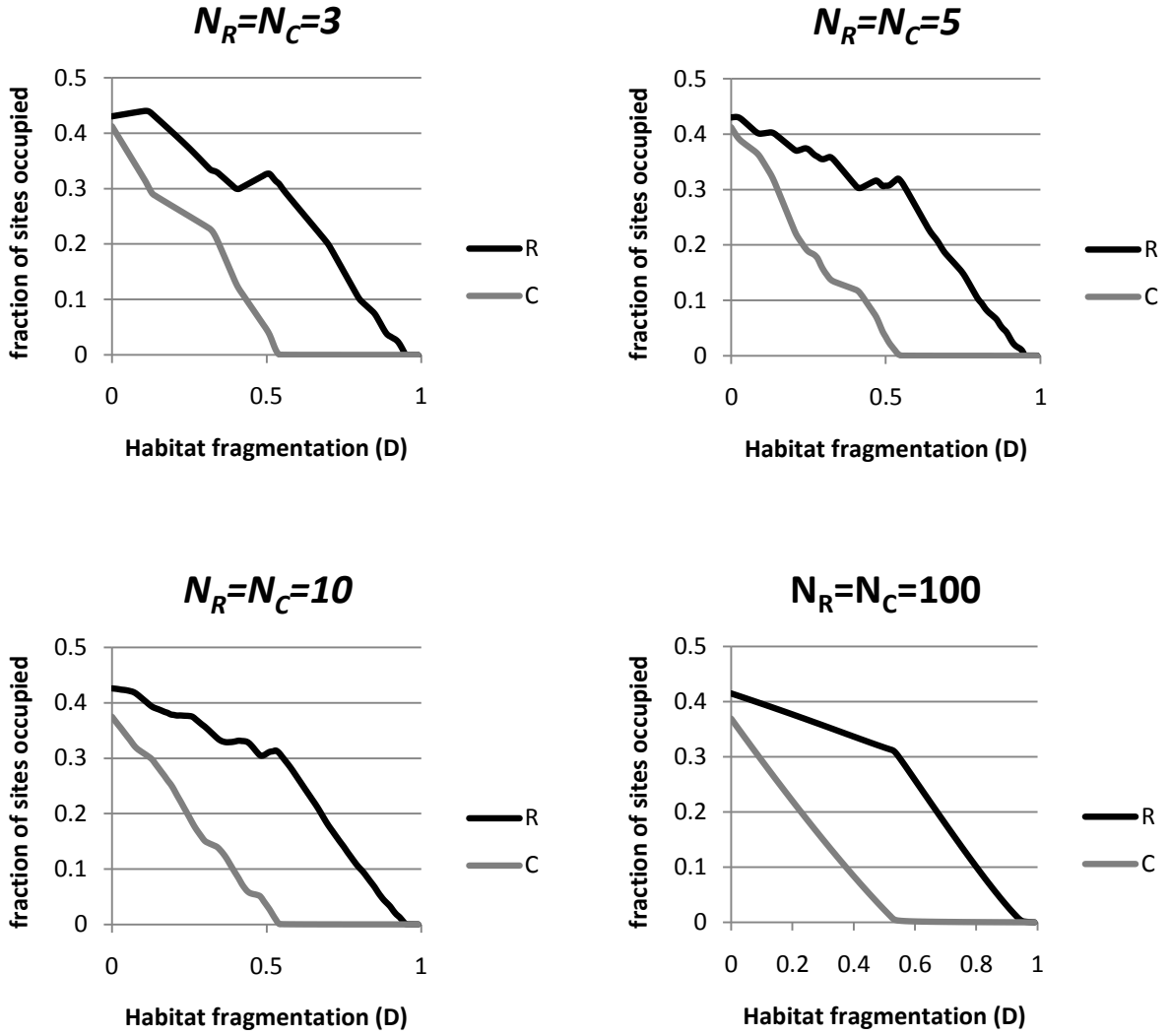


Figure 1. The impact of habitat fragmentation D on the total abundance of resource species (R) and consumer species (C) for different numbers of resource species N_R and consumer species N_C included. Abrupt changes in the impact of habitat fragmentation on the total abundance of resource and consumer species can be observed when the number of species included N is low. If the total number of species included N goes to infinity, the slopes $d\hat{R}_{tot}/dD$ and $d\hat{C}_{tot}/dD$ become ‘seemingly’ constant. Type of model: mean-field. Parameter settings: $c_{max}=1$, $\mu=0.8$, $\psi=0.6$, $e_R=0.05$, $e_C=0.05$, $f=0.00001$.

3.2 EXTINCTION AND RE-ESTABLISHMENT DUE TO COMPETITION IN THE MEAN FIELD MODEL

Within the for this study newly developed model, competition may cause species to go extinct and re-establish with increasing habitat fragmentation. Although it is not the aim of this research, this is an important property of the model, since it shows that habitat fragmentation may liberate species from the pressure imposed by a better competitor.

The fact that habitat fragmentation only has a negative effect on odd-numbered species with increasing habitat fragmentation, mentioned earlier in this paper, has an important consequence for the order wherein species may go extinct due to competitive exclusion. If species go extinct due to competition with increasing habitat fragmentation, the odd-numbered species with the highest number will go extinct first. The odd-numbered species with the second highest number will be the next one to go extinct, this order of extinction continues, until species bc goes extinct. Due to the extinction of species bc , all formerly odd-numbered species become even-numbered. Habitat fragmentation now has a positive effect on the abundance of the extinct species and with increasing habitat fragmentation all species that are extinct due to competition will re-establish (see figure 2). If and how many species go extinct due to competitive exclusion depends on the height of e_R and c_{\max} and on the number of species N included in the model.

In the for this study newly developed model the size of Δc and Δc_{bc} , decreases with increasing N , where $\Delta c = c_{i+1} - c_i$ and $\Delta c_{bc} = c_{bc} - c_{\min}$ and c_{\min} refers to the minimum colonization rate necessary for survival. Because Δc and Δc_{bc} decreases, the difference in abundance between odd- and even-numbered species also decreases with increasing N . This in turn makes competitive exclusion less likely to occur. The in the here studied model included relation between N and Δc thus leads to the, at first sight counter intuitive, result that the occurrence of competitive exclusion decreases, as the number of species included N increases (see figure 3).

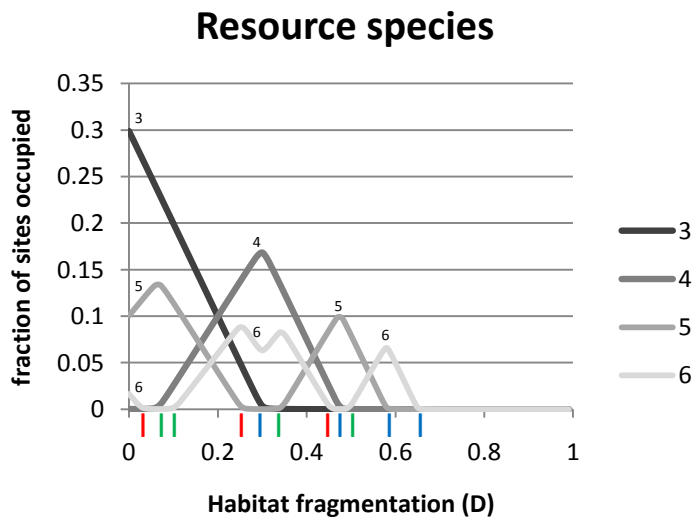


Figure 2. If the total number of species included N is low, species might go extinct due to competitive exclusion. In the here presented example species 4, 5 and 6 are, or go, extinct for certain values of habitat fragmentation D due to competitive exclusion (indicated in red). As habitat fragmentation increases further these species re-establish because the abundance of better competitors declines (indicated in green). Eventually all species go extinct due to habitat fragmentation itself (indicated in blue). Parameter settings: $N_R=6$, $\mu=0$, $e_R=0.35$, $f=0.00001$. Species 1 and species 2 are extinct for all values of habitat fragmentation D .

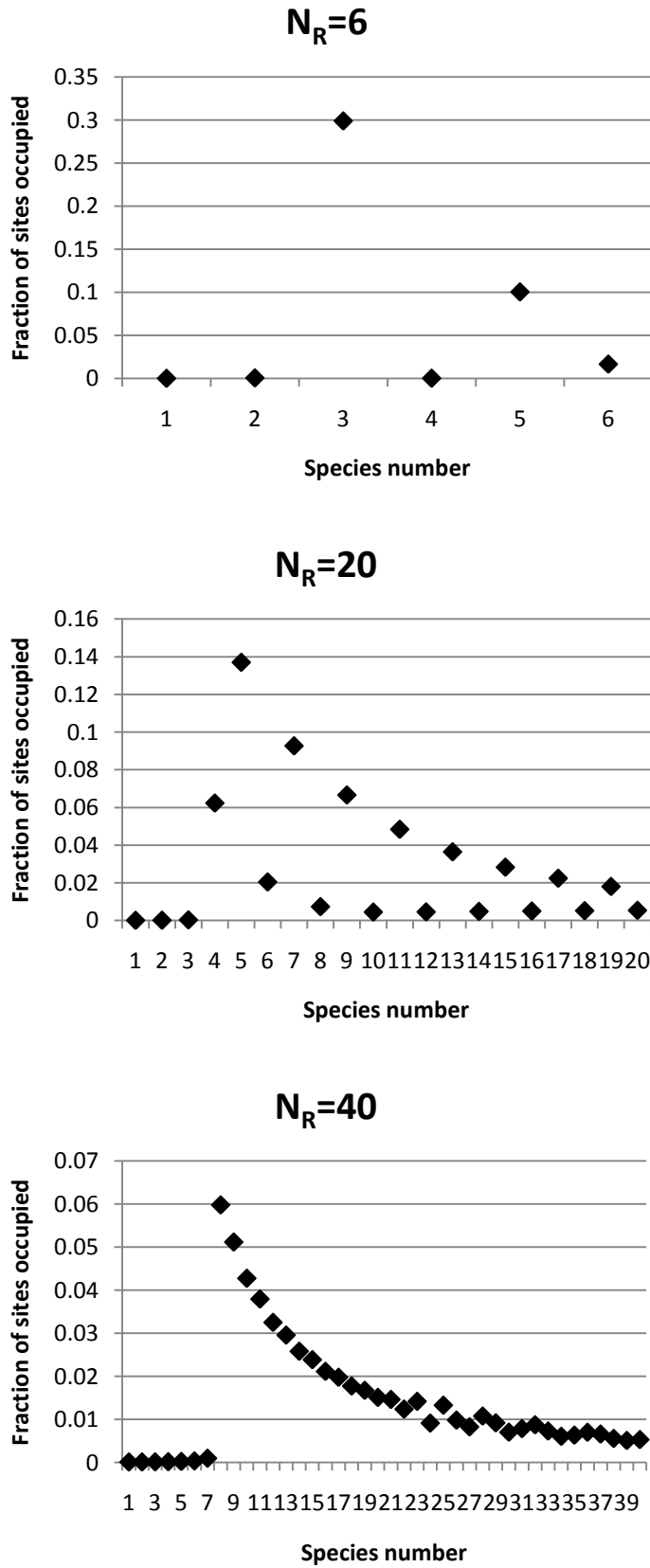


Figure 3. In the graphs on the left, the abundance of *individual* resource species is shown for different values of the total number of species N incorporated.

As the number of species N increases, the difference in abundance between ‘odd-numbered’ and ‘even-numbered’ species decreases. As a consequence competitive exclusion is unlikely to occur when the value of N is high.

The most competitive species (species 1 till species bc) are extinct because their colonizing ability c_i is smaller than extinction rate e_R . All other species that are (almost) extinct, are extinct because they are outcompeted by better competitors.

Type of model: mean-field

Parameter settings: $D=0$, $\mu=0$, $e_R=0.35$, $f=0.00001$

3.3 EXTINCTION OR ESTABLISHMENT DUE TO HABITAT FRAGMENTATION IN THE MEAN FIELD MODEL

The influence of habitat fragmentation on the extinction or re-establishment of species can be further studied by solving $\hat{R}_i=0$ and $\hat{C}_i=0$ for D . The solution of this problem is as follows:

$$D_{Ri} = 1 - \frac{e_R}{c_{Ri}} - \frac{\mu}{c_{Ri}} \hat{C}_{tot}$$

$$D_{Ci} = 1 - \frac{e_C + \psi}{c_{Ci}} + \frac{\psi}{c_{Ci}} \hat{R}_{tot}$$

Let us first consider a scenario where top-down control μ and donor control ψ are zero. In this case one can clearly see that $D_i < D_{i+1} < D_{i+2}$ and so on. In this scenario species will thus go extinct due to habitat fragmentation in order of their competitive rank. The most competitive species will go extinct first as habitat fragmentation increases, followed by the next best competitor and so on. Also when competitive exclusion occurs in the model, this order remains intact (see figure 2).

A scenario where top-down control μ and donor control ψ are not zero however requires further analysis. Determining D_{Ri} and D_{Ci} now is more difficult, because \hat{R}_{tot} and \hat{C}_{tot} are influenced by habitat fragmentation D themselves. This dependence of \hat{R}_{tot} and \hat{C}_{tot} on D makes three scenario's possible for an individual species i . (1) Species i will remain in the same state (extinct or present) for all values of D , (2) if species i is not extinct already it will go extinct due to habitat fragmentation as habitat fragmentation D increases further and (3) if species i is not present already it will establish due to habitat fragmentation as habitat fragmentation D increases. Scenario 1, 2 and 3 are true for respectively resource species (above) and consumer species (below) when the following is true:

Scenario 1 (same state)	Scenario 2 (extinction)	Scenario 3 (establishment)
$\frac{d\hat{C}_{tot}}{dD} = -\frac{c_{Ri}}{\mu}$	$\frac{d\hat{C}_{tot}}{dD} > -\frac{c_{Ri}}{\mu}$	$\frac{d\hat{C}_{tot}}{dD} < -\frac{c_{Ri}}{\mu}$
$\frac{d\hat{R}_{tot}}{dD} = \frac{c_{Ci}}{\psi}$	$\frac{d\hat{R}_{tot}}{dD} < \frac{c_{Ci}}{\psi}$	$\frac{d\hat{R}_{tot}}{dD} > \frac{c_{Ci}}{\psi}$

As mentioned in paragraph 4.1, $d\hat{R}_{tot}/dD$ can only be bigger than zero if donor control ψ is small. The consequence of a low donor control ψ is a high value for c_{Ri}/ψ . As a consequence of this interrelationship, $d\hat{R}_{tot}/dD$ is always smaller than c_{Ci}/ψ , thus scenario 1 and scenario 3 cannot be true for consumer species. Consumer species will thus always follow scenario 2, they will go extinct with increasing habitat fragmentation D .

All scenario's are however possible for resource species, including scenario 3, the scenario wherein the number of species increases while habitat fragmentation is increasing. Scenario 3 is possible, even when the value of top-down control μ is low. The first species to re-establish in case of scenario 3 will be species $bc-1$. As long as $d\hat{C}_{tot}/dD$ remains the same, all species however establish with increasing habitat fragmentation D , because $c_{Rbc-1} > c_{Rbc-2} > c_{Rbc-3} \dots > c_{NR}$. In the case of scenario 3, species $bc-1$ will thus be the first one to establish, followed by species $bc-2$ and so on. Resource species will continue to establish until species N_R establishes, or until all consumers have gone extinct. In this case $d\hat{C}_{tot}/dD$ becomes zero (scenario 2). Resource species will then thus start to go extinct again as habitat fragmentation increases.

On the next two pages examples of scenario 2 and 3 are shown (figure 4 and 5). Even if the total abundance of resource and consumer species, and the abundance of the species present at no habitat fragmentation ($D=0$) is the same, the impact of habitat fragmentation on the species richness of resource species can be very different, depending on the strength of top-down control μ and donor control ψ .

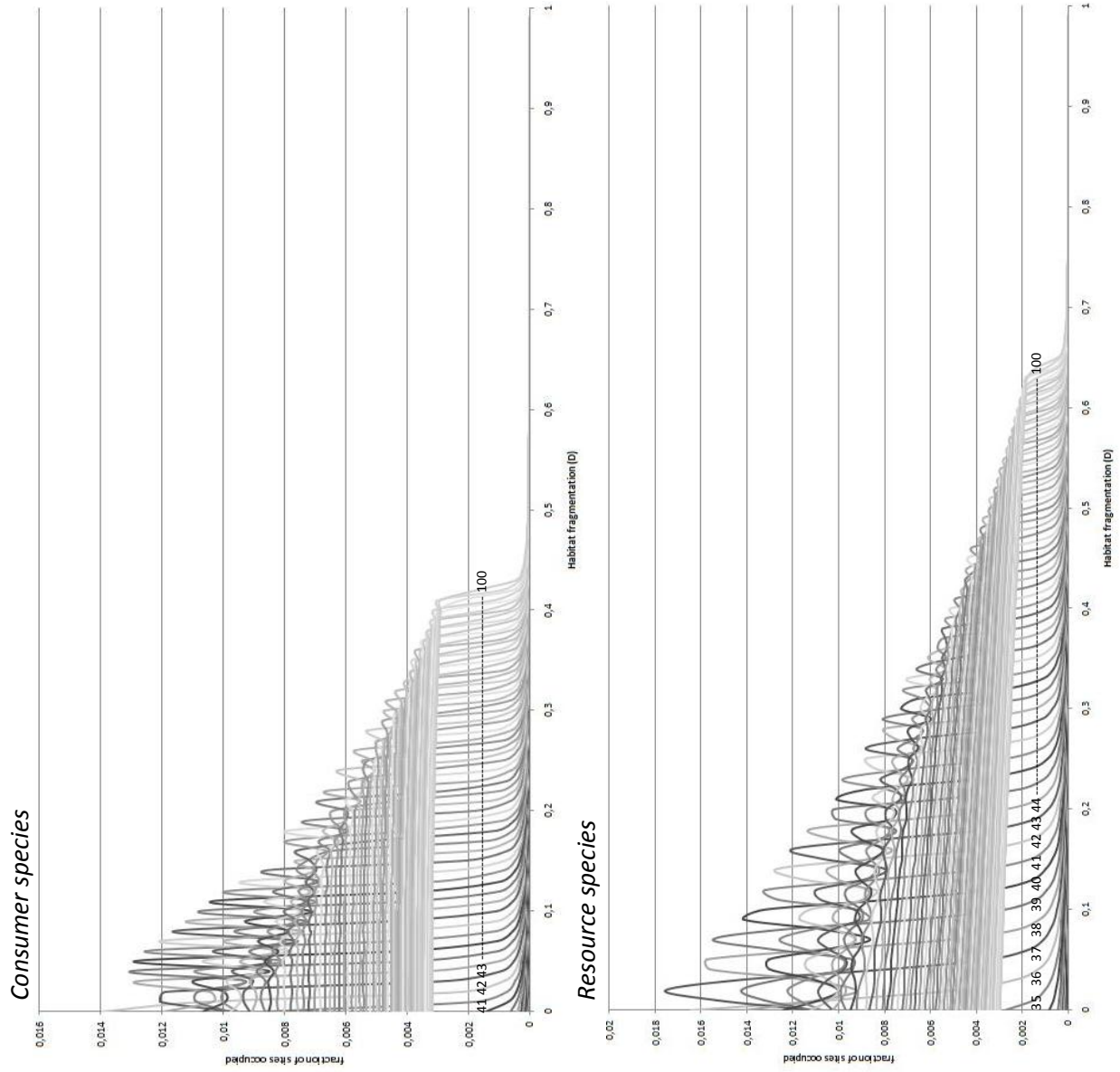


Figure 4. Habitat fragmentation is not beneficial for resource species when there is no top-down control ($\mu=0$). As habitat fragmentation increases, both resource and consumer species go extinct in order of their competitive rank.

The total abundance of resource and consumer species and the abundance of individual species at $D=0$ is more or less similar in the cases presented in figure 4 and figure 5. The impact of habitat fragmentation on these individual abundances however is fairly different.

The numbers next to the lines indicate the number (i) of a species. Species go extinct in order of their ranking. The best competitor, with lowest colonizing ability is the first one to go extinct due to habitat fragmentation.

Type of model: mean-field

Parameter settings: $N_R=100$, $N_C=100$, $c_{\max}=1$, $\mu=0$, $\psi=0.6$, $e_R=0.35$, $e_C=0.05$, $f=0.00001$.

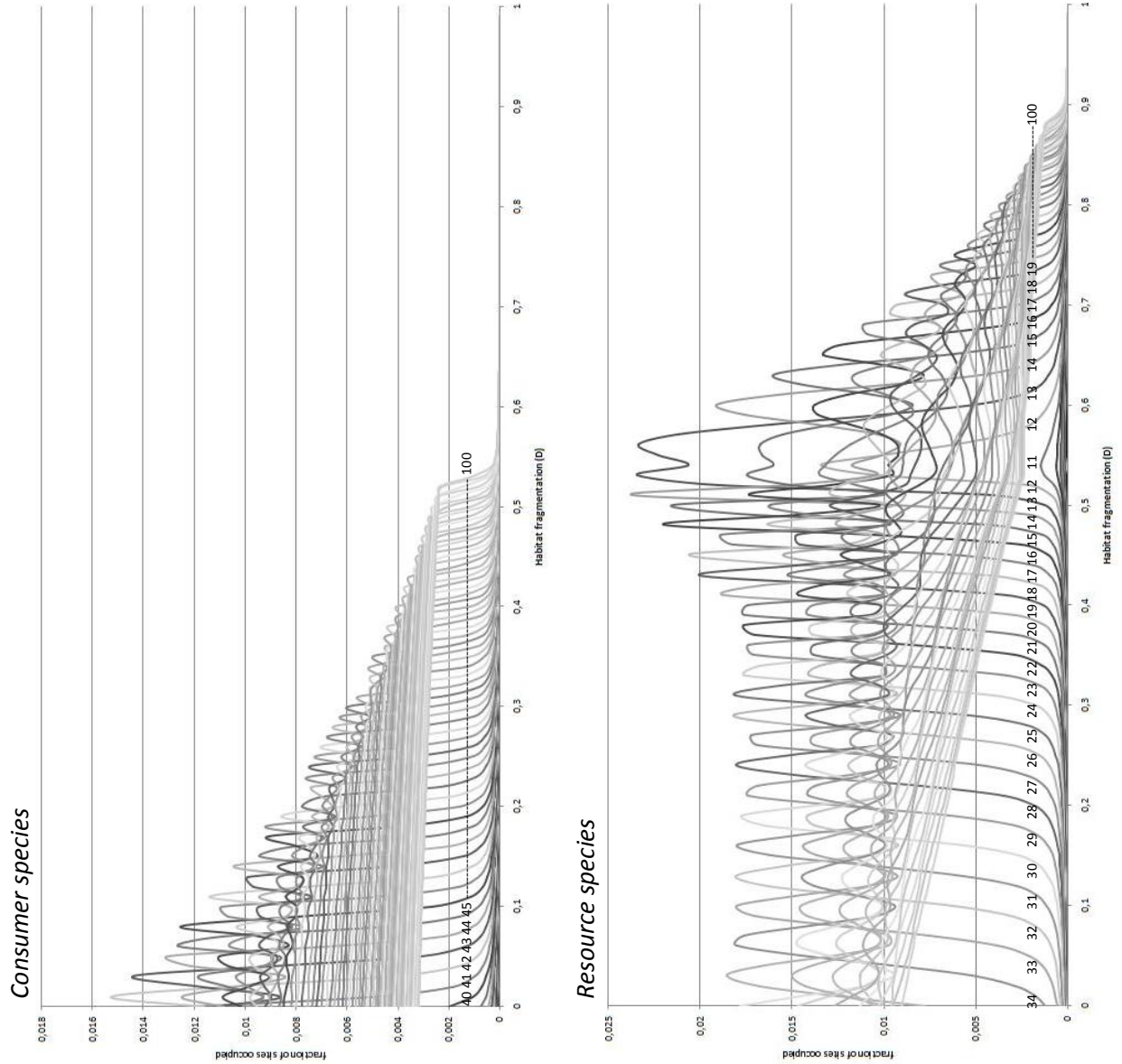


Figure 5. Habitat fragmentation can be beneficial for resource species. Even though the total abundance of resource species declines, more and more resource species establish as habitat fragmentation increases. The establishment of resource species continues until all consumers are extinct.

The total abundance of resource and consumer species and the abundance of individual species at $D=0$ is more or less similar in the cases presented in figure 4 and figure 5. The impact of habitat fragmentation on these individual abundances however is fairly different.

The numbers next to the lines indicate the number (i) of a species. Species establish or go extinct in order of their ranking. The best competitors, with lowest colonizing ability, are the last ones to establish due to decreased impact of top-down control and also go extinct first due to habitat fragmentation (last in first out).

Type of model: mean-field

Parameter settings: $N_R=100$, $N_C=100$, $c_{max}=1$, $\mu=0.8$, $\psi=0.6$, $e_R=0.05$, $e_C=0.05$, $f=0.00001$.

3.4 EXTINCTION AND (RE-)ESTABLISHMENT IN THE SPATIALLY EXPLICIT MODEL

The difference between the impact of habitat fragmentation on the abundance of odd-numbered and the impact of habitat fragmentation on the abundance of even-numbered species, does not exist in the spatially explicit model. As a consequence there is also no difference between the impact of habitat fragmentation on the total abundance of resource and consumer species between an even and odd total number of species *NBGO* whereof the abundance is bigger than zero. In the spatially explicit model, in case of no, or little, top-down control the abundance of species *bc* is negatively affected by habitat fragmentation, while the abundance of all species that are not as competitive as species *bc* is positively affected by habitat fragmentation in the spatially explicit model. Different from what is observed in the mean field model, a clear difference thus is observed between the impact of habitat fragmentation on species *bc* and the impact of habitat fragmentation on all species that are not as competitive as species *bc* within the spatially explicit model.

As a consequence of this different impact of habitat fragmentation, the occurrence of competitive exclusion also differs between the mean field and the spatially explicit model. Within the spatially explicit model, competitive exclusion does not occur with odd-numbered species only, as is the case in the mean-field model. It occurs with the most uncompetitive species included within the spatially explicit model, independent of the evenness or oddness of their number. In practice, the occurrence of competitive exclusion within the spatially explicit model however is uncommon when the lattice size of the model is big. Up till 50 different species per trophic level can be included within the spatially explicit model without the occurrence of competitive exclusion, when its lattice size is equal to or bigger than 500×500 , its extinction rate is equal to or higher than 0.05 and when the external influx f is equal to or higher than 0.0001.

Other than the impact of habitat fragmentation on the abundances of individual species and the occurrence of competitive exclusion, the extinction or establishment of species due to habitat fragmentation is similar in both models. Extinction of resource and consumer species, in a scenario with no or a weak impact of top-down control μ , occurs in the same order as in the mean field model. Likewise, the establishment of resource species, in a scenario with a stronger impact of top-down control μ , occurs in the same order as the order found within the mean field model. The impact of habitat fragmentation on the extinction or establishment of species due to habitat fragmentation thus is very similar in the mean-field and the spatially explicit model.

As in the mean field model, resource species *bc* is the most abundant species, even shortly before it goes extinct or shortly after it has established within the spatially explicit model. Graphs showing the relation between habitat fragmentation and the abundance of individual species in the spatially explicit model therefore look very similar to the graphs of the mean field model, shown in figure 4 and 5. The only difference between these graphs is the abundance of odd-numbered species that are not as competitive as species *bc*.

3.5 THE INTERPLAY BETWEEN TOP-DOWN CONTROL μ AND DONOR CONTROL ψ

Intuitively one would expect that the impact of consumer species on the total abundance and species richness of resource species will only get bigger as the strength of top-down control μ increases. Top-down control μ however not only affects the abundance of resource species, it also affects the total abundance of consumer species when the value of donor control ψ is bigger than zero. A high value of top-down control robs consumer species of their resource. This causes a decline in total abundance of consumer species with increasing top-down control μ . As the *strength* of top-down control increases, its *impact* on resource species is therefore reduced, because the abundance of consumer species declines with increasing top-down control (see figure 6).

The negative impact of top-down control μ , via donor control ψ , on consumer species is especially strong within the spatially explicit model, because top-down control μ causes consumer species to be unevenly distributed over sites with and without resource species. Within the spatially explicit model resource species have a higher probability of dying in sites where consumer species are present due to top-down control μ . As a consequence consumer species are more often found in sites where no resource species are present, which increases their probability of dying strongly via donor control ψ . Within the mean field model this effect is less strong, because consumer species are assumed to be equally distributed over sites wherein resource species are present and sites wherein resource species are not present.

For high values of donor control ψ within the spatially explicit model, the decline in the abundance of consumer species can be so strong that there is an optimum value for top-down control μ where its impact on resource species is biggest. After this optimum value the abundance of resource species starts to increase again even though the strength of top-down control μ increases. This is not possible within the mean-field model, because within the mean-field model an increase in abundance of resource species will always lead to an increase in total abundance of consumer species via donor control ψ (see figure 7 and 8).

The optimum value, wherefore the impact of top-down control on resource species is biggest is also found within the spatially explicit model when studying the impact of top-down control on the abundance of individual species. As top-down control increases, both resource and consumer species go extinct in order of their competitive rank, where the most competitive species, species *bc*, is the first one to go extinct. This order of extinction is the same in the spatially explicit model and the mean field model. However, if, within the spatially explicit model, top-down control μ increases further than its optimum value, resource species start to re-establish again in reversed order. This leads to the counterintuitive result that the same resource species is dominant for a low and a high value of top-down control μ (see figure 9).

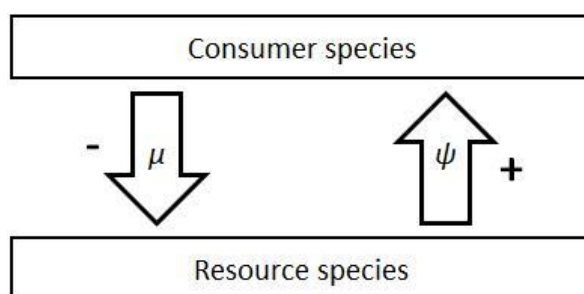


Figure 6. The interplay between top-down control μ and donor control ψ . Top-down control μ has a direct negative effect on the abundance of resource species. Indirectly it however also has a negative effect on the abundance of consumer species, because the abundance of resource species and the abundance of consumer species is positively related via donor control ψ .

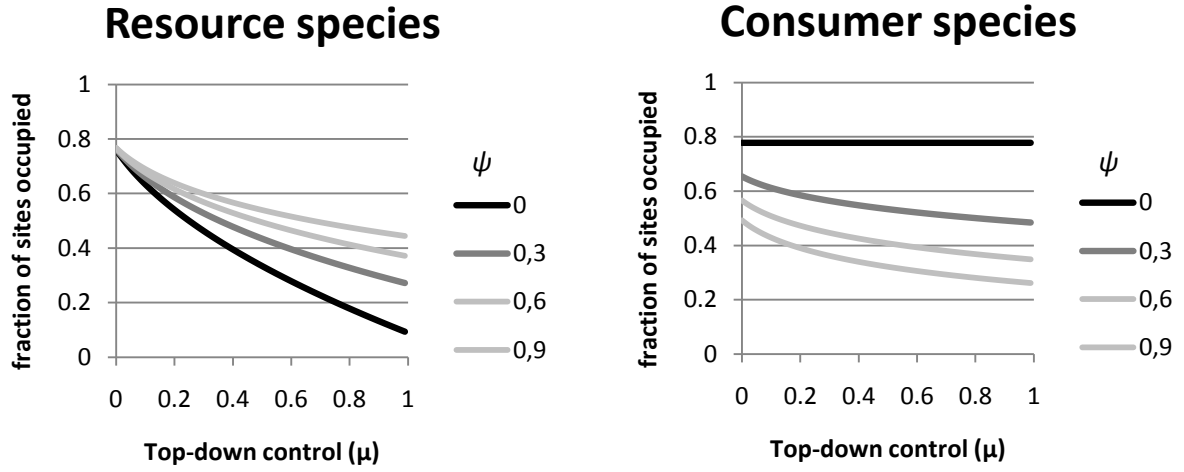


Figure 7. The impact of top-down control μ on the total abundance of resource species (left) and consumer species (right) for different values of donor control ψ in the mean field model. With increasing top-down control the abundance of both resource and consumer species declines, unless donor control $\psi=0$. Parameter settings: $N_R=100$, $N_C=100$, $D=0$, $c_{\max}=1$, $e_R=0.05$, $e_C=0.05$, $f=0.00001$.

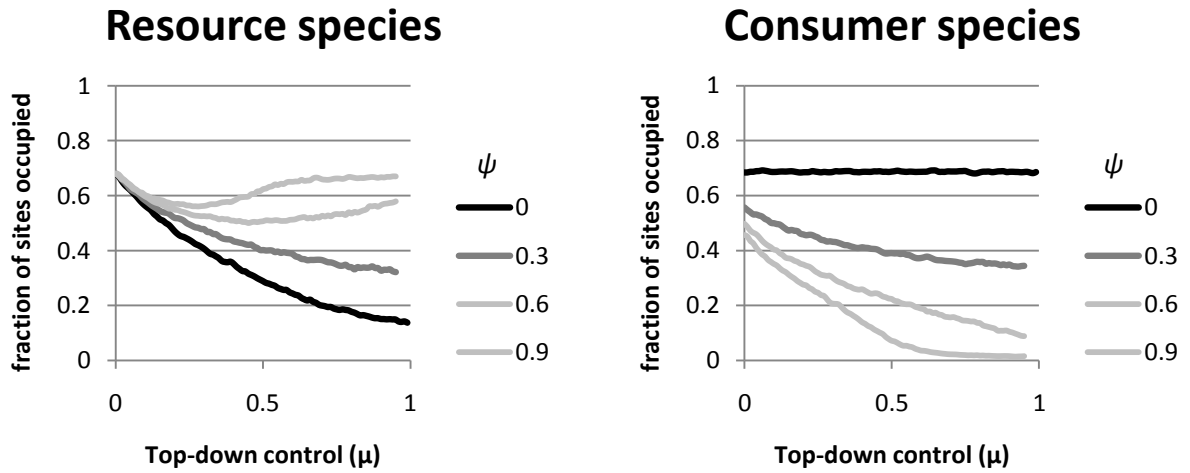


Figure 8. The impact of top-down control μ on the total abundance of resource species (left) and consumer species (right) for different values of donor control ψ in the spatially explicit model. With increasing top-down control the abundance of consumer species declines, unless donor control $\psi=0$. For high values of donor control ψ within the spatially explicit model, the decline in the abundance of consumer species can be so strong that there is an optimum value for top-down μ control where its *impact* on resource species is biggest. After this optimum value the abundance of resource species thus starts to increase again even though the *strength* of top-down control μ increases. Parameter settings: $N_R=20$, $N_C=20$, $D=0$, $c_{\max}=0.2$, $e_R=0.05$, $e_C=0.05$, $f=0.0001$, $m=250$, $dT=0.1$.

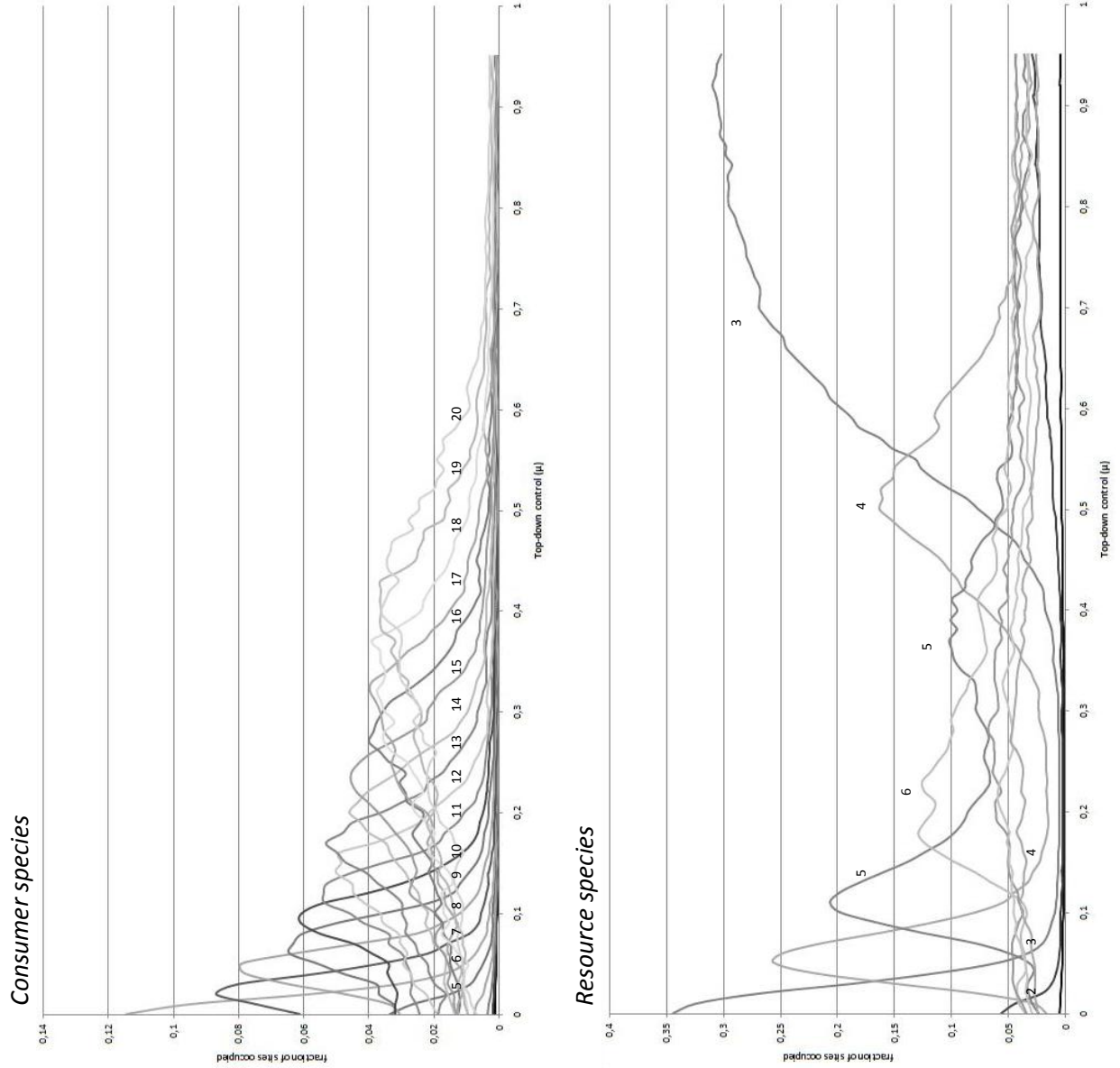


Figure 9. As the *strength* of top-down control μ increases, its *impact* on resource species is reduced, because the abundance of consumer species declines with increasing top-down control. In the here presented case, this causes the same resource species to be dominant for a low and a high value of donor control μ .

The numbers next to the lines indicate the number (*i*) of a species. Species establish or go extinct in order of their ranking. The best competitors, with lowest colonizing ability, are the first ones to go extinct as top-down control μ increases. As top-down control μ increases further and the impact of top-down control is reduced, they are also the last ones to re-establish.

Type of model: spatially explicit

Parameter settings: $N_R=20$, $N_C=20$, $D=0$, $c_{\max}=0.2$, $\psi=0.9$, $e_R=0.05$, $e_C=0.05$, $f=0.0001$, $m=250$, $dT=0.1$.

3.6 THE SPATIAL DISTRIBUTION OF INDIVIDUAL SPECIES

Within the spatially explicit model consumer species are not only unevenly distributed over sites with and without resource species, as mentioned in the former paragraph, they are also unevenly distributed over different resource species types. At the position where consumer species are present, resource species with a low competitive strength and thus a high colonizing ability are substantially more abundant. During time, consumer species however are moving from an area with resource species that are weak competitors to an area with resource species that are strong competitors. This is probably caused by a higher density of resource species in the area where the highly competitive resource species are present. These highly competitive resource species however cannot maintain themselves under the pressure imposed by consumers, they go extinct in this area and the area gets occupied by resource species that are weak competitors. The weakest competitors, with highest colonizing ability, are the first to colonize the area wherein resource species have gone extinct due to the presence of consumers. Consumer species probably have the lowest impact on these resource species because they have a high colonization ability, therefore these resource species can maintain themselves in the presence of consumer species. These resource species are however in time replaced by resource species that are better competitors. Consumer species moving in a certain direction, thus leave an array of resource species behind ordered from highest rank to lowest rank (see figure 10).

The array of resource species left behind illustrates the impact top-down control has on individual resource species. Presence of consumer species has a strong negative effect on the abundance of the best competitor bc , but promotes the abundance of all weaker competitors, especially the abundance of species $bc+1$ (see figure 9 and 10). There is thus not only a difference between the mean field and the spatially explicit model in impact of top-down control μ on the total abundance of resource and consumer species, also the impact of top-down control on the abundance of individual species differs between the mean field and the spatially explicit model. Within the mean field model, all odd-numbered species are negatively affected by consumer species, including species bc and all even numbered species are positively affected by the presence of consumer species. Within the spatially explicit model, there is no difference between odd- and even numbered species. Presence of consumer species negatively affects the abundance of the best competitor bc , but seems to promote the abundance all weaker competitors, especially the abundance of species $bc+1$.

The impact of consumer species on resource species bc can be highly influenced by the presence of resource species that are weaker competitors within the spatially explicit model. As shown in figure 10, weak competitors are relatively more often present at sites where consumer species are also present. Their ability to colonize sites that have become empty due to top-down control μ , reduces the extent wherein consumer species are confronted with a lack of resource strongly. A strong mutual beneficial relation thus exists between resource species that are weak competitors and consumer species. Consumer species cause resource species that are strong competitors to go extinct, providing resource species that are weak competitors with an area to colonize. For consumer species it is important that the area where they are present gets re-colonized quickly, because the impact of donor control ψ would otherwise be too strong. The strong colonizing ability of resource species that are weak competitors thus is beneficial for consumer species.

Within figure 10, the careful observer may have noticed an area, not indicated with black dots and arrows, where consumer species have caused the extinction of the most competitive resource species. In this 'third' area the resource species that is the weakest competitor has not managed to establish. Clearly consumer species are doing less well in this area.

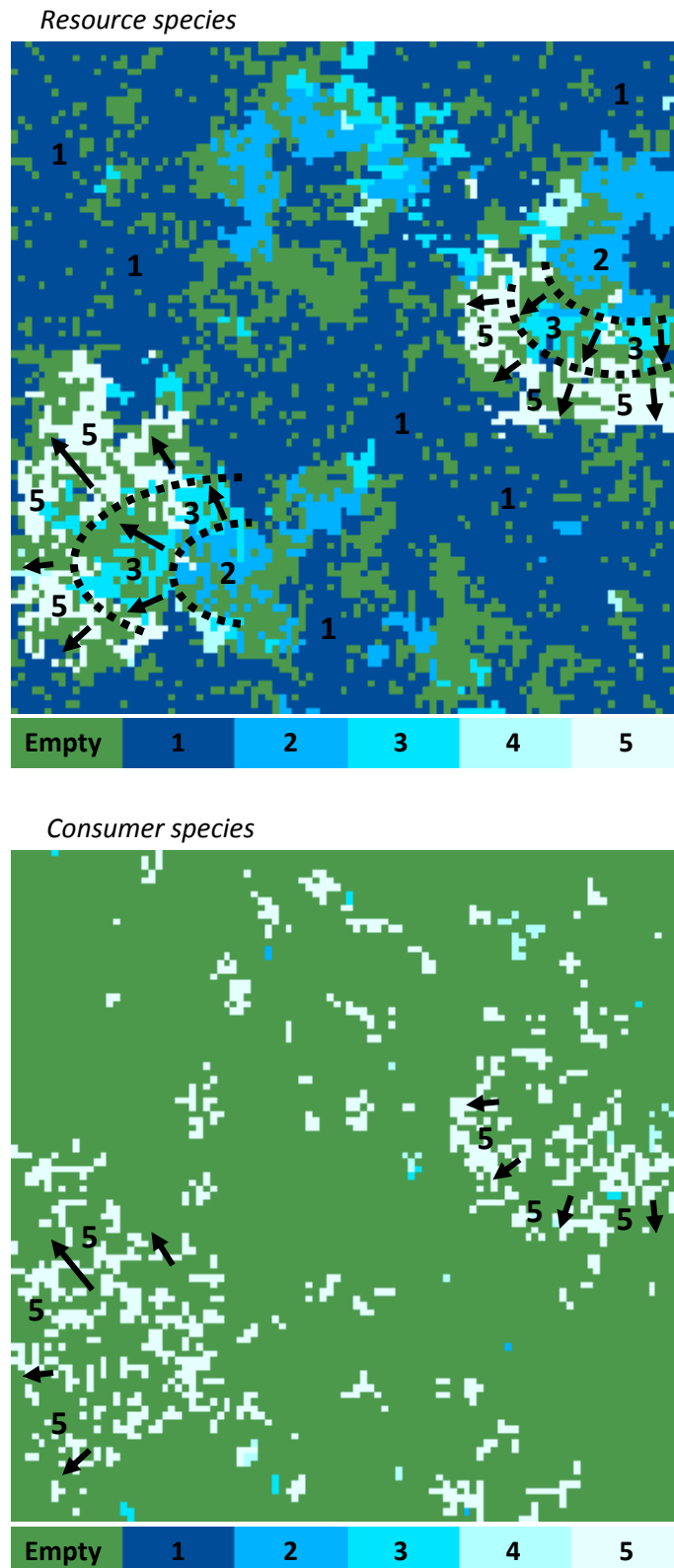


Figure 10. The spatial distribution of species in the spatially explicit model. Consumer species moving in a certain direction, leave an array of resource species behind ordered from highest rank to lowest rank.

During time, consumer species are moving from an area with resource species that are weak competitors to an area with resource species that are strong competitors (indicated with the black arrows). This is probably caused by a higher density of resource species in the area where the highly competitive resource species are present. Highly competitive resource species cannot maintain themselves under the pressure imposed by consumers, they go extinct in this area. The weakest competitors, with highest colonizing ability, are the first to colonize the area wherein resource species have gone extinct due to the presence of consumers. Consumer species probably have the lowest impact on these resource species because they have a high colonization ability, therefore these resource species can maintain themselves in the presence of consumer species. These resource species are however in time replaced by resource species that are better competitors.

Type of model: spatially explicit

Parameter settings: $N_R=5$, $N_C=5$, $c_{max}=0.2$, $\mu=0.7$, $\psi=0.8$, $e_R=0.01$, $e_C=0.05$, $f=0.0001$, $m=100$, $dT=0.1$.

3.7 EXTINCTION OR ESTABLISHMENT OF SPECIES DUE TO MIGRATION BETWEEN AREAS OF DIFFERENT SIZE

The model that describes the impact of migration between areas of different size can be used to describe migration between a potentially unlimited number of areas. The impact of migration between areas of different size is however not principally different when one models migration between two areas of different size, or between many areas of different size. Studying the impact of migration between two areas of different size thus seems to be sufficient.

As shown in the former paragraph habitat fragmentation D can have either a beneficial or a negative impact on resource species richness, depending on the value of top-down control μ and donor control ψ . Similarly species richness of resource species can be either higher, or lower in a small area when compared to a big area, depending on the strength of top-down control μ and donor control ψ . The species richness of consumer species is always lower in small areas when compared to a big area.

In a scenario where the species richness of resource species is higher in small areas, increasing the rate of successful migration θ between areas reduces the species richness of resource species in small areas. As the rate of successful migration θ increases, abundance and species richness of consumer species increases strongly within small areas. This increased abundance of consumer species leads to a stronger impact of top-down control μ on resource species, leading to a lower abundance and species richness of resource species in small areas (see figure 11). Unfortunately all consumer species that manage to establish in the small area where already present in one of the larger areas, while the resource species that have gone extinct in small areas where not present in bigger areas. The system as a whole thus loses resource species as the rate of successful migration θ increases.

As the rate of successful migration θ increases, resource species are lost, some consumer species that were not present within the system as a whole however may manage to establish. Due to the increased rate of successful migration θ the abundance of resource species in big areas increases slightly. Because more resource species from small areas manage to establish in big areas. Due to this slight increase in the abundance of resource species, more resource is available for consumer species, which may lead to the establishment of new consumer species in big areas.

Small areas, where resource species are lost, are much more affected by migration than big areas, where consumer species are gained. As big areas tend to contain more individuals than small areas, big areas also produce more migrants than small areas do. The impact of a small area on a big area via migration thus is smaller than the impact of a big area on a small area. Consequentially many resource species are lost as the rate of successful migration θ increases while only a few consumer species are gained.

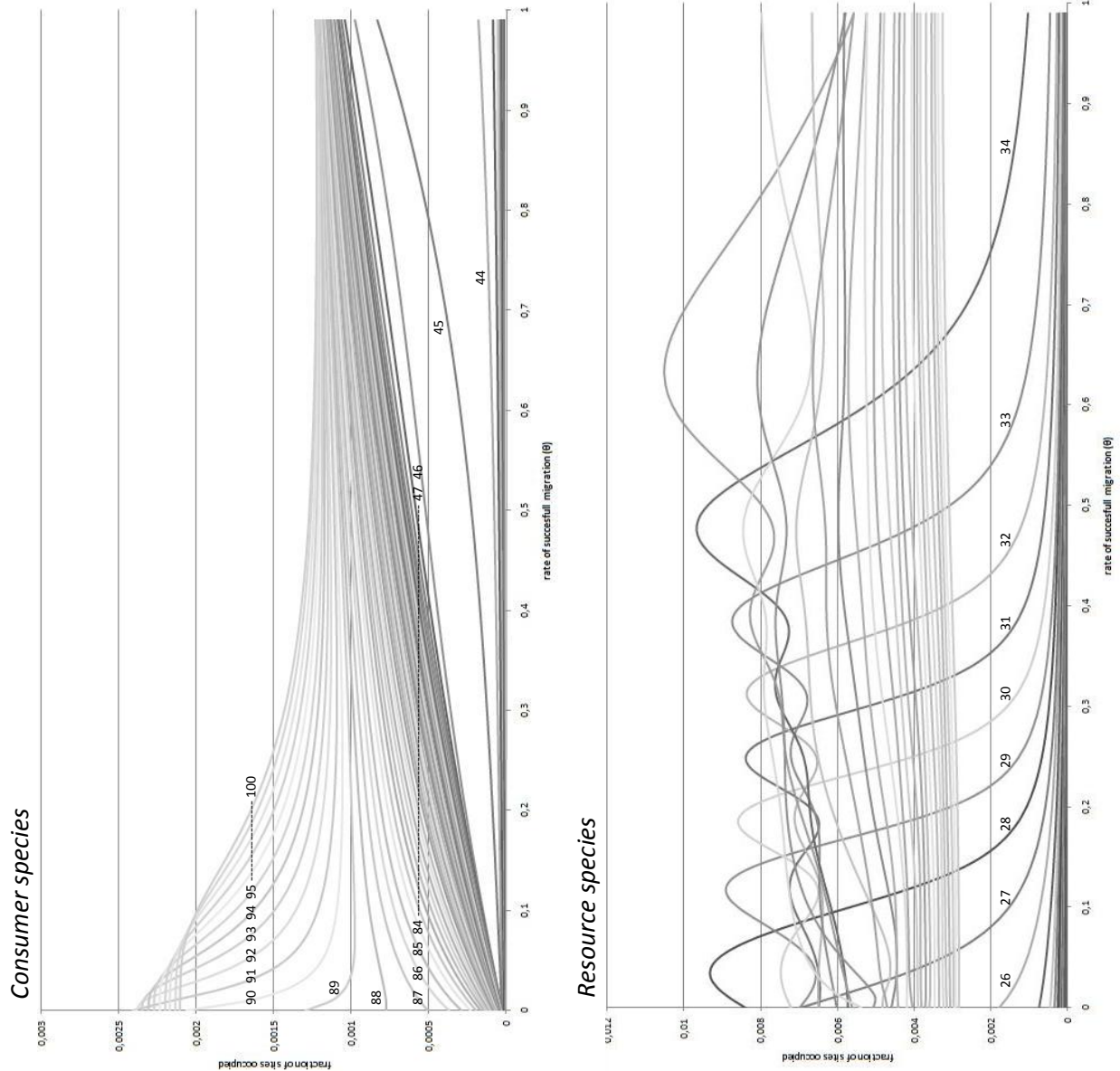


Figure 11. Migration between areas of different size is beneficial for consumer species, but leads to the loss of resource species in small areas. In the here shown scenario migration is possible between two areas, one with size $P=1$ and one with size $P=0.45$. In this figure the abundance of individual resource and consumer species is shown within the area that has size $P=0.45$. The abundance of individual species in the area with size $P=1$ is almost unaffected by migration θ .

All consumer species that successfully establish with increasing migration in the area with size $P=0.45$, where already present in the area with size $P=1$. The resource species that go extinct due to an increased migration however where not present in the area with size $P=1$.

The numbers next to the lines indicate the number (i) of a species. Resource species go extinct in order of their ranking. The best competitor, with lowest colonizing ability is the first one to go extinct due to an increase in migration rate θ . Consumer species establish in reversed order, the species with the highest colonizing ability will be the first one to establish.

Type of model: migration model

Parameter settings: $N_R=100$, $N_C=100$, $C_{max}=1$, $d=0.1$, $\mu=0.8$, $\psi=0.6$, $e_x=0.05$, $e_y=0.05$, $f=0.00001$.

4. Discussion

4.1 RESEARCH QUESTION 1: THE EFFECT OF HABITAT FRAGMENTATION ON SPECIES RICHNESS

The impact of habitat fragmentation on the species richness of an ecosystem wherein trophic interactions and competitive coexistence, made possible via a competition-colonization trade-off, co-occur depends on two circumstances, namely the strength of the trophic interactions and the potential occurrence of competitive exclusion.

Results of the mean field and the spatially explicit model, presented in this thesis clearly show that, if no species are excluded from such an ecosystem due to competition, resource species can be gained with increasing habitat fragmentation when trophic interactions, i.e. top-down control μ and donor control ψ , are relatively strong. Consumer species are lost independent of the strength of trophic interactions with increasing habitat fragmentation although the speed wherein consumer species are lost with increasing habitat fragmentation may vary for different values of top-down and donor control. If the strength of trophic interactions is weak, resource species richness is affected by habitat fragmentation in the same way as the species richness of consumer species, they go extinct with increasing habitat fragmentation.

The finding that resource species are gained with increasing habitat fragmentation when trophic interactions are strong, has important consequences for those who wish to conserve biodiversity. If the in this thesis sketched scenario is true, highly fragmented landscapes will provide safe Heaven for species on a low trophic level when trophic interactions are strong. Low fragmented landscapes will in turn provide habitat for species on a high trophic level. It will then depend on the type of species one wishes to conserve, whether or not habitat fragmentation has a negative impact on them.

If one wishes to gain insight in the potential impact of habitat fragmentation on the species richness of a group of species belonging to the same trophic level, it is thus of importance to determine the strength of trophic interactions. This importance is clearly shown in figure 4 and figure 5. Within the cases presented in these figures, the abundance of individual species and the type of species present are similar when there is no habitat fragmentation ($D=0$). The impact of habitat fragmentation on these at first sight similar ecosystems however is fairly different.

The above described impact of habitat fragmentation on species richness can however be strongly reduced due to the occurrence of competitive exclusion. In a scenario where species go extinct with increasing habitat fragmentation, weak competitors get the opportunity to (re-)establish with increasing habitat fragmentation. In a scenario where species establish with increasing habitat fragmentation, the establishing species may cause the extinction of weaker competitors. The impact of habitat fragmentation, either negative or positive, on species richness can thus be reduced by the occurrence of competitive exclusion, because the establishment of one species leads to the extinction of another species, or the other way around.

4.2 RESEARCH QUESTION 2: THE EFFECT OF HABITAT FRAGMENTATION ON SPECIES TYPE

Although the occurrence of competitive exclusion may reduce the impact of habitat fragmentation on species richness, the impact of habitat fragmentation on species type remains intact. Not only the impact of habitat fragmentation on the species richness of resource species is opposite in a scenario with strong and a scenario with no or weak trophic interactions. Also the type of species influenced by habitat fragmentation is opposite. In the case of no or weak trophic interactions the best competitor, with lowest colonizing ability, is the first one to go extinct due to habitat fragmentation, while in the case of strong trophic interactions the least best competitor is the first one to establish due to habitat fragmentation. Independent of the strength of trophic interactions consumer species will go extinct due to habitat fragmentation where the best competitor, with lowest colonizing ability, is the first one to go extinct due to habitat fragmentation.

In a scenario where competitive exclusion occurs, the same type of species will remain to go extinct or establish due to habitat fragmentation. In a scenario with no or weak trophic interactions, the resource species present in the system will thus remain to become less competitive with increasing habitat fragmentation, while in a scenario with strong trophic interactions resource species become more competitive, independent of the occurrence of competitive exclusion. The type of species present in a low fragmented landscape will thus differ from the type of species present in a highly fragmented landscape. If the species present in a low fragmented landscape will be either more or less competitive than the species present in a highly fragmented landscape, depends on the strength of trophic interactions.

Competitive exclusion thus might reduce the impact of habitat fragmentation on species richness, it does not reduce the impact of habitat fragmentation on species type. A highly fragmented landscape will thus contain different species when compared to a low fragmented landscape. If one wishes to conserve as much species as possible, it might be worth considering to conserve both types of landscapes.

4.3 THE OCCURRENCE OF COMPETITIVE EXCLUSION

Since the occurrence of competitive exclusion influences the impact of habitat fragmentation on species richness, it is important to gain knowledge about the type of ecosystems wherein competitive exclusion is likely to occur. In the above presented results, a relation between the number of species N included in the model and the occurrence of competitive exclusion, is shown. As the number of species N increases, the occurrence of competitive exclusion is reduced. At first sight this relation may seem counterintuitive. It however may not have to be as odd as it seems at first sight. Essentially this result shows that if the difference between species, in this case represented by $\Delta c = c_{i+1} - c_i$, declines, the occurrence of competitive exclusion is less probable. A small Δc prevents one species from being very abundant, which leads to the competitive exclusion of another species. Some taxa such as plants and insects are known for the great number of species they contain, but also for the sometimes relatively small functional differences found between two species. This relatively small differences in functional properties might be an explanation for a limited occurrence of competitive exclusion within such a taxon. In essence one could state that as the *range* wherein species can potentially vary, in this model expressed by $c_{\max} - c_1$, increases, the occurrence of competitive exclusion becomes more likely. If the *difference* between species, in this model represented by $\Delta c = c_{i+1} - c_i$, decreases, competitive exclusion is less likely to occur. Difference in functional properties between competing species can thus be used as an indication for the extent wherein it is likely that competitive exclusion occurs.

4.4 COMPARISON OF THE MEAN FIELD MODEL WITH THE MODEL OF TILMAN *ET AL.* (1994, 1997)

Several aspects of the for this study newly developed model, are not only a property this model, they are also a property of the model of Tilman *et al.* (1994, 1997). Among these properties is the positive impact of habitat fragmentation on even-numbered species and the negative impact of habitat fragmentation on odd-numbered species, described in paragraph 3.1, as was recently published by Morozov & Li (2008). Also the occurrence of competitive exclusion which causes species to go extinct and re-establish with increasing habitat fragmentation found in the for this study developed model, is a property of the model of Tilman *et al.* (1994, 1997). This is an important finding, since it shows that habitat fragmentation may liberate species from the pressure imposed by a better competitor and thus may strongly reduce the negative impact of habitat fragmentation on species richness. Surprisingly this point is not stressed by the papers of Tilman *et al.* (1994, 1997), or in papers using Tilmans model as a base for further research.

An important difference between the in this thesis presented model and the model of Tilman *et al.* (1994, 1997) is the relation between the number of species N included in the for this study newly developed model and the occurrence of competitive exclusion, described in paragraph 3.2. This difference is caused by the different way wherein trade-offs are described. The trade-offs proposed by Tilman *et al.* (1994, 1997) are defined in such a way that $\Delta c = c_{i+1} - c_i$ and $\Delta c_{bc} = c_{bc} - c_{min}$, where c_{min} refers to the minimum colonization rate necessary for survival, is independent of the number of species included. In the for this study developed model the size of Δc and Δc_{bc} , decreases with increasing N . Because Δc and Δc_{bc} decreases, the difference in abundance between odd- and even-numbered species decreases, which in turn makes competitive exclusion less likely to occur. This result is counterintuitive, but as described in the former paragraph this difference between Tilmans model and the for this study newly developed model does not have to be as odd as it may seem at first sight.

4.5 COMPARISON OF THE MEAN FIELD MODEL WITH THE MODEL OF SWIHART *ET AL.* (2001)

The original two-species model of Swihart *et al.* (2001) has for this study been translated into a model where the original ‘prey’ and ‘predator’ in the model of Swihart *et al.* (2001) are converted into respectively a group of resource species and a group of consumer species that follow a trade-off. The abundance of ‘prey’ in the original model of Swihart *et al.* (2001) is thus comparable with the total abundance of resource species in the newly developed model, and the abundance of ‘predators’ is comparable with the total abundance of consumer species. Indeed this comparison is applicable. All scenario’s sketched by Swihart *et al.* (2001) can be found in the for this study newly developed model for similar parameter settings, as long as the number of species included N is large. The total abundances of resource and consumer species thus respond in a similar way to habitat fragmentation as the original state variables ‘prey’ and ‘predator’ in the model of Swihart *et al.* (2001).

One of the scenarios sketched by Swihart *et al.* (2001) is a scenario where the abundance of prey species increases with increasing habitat fragmentation. This scenario occurs when the value of top-down control μ is bigger than the colonization rate c of ‘prey’. Similarly an increase in total abundance of resource species occurs in the for this study newly developed model when the value of μ is relatively high and the value of c_{Rmax} is relatively low. Intuitively one would relate this scenario with the increase in species richness found within the for this study newly developed model. A logical, direct relation between the total abundance of resource species and the species richness would then be assumed to be there. Surprisingly, establishment of resource species may occur even when the total abundance of resource species declines strongly with increasing habitat fragmentation (see figure 1 and figure 5). The often assumed relation between the total abundance of a group of species and the species richness of this group is not confirmed by the for this study developed model. The species richness of resource species may very well increase while the total abundance of resource species declines with increasing habitat fragmentation when trophic interactions are strong.

A scenario where the total abundance of resource species declines with increasing habitat fragmentation even seems to be the most likely scenario, when a large number of species N_R is included in the model. A scenario where the total abundance of resource species increases with increasing habitat fragmentation requires a relatively low value of c_{Rmax} . This scenario thus requires a relatively small range wherein species can differ in colonizing ability. If there is a high number of resource species N_R included in the model, it does not seem to be realistic to keep this range, and thus the height of c_{Rmax} , small enough for this scenario to occur.

4.6 DIFFERENCES BETWEEN THE MEAN FIELD AND THE SPATIALLY EXPLICIT MODEL

One of the essential differences between the mean field and the spatially explicit model is that, within the spatially explicit model, habitat fragmentation has a negative impact on the abundance of resource species *bc* and a positive impact on the abundance of all resource species that are not as competitive as species *bc* in case of weak trophic interactions. In case of strong trophic interactions this is the other way around. Within the mean field model this difference in impact of habitat fragmentation occurs between odd- and even-numbered species.

Although this is a big difference between the mean field and the spatially explicit model, it is not of essential influence on the impact of habitat fragmentation on the extinction and/or establishment of species. Both within the mean field and the spatially explicit model the resource species that is the best competitor is the first one to go extinct in case consumer species have no or only a weak impact on resource species. In the case of a strong impact of consumer species on resource species, the extinct resource species that is the least best competitor is the first one to establish. Also, in both models, increasing habitat fragmentation leads to the loss of consumer species, where the best competitor is the first one to go extinct, independent of the strength of trophic interactions.

As a consequence of the difference in impact of habitat fragmentation on individual species between the mean field and the spatially explicit model, the species that are affected by competitive exclusion are also different in the mean field and the spatially explicit model. In the spatially explicit model both even- and odd-numbered species that are weak competitors are affected by competitive exclusion and not only odd-numbered species which is the case in the mean field model. Again however, the essential finding brought forward in paragraph 4.3, that an increase in the *range* wherein species can potentially vary makes the occurrence of competitive exclusion more likely, while a decrease in *difference* between species ($\Delta c = c_{i+1} - c_i$) makes the occurrence of competitive exclusion less likely is also true for the spatially explicit model.

Another difference between the mean field and the spatially explicit model is found in the interplay between top down control and donor control. The spatial explicit model shows that, other than the mean field model, the strength of top-down control does not necessarily mean that its impact on resource species will also be big. Consumer species that increase the death rate of resource species may hamper their own population growth because they are faced with a lack of resource in the sites wherein they are present. Within the spatially explicit model strong trophic interactions thus not necessarily mean a strong impact of consumer species on resource species. Consequentially the scenario where resource species establish with increasing habitat fragmentation does not necessarily have to occur within the spatially explicit model when trophic interactions are strong. This scenario only occurs when the *impact* of consumer species on resource species is strong. The highest impact of consumer species on resource species total abundance and species type might be obtained for intermediate values of top-down and donor control.

Furthermore striking spatial patterns are found in the spatially explicit model. They clearly show the impact consumer species have on resource species, namely the release of competitive exclusion. Very interesting is also the observed mutualistic relation between resource species that are weak competitors and consumer species. These findings might be a starting point for further research.

4.7 RESEARCH QUESTION 3: THE EFFECT OF MIGRATION BETWEEN AREAS OF DIFFERENT SIZE

The results shown by the migration model clearly show that an increased migration between areas of different size will lead to the loss of resource species in a scenario where trophic interactions are strong and where no competitive exclusion occurs (see figure 11). Resource species that are not present in big areas will go extinct in small areas. Some consumer species, not present in small areas, might be gained in big areas as the rate of migration increases, because the total abundance of resource species in big areas increases due to an increased migration of resource species from small areas to big areas. Small areas produce not as much migrants as big areas, therefore amount of consumer species will probably be relatively small, while the loss of resource species will be big.

This finding has important consequences for conservationists. Promoting migration, for instance by building a corridor or by developing an ecological main structure, will probably not be beneficial for the species richness of resource species when the impact of consumer species on resource species is strong.

In a scenario where competitive exclusion does occur the species richness of resource species and consumer species does not necessarily have to be different when comparing a big area with a small area. The type of species present in small and big areas however will be different. Increasing migration between big and small areas makes the group of species present in big and small areas more alike. In case competitive exclusion occurs, increasing migration between big and small areas will then thus lead to the loss of both consumer and resource species.

4.8 TAKE HOME MESSAGE FOR ECOLOGISTS

An important take home message that can be learned from this study is that the commonly applied concept of trade-offs, used as an explanation for the coexistence of competing species, may deliver a very different outcome when studied in the context of trophic interactions. Results of this study show that when an external factor such as habitat fragmentation influences two trophic levels at the same time, the impact of this external factor on the lowest trophic level can be opposite to its original impact, depending on the strength of top-down and the strength of donor control. This is probably not only true for the 'external factor' habitat fragmentation and not only true for the competition-colonization trade-off. If one uses a trade-off in order to explain the impact of an external factor on the type of species and the species richness of a group of species, it is thus of importance to be aware of the potential impact trophic interactions may have on this group of species.

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Appendix 1

Description, units, values of model variables and parameters and symbols.

Parameters and symbols used within models				
Symbols	Description	Unit	Value(s)	Model(s)
D	fraction of sites destroyed		0 – 1	Mean fld / Spatial
R _i	fraction of sites occupied by resource species <i>i</i>		0 – 1	Mean fld / Spatial
C _i	fraction of sites occupied by consumer species <i>i</i>		0 – 1	Mean fld / Spatial
R _{iq}	fraction of sites occupied by resource species <i>i</i> in habitat area <i>q</i>		0 – 1	Migration
C _{iq}	fraction of sites occupied by consumer species <i>i</i> in habitat area <i>q</i>		0 – 1	Migration
P	the size of area <i>q</i>		0 – 1	Migration
<i>i</i>	number and competitive rank of a species		1 - N _R or 1 - N _C	Mean fld / Spatial / Migration
<i>j</i>	number of a species that is more competitive than species <i>i</i>		1-(<i>i</i> -1)	Mean fld / Spatial / Migration
C _{Ri}	colonization rate of resource species <i>i</i>	yr ⁻¹	def. by trade-off	Mean fld / Spatial / Migration
C _{ci}	colonization rate of consumer species <i>i</i>	yr ⁻¹	def. by trade-off	Mean fld / Spatial / Migration
d	proportion of colonizers that attempt to migrate to a new area		0 – 1	Migration
θ	migration success, fraction of migrants that reach a new area		0 – 1	Migration
N _R	number of resource species		unlimited	Mean fld / Spatial / Migration
N _C	number of consumer species		unlimited	Mean fld / Spatial / Migration
N _p	number of area's		unlimited	migration
e _R	extinction rate of resource species	yr ⁻¹	0.05 - 0.6	Mean fld / Spatial / Migration
e _C	extinction rate of consumer species	yr ⁻¹	0.05 - 0.6	Mean fld / Spatial / Migration
ψ	bottom-up control, ability of a consumer species to survive without resource species	yr ⁻¹	0 – 1	Mean fld / Spatial / Migration
μ	top-down control, impact of consumer species on the death rate of resource species	yr ⁻¹	0 - 1	Mean fld / Spatial / Migration
f _R	external influx of resource species	yr ⁻¹	0 – 0.001	Mean fld / Spatial / Migration
f _C	external influx of consumer species	yr ⁻¹	0 – 0.001	Mean fld / Spatial / Migration
Other symbols				
Symbols	Description			
B _c	number and competitive rank of the best competitor whereof the abundance is bigger than zero.			
NBG0 _R	number of resource species whereof the abundance is bigger than zero			
NBG0 _C	number of consumer species whereof the abundance is bigger than zero			
Δc	Difference between colonizing abilities, depending on the number of species included, Δc = C _{i+1} -C _i			

Appendix 2

Derivation of the solution of $d\hat{R}_{tot}/dt$ and $d\hat{C}_{tot}/dt$ for 0.

Step 1: Solution $d\hat{R}_i/dt$ and $d\hat{C}_i/dt$ for 0

$$\begin{aligned}\hat{R}_{i,(i-bc+1)odd} &= \frac{c_{Rbc}c_{Rbc+2}}{c_{Rbc+1}c_{Rbc+3}} \dots \frac{c_{i-2}}{c_{i-1}} (1-D) - \frac{c_{Rbc+1}c_{Rbc+3}}{c_{Rbc}c_{Rbc+2}} \dots \frac{1}{c_i} e - \frac{c_{Rbc+1}c_{Rbc+3}}{c_{Rbc}c_{Rbc+2}} \dots \frac{1}{c_i} \mu \hat{C}_{tot} \\ \hat{R}_{i,(i-bc+1)even} &= \frac{c_{Rbc}c_{Rbc+2}}{c_{Rbc+1}c_{Rbc+3}} \dots \frac{1}{c_i} (D-1) + \frac{c_{Rbc+1}c_{Rbc+3}}{c_{Rbc}c_{Rbc+2}} \dots \frac{c_{i-2}}{c_{i-1}} e + \frac{c_{Rbc+1}c_{Rbc+3}}{c_{Rbc}c_{Rbc+2}} \dots \frac{c_{i-2}}{c_{i-1}} \mu \hat{C}_{tot} \\ \hat{C}_{i,(i-bc+1)odd} &= \frac{c_{Cbc}c_{Cbc+2}}{c_{Cbc+1}c_{Cbc+3}} \dots \frac{c_{i-2}}{c_{i-1}} (1-D) - \frac{c_{Cbc+1}c_{Cbc+3}}{c_{Cbc}c_{Cbc+2}} \dots \frac{1}{c_i} (e + \psi) + \frac{c_{Cbc+1}c_{Cbc+3}}{c_{Cbc}c_{Cbc+2}} \dots \frac{1}{c_i} \psi \hat{R}_{tot} \\ \hat{C}_{i,(i-bc+1)even} &= \frac{c_{Cbc}c_{Cbc+2}}{c_{Cbc+1}c_{Cbc+3}} \dots \frac{1}{c_i} (D-1) + \frac{c_{Cbc+1}c_{Cbc+3}}{c_{Cbc}c_{Cbc+2}} \dots \frac{c_{i-2}}{c_{i-1}} (e + \psi) - \frac{c_{Cbc+1}c_{Cbc+3}}{c_{Cbc}c_{Cbc+2}} \dots \frac{c_{i-2}}{c_{i-1}} \psi \hat{R}_{tot}\end{aligned}$$

Step 2:

$$\begin{aligned}\hat{R}_{tot} &= \sum_{i=1}^{NR} \hat{R}_i \\ \hat{R}_{tot,RNB}^{odd} &= 1 - D - \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{1}{c_{RBC}} e - \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{1}{c_{RBC}} \mu \hat{C}_{tot} \\ \hat{R}_{tot,RNB}^{even} &= 1 - (1 - \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{c_{RBC}}{c_{RBC+1}}) D - \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{c_{RBC}}{c_{RBC+1}} \\ \hat{C}_{tot} &= \sum_{i=1}^{NC} \hat{C}_i \\ \hat{C}_{tot,CNB}^{odd} &= 1 - D - \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{1}{c_{CBC}} (e + \psi) + \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{1}{c_{CBC}} \psi \hat{R}_{tot} \\ \hat{C}_{tot,CNB}^{even} &= 1 - (1 - \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{c_{CBC}}{c_{CBC+1}}) D - \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{c_{CBC}}{c_{CBC+1}}\end{aligned}$$

Step 3:

$$\begin{aligned}\frac{\hat{R}_{tot, RNB\text{Rodd}}}{dD} &= -1 - \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{\mu}{c_{RBC}} \left(\frac{dC_{tot}}{dD} \right) \\ \frac{\hat{R}_{tot, RNB\text{Reven}}}{dD} &= -1 + \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{c_{RBC}}{c_{RBC+1}} \\ \frac{\hat{C}_{tot, CNBRodd}}{dD} &= 1 + \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{\psi}{c_{CBC}} \left(\frac{\hat{R}_{tot}}{dD} \right) \\ \frac{\hat{C}_{tot, CNB\text{Reven}}}{dD} &= -1 + \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{c_{CBC}}{c_{CBC+1}}\end{aligned}$$

Step 4:

$$\begin{aligned}\frac{\hat{R}_{tot, RNB\text{Rodd}, CNBRodd}}{dD} &= - \frac{(c_{NR}c_{NR-2} \dots c_{RBC})(c_{NC}c_{NC-2} \dots c_{CBC}) - (c_{NR-1}c_{NR-3} \dots c_{RBC})(c_{NC}c_{NC} \dots c_{CBC})\mu}{(c_{NR}c_{NR-2} \dots c_{RBC})(c_{NC}c_{NC-2} \dots c_{CBC}) + (c_{NR-1}c_{NR-3} \dots c_{RBC+1})(c_{NC-1}c_{NC-3} \dots c_{CBC+1})\mu\psi} \\ \frac{\hat{R}_{tot, RNB\text{Rodd}, CNB\text{Reven}}}{dD} &= -1 + \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{\mu}{c_{RBC}} - \left(\frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{\mu}{c_{RBC}} \right) \left(\frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{c_{CBC}}{c_{CBC+1}} \right) \\ \frac{\hat{R}_{tot, RNB\text{Reven}}}{dD} &= -1 + \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{c_{RBC}}{c_{RBC+1}} \\ \frac{\hat{C}_{tot, RNB\text{Rodd}, CNBRodd}}{dD} &= - \frac{(c_{NR}c_{NR-2} \dots c_{RBC})(c_{NC}c_{NC-2} \dots c_{CBC}) + (c_{NR}c_{NR-2} \dots c_{RBC})(c_{NC-1}c_{NC-3} \dots c_{CBC+1})\psi}{(c_{NR}c_{NR-2} \dots c_{RBC})(c_{NC}c_{NC-2} \dots c_{CBC}) + (c_{NR-1}c_{NR-3} \dots c_{RBC+1})(c_{NC-1}c_{NC-3} \dots c_{CBC+1})\mu\psi} \\ \frac{\hat{C}_{tot, RNB\text{Reven}, CNBRodd}}{dD} &= -1 - \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{\psi}{c_{CBC}} + \left(\frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{\psi}{c_{CBC}} \right) \left(\frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{c_{RBC}}{c_{RBC+1}} \right) \\ \frac{\hat{C}_{tot, CNB\text{Reven}}}{dD} &= -1 + \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{c_{CBC}}{c_{CBC+1}}\end{aligned}$$

Step 5:

$$\begin{aligned}
\hat{R}_{tot, RNB\text{Rodd}, CNB\text{Rodd}} &= 1 - \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{1}{c_{RBC}} e \dots \\
&\dots - \frac{(c_{NR}c_{NR-2} \dots c_{RBC})(c_{NC}c_{NC-2} \dots c_{CBC}) - (c_{NR-1}c_{NR-3} \dots c_{RBC})(c_{NC}c_{NC} \dots c_{CBC})\mu}{(c_{NR}c_{NR-2} \dots c_{RBC})(c_{NC}c_{NC-2} \dots c_{CBC}) + (c_{NR-1}c_{NR-3} \dots c_{RBC+1})(c_{NC-1}c_{NC-3} \dots c_{CBC+1})\mu\psi} D \\
\hat{R}_{tot, RNB\text{Rodd}, CNB\text{Reven}} &= 1 - \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{1}{c_{RBC}} e \dots \\
&\dots - (1 - \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{\mu}{c_{RBC}} + (\frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{\mu}{c_{RBC}})(\frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{c_{CBC}}{c_{CBC+1}}))D \\
\hat{R}_{tot, CNB\text{Reven}} &= 1 - \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{c_{RBC}}{c_{RBC+1}} - (1 - \frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{c_{RBC}}{c_{RBC+1}})D \\
\hat{C}_{tot, RNB\text{Rodd}, CNB\text{Rodd}} &= 1 - \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{1}{c_{CBC}} (e + \psi) \dots \\
&\dots - \frac{(c_{NR}c_{NR-2} \dots c_{RBC})(c_{NC}c_{NC-2} \dots c_{CBC}) + (c_{NR}c_{NR-2} \dots c_{RBC})(c_{NC-1}c_{NC-3} \dots c_{CBC+1})\psi}{(c_{NR}c_{NR-2} \dots c_{RBC})(c_{NC}c_{NC-2} \dots c_{CBC}) + (c_{NR-1}c_{NR-3} \dots c_{RBC+1})(c_{NC-1}c_{NC-3} \dots c_{CBC+1})\mu\psi} D \\
\hat{C}_{tot, RNB\text{Reven}, CNB\text{Rodd}} &= 1 - \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{1}{c_{CBC}} (e + \psi) \dots \\
&\dots - (1 + \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{\psi}{c_{CBC}} - (\frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{\psi}{c_{CBC}})(\frac{c_{NR-1}c_{NR-3}}{c_{NR}c_{NR-2}} \dots \frac{c_{RBC}}{c_{RBC+1}}))D \\
\hat{C}_{tot, CNB\text{Reven}} &= 1 - \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{c_{CBC}}{c_{CBC+1}} - (1 - \frac{c_{NC-1}c_{NC-3}}{c_{NC}c_{NC-2}} \dots \frac{c_{CBC}}{c_{CBC+1}})D
\end{aligned}$$