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Ecological Informatics: An Agent Based Model on Coexistence Dynamics

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Ecological Informatics: An Agent Based Model on Coexistence Dynamics

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by

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ABSTRACT

Ecological Informatics: An Agent Based Model on Coexistence Dynamics

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The coexistence of species is probably one of the most interesting and complex phenomenon in nature. We constructed an agent based model to study the coexistence dynamics of prey - predator populations by varying productivity levels of producers in fragmented and connected habitats along with different levels of quality of predators. Our results indicated that productivity levels of producers in fragmented and connected habitats along with levels of predator quality are significantly responsible for overall predator - prey population size and survivorship. In the absence of predation, competition between identical prey populations is more probable in connected habitats than in unfragmented or fragmented habitats. Implementing low quality predators in the habitats positively influences the overall coexistence dynamics whereas implementing high quality predators tend to decrease the prey populations. Fragmented habitats provide for greater prey population survival time in highly productive environments but low prey population survival time in less productive environments.

DEDICATION

To my dearest mom,

JAYA THAPA

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First, I would like to express my gratitude towards Dr. Istvan Karsai, Professor, Department of Biological Sciences, at East Tennessee State University (ETSU), Johnson City, Tennessee. I am forever indebted to him for these past three years as in these years, I not only received an opportunity to learn and practice novel means of science through artificial life and informatics study but also developed myself personally bottom – up. I am honored to work with such an honest and ardent scientific genius.

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CHAPTER 1

INTRODUCTION

Habitat Fragmentation

One form of habitat fragmentation occurs when anthropogenic habitat changes lead to mosaic landscapes of habitat patches which is surrounded by more or less optimal habitats impeding movements of organisms (Wu 2009). Habitat fragmentation can be defined as the discontinuity in the spatial distribution of resources and other vital elements supporting survival conditions that then negatively influences occupancy, reproduction and survival of populations (Franklin et al. 2002). Fragmentation affects populations by reducing the size of optimal habitats which results in smaller population sizes that are vulnerable to bigger changes even under minimal fluctuations of demographic factors (Krohne 2001, 137 – 139 p). Fragmentation of landscapes is a universal source of environmental and global species change (Fischer and Lindenmayer 2007; Gliwicz and Wrzosek 2008; Blackburn et al. 2017) . The four basic and most prominent effects of fragmentation on habitat patterns are decrease in amount of habitat, increase in patchiness of habitat, reduction in size of the habitat patches and increase in isolation of habitat patches (Fahrig 2003). Habitat loss and habitat fragmentation occur together (Fahrig 1997) and are one of the major challenges to biodiversity and ecosystem conservation processes (Schweiger et al. 2000; Fahrig 2003; Aguirre and Dirzo 2008; Salau et al. 2012; Brudvig et al. 2015; Prugh 2009).The effects of habitat fragmentation intensify the effects of habitat loss and hence, lead to greater population decline (Bender et al. 1998). Fragmentation also exposes organisms to different physical and biological conditions at an ecosystem boundary or within connecting ecosystems creating edge effects (Fisher and Lindenmayer 2007). Edge effects might cause altercation in biotic and abiotic conditions (physical conditions) which in return affects the organisms living in such fragmented habitats (Murcia 1995). A study conducted in ecologically critical sagebrush communities in Utah indicated that the proportion of active burrows, photo counts and fecal pellets for inhabiting pygmy rabbits was reduced significantly in edge habitats, suggesting a smaller population near habitat edge (Pierce et al. 2011). Fragmented habitats which have been stripped of their attractiveness are also responsible for reduced plant – pollinator interactions which eventually leads to reduced diversity and abundance of producers and results in extinction of populations in such habitats (Rathcke and Jules 1993; Aguirre and Dirzo 2008; Andrieu et al. 2009). A study carried out to measure the effect of forest fragmentation on male euglossine bees' population by Powell and Powell (1987). It was observed that the rate at which the bees visited the same three chemical attractants was lower in small forest fragments than in continuous forests. Also, it has been shown that the smaller the size of the fragmented land, the lesser the presence of pollinator species in such locations (Aguirre and Dirzo 2008). Habitat fragmentation also leads to formation of regional metapopulation (Taylor 1991; Krohne 1997; Fahrig 2003; Wu 2009). Metapopulation theory differs from island biogeography (MacArthur and Wilson 1967) in that it focuses on networks of small patches lacking mainland habitat and is restricted to dynamics of only one species (Harrison and Bruna 1999). Metapopulations are basically a group of sub-populations with local extinctions and regional recolonization or dispersal (Wu 2009). Studies done on Glanville fritillary butterfly (*Melitaea cinxia)*, suggested that metapopulations in smaller patch networks are often more at risk than the metapopulations in large and well connected networks (Hanski 1998). The effects of habitat fragmentation could be more complex because its results depend upon how species react to the features in fragmented habitats and their interactions with other species in such habitats. Species confined to fragmented habitats also have less time to adapt to the newly changed environment especially for the non-edge species which adds to the detrimental effects of habitat fragmentation (Wu 2009).

Corridor Connectivity

A relative level to which landscapes assist or hinder the movement of organisms between resource patches can be defined as connectivity (Tischendorf and Fahrig 2000). Connectivity is a fundamental concept and is basically a measure of habitat patch, rather than of total function of landscapes (Moilanen and Hanski 2001; Taylor et al. 2006). Corridors, which are narrow strips of habitats establish connectivity among different isolated habitats (Rosenberg et al. 1997; Levey et al. 2005; Watkins et al. 2011; Brudvig et al. 2012) thereby connecting two or more larger habitat patches, improving and maintaining the viability of specific species' population in those habitat patches (Beier and Noss 1998; Fisher and Lindenmayer 2007). Corridors connect local sub-populations into a single meta-population, hence, lowering the risks of local extinctions caused by human activities and ensuring long – term survival (Watkins et al. 2011). Landscape connectivity is also vital for preserving the ecological and genetical diversity of populations threatened by habitat fragmentation and climate change (Rayfield et al. 2016). The problem arising due to resources scarcity and habitat fragmentation could be addressed by allowing species to move freely between the patches of fragmented landscapes (Watkins et al. 2011; Salau et al. 2012). One of the pioneering studies in the field of corridor connectivity was conducted in a vole population to see the effects of biological corridors (La Polla and Barrett 1993). The study demonstrated that male voles' movements between the patches with corridors was significantly higher than between the patches lacking corridors (La Polla and Barrett 1993). Similarly, studies done in movement patterns of Oregon salamander (*Ensatina eschscholtzii*) (Rosenberg et al. 1997) and butterflies at the Savannah River Site in South Carolina (Haddad 1999) suggested that corridors do have effects that increase inter-patch movements and hence, population density. A study performed on the role of shrub strips' as corridor by passerine birds in northeastern Poland showed that corridors not only facilitated birds' movement towards littoral lakes in search of prey (dipterans, hymenopterans and lepidopteran larvae), but also helped them guide their directions of flight (Dmowski and Kozakiewicz 1990). According to Ament et al. (2014), one importance of connectivity besides daily travel and migration is that it provides dispersal. Dispersal is movement of individuals that allow continued genetic and demographic connectivity among populations (Holyoak and Lawler 1996; Ament et al. 2014). Dispersal is vital for efficient connectivity (Vasudev et al. 2015). Recent studies have shown that Canada lynx (*Lynx canadensis*) populations which listed as threatened under the US Endangered Species Act (Bayne et al. 2008) in northern Rocky Mountains, rely on such dispersal behaviors using corridors to maintain healthy population connectivity between Canada and the US (Squires et al. 2013). Biodiversity conservation in landscapes experiencing climate and land – use changes requires planning that incorporates habitat networks facilitating dispersal at various spatial scales (Rayfield et al. 2016). The effectiveness of corridors has also been highlighted by many studies involving habitat patch connectivity and population survival, in white – footed mice (Fahrig and Merriam 1985), designing a conservation plan for protecting the habitat for white giant pandas in the Qionglai mountain range in China (Xu et al. 2006), studying the coexistence dynamics of predator – prey population dynamics (Karsai and Kampis 2011), studying movement of jaguars through conservation corridors (Watkins et al. 2011) and studying conditions preventing extinctions of cougar population in the Santa Ana Mountains of southern California (Beier 1993).

Corridors have not always been shown to be effective by all the studies. In one of such cases, it has been shown that that open corridor connectivity could lead to increased invasion of exotic species which could eventually lead to decreased red ants species diversity (Resasco et al. 2014). In another such study, it was shown that corridors were responsible for elevated local fire temperatures during burns because of increased inter – patch connectivity and through within-patch edge effects (Brudvig et al. 2012).

Competition, Predation, and Coexistence

The model for growth of single species in an unchanging environment, proposed by Thomas R. Malthus (1798) which theorized exponential population growth written as $\frac{dx}{dt} = r \cdot x$, where x = the number of population and r = constant rate of increase, served as the backbone for all deterministic models of interactions between species (Wangersky 1978). It was not until 1838 when P.F. Verhulst, a Belgian mathematician proposed a logistic growth rate for population increase (Bacaer 2011, 31 – 41 p). The logistic growth rate modified the exponential growth rate by introducing the idea of density dependence or intraspecific competition which means that the performance of a population is determined by the number of individuals within that population and is written as $\frac{dN}{dt} = r \cdot N \left(\frac{K-N}{K}\right)$ where K = carrying capacity, N = population density and r = is the rate of intrinsic growth under specified environmental conditions (Ayala 1970; Vandermeer 2010). The logistic growth equation can easily be expanded to the cases of two or more species competing for the same resource (Ayala 1970). Lotka (1925) and Volterra (1931) considered two species interactions in their famous competition equation which is written as

$$\frac{dN_1}{dt} = r_1 N_1 \left(\frac{K_1 - N_1 - \alpha N_2}{K_1}\right)$$

$$\frac{dN_2}{dt} = r_2 N_2 \left(\frac{K_2 - N_2 - \beta N_1}{K_2}\right)$$

where N_1 and N_2= population size of species I and species II respectively, t = time, r_1 and r_2= intrinsic rates of population increase and K_1 and K_2 = carrying capacity of population I and population II respectively, α = effect an individual of species 2 has on the carrying capacity of species 1, β = effect an individual of species 1 has on the carrying capacity of species 2 (Ayala 1970; Tilman 1980; Jungck 1997; Karsai et al. 2016).

Gause's principle (1934) which stated that identical competitors cannot coexist was conceived as an empirical testing of Lotka – Volterra equations (Hardin 1960). For coexistence to occur, the two-competing species either compete for different resources or each species use different resources (Ayala 1970). This idea of competitive exclusion has been one of the most important ecological principles for the past century (Neill et al. 2009). This principle however, contradicts with the observed biodiversity (Kalmykov and Kalmykov 2012). Indeed, the competitive exclusion principle is only valid in the case of fixed resource densities (Armstrong and McGehee 1980) and based on oversimplified theories about the nature of competition process between species (Ayala 1970). Another flaw of the model is that it neglects the ages and sizes of the participating individual organisms (Vance 1984). The model fails to accommodate density – independent factors such as age related deaths, accidental deaths, sex ratio, mating success and gender related mortality which could alter the speed of population growth and hence, the population of interacting species (Schmickl and Karsai 2010). It lacks explanation of how species use a resource and how they hinder each other's abilities to acquire the resource (Vance 1984). A study done on five species of congeneric warblers and their homogenous habitats in boreal forests showed that variation of feeding position within the tree, difference in individual behavior and nesting dates helped reduce competition and allowed coexistence (MacArthur 1958). The outcome of such competition need not be extinction of one of the participating species, but rather adaptive changes within the species that enhance survival (Levin 1970). Competition and coexistence are the major ecological processes that shape the structure of a closed community, its constituent elements and response to disturbance (Fargione and Tilman 2002). Competition effects the natural balance between species either by character displacement which leads to separation of morphological and physiological traits in species in the long run, or by extinction of one of the species because of interspecific competition as a short – term effect (Krohne 2001, 228 – 232 p).

Predation of competing species, on the other hand, has been regarded as a potentially important factor leading to coexistence (Caswell 1978; Chase et al. 2002). Competition and predation are not independent of one another (Gurevitch et al. 2000). Carnivory and herbivory are two forms of predation (Krohne 2001, 245 p). Animal species diversity in a habitat may results from predator effects on herbivores (Paine 1966; Gliwicz and Wrzosek 2008). A study done on structure of freshwater animal communities showed that fish predation played a role in maintaining coexistence among zooplankton (Hall et al. 1970). Similarly, the work by Paine (1966) showed that after elimination of predator starfish *Pisaster,* the number of overall species present around the coastline was reduced from 15 to 8, which shows that lack of predation resulted in a less diverse local community. Both systems studied above are large and complex enough to resemble an open model system containing many different cells for prey refuge where predation is irregular rather than continuous (Caswell 1978). Fluctuations in such intensity of predation was the key to maintain the overall aquatic community structure of *Chaoborus* species in the study done by (Garcia and Mittelbach 2008)

The explanations for coexistence within a given trophic level are usually tied to competition by understanding species' interactions where competition does not exclude members of the assemblage (Caswell 1978). Gurevitch et al. (2000) concluded from their experiment that predation does reduce the intensity of the competition, but other studies have shown an increase, a decrease or no significant effect at all on competition (Chase et al. 2002). This diversity of results can be attributed to the dependence of coexistence on the ratio of interspecific effects to intraspecific effects, and how these effects depend upon other factors like resource availability and predation (Chase et al. 2002; Karsai et al. 2016). For a clearer understanding of when and why predation affects competition, it is essential that biases in experimental systems be considered (Chase et al. 2002). The review of interactions between predation and competition by Chase et al. (2002) is based on top down (stepwise design) models (Karsai et al.2016). The authors emphasize that new theories should not solely concentrate on adding extra details to remedy the issue of simplifications such as homogenous population and constant life history parameters of top down models, but rather implement relative frequencies of positive and negative effects of predation on coexistence and spatial and other forms of heterogeneity in non – equilibrial open systems.

Role of Agent Based Models in Studying Population Dynamics

Implementing positive and negative effects of predation on species coexistence can be done via the dispersal of the predator and prey and its resultant effects on the extinction rates of the prey (Shurin and Allen 2001). Creating spatial and other forms of heterogeneity through dispersal could be achieved by effective landscape connectivity (Fahrig and Merriam 1994; Tischendorf and Fahrig 2000; Watkins et al. 2011). Modeling such predator mediated coexistence studies requires a balance of parametric values (Caswell 1978) as such dynamics results principally from the behavior of the individual members of the population and local interactions between them. Hence, it is important to understand behaviors of individual members and their interactions to successfully model population dynamics (Karsai et al. 2016). The search for such knowledge is often assisted by bottom – up simulation models such as cellular automata and agent-based models (Grimm et al. 2005). In cellular automata (von Neumann 1966), agents simultaneously perform actions at constant time steps (Castiglione 2006). Beginning with von Neumann's work as cellular automata (1966), agent – based computer modeling techniques have been applied to study diverse complex systems such as human social phenomenon, migration, interaction with the environment, propagation of diseases, and population dynamics (Epstein et al. 1996, 2 - 26 p). Bottom- up simulation modeling helps us to accumulate relevant information about individuals at a lower level of the system and observe the emergence of system – level properties related to complex systems (Auyang 1999, 2 – 174 p; Grimm et al. 2005). Such system – level properties are then observed as emergent behavior (emergent properties) (Castiglione 2006). This global behavior emerges as an outcome of many individuals, following behavioral rules, living together within a given environment, and interacting with each other and with the environment (Borshchev and Filippov 2004). Agent based models can also be used to investigate how population-level effects like stability, persistence and coexistence can be based upon local interactions and movements of organisms (DeAngelis and Mooij 2005). Agent based models allow the inclusion of individual variation in greater detail (DeAngelis and Mooij 2005) than classical differential – equation and difference equation models such as Lotka (1925) and Volterra (1931), which is vital for continued development of ecological and evolutionary theory. Agent based models are also better in comparison to classical differential models in representing situations in which even small fluctuations can drive a system into unknown and totally different states such as prey – predation systems. This is vital in the case of complex biological systems, as a single entity (such as a virus or a malignant cell) could possibly affect the entire system. In contrast, differential equation models tend to model the average behavior of the system and fail to address smaller variability (Castiglione 2006). Bottom – up models are virtual laboratories where controlled experiments are used to differentiate noise from signal. Theories of complex systems are unlikely to be reducible to analytic equations alone, but are more likely to be represented by sets of conceptually simple mechanisms that produce different dynamics and outcomes in different contexts (Koch 1973; DeAngelis and Mooij 2005; Grimm et al. 2005).

The goal of this study was to explore the coexistence dynamics of prey - predator populations within fragmented and connected fragmented habitat systems using a minimalistic agent based model. The habitat systems were comprised of producers having variable regeneration times along with prey populations and predators with various quality levels. In the model system, producers with varying regeneration time were the main source of energy that were consumed by prey populations (herbivores) as their source of energy. The prey population was then consumed by predators (carnivores). The predator and prey populations each have unique life history parameters. The response to varying levels of regeneration times of producers combined with quality of predators within the habitats types was studied via population size and survival times. Apart, from tri – trophic coexistence dynamics, the study also explored how competition between two prey populations sharing similar life history parameters (Prey Population type I and Prey Population type II) and predators influenced the overall coexistence dynamics. In the present model, only consumption, reproduction and predation are assumed at the individual level (Karsai and Kampis 2011) while density-dependent and other dynamics arise as emergent consequences of the context – independent individual interactions. This study tested the following hypotheses:

$H_{0:}$ Different habitat types with varying producer regeneration times and levels of predator quality have no significant effect on overall predator – prey population size and survivorship.

$H_{A:}$ There is significant influence of different habitat types combined with varying producer regeneration times and levels of predator quality on overall predator – prey population size and survivorship.

H_{I}: In absence of predators, coexistence between two identical prey populations is more probable in connected habitats.

H_{II}: Within different habitats with two identical prey populations, implementing low quality predators enhances their survival of both prey populations hence, positively influencing the coexistence dynamics.

$H_{III:}$ Within the different habitats with two identical prey populations, implementing high quality predators leads to decline of prey populations hence, negatively influencing the coexistence dynamics.

H_{IV}: In highly productive environment with predators, fragmented habitats provide for better coexistence between two identical prey populations.

H_{V}: In less productive environment with predators, unfragmented and connected habitats provide for better coexistence between two identical prey populations.

CHAPTER 2

MATERIALS AND METHODS

A coexistence dynamics agent based model was built using Netlogo 5.2.0 with sub-models that allowed parameter sweeps for habitat types, quality levels of predators and regeneration times of producers. For each combination of input conditions, the population dynamics simulations were iterated 50 times; each simulation was run for 10,000 time-ticks using behaviorspace in Netlogo 5.2.0 which allowed to systematically vary the model's settings and record the results of each of such model run. The obtained data was saved in Microsoft Excel 2016. The data was then imported to conduct various general linear mixed model Anova (Type III) analyses and Kruskal – Wallis Tests (with Dunn's Test for pairwise tests) to study the level of significance of studied parameters on prey-predator population size and survivorships using RStudio (version 3.3.1).

Purpose

The purpose of the model is to study the coexistence dynamics within simulated habitat systems with varying degrees of connectivity containing a single producer species with varying regeneration times, two different consumers, and a predator species having varying levels of quality. The resulting population size and their persistence times are emergent outcomes of the model system. The model is minimalistic in terms of agents, and their interactions with other agents and their environment. The model is driven by simple energy flow within trophic levels. The goal of this study is to be able to understand various driving factors behind the coexistence of species within such systems.

State Variables and Scales

The model consists of a varying number of producers, prey and predators in a habitat system. The models have three different kinds of mobile agents: prey agents type I (Prey I), prey agents type II (Prey II) and predator agents (Predator); each with their individual life history parameters and rule set (Table 1). Both predators and preys are consumers. All agents belonging to the same species are identical except for their identity, heading, positon and individual energy level. These variables are randomized at the start of each simulation, which is updated during each step. The same type of agents add up after each iteration to form a population, that is updated every tick (time unit). The two types of prey consume the producers in the similar manner. The producers in the habitat systems are represented by random green patches. Producers regenerate after varied amount of time ($Time_{regeneration}$) while the prey population reproduces per their fixed reproduction rate (R_{preyI}, R_{preyII} and $R_{predator}$) and energy level (E) (Table 1) which are then consumed by predators thereby increasing their energy levels. Hence, behaviors can be converted into one single common currency named “energy”. Energy not only relates to the well – being of organisms, but also expresses the level of food and determines the expected lifetime of organisms (Karsai and Kampis 2011).

The habitat environment consists of discrete n * n patches (Table 1). The habitat is modeled as a rectangular torus world having boundaries of reflecting walls. The mobile agents can be located randomly anywhere within the habitat but not at the boundaries. The reflecting walls also serve to implement fragmentation in the system and function similarly to roads, canals, fences, or hard boundaries (Karsai and Kampis 2011). Corridor connectivity is implemented in the model via small openings in the reflecting walls. The reflecting walls are generally impenetrable by mobile agents, but when connectivity is introduced through small openings, agents can pass through. The corridors have been simplified into small openings only and lack any fundamental dimensional parameters like length or breadth. The model is focused on the quantitative effects of such connectivity levels on habitat systems. Time is measured in ticks (steps) until the end of simulation at (T_{max}) (Table 1) and time proceeds in discrete steps. For experimental purposes, the linear size of the habitat n was assumed to be 200. The speed (V) of the individual agents was set to 0.9 Length Unit per time tick. Hence, if we consider one time tick to be consistent with 1 day, the entire habitat area (from right end to the left end) is explorable in roughly about 7.5 months. This helps us to establish that the area is large enough to capture large – scale spatiotemporal dynamics like real systems (Karsai and Kampis 2011). The selection of appropriate scales allowed us to grasp many generations of spatiotemporal dynamics. All the relevant parameters are listed in Table 1.

Table 1. State variables and processes

State variables	**Notation**	**Value**	**Units**
Prey agents Type I	Prey I	$N_{preyI\ (T = 0)} = 1000$	Individuals
Prey agents Type II	Prey II	$N_{preyII\ (T = 0)} = 1000$	Individuals
Predator agents	Predator	$N_{predator\ (T = 0)} = 100$	Individuals
Prey I population size	N_{preyI}	Stochastic – Updated each tick	Individuals
Prey II population size	N_{preyII}	Stochastic – Updated each tick	Individuals
Predator population size	$N_{predator}$	Stochastic – Updated each tick	Individuals

State Variables	Notation	Value	Units
Habitat dimension	n * n	100 * 100	(Length Unit)^2
Initial time	T_0	0	Ticks
Maximum time	T_{max}	10,000 or until extinction	Ticks
Prey I survival time	$Time_{preyI}$	Stochastic – Updated each tick	Ticks
Prey II survival time	$Time_{preyII}$	Stochastic – Updated each tick	Ticks
Predator survival time	$Time_{predator}$	Stochastic – Updated each tick	Ticks
Prey I gain from food	$Gain_{preyI}$	4	Energy Units (EU)
Prey II gain from food	$Gain_{preyII}$	4	Energy Units (EU)
Predator gain from food	$Gain_{predator}$	Varied (10, 20, 30, 40, 50, 60)	Energy Units (EU)
Energy level	E	Stochastic – Updated each tick	Energy Units (EU)
Grass regeneration time	$Time_{regeneration}$	Varied (1, 10, 20, 30, 40, 50, 60, 70 ,80 ,90, 100)	Ticks
Prey I reproduction rate	R_{preyI}	15	Percentage

State Variables	Notation	Value	Units
Prey II reproduction rate	R_{preyII}	15	Percentage
Predator reproduction rate	$R_{predator}$	15	Percentage
Speed	V	0.9	Length Unit/ Tick
Turning angle	U	Random 50	Degrees
Test interval	t	50 – 10,000	Ticks

Process Overview and Scheduling

At each discrete time step, each agent performs a series of activities in sequential order. The agents (Prey I, Prey II and Predators) move randomly in space, consume available food, reproduce if they meet a certain energy thresholds and die if the energy is below the level required to carry out life processes including foraging and reproduction. The agents move in a randomly selected direction based on speed (V) and turning angle (U) (Table 1 and Table 2). The producers (green patches) are the food sources for prey individuals. The basic life process of a producer is shown in Figure 1. As the countdown to regenerate equals to, or becomes less than zero, the green patches regenerate. Agents move randomly (random walk) and lose 1 Energy Unit (E. U). Prey individuals will consume the food and gain energy equivalent to prey gain from food ($Gain_{preyI}$ and $Gain_{preyII}$) (Table 1) set in the model (Figure 2). Similarly, predators will hunt prey individuals and gain energy equivalent to predator gain from food ($Gain_{predator}$) (Table 1) set in the model (Figure 3). Reproduction is asexual and occurs with a fixed probability for prey (R_{preyI}, R_{preyII}) and predator ($R_{predator}$) respectively (Table 1). The energy reserve of the parent is shared equally with the new offspring and introduced to the environment. If the energy is greater than zero, the new individual survives. Death results when the energy level of prey or predator reaches zero (E < = 0) (Figure 2 and Figure 3). It also occurs for prey when they are consumed by predators. Thus, “energy” directly translates to lifespan of prey and predator individuals (Karsai and Kampis 2011).

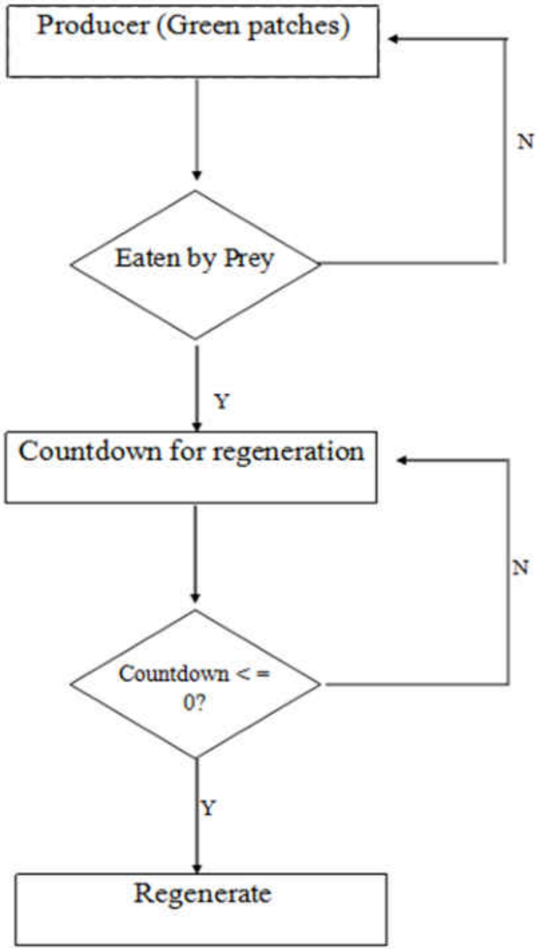

Figure 1. Schematic view of producer’s behavior

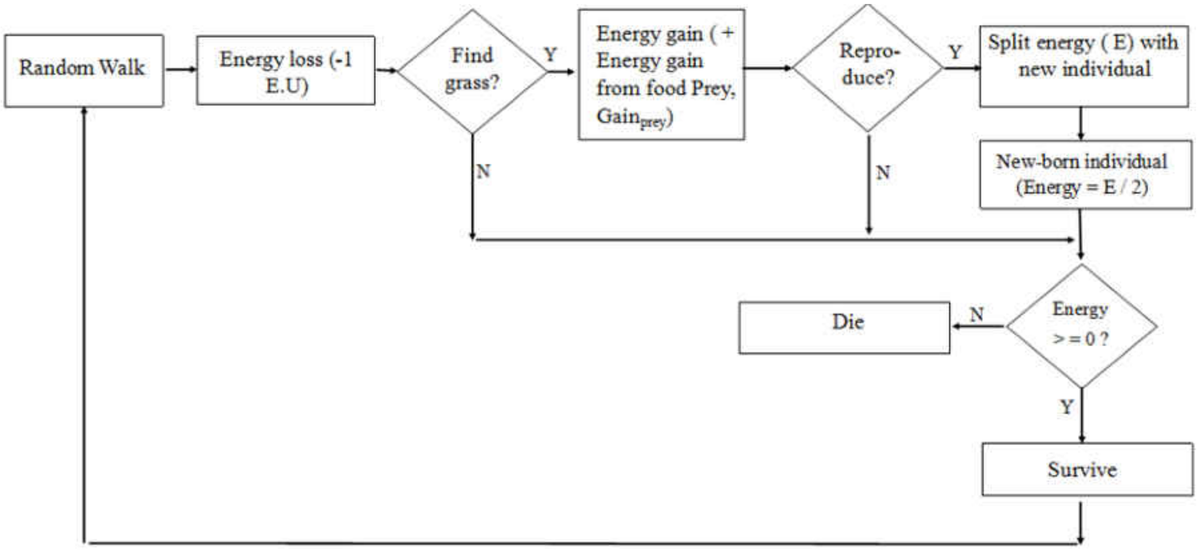

Figure 2. Schematic view of prey's behavior

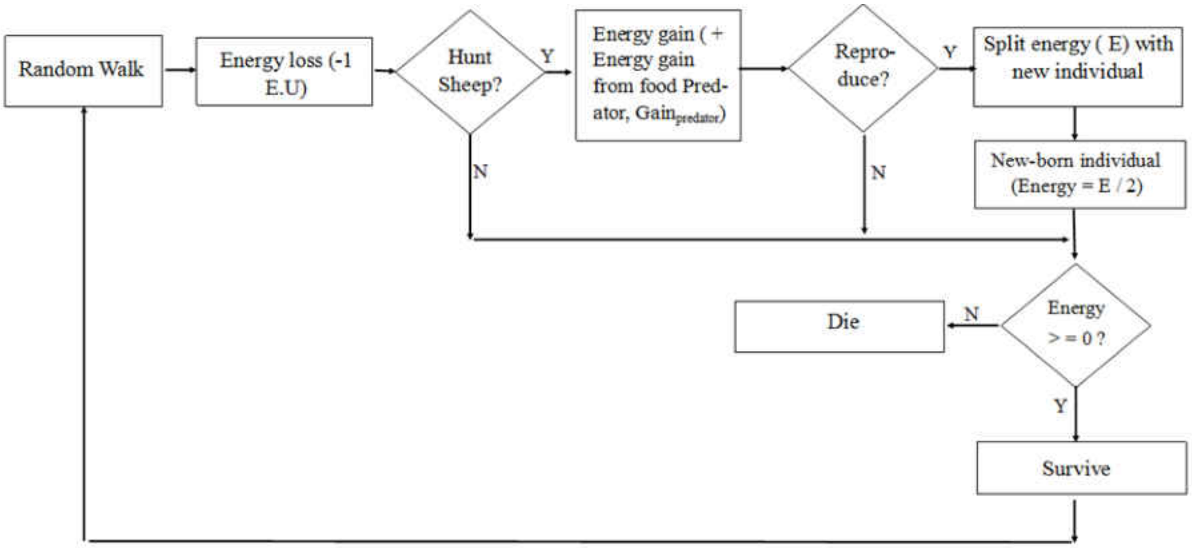

Figure 3. Schematic view of predator's behavior

Design Concepts

The following are some basic principles of the model system.

Emergence

In this model, the population dynamics of prey – predators such as coexistence (prey – predator populations, prey-predator survival times) and population fluctuations are emergent outcomes of complex interactions between the individuals and their environments. It is based on simple individual properties such as consumption, predation and reproduction (Karsai and Kampis 2011).

Adaptation

Adaptation is not explicitly modeled in the system, although extensions of the model that includes adaptation could be added (Polhill et al. 2008). The mobile agents (prey individuals and predators) could be made more aware of their surroundings by letting them sense if there is food or danger in front of them. If there are food patches, they could proceed with their movements but on sensing danger (predators), they could change their heading per same logic. Similarly, the width of the corridors can be increased to allow for more dispersal. Such adjustments could influence the rate of interactions between the agents which might affect the overall population dynamics.

Fitness

Fitness is not explicitly modeled in the system. Fitness is measured in terms of energy of the agents. The ability of an agent to successfully forage and reproduce is dependent upon its corresponding energy level. The energy level is dependent on the food consumed by the agents. Hence, energy influences the overall fitness state of the system.

Prediction

Agents cannot predict the interactions between other agents or the environment itself. Neither they can predict subsequent population dynamics. The agents do not have any memory or learning mechanisms. However, certain extensions that allow the capabilities for such could be added to the model.

Sensing

The agents know their internal states such as speed (V), turning angle (U), reproduction rates ($R_{preyI,}$ R_{preyII}, $R_{predator}$) and energy gain from food ($Gain_{preyI}$ and $Gain_{preyII}$, $Gain_{predator}$) and interact accordingly. Collison between two mobile agents is vital for predation. Predator individuals on colliding with prey individuals consume them and increase their energy level by the amount equivalent to predator gain from food. Similarly, prey individuals encountering green patches consume them and increase their energy level by amount equivalent to prey gain from food.

In this model, the agents cannot sense the presence of surrounding prey or predators, but it is determined stochastically. Also, the surrounding reflecting border walls and openings in such walls cannot be sensed by the agents but are found through random walk. The agents cannot cross the reflecting walls and borders unless there is an opening.

Interaction

The local interactions between two different agents, or an agent and their environment, lead to complex emergent outcomes. The interactions take place in the form of predation. It is applicable to both Prey I and Prey II and Predators. The energy transfer occurring at various trophic levels (from producers to prey to predators) is the primary factor regulating the energy levels of agents. The systems with varying regeneration time of producers will support varying size of prey population dependent on them for energy. This could significantly affect the population size and effect the intensity of prey - predator interactions. More than one individual could occupy the same spatial location, but a prey individual is only consumed by a single predator (Karsai and Kampis 2011).

Stochasticity

We used the built – in random number generator “Mersenne Twister” (Abrahamson and Wilensky 2004) of the simulation platform to iterate the stochastic events within the model. Prey I population size (N_{preyI}), Prey II population size (N_{preyII}), Predator population size ($N_{predator}$) Prey I survival time ($Time_{preyI}$), Prey II survival time ($Time_{preyII}$), Predator survival time ($Time_{predator}$) (Table 1) are some of the stochastic events. Whereas, initial number of Prey I population size ($N_{preyI\,(T = 0)}$), initial number of Prey II population size ($N_{preyII\,(T = 0)}$), initial number of Predator population size ($N_{predator\,(T = 0)}$), initial Prey I energy level ($E_{preyI\,(T = 0)}$), initial Prey II energy level ($E_{preyII\,(T = 0)}$), initial Predator energy level ($E_{predator\,(T = 0)}$), initial speed and random orientation in habitat space are provided as an initial external input (Table 2) in the system.

Collectives

The major groups of individuals are prey and predator populations. Initial numbers of prey and predators are both provided as external input, while the subsequent populations at the end of simulations after each set of iteration are total function of stochastic nature of the model.

Observation

The simulation platform offers a 2-D spatial plot of the habitat systems as well as options to optimize it into a 3-D interface to monitor the system behavior. The following are monitored and saved into a Microsoft Excel file for further analyses: all model parameters, Prey I population size, Prey II population size, Predator population size, Prey I survival time, Prey II survival time, Predator survival time and phase volume. To test our hypothesis and conduct statistical analyses, general linear mixed models Anova (Type "III") and Kruskal – Wallis Tests in RStudio (version 3.3.1 – "Bug in Your Hair") was used extensively.

Initialization

When the simulated experimental systems are initialized at Time (T_0) = 0, green patches are brought into a saturated state as well as initial number of prey I individuals ($N_{preyI\ (T = 0)}$), initial number of prey II individuals ($N_{preyII\ (T = 0)}$) and initial number of predator individuals ($N_{predator\ (T = 0)}$) are placed randomly into the habitat systems with random directional headings and energy (between 0 and twice $Gain_{prey}$ and $Gain_{pred}$ respectively). The initial values of our simulation were selected based on experiments carried out by Karsai and Kampis (2011). The initial parameters settings of the model are listed in Table 2 below.

Table 2. Initial parameters of the model

State variables	**Notation**	**Initial values**	**Units**
Initial Prey I population size	$N_{preyI\ (T = 0)}$	1000	Individuals
Initial Prey II population size	$N_{preyII\ (T = 0)}$	1000	Individuals
Initial Predator population size	$N_{predator\ (T = 0)}$	100	Individuals
Initial Prey I energy level	$E_{preyI\ (T = 0)}$	4	Energy Units (EU)
Initial Prey II energy level	$E_{preyII\ (T = 0)}$	4	Energy Units (EU)
Initial Predator energy level	$E_{predator\ (T = 0)}$	10	Energy Units (EU)
Speed	V	0.9	Length Unit / Tick
Turning angle	U	*Random 50	Degrees
Prey I reproduction - rate	$R_{preyI\ (T = 0)}$	15	Percentage
Prey II reproduction - rate	$R_{preyII\ (T = 0)}$	15	Percentage
Predator reproduction - rate	$R_{predator\ (T = 0)}$	15	Percentage

Note: *Random yields a numerical value between 0 and given value using the random number generator of the Netlogo 5.2.0 simulation platform.

Submodels

The submodels that represent the processes listed in “process overview and scheduling” of the model description are explained in detail below

The Overall Tasks of Agents

The primary agents involved in the model are stationary producers (green patches or grass), mobile prey populations (type I and type II) and mobile predators (with varying quality level). At each time step, every individual mobile agent performs the following sequential actions: they move randomly in given habitat types, consume available food, reproduce if they have sufficient energy (in case for prey and predator) or proper countdown level (in case of producers) and die if the energy is less than or equal to zero (in case of prey individuals and predator individuals) or on being eaten by prey (in case of producers). The submodels and initial model parameter values were chosen based on pre-experiments and studies performed by Karsai and Kampis (2011).

Habitat Types

We used habitats with different levels of fragmentation (W) with and without connectivity (C). The following habitat system arrangements were rigorously studied:

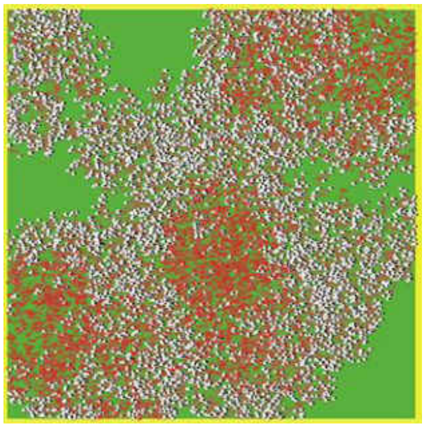

Figure 4. Habitat Type W0C0 (Fragmentation level = 0, Connectivity level = 0).

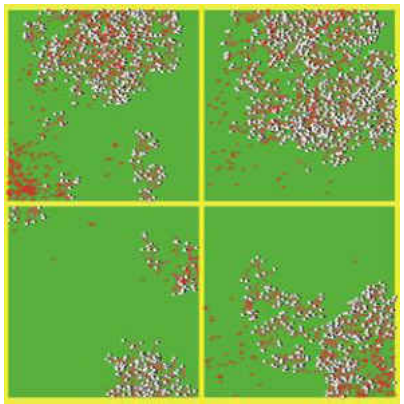

Figure 5. Habitat Type W1C0 (Fragmentation level = 1, Connectivity level = 0).

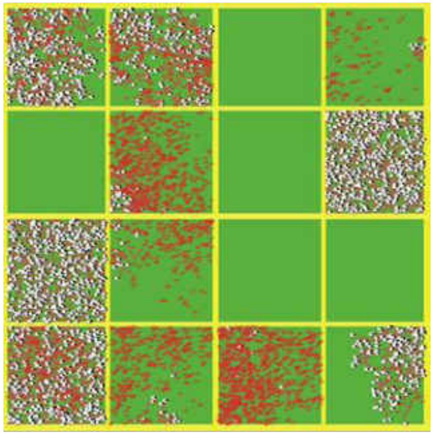

Figure 6. Habitat Type W2C0 (Fragmentation level = 2, Connectivity level = 0).

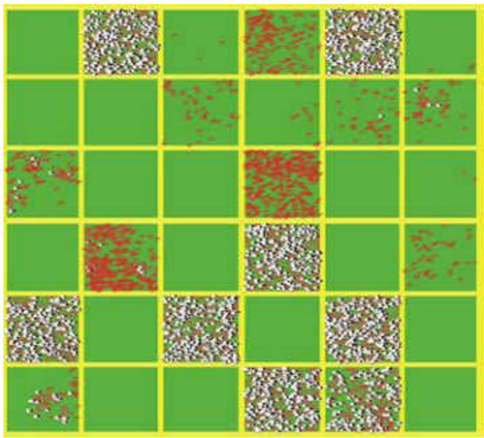

Figure 7. Habitat Type W3C0 (Fragmentation level = 3, Connectivity level = 0).

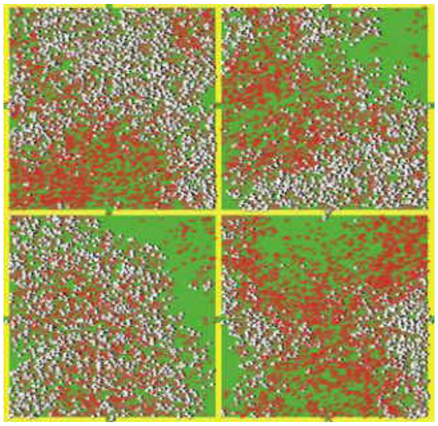

Figure 8. Habitat Type W1C1 (Fragmentation level = 1, Connectivity level = 1).

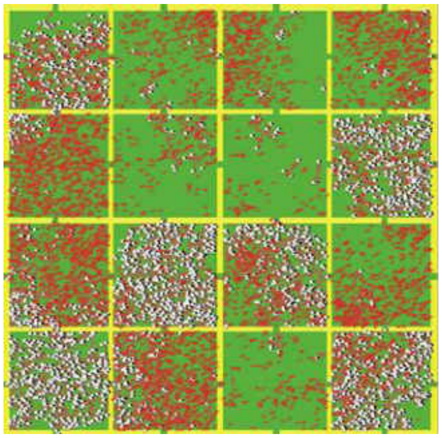

Figure 9. Habitat Type W2C2 (Fragmentation level = 2, Connectivity level = 2).

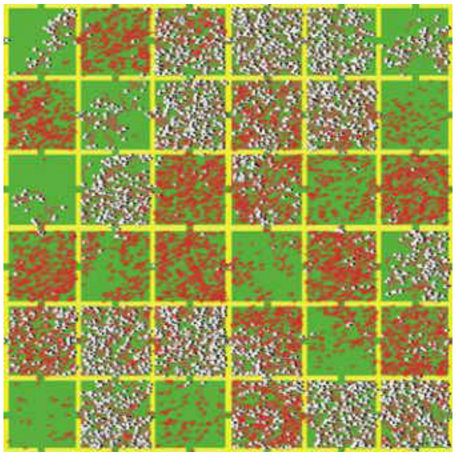

Figure 10. Habitat Type W3C3 (Fragmentation level = 3, Connectivity level = 3).

Predator Quality

We used predators with varying level of quality to understand their impact upon prey population and hence, overall coexistence dynamics within the model system. The numerical equivalent to determine different types of predators in the system was given by the state variable predator gain from food i.e., "$\text{Gain}_{\text{predator}}$". It determines the numerical value of Energy Units (EU) that predator populations can obtain on consuming food (prey population). This value was externally controlled and manipulated. The predators with low predator gain values obtained lower energy per unit food (prey agents) consumed in comparison to the predators with higher predator gain values who obtained higher energy per unit same food (prey agents). For example, the predators having predator gain from food ($\text{Gain}_{\text{predator}}$) = 10 were low quality predators and obtained 10 Energy Units (EU) per unit food consumed whereas, the predators having predator gain from food ($\text{Gain}_{\text{predator}}$) = 60 were high quality predators and obtained 60 Energy Units (EU) per unit same food. A high-quality predator gained more energy from food which implied that it could move farther and forage more before it eventually died out due to starvation or lack of energy. This also meant increased energy reserves and increased predator lifetimes resembling that of fast moving and efficient natural predators controlling large areas of natural habitats (Karsai and Kampis, 2011).

Grass Regeneration Time

We used producers with varying regeneration times to study their impacts on abundance of prey populations and hence, overall coexistence dynamics. It is the internal timer of the model system which is responsible to initiate the countdown for regrowth of the producers once they were consumed by the prey population. The timer was experimentally set to either lower values or higher values. The producers which took $\text{Time}_{\text{regeneration}} = 1$ were fast regenerating producers and took 1 time tick to regenerate whereas the producers which took $\text{Time}_{\text{regeneration}} = 100$ were slower regenerating producers and took 100 time ticks to regenerate.

Random Walk

Initially, prey populations, either only ($N_{\text{preyI (T = 0)}} = 1000$), or ($N_{\text{preyII (T = 0)}} = 1000$), or both ($N_{\text{preyI (T = 0)}}$ and $N_{\text{preyII (T = 0)}} = 1000$) and predator populations ($N_{\text{predator (T = 0)}} = 100$) are placed randomly within the model space at time (T) = 0 ticks (T_0; Table 1). The agents have their own state variables like speed (V), Turning angle (U), initial energy ($E_{\text{preyI (T = 0)}}$ or $E_{\text{preyII (T = 0)}}$) for prey population and initial energy ($E_{\text{predator (T = 0))}}$ for predator population. Their movement in random headings with speed (V) is stochastic. As they move through one Length Unit per time tick in the given space, they lose energy worth one Energy Unit (EU) which needs to be compensated for in succeeding procedures for their survival. They perform this movement each time-step till they survive within the system and is updated at each time tick. This energy loss needs to be compensated for in succeeding time intervals.

Foraging and Energy Compensation

This process guides the mobile agents to obtain food resources. The agents need to compensate the lost energy during random walk by successful foraging. However, the agents do not have any predetermined knowledge of their surroundings. As time proceeds, successful foraging occurs by means of random collisions between two different types of mobile agents (prey and predator). At time of initialization i.e., (T) = 0 tick, the energy level for prey and predator agents is given as follows:

$$\text{Prey Energy level } (E_{prey}) = E_{preyI\,(T=0)} \text{ or } (E_{preyII\,(T=0)}) \qquad \text{(Eq. 1)}$$

$$\text{Predator Energy level } (E_{predator}) = E_{predator\,(T=0)} \qquad \text{(Eq. 2)}$$

As time proceeds, random walk leads to collision between prey and predator agents. If prey agents stumble across green patches (grass), they consume the grass and gain energy equivalent to Gain_{preyI} or Gain_{preyII} which is set externally in the model. The energy gained is then added to the preexisting energy level and the total energy level (E) is updated. So, at time (T) = 1 tick, the energy level of prey agents is updated as given below:

$$\text{Energy level } (E_{prey\,(1)}) = E_{preyI\,(T=1)} \text{ or } E_{preyII\,(T=1)} + \text{Gain}_{preyI} \text{ or } \text{Gain}_{preyII} \qquad \text{(Eq. 4)}$$

Since, we ran this simulation for 10,000 time-ticks, the energy level at each further time step (T > 1) will be updated sequentially as given below:

$$\text{Energy level } (E_{prey\,(1+n)}) = E_{preyI\,(T=1+n)} \text{ (or } E_{preyII\,(T=1+n)}) + \text{Gain}_{preyI} \text{ (or } \text{Gain}_{preyII}) \qquad \text{(Eq. 5)}$$

Where the value of n ranges from 1 to 9999th steps.

Similarly, if a predator agent collides with a prey agent in its location, or if a prey agent collides with a predator agent in its location, the prey is consumed and predator gains energy equivalent to $\text{Gain}_{\text{pred}}$ which is set externally in the model. The energy gained is then added to the preexisting energy level and the total energy level (E) is then updated. So, at time (T) = 1 tick, the level of energy for predator energy is updated as given below:

$$\text{Energy level } (E_{\text{predator }(1)}) = E_{\text{predator }(T = 1)} + \text{Gain}_{\text{predator}} \qquad \text{(Eq. 6)}$$

This simulation was run for 10,000 time-ticks and the energy level at each time steps ($T > 1$) was updated sequentially as given below:

$$\text{Energy level } (E_{\text{predator }(1 + n)}) = E_{\text{predator }(1 + n)} + \text{Gain}_{\text{predator}} \qquad \text{(Eq. 7)}$$

Where the value of n ranges from 1 to 9999th steps.

Hence, in any given time step, it is necessary for agents to maintain their energy level (E) greater than zero ($E > 0$) to reproduce and survive.

Reproduction

Regeneration of producers (technically producer reproduction within the model means its regeneration based on specific regeneration time) in case of producers (grass) occurs when it is consumed by prey agents in the model. Upon being consumed, the green patches turn into brown patches. This process initiates the countdown which is built into the model based on its corresponding regeneration time ($\text{Time}_{\text{regeneration}}$). There is a timer which stores current countdown in the model. As the value of the timer reaches equal or less than zero i.e. countdown < = 0, the brown patches turn into green patches which means the plant has regenerated. In the model, the regeneration time could be varied from 1 to 100 with single unit increments. Also, this means that producers with lower regeneration time reproduces or regenerates faster than the producers with higher regeneration time which regenerates slower. A habitat system with producers having regeneration time ($\text{Time}_{\text{regeneration}}$) = 1 regenerates 100 times faster than producers with regeneration time ($\text{Time}_{\text{regeneration}}$) = 100.

This reproduction behavior changes in case of prey and predator agents as reproduction occurs asexually with fixed probability of $R_{\text{preyI},}$ R_{preyII} and R_{predator} respectively. The higher the probability of reproduction i.e. $R_{\text{preyI},}$ R_{preyII} and R_{predator} value, the higher chances that it will reproduce. After reproduction, the energy is divided equally between parent and offspring. Hence, if before reproduction parents had energy (E) = "x" Energy Unit, after successful reproduction, the offspring and parents both will have energy (E) = "x / 2" Energy Unit. The offspring are then randomly placed in the model space with random headings and they start the same life processes.

Death

Death of plant, or producers, occurs on being eaten by the prey agents. Similarly, the death occurs for prey on being consumed by predators. Death also occurs in both prey and predator agents if their energy level reaches zero or equal to zero i.e., E_{preyI} or $E_{\text{preyII}} < = 0$ or $E_{\text{predator}} < = 0$. During each n^th^ time step, 1 Energy Unit (EU) is deducted from their energy deposits. This energy needs to be compensated by consuming food. If they can successfully forage, they will survive and carry on their life processes as mentioned earlier. On failing to do so, each successive time step will reduce their energy level potentially to a point when they have no energy reserve left to carry on any life functions which results in their death. Thus, energy directly translates to the available lifetime of prey and predator individuals (Karsai and Kampis 2011).

Simulation Experiments

We conducted the following experiments to study the coexistence dynamics using our agent based model.

Experiment of Varying Regeneration Times, Habitat Types and Quality Levels of Predators

The regeneration times of the producers were varied and its effects on prey – predator populations and their survival times was studied within different types of habitats with fragmentation (W) and connectivity or openings (C). Seven different habitat types (W0C0, W1C0, W2C0, W3C0, W1C1, W2C2 and W3C3; where W = level of fragmentation and C = level of connectivity) were set up with the combination of eleven varied producer regeneration times ($Time_{regeneration}$ = 1, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100; 1 being faster regenerating producers within the habitats or high production environment whereas 100 being the slower regenerating producers or low production environment within the habitats) and six levels of predator quality ($Gain_{predator}$ = 10, 20, 30, 40, 50, 60; 10 being the least efficient predators whereas 60 being the most efficient predators). Each experiment was run for 10,000 time steps (T_{max}) or until extinction of the population. Fifty parallel simulations were carried out for each unique experimental setting to measure the variability of the coexistence dynamics in such settings.

Experiment of Identical Competition

For this experimental study, two prey populations with identical life history parameters were implemented in the model. The regeneration times of producers ($Time_{regeneration}$) were varied across a wide range i.e., ($Time_{regeneration}$ = 1, 10, 20, 30, 40, 50, 60, 70, 80, 90 and 100; 1 being faster regenerating producers within the habitats whereas 100 being the slower regenerating producers within the habitats) in each of the seven different habitat types (W0C0, W1C0, W2C0, W3C0, W1C1, W2C2 and W3C3; where W = level of fragmentation and C = level of connectivity) mentioned above. Each experiment was run for 10,000 time steps (T_{max}) or until extinction of the population. Fifty parallel simulations were carried out for each unique experimental setting to measure the variability of the coexistence dynamics in such settings.

Experiment of Non – Identical Competition

For this experimental study, two prey populations with non – identical life history parameters were implemented in the model. The amount of energy gained from food for Prey I population was kept constant ($Gain_{preyI}$ = 4 EU) but the amount of energy gained from food for Prey II population was reduced by half i.e., ($Gain_{preyII}$ = 2 EU) resulting in two non-identical population where one was twice as efficient (Prey I) than other (Prey II). Other parameters for the experiment were set to standard initial values (Table 2). Seven habitat systems (W0C0, W1C0, W2C0, W3C0, W1C1, W2C2 and W3C3; W = level of fragmentation and C = level of connectivity) were studied. Similarly, regeneration times of producers was varied across a wide range i.e., ($Time_{regeneration}$ = 1, 10, 20, 30, 40, 50, 60, 70, 80, 90 and 100; 1 being faster regenerating producers within the habitats whereas 100 being the slower regenerating producers within the habitats) in each of the habitat types mentioned above. Each experiment was run for 10,000 time steps (T_{max}) or until extinction of the population. Fifty parallel simulations were carried out for each unique experimental setting to measure the variability of the coexistence dynamics in such settings.

Experiment of Predation and Competition

For this experimental study, varying levels of quality of predators were introduced in one high production and low production environment respectively. A non – biased predator of the prey populations was implemented in to the model system. Predators with 6 different quality levels ($Gain_{predator}$ = 10, 20, 30, 40, 50 and 60) were studied. The quality levels determined the numerical equivalent of Energy Units (EU) that predator populations obtained ($Gain_{predator}$) on consuming food (prey populations). Low quality predators gained between 10 – 30 EU per unit food consumed and were less efficient predators whereas high quality predators gained between 40 – 60 EU per unit same food consumed and were highly efficient predators. This study was performed under two levels of producer regeneration times i.e., $Time_{regeneration}$ = 10 and 50 to mimic habitats with higher and lower productivity respectively. Three contrasting habitat settings (W0C0, W3C0 and W3C3; W = level of fragmentation and C = level of connectivity) were used to study the overall dynamics. These three habitats were chosen because it represented the highest possible values of fragmentation (W) and connectivity (C) levels within unfragmented, fragmented and connected habitat types respectively. Each experiment was run for 10,000 time steps (T_{max}) or until extinction of the population. Fifty parallel simulations were carried out for each unique experimental setting to measure the variability of the coexistence dynamics in such settings.

CHAPTER 3

RESULTS

The experimental parameters chosen for inclusion in the model was based on prior studies performed by Karsai and Kampis (2011) and sensitivity analyses performed during current study. Each prey – predator population size as well as their survival times in various habitat systems (each individual unique point in the figures and the boxplots) below represents the average value (mean) of end points from fifty parallel simulations. Each simulation was run for 10,000 time steps using behaviorspace in Netlogo 5.2.0.

Combined Effects of Different Habitat Types, Varying Regeneration Times of Producers and Levels of Predator Quality in Coexistence Dynamics

We hypothesized that different habitat types with the combination of varying producer regeneration times and levels of predator quality significantly affect prey – predator population size as well as their survival time. The obtained experimental data were analyzed and patterns of prey and predator populations and survival times in unconnected fragmented habitats and connected habitats were studied to test our prediction. To test this prediction, seven different habitat types (W0C0, W1C0, W2C0, W3C0, W1C1, W2C2 and W3C3; where W = level of fragmentation and C = level of connectivity) were set up with the combination of eleven varied time steps of producer regeneration times ($\text{Time}_{\text{regeneration}}$ = 1, 10, 20, 30, 40, 50, 60, 70, 80, 90, 100; 1 being faster regenerating producers within the habitats or high productive environment whereas 100 being the slower regenerating producers or low productive environment within the habitats) and six levels of predator quality ($\text{Gain}_{\text{predator}}$ = 10, 20, 30, 40, 50, 60; 10 being the least efficient predators whereas 60 being the most efficient predators).

A mixed Anova model in the general linear model framework was used to statistically confirm if there were significant effects of different habitat types, varying regeneration times of producers and quality levels of predators in coexistence dynamics of prey – predator population. Coexistence dynamics was expressed as mean values of state variables such as prey population size (N_{preyI}), predator population size ($N_{predator}$), prey survival time ($Time_{preyI}$) and predator survival time ($Time_{predator}$). The final models and their residual plots revealed that different habitat types, varying regeneration times of producers and quality levels of predators were significantly responsible for determining mean prey population size ($p < 0.01$) (Table 3; Figure 11), mean predator population size ($p < 0.01$) (Table 4; Figure 12) as well as determining prey population survival time ($p < 0.01$) (Table 5; Figure 13) and predator population survival time ($p < 0.01$) (Table 6; Figure 14) when one or more population was extinct during experimental runs. The residual plots of these models showed no obvious patterns and were finally accepted.

Table 3. An Anova table showing highly significant effects of different habitat types, varying regeneration times of producers and quality levels of predators on sqrt (sqrt (Mean Prey Population Size)).

Sources of Variation	Df	F Value	Parameter Estimates	Std. Error	T Value
Intercept	1	886.17*	5.25	0.17	29.77*
Habitat W1C0	1	8.70*	0.29	0.1	2.95*
Habitat W2C0	1	8.06*	0.36	0.11	2.84*
Habitat W3C0	1	4.45**	0.33	0.15	2.11**
Habitat W1C1	1	30.69*	0.45	0.08	5.54*
Habitat W2C2	1	67.40*	0.66	0.08	8.21*
Habitat W3C3	1	73.10*	0.7	0.008	8.55*
Producer Regeneration Time	1	4.2**	-0.002	0.001	(-2.05) **
Predator Quality Levels	1	23.29*	-0.009	0.002	(-4.29) *
Mean Prey Population	1	697.12*	0.0003	0.00001	26.403*
Mean Predator Population	1	0.034	0.000006	0.00001	0.6
Residuals	247				

p values < 0.01
****p values < 0.05***

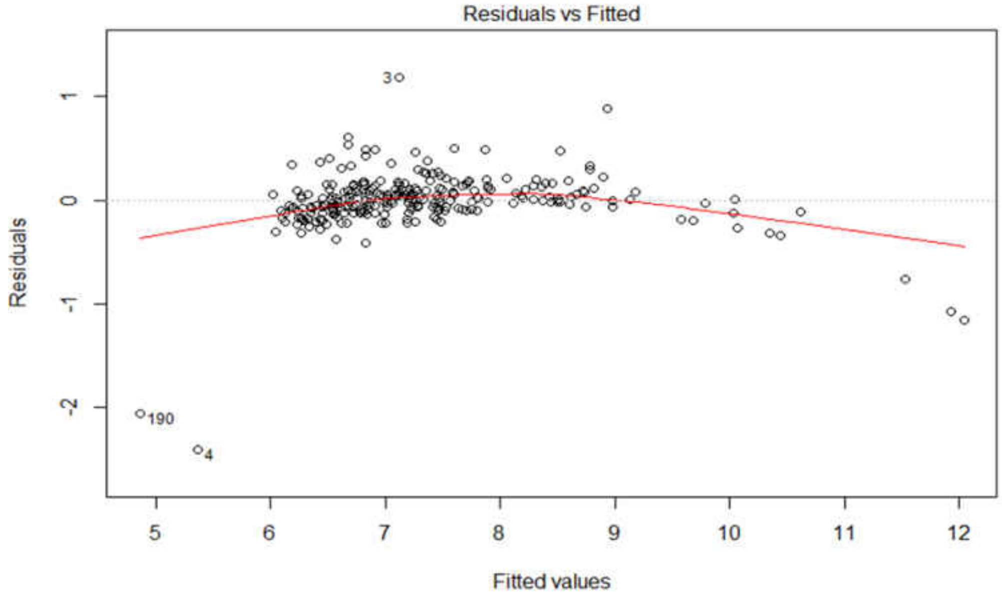

Figure 11. Residual plot of the most fitted model for standardized residual of sqrt (sqrt (Mean Prey Population)) vs predicted residuals of sqrt (sqrt (Mean Prey Population)). This model was accepted because it did not show any obvious pattern (Adjusted R-squared = .91).

Table 4. An Anova table showing highly significant effects of different habitat types, varying regeneration times of producers and quality levels of predators on sqrt (sqrt (Mean Predator Population Size)).

Sources of Variation	Df	F Value	Parameter Estimates	Std. Error	T Value
Intercept	1	224.7*	3.7	0.24	14.9*
Habitat W1C0	1	31.36*	-0.78	0.13	(-5.60) *
Habitat W2C0	1	25.8*	-0.9	0.17	(-5.08) *
Habitat W3C0	1	95.25*	-2.15	0.22	(-9.76) *
Habitat W1C1	1	29.7*	-0.6	0.11	(-5.45) *
Habitat W2C2	1	3.24	-0.2	0.11	(-1.80)
Habitat W3C3	1	0.01	0.002	0.11	0.1
Producer Regeneration Time	1	137.8*	0.01	0.001	(-11.74) *
Predator Quality Levels	1	129.26*	0.003	0.002	11.37*
Mean Prey Population	1	5.5**	0.00004	0.00002	2.34**
Mean Predator Population	1	300.48*	0.0002	0.00001	17.33*
Prey Survival Time	1	77.28*	0.0003	0.00004	(-8.80) *
Predator Survival Time	1	286.82*	0.0006	0.00004	16.94*
Residuals	245				

p values < 0.01

*****p values < 0.05***

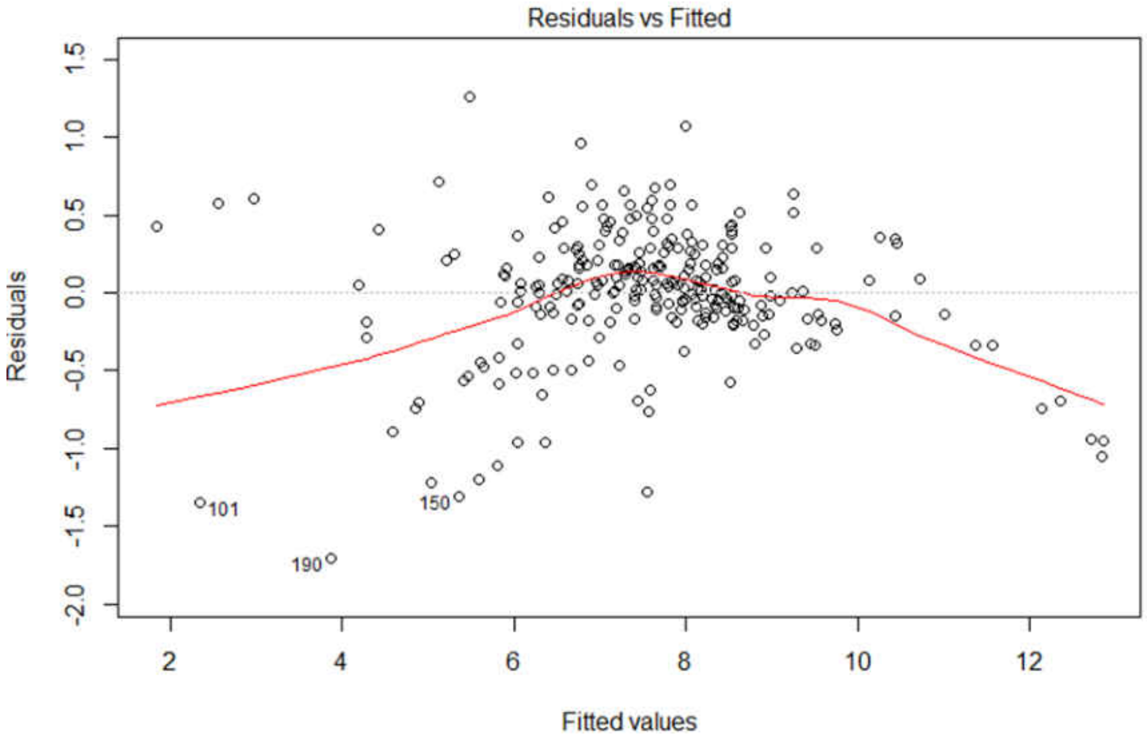

Figure 12. Residual plot of the most fitted model for standardized residual of sqrt (sqrt (Mean Predator Population)) vs predicted residuals of sqrt (sqrt (Mean Predator Population)). This model was accepted because it did not show any obvious pattern (Adjusted R – squared = 0.93).

Table 5. An Anova table showing highly significant effects of different habitat types, varying regeneration times of producers and quality levels of predators on log (log (Mean Prey Survival Time)).

Sources of Variation	Df	F Value	Parameter Estimates	Std. Error	T Value
Intercept	1	5130.3**	2.17	0.03	71.62
Habitat W1C0	1	34.22**	-0.07	0.01	(-5.85) **
Habitat W2C0	1	58.21**	-0.09	0.01	(-7.63) **
Habitat W3C0	1	67.24**	-0.01	0.01	(-8.20) **
Producer Regeneration Time	1	0.14**	-0.003	0.0003	(-9.91) **
Predator Quality Levels	1	0.02**	-0.001	0.0003	(-4.52) **
Predator Survival Time	1	0.08**	0.0002	0.00003	7.62**
Residuals	103				

*p values < 0.01
**p values < 0.05

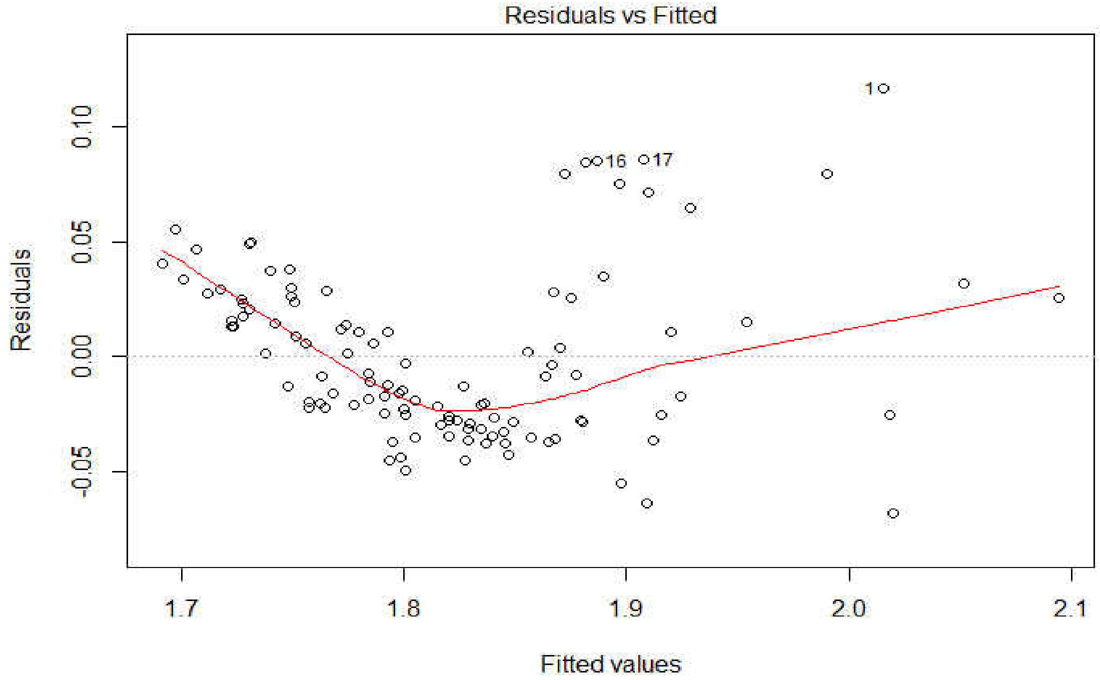

Figure 13. Residual plots of the most fitted model for standardized residual of log (log (Mean Prey Survival Time)) vs predicted residuals of log (log (Mean Prey Survival Time)). This model was accepted because it did not show any obvious pattern (Adjusted R-squared = 0.81).

Table 6. An Anova table showing highly significant effects of different habitat types, varying regeneration times of producers and quality levels of predators on log (log (Mean Predator Survival Time)).

Sources of Variation	Df	F Value	Parameter Estimates	Std. Error	T Value
Intercept	1	612.78**	1.45	0.05	24.75**
Habitat W1C0	1	44.08**	0.01	0.01	6.64**
Habitat W2C0	1	48.44**	0.01	0.01	6.96**
Habitat W3C0	1	40.44**	0.01	0.01	6.36**
Producer Regeneration Time	1	12.659**	-0.002	0.0005	(-3.55) **
Predator Quality Levels	1	240.01**	0.006	0.0003	15.49**
Predator Survival Time	1	14.22**	0.00004	0.00001	3.77**
Residuals	103				

p values < 0.01

*****p values < 0.05***

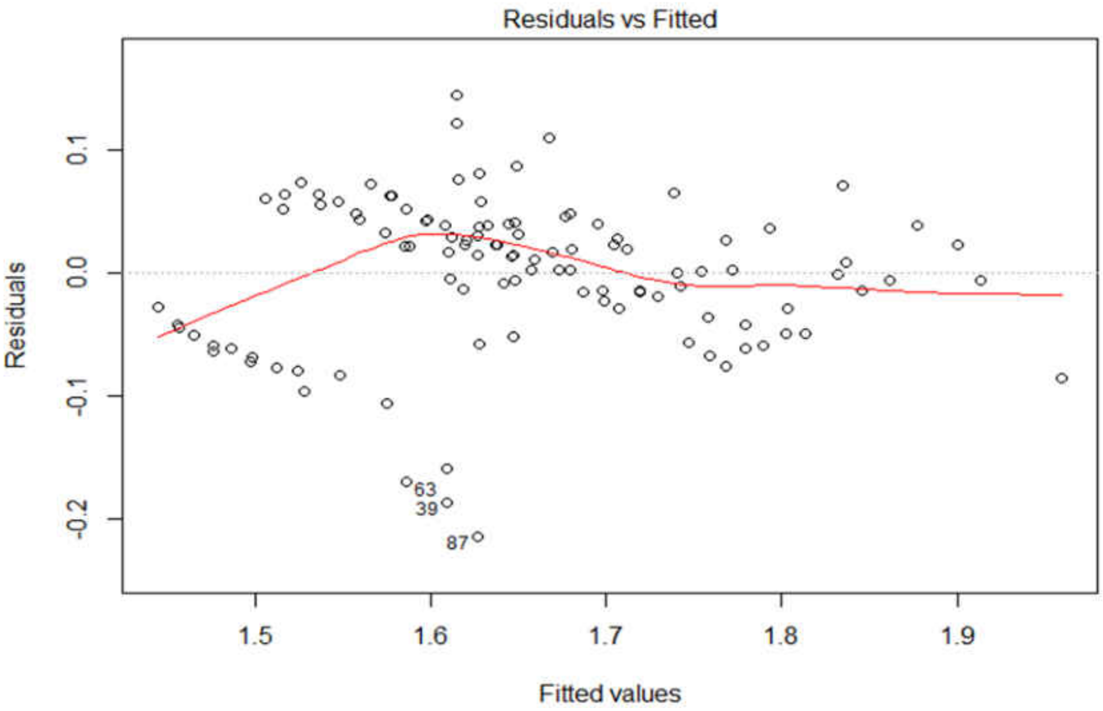

Figure 14. Residual plots of the most fitted model for standardized residual of log (log (Mean Prey Survival Time)) vs predicted residuals of log (log (Mean Prey Survival Time)). This model was accepted because it did not show any obvious pattern (Adjusted R-squared = 0.74).

Prey and Predator Population Size Dynamics in Unconnected Habitats

Besides the statistical analyses conducted for global effects as mentioned above (Table 3 – 6, Figure 11 – 14), further analyses were carried out to study the individual effects of each of the studied parameters on prey – predator population dynamics in unfragmented and fragmented habitats. It was observed that distribution of population size was significantly different across regeneration times of producers for prey population size (Kruskal – Wallis H: 127, $p < 0.01$, N = 264) (Figure 15a) as well as predator population size (Kruskal - Wallis H: 39.487, $p < 0.01$, N = 264) (Figure 15b).

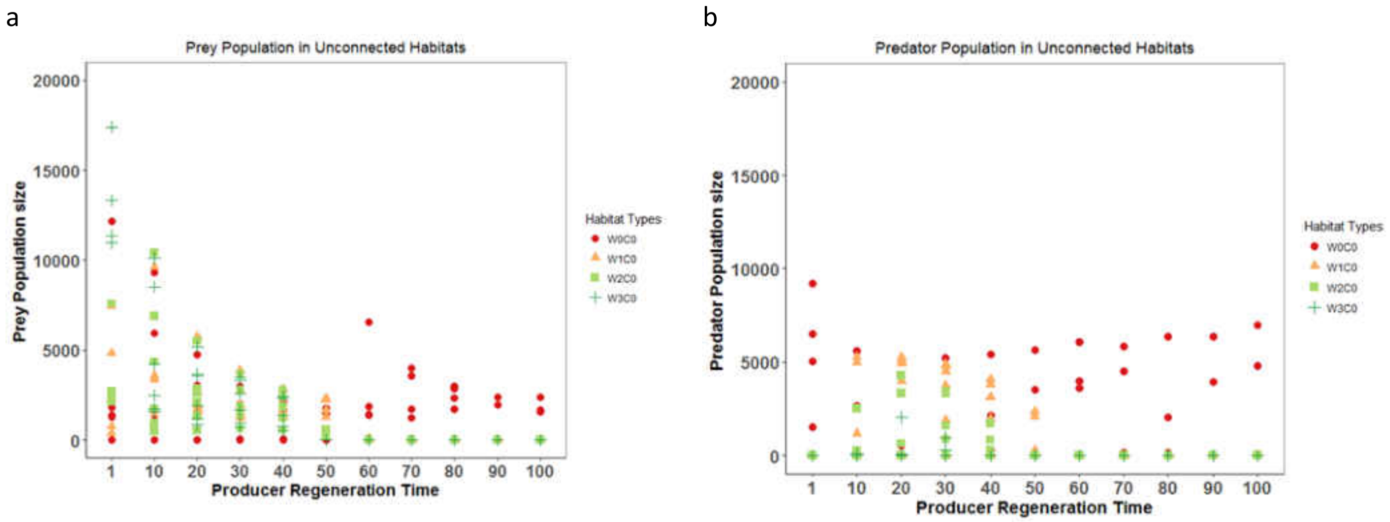

Figure 15. Prey - predator population size across unconnected habitat types as a function of producer regeneration times. a) Prey population size. b) Predator population size.

The distribution of prey population size was not significantly different across unfragmented (W0C0) and fragmented habitats (W1C0, W2C0 and W3C0) but was significantly different across quality levels of predators ($\text{Gain}_{\text{predator}}$) (Kruskal - Wallis H: 35.78, $p < 0.01$, N = 264; most significant differences occurring between levels of 10 – 50, 10 – 60, 20 – 50, 20 – 60, 30 – 50, 30 – 60 and 40 – 60 ($p < 0.01$) based on pairwise comparisons using Dunn’s Test) (Figure 16a). In contrast to prey population, we observed that the distribution of predator population was significantly different across unfragmented and fragmented habitats (Kruskal – Wallis H: 32.912, $p < 0.01$, N = 264; non-significant difference occurring only between habitat types W2C0 – W3C0 ($p > 0.05$) based on pairwise comparison using Dunn’s Test) (Figure 16b) and their quality levels (Kruskal - Wallis H: 16.324, $p < 0.01$, N = 264; most significant differences occurring between levels of 20 – 50, 20 – 60 and 30 – 60 ($p < 0.01$) based on pairwise comparison using Dunn’s Test) (Figure 16b).

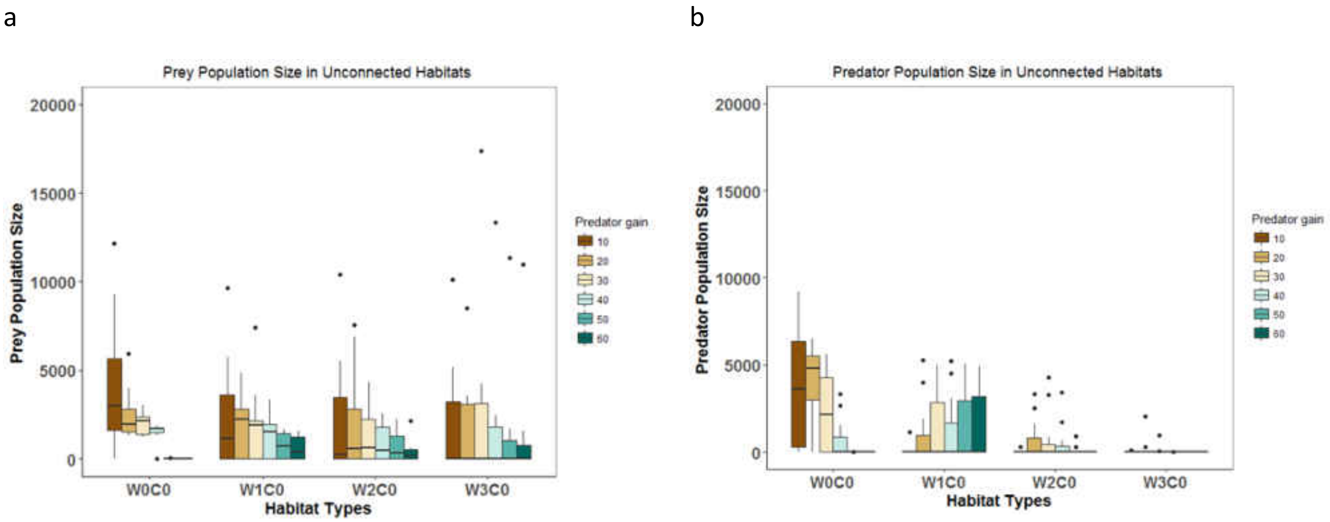

Figure 16. Prey - predator population size across predator quality levels as a function of unconnected habitat types. a) Prey population size. b) Predator population size.

Prey and Predator Survival Time Dynamics in Unconnected Habitat

Besides the statistical analyses conducted for global effects (Table 3 – 6, Figure 11 – 14), further analyses were also carried out to study the individual effects of each studied parameters on prey – predator survival time within unfragmented and fragmented habitats. In unfragmented habitats (W0C0), 43% of the experimental runs resulted in prey survival time of less than 5,000 time – steps (T_{max} = 10,000 time steps). 90% of such cases occurred when producers regenerated slowly ($Time_{regeneration =}$ 60 – 100). Similarly, in fragmented habitats (W1C0, W2C0 and W3C0), 51% of the experimental runs resulted in prey survival time of less than 5,000 time – steps (T_{max} = 10,000 time steps). 93% of such cases occurred when producers regenerated slowly ($Time_{regeneration}$ = 60 – 100) (Figure 17 a). Predator population on the other hand, survived for less than half of its possible maximum survival time (T_{max} = 10,000 time steps) i.e., 5,000 time – steps in 64% of the total experimental runs in unfragmented habitats (W0C0) and 82% in fragmented habitats (W1C0, W2C0, W3C0) (Figure. 17b).

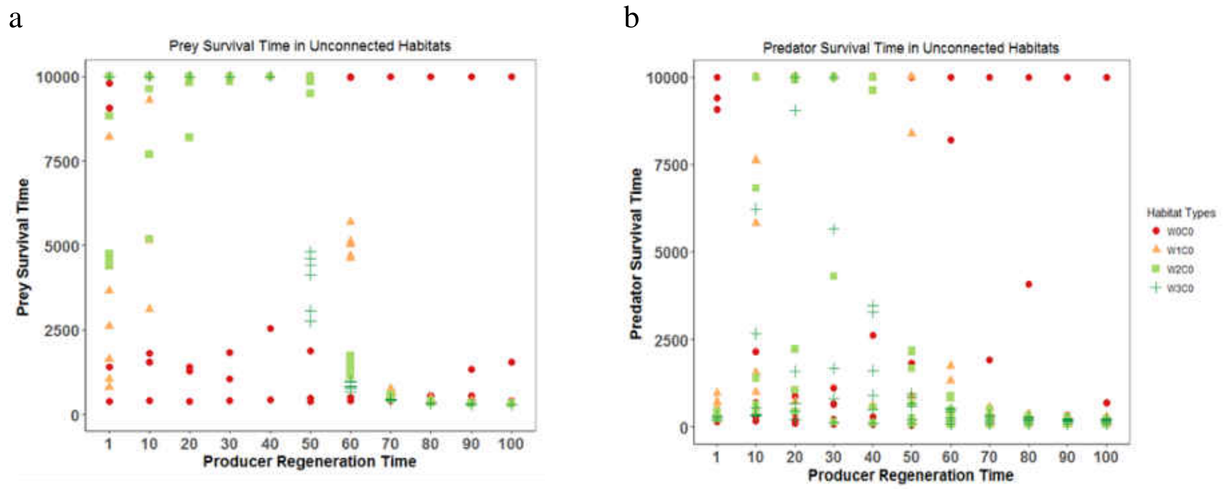

Figure 17. Prey-Predator survival time across unconnected habitat types as a function of producer regeneration time. a) Prey survival time b) predator survival time.

In unfragmented habitats (W0C0), prey population survived an average of 5,978 time steps in the presence of low quality predators (Gain$_{predator}$ = 10 - 30) and an average of 5,860 time steps in presence of high quality predators (Gain$_{predator}$ > 30) (Figure 18a). Whereas in fragmented habitats (W1C0, W2C0 and W3C0), survival time of prey population decreased to an average of 5,300 time steps in the presence of low quality predators and an average of 4,951 time steps in the presence of high quality predators (Figure 18a).

In unfragmented habitats (W0C0), low quality or less efficient predator population (Gain$_{predator}$ = 10 – 30) survived an average of 2,887 time steps while high quality or highly efficient predators (Gainpredator > 30) surved an average of 4,990 time steps. Whereas in fragmented habitats (W1C0, W2C0 and W3C0), survival time of low quality or less efficient predator population decreased to an average of 2,163 time steps and an average of 2,449 time steps for high quality of highly efficient predators (Figure 18 b).

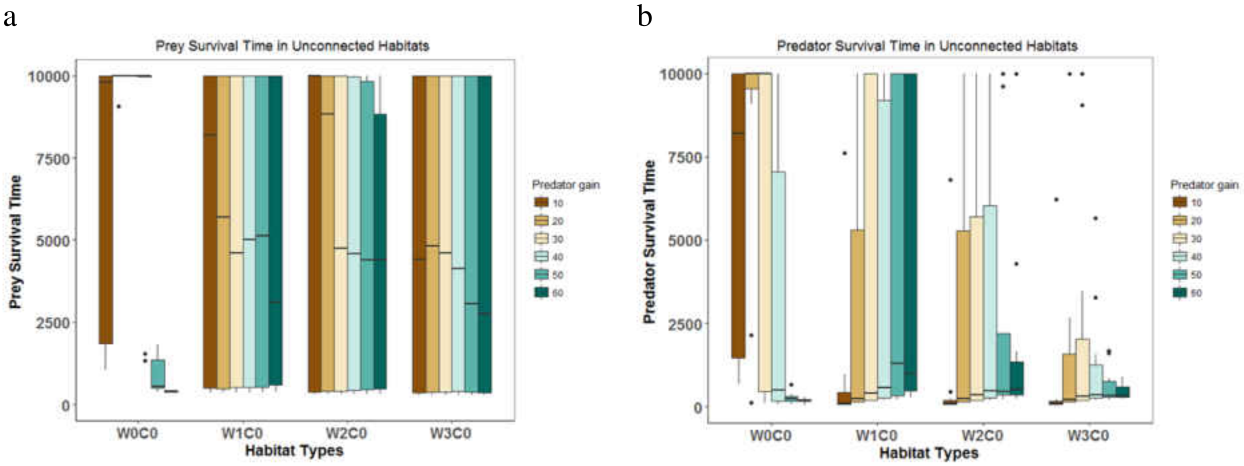

Figure 18. Prey - predator survival time across predator quality levels as a function of unconnected habitat types. a) Prey survival time. b) Predator survival time.

Prey and Predator Population Size Dynamics in Connected Habitats

Implementing connectivity (when $C > 0$; W1C1, W2C2 and W3C3), resulted in population size increase for both prey and predator populations across entire range of producer regeneration times ($\text{Time}_{\text{regeneration}} = 1 – 100$) (Figure 19a and 19b) compared to the habitats without connectivity (Figure 15a and 15b). Besides the statistical analyses conducted for global effects as mentioned above (Table 3 – 6 and Figure 11 - 14), further analyses were carried out to study the individual effects of each of the studied parameters on prey – predator population size in connected habitats. It was observed that distribution was significantly different across regeneration time of producers for prey population size (Kruskal - Wallis H: 45.06, $p < 0.01$, N = 198) (Figure 19a) as well as predator population size (Kruskal - Wallis H: 108, $p < 0.01$, N = 198) (Figure 19b).

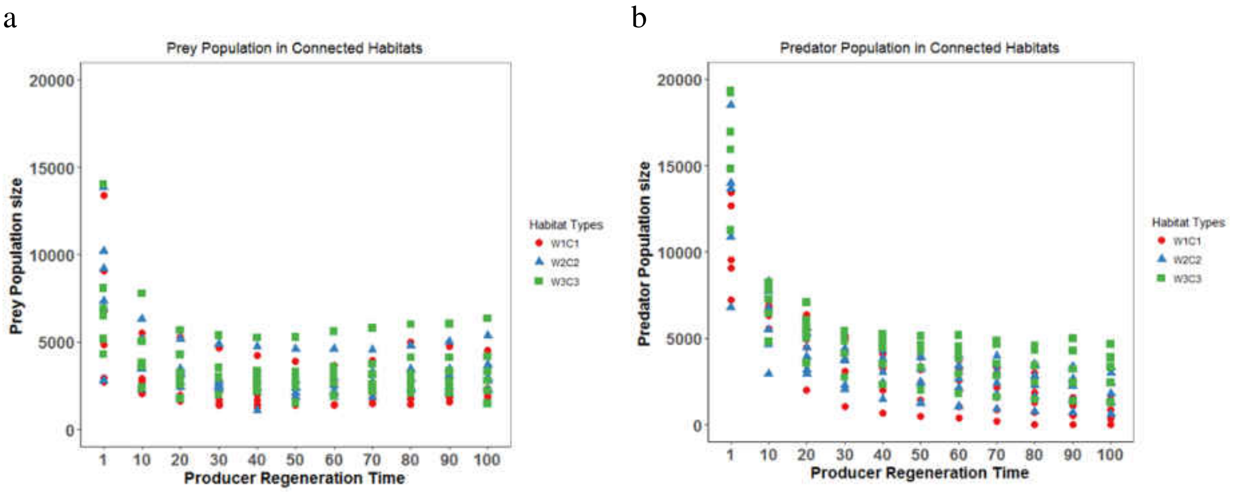

Figure 19. Prey - predator population size across connected habitat types as a function of producer regeneration time. a) Prey population size. b) Predator population size

Similarly, implementing connectivity led to decline in prey population and increase in predator population with increase in quality levels of predators ($Gain_{predator}$) (Figure 20a and 20b) compared to habitats without connectivity (Figure 16a and 16b). The distribution of prey population size was significantly different across connected habitat types (W1C1, W2C2 and W3C3) (Kruskal - Wallis H: 22.50, $p < 0.01$, N = 198; non-significant difference occurring only between habitat type W2C2 – W3C3 ($p > 0.05$) based on pairwise comparisons using Dunn's Test) (Figure 16a) as well as across quality levels of predators ($Gain_{predator}$) (Kruskal - Wallis H: 109.94, $p < 0.01$, N = 198; non-significant differences occurring between levels of 30 – 40, 30 – 60, 40 – 50 and 50 – 60 ($p > 0.01$) based on pairwise comparisons using Dunn's Test) (Figure 20a).

Similarly, we observed that distribution of predator population was significantly different across connected habitats (Kruskal – Wallis H: 18.47, $p < 0.01$, N = 198; most significant differences occurring between habitat types W1C1 – W3C3 and W2C2 – W3C3 ($p < 0.01$) based on pairwise comparison using Dunn's Test) (Figure 20b) as well as their quality levels (Kruskal - Wallis H: 16.324, $p < 0.01$, N = 264; most significant difference occurring between levels of 10 – 20, 10 – 30, 10 – 40 , 10 – 50, 10 – 60, 20 – 40 , 20 – 50 and 20 -60 ($p < 0.01$) based on pairwise comparison using Dunn's Test) (Figure 20b).

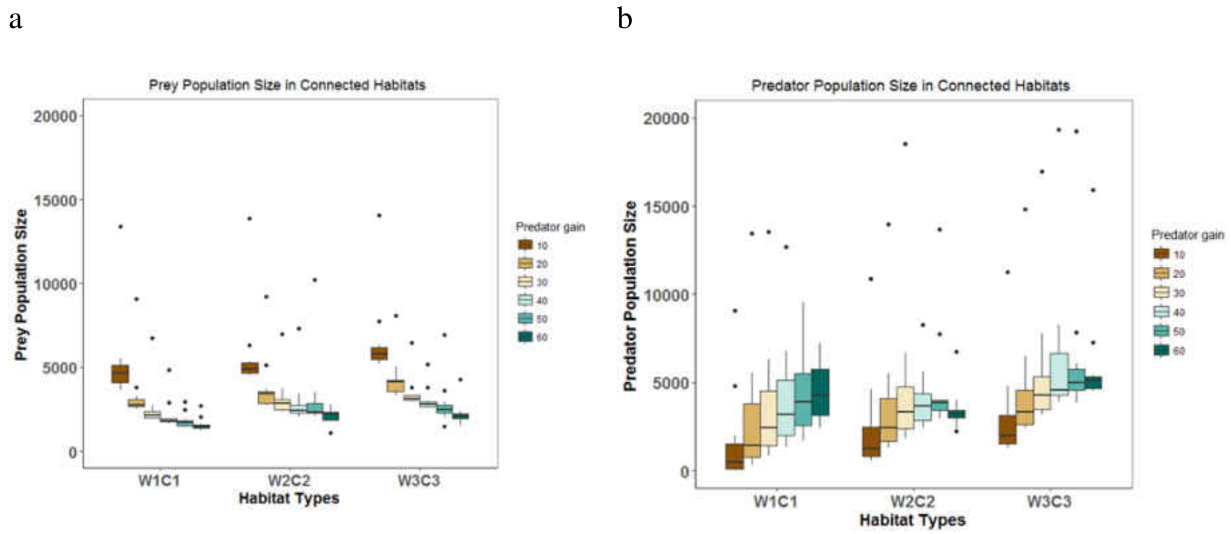

Figure 20. Prey-predator population size across quality levels of predators as a function of connected habitat types. a) Prey population size. b) Predator population size.

Prey and Predator Survival Time Dynamics in Connected Habitats

Besides the statistical analyses conducted for global effects (Table 3 – 6, Figure 11 -14), further analyses were also carried out to study the individual effects of each studied parameters on prey – predator survival time within connected habitats. Implementing connectivity (when C > 0, W1C1, W2C2 and W3C3) led to only 0.01% of the experimental runs resulting in prey survival time of less than 5,000 time steps (down from 51% in fragmented habitats) (T_{max} = 10, 000 time steps) across entire range of producer regeneration time (Figure 21a). Similarly, only 0.03% of the experimental runs resulted in predator survival time of less than 5,000 time steps (down from 82% in fragmented habitats) (T_{max} = 10,000 time steps) across entire range of producer regeneration time (Figure 21b).

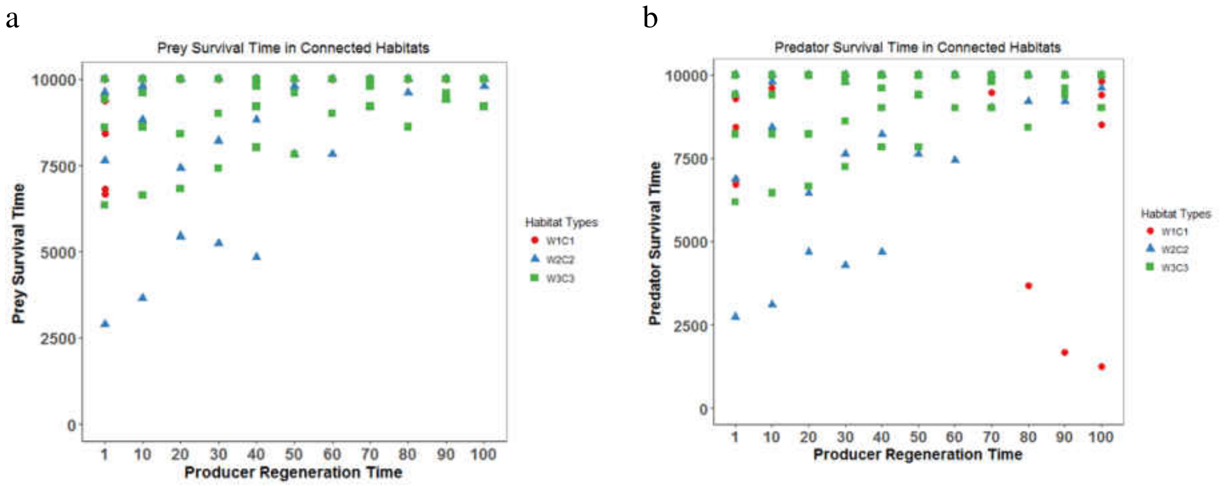

Figure 21. Prey-predator population size across connected habitat types as a function of producer regeneration time. a) Prey survival time. b) Predator survival time

Implementing connectivity also led to increase in average prey population survival time to 9,993 time – steps (up from 5,300 time steps in fragmented habitats) (T_{max} = 10, 000 time steps) in the presence of low quality predators ($Gain_{predator}$ = 10 - 30) and to 9,159 time steps (up from 4,951 time steps in fragmented habitats) (T_{max} = 10, 000 time steps) in presence of high quality predators ($Gain_{predator}$ > 30) (Figure 22a). Similarly, implementing connectivity led to increase in average low quality predator survival time to 9,730 time steps (up from 2,163 time – steps in fragmented habitats) and high quality predator survival time to 9,028 time steps (up from 2,449 time steps in fragmented habitats) (Figure 22b).

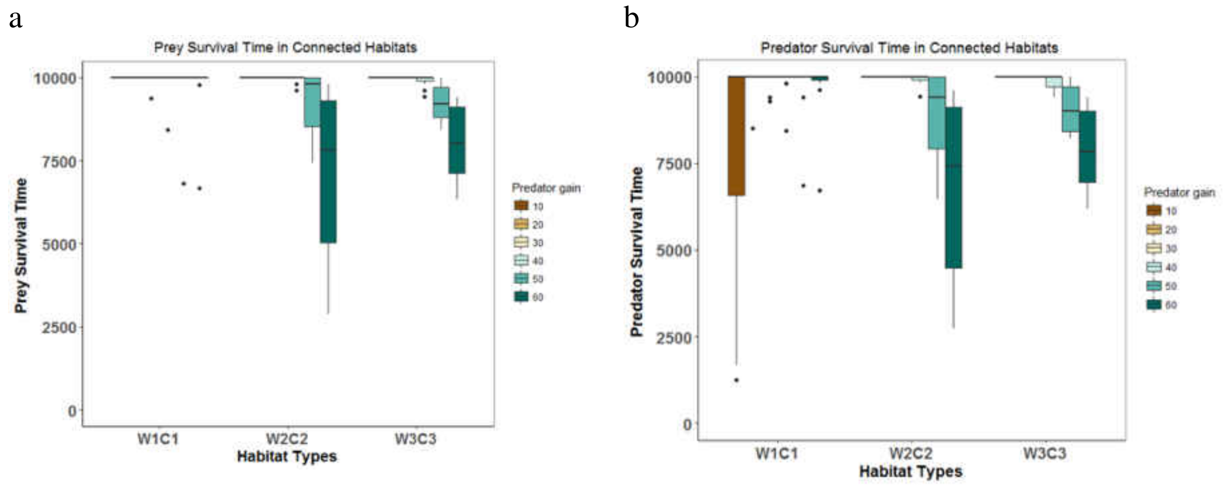

Figure 22. Prey - predator survival time across predator quality level as a function of connected habitat systems. a) Prey survival time. b) Predator survival time.

Two Prey Populations with Identical Life Histories and Coexistence Dynamics

When two identical species compete for same resources they cannot coexist (Gause 1934). We hypothesized that within different habitat types (W0C0, W1C0, W2C0, W3C0, W1C1, W2C2 and W3C3; W = level of fragmentation and C = level of connectivity), with two identical prey populations (Prey I and Prey II), survival time of prey populations is affected by the varying producer regeneration times. We also predicted that coexistence dynamics of two identical populations is better favored in connected habitat types.

In case of competition between two identical prey populations, it was observed that faster regenerating producers supported stable population dynamics over extended period without extinction of either prey population whereas extinction occurred when producers were regenerating slowly ($\text{Time}_{\text{regeneration}} = 60 – 100$). In fact, 100% of the observed population extinctions occurred when slow regenerating producers were present ($\text{Time}_{\text{regeneration}} = 60 – 100$). The distribution of population survival times across regeneration times of producers were significantly different for Prey I survival time (Kruskal – Wallis H: 39.01, $p < 0.05$, N = 77) and Prey II survival time (Kruskal – Wallis H: 37.38, $p < 0.05$, N = 77).

Survival time of identical prey populations was also influenced by arrangement of the habitat types the populations resided in. The distribution of survival time across habitats was significantly different for Prey I survival time (Kruskal - Wallis H: 19.25, $p < 0.05$, N = 77; most significant differences arising between habitat types W0C0 - W3C3 ($p < 0.01$), W1C0 - W3C3($p < 0.01$), W2C0 – W3C3 ($p < 0.01$), W3C0 – W3C3 ($p < 0.01$) based on pairwise comparisons using Dunn's - Test) and Prey II survial time (Kruskal - Walis H: 18.21, $p < 0.05$, N = 77; most significant differences arsing between habitat types W0C0 - W3C3 ($p < 0.01$), W1C0 - W3C3($p < 0.01$), W2C0 – W3C3 ($p < 0.01$), W3C0 – W3C3 ($p < 0.01$) based on pairwise comprisons using Dunn's Test).

Habitat types (W0C0, W3C0 and W3C3) were further analyzed to study any possible relations between a certain habitat types and coexistence dynamics.

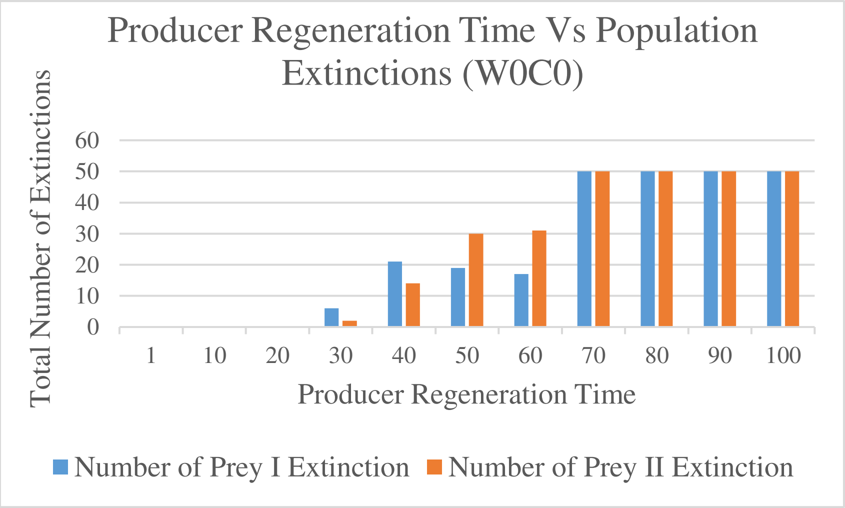

Figure 23. The number of extinctions of Prey I and Prey II populations as a function of the regeneration times of the producers in habitat system W0C0. 50 parallel simulations were run until maximum time (T_{max}). All parameters were set as per Table 2.

These three habitats were chosen because it represented the highest possible values of fragmentation (W) and connectivity (C) levels within our studied unfragmented, fragmented and connected habitats settings respectively. In unfragmented habitats (W0C0), both prey population coexisted when $\text{Time}_{\text{regeneration}}$ was in the range of 1 – 20 whereas, equal number of extinctions were observed when $\text{Time}_{\text{regeneration}}$ = 70 – 100 (Figure 23). Competition between the two-prey population (Gause Law, 1934) was observed when $\text{Time}_{\text{regeneration}}$ = 30 – 60 (Figure 23).

In fragmented habitats (W3C0), both prey population coexisted over a wider range of producer regeneration times ($\text{Time}_{\text{regeneration}}$ = 10 – 40) while both prey population declined to extinction when the regeneration of producers was slow ($\text{Time}_{\text{regeneration}}$ = 50 – 100) (Figure 24). Only one extinction was observed in case of Prey I population when $\text{Time}_{\text{regeneration}}$ = 50 (Figure 24).

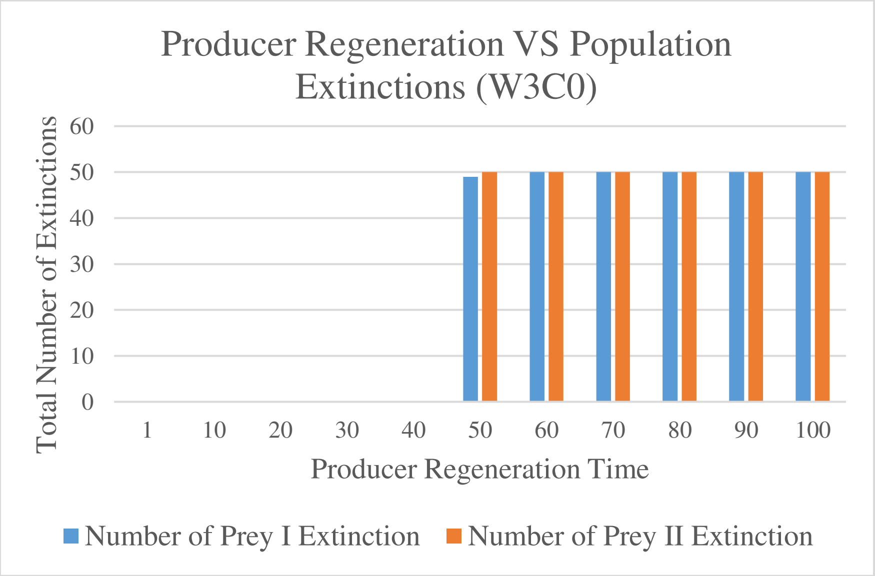

Figure 24. The number of extinctions of Prey I and Prey II populations as a function of the regeneration times of the producers in habitat system W3C0. 50 parallel simulations were run until maximum time (T_{max}). All parameters were set as per Table 2

In connected habitats (W3C3), however, both prey population coexisted across entire range of producer regeneration times ($\text{Time}_{\text{regeneration}}$ = 10 – 100) (Figure 25). Only one extinction was observed in case of Prey II population when $\text{Time}_{\text{regeneration}}$ = 70 (Figure 25).

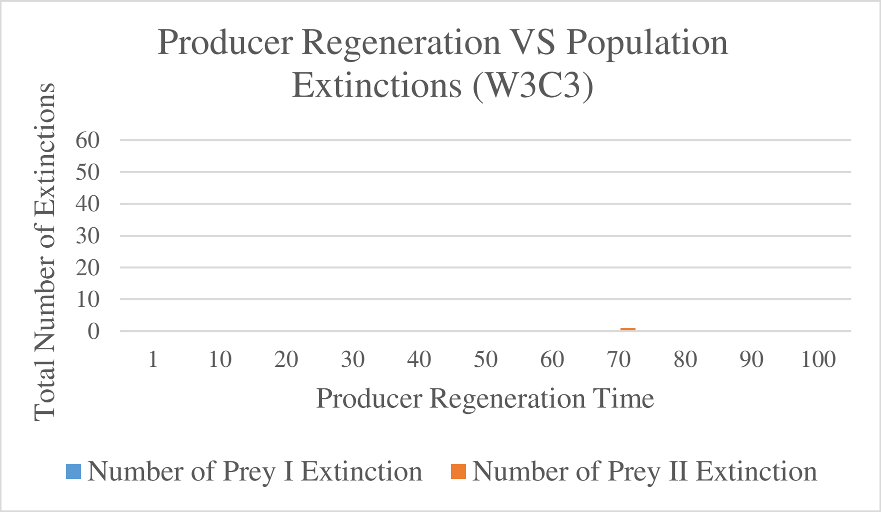

Figure 25. The number of extinctions of Prey I and Prey II populations as a function of the regeneration times of the producers in habitat system W3C3. 50 parallel simulations were run until maximum time (T_{max}). All parameters were set as per Table 2.

Two Prey Populations with Non – Identical Life Histories and Coexistence Dynamics

We hypothesized that non – identical life history parameters could alter the competitive and coexistence dynamics of participating prey populations. To test this prediction, the amount of energy gained from food for Prey I populations was kept constant ($Gain_{preyI}$ = 4 EU) but the amount of energy gained from food for Prey II populations was reduced by half i.e., ($Gain_{preyII}$ = 2 EU) resulting in two non-identical population where one was twice as efficient (Prey I) than other (Prey II). Other parameters for the experiment were set to standard initial values (Table 2). In case of non – identical prey populations, more efficient prey population (Prey I) survived an average of 7,676 time steps whereas less efficient prey population (Prey II) survived an average of only 72 time steps (T_{max} = 10,000 time steps for both populations). The distribution of survival time across producer regeneration time was significantly different for Prey I survival time (Kruskal – Wallis H: 29.40, $p < 0.05$, N = 77) while it was not significantly different for Prey II survival time.

However, it was observed that coexistence dynamics between non-identical prey populations was significantly shaped by arrangement of the habitat types the population resided in. The distribution of survival times across habitats was significantly different for Prey I survival time (Kruskal – Wallis H: 20.70, $p < 0.05$, $N = 77$; most significant difference occurring between habitat types W3C0 – W1C1, W3C0 – W2C2 and W3C0 – W3C3 based on pairwise comparisons using Dunn’s Test) and Prey II survival time (Kruskal – Wallis H: 61.462, $p < 0.05$, $N = 77$; the most significant difference occurring between habitat types W1C0 – W3C3, W2C0 – W3C3 and W3C0 – W3C3 based on pairwise comparisons using Dunn’s Test) as shown in (Figure 26).

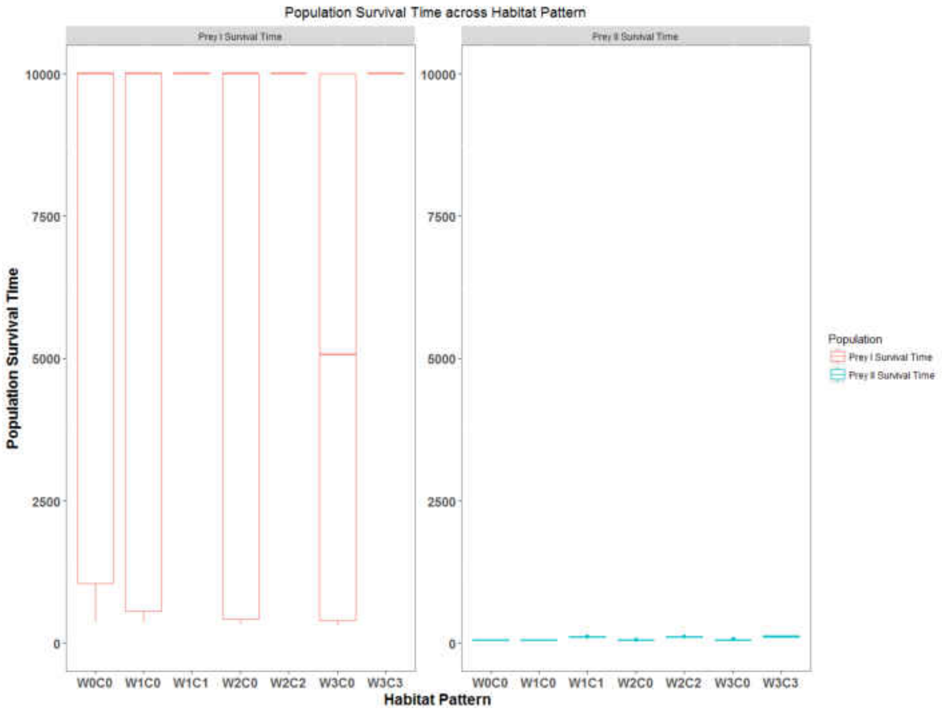

Figure 26. Population survival times of non - identical competitors as a function of habitat patterns. The survival dynamics of Prey I population whose $\text{Gain}_{\text{preyI}}$ was kept constant is shown in the left while the survival dynamics of the Prey II population whose $\text{Gain}_{\text{preyII}}$ was reduced to half is shown in right. Reducing ability to obtain energy from food drastically impacted survivability for Prey II population.

To understand further how the non-identical life history parameters affected the coexistence dynamics between the two-prey population, a set of new experiments was carried out where all the parameters were set to standard initial values (Table 2) but amount of energy gained from food for Prey II population ($Gain_{preyII}$) was gradually increased through 1 – 8 Energy Units with increment of 1 Energy Units in each experimental set up within three contrasting habitat types (W0C0, W3C0 and W3C3; W = level of fragmentation and C = level of connectivity). These three habitats were chosen because it represented the highest possible values of fragmentation (W) and connectivity (C) levels within our studied unfragmented, fragmented and connected habitat types respectively. The regeneration time of producer ($Time_{regeneration}$) was kept constant at 10 for this experiment. Each experiment was run for 10,000 time steps (T_{max}) or until extinction of the population. 50 parallel simulations were carried out for each unique experimental setting to measure the variability of the coexistence dynamics in such settings.

It was observed that when prey II population were the less efficient ones ($Gain_{preyII}$ < = 3 EU), their average survival time decreased to less than 250 time steps (T_{max} = 10,000 time steps) (Figure 27) whereas when they were the more efficient ones ($Gain_{preyII}$ > 5), their average survival time drastically increased to T_{max} (T_{max} = 10,000 time steps) (Figure 27). The two population could coexist only when they both had the same level of efficiency ($Gain_{preyI}$ = $Gain_{preyII}$ = 4EU) as shown in (Figure 27). This population shifted from lower to high survivability as the efficiency was increased gradually and it was noteworthy that this occurred simultaneously when survivability of other prey population (Prey I) shifted from higher to lower survivability as shown in (Figure 27).

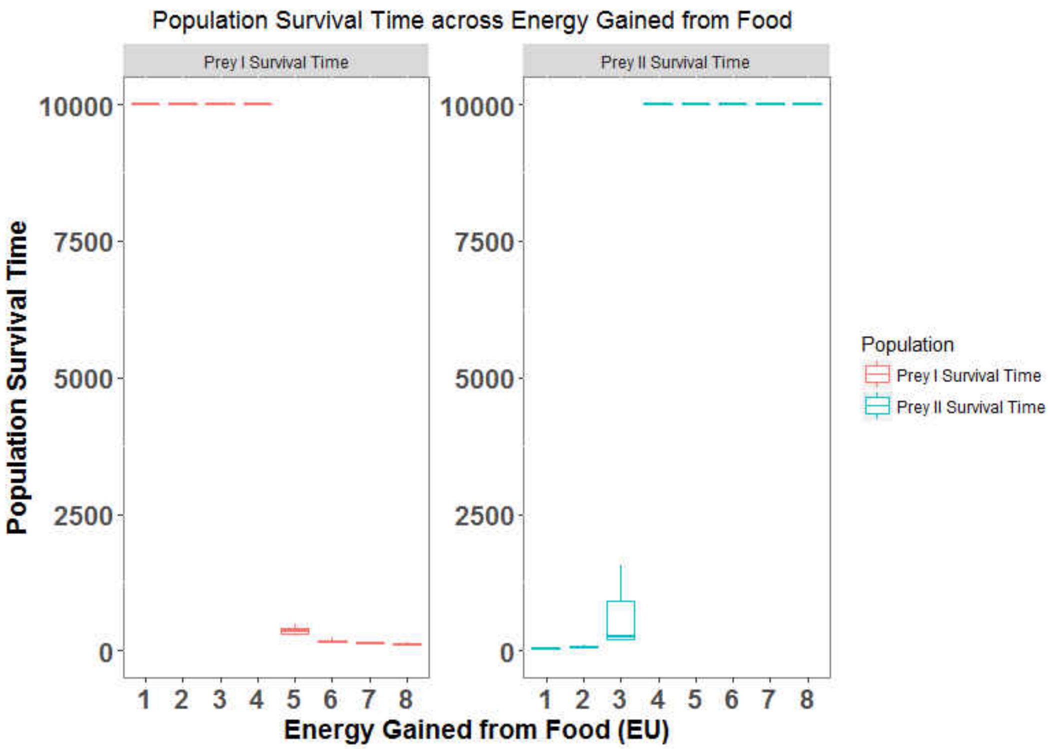

Figure 27. Population survival times of non-identical prey populations as a function of varying energy gain from good of Prey II ($Gain_{preyII}$). The survival time started out low for Prey population II when $Gain_{preyII} < 3$ but as $Gain_{preyII} > 5$ it outlived Prey I. The population only coexisted at equal $Gain_{prey}$ value of 4 for both population; below or above the value of which the population showed a strong shift from negative to positive in survivability.

The Effects of Interactions Between Predation and Competition on Coexistence Dynamics

We hypothesized that implementing lower quality predator populations in the system with two identical prey populations will ensure greater survivability of both prey species and hence, enhance coexistence. We also predicted that higher quality predators in contrast, will reduce the prey populations and their survivability significantly contrary to hypothesis of Paine (1964) and Hall et al. (1970) that predation solely promotes coexistence by limiting one monopolizing species to out – perform another species.

When Time$_{regeneration}$ = 10

When productivity of habitats was higher, implementing low quality or less efficient predators (Gain$_{predator}$ = 10 – 30 EU) within in the habitats resulted in larger prey population size (Figure 28). In contrary, implementing high quality or more efficient predators (Gain$_{predator}$ = 40 – 60 EU) within the habitats resulted in decline and hence, smaller prey population size due to over exploitation (Figure 28).

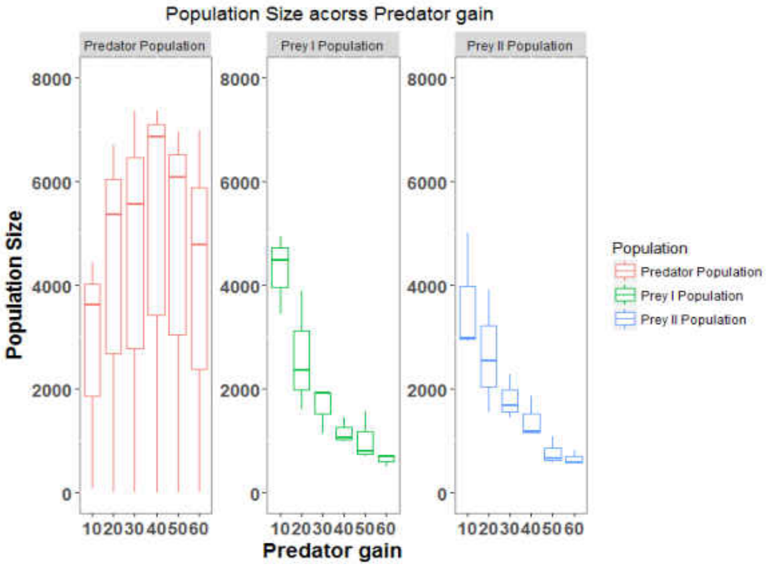

Figure 28. Population size as a function of quality levels of predators. Both prey population occurred in higher number when lower quality predators were present. As predators' efficiency was increased, the prey population faced massive decline due to overexploitation by predators

The distribution of population size across quality levels of predators (Gain$_{predator}$) was significantly different for Prey I population (Kruskal – Wallis H: 14.42, $p < 0.05$, N = 18; most significant differences arising between Gain$_{predator}$ 10 – 40 ($p < 0.01$), 10- 50 ($p < 0.01$), 10 – 60 ($p < 0.01$) and 20 – 60 ($p < 0.01$) based on pairwise comparison using Dunn's Test) and Prey II Population (Kruskal – Wallis H: 14.60, $p < 0.05$, N = 18; most significant differences arising between Gain$_{predator}$ 10 – 50 ($p < 0.01$), 10 – 60 ($p < 0.01$), 20 – 50 ($p < 0.01$) and 20 – 60 ($p < 0.01$) based on pairwise comparison using Dunn's Test).

Similarly, implementing fragmentation (W3C0) led to higher survival times in both prey populations than implementing unfragmented (W0C0) or connected habitats (W3C3) (Figure29).

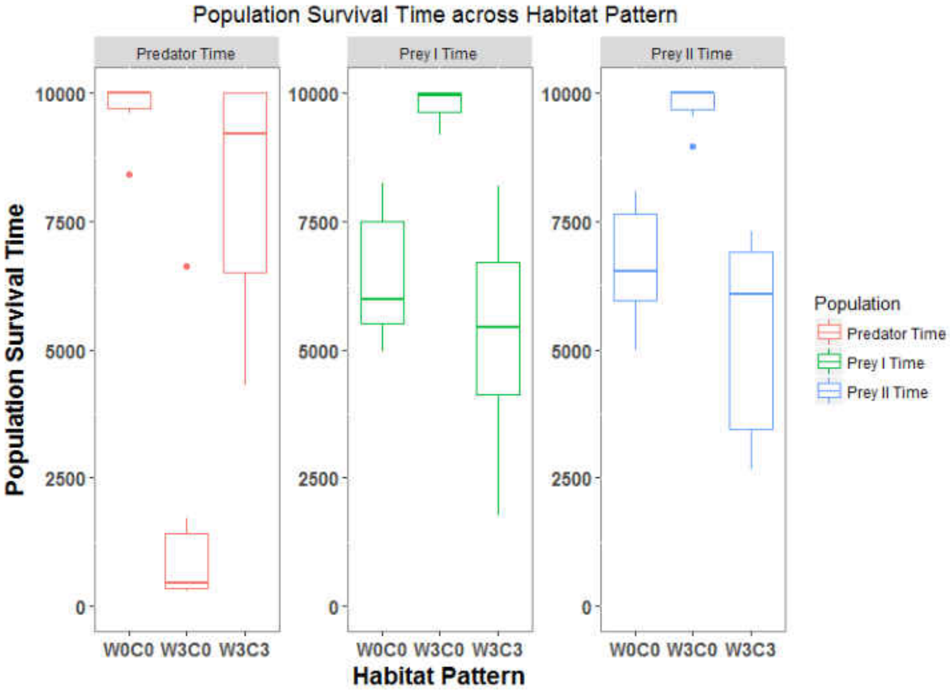

Figure 29. Population survival time as a function of habitat types. Fragmented habitats were better suited for survivability of both prey population in comparison to unfragmented and connected habitats when predators were included in the systems. This happened as fragmented habitat provided temporary refuge which helped minimize impacts of overexploitation. The predator population however, flourished in unfragmented and connected habitats.

In contrast, the predator survival time was higher in unfragmented and connected habitat types. The distribution of survival time across habitat types was significantly different in case of Prey I population (Kruskal – Wallis H: 11.84, $p < 0.05$, N = 18; most significant differences arising between habitat types W0C0 – W3C0 ($p < 0.01$) and W3C0 – W3C3 ($p < 0.01$) based on pairwise comparison using Dunn's Test), Prey II population (Kruskal – Wallis H: 12.06, $p < 0.05$, N = 18; most significant differences arising between habitat types W0C0 – W3CO ($p <$

0.01) and W3C0 – W3C3 ($p < 0.01$) based on pairwise comparison using Dunn's Test) and Predator population (Kruskal – Wallis H: 11.20, $p < 0.05$, N = 18; most significant difference arising between habitat types W0C0 – W3C0 ($p < 0.01$) based on pairwise comparison using Dunn's Test).

When $\text{Time}_{\text{regeneration}} = 50$

When the productivity of habitats decreased, it was observed that the overall predator – prey population size was smaller (Figure 30) than in comparison to the habitat systems where productivity was higher ($\text{Time}_{\text{regeneration}} = 10$; Figure 28).

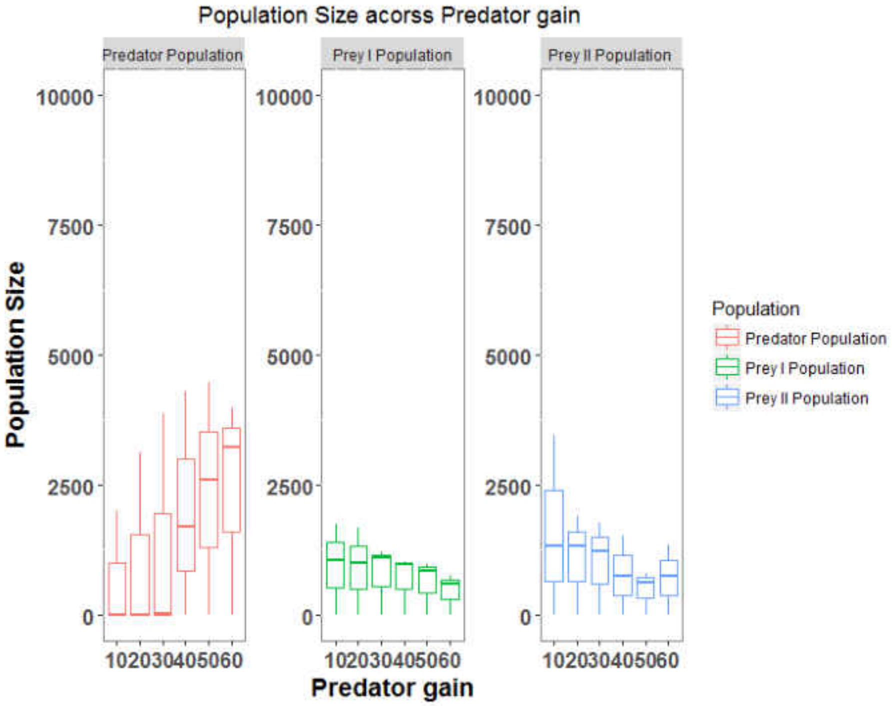

Figure 30. Population size as a function of quality levels of predators. Overall population size was smaller compared to $\text{Time}_{\text{regeneration}} = 10$ (Fig. 28). Both prey population size occurred in higher number when lower quality predators were present. Increasing efficiency of predators reduced the prey population but the amplitude of overall population size was smaller as compared to when $\text{Time}_{\text{regeneration}} = 10$ (Fig. 28).

Similar population fluctuation dynamics occurred as when $\text{Time}_{\text{regeneration}} = 10$ but with much lower amplitude (Figure 30). Implementing low quality or less efficient predators

($\text{Gain}_{\text{predator}}$ = 10 – 30 EU) still resulted in higher prey population size than implementing high quality predators ($\text{Gain}_{\text{predator}}$ = 40 – 60 EU) but the population size did not fluctuate as heavily as in case of highly productive habitats (Figure 28 and Figure 30). The distribution of survival time across levels of predator quality was not significantly different in case of Prey I population (Kruskal – Wallis H: 2.88, $p > 0.05$, N = 18) as well as Prey II population (Kruskal - Wallis H: 1.55, $p > 0.05$, N = 18).

Similarly, when the productivity of the habitats was lower, implementing fragmentation (W3C0) led to decline and eventual extinction of both prey - predator population. However, the predator – prey population survived in unfragmented (W0C0) and connected habitats (W3C3) (Figure 31).The distribution of population size across habitat types was significantly different in case of Prey I population (Kruskal – Wallis H: 11.41, $p < 0.05$, N = 18; most significant differences arising between habitat types W0C0 – W3C0 ($p < 0.01$) and W3C0 – W3C3 ($p < 0.01$) based on pairwise comparison using Dunn's Test), Prey II population (Kruskal – Wallis H:14.52, $p < 0.05$, N = 18; most significant differences between habitat types W0C0 – W3C0 ($p < 0.01$)and W3C0 – W3C3 ($p < 0.01$) based on pairwise comparison using Dunn's Test) and Predator population (Kruskal – Wallis H: 12.80, $p < 0.05$, N = 18; most significant difference arising between habitat types W3C0 – W3C3 ($p < 0.01$) based on pairwise comparison using Dunn's Test).

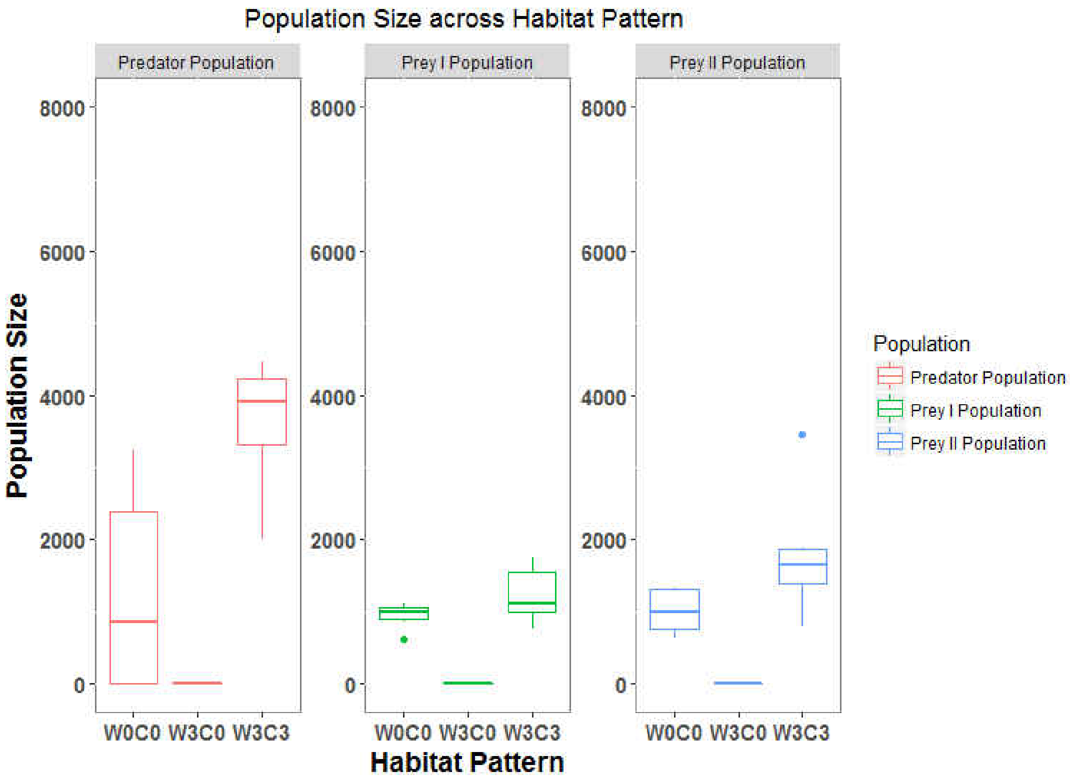

Figure 31. Population size as a function of habitat types. Both predator – prey populations faced massive decline to extinction within unfragmented habitats (W3C0) but survived within unfragmented (W0C0) and connected habitat types (W3C3).

In contrast to the habitats whose productivity was higher ($\text{Time}_{\text{regeneration}}$ = 10; Figure 29), implementing fragmentation (W3C0) led to lower survival time of both prey population than in unfragmented habitats (W0C0) and connected habitats (W3C3) as shown in Figure 32. This pattern was similar for predator population. The distribution of survival time across habitat types was significantly different in case of Prey I population (Kruskal – Wallis H: 11.415, $p < 0.05$, N = 18; most significant difference arising between habitat types W0C0 – W3C0 ($p < 0.01$) and W3C0 – W3C3 ($p < 0.01$) based on pairwise comparison using Dunn's Test), Prey II population (Kruskal – Wallis H: 9.58, $p < 0.05$, N = 18; most significant difference arising between habitat types W0C0 – W3C0 ($p < 0.01$) and W3C0 – W3C3 ($p < 0.01$) based on pairwise comparison using Dunn's Test) and Predator population (Kruskal – Wallis H: 7.61, $p < 0.05$, N= 18; the major difference arising between habitat types W3C0 – W3C3, $p < 0.01$ based on pairwise comparison using Dunn's Test).

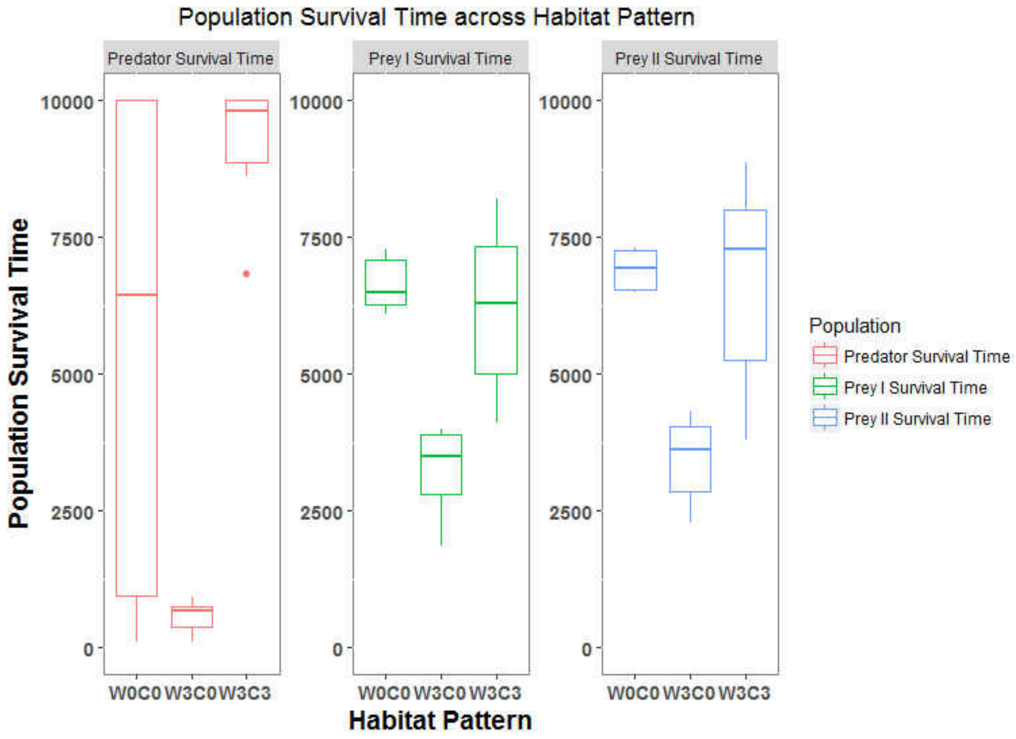

Figure 32. Population survival time as a function of habitat types. Unfragmented (W0C0) and connected habitats (W3C3) were better suited for survival of both predator - prey population than fragmented habitats (W3C0) as compared to when $\text{Time}_{\text{regeneration}} = 10$ (Figure 29).

CHAPTER 4

DISCUSSIONS

The agent based model we developed is an abstract and minimalistic model for studying prey – predator coexistence dynamics and unlike classical Lotka -Volterra models, carrying capacities and competition coefficients are not explicitly implemented into the model system (Karsai et al. 2016). Instead of using an explicit competition coefficient, we relied upon interactions amongst individuals and their corresponding environments (Process overview and Scheduling; Figure 1 – 3). Similarly, instead of implementing carrying capacity directly, we built a model system where energy flow occurs between trophic levels i.e., from producers to consumers (prey populations) to predators (Karsai et al. 2016). This simple setup facilitated the outcomes of complex emergent dynamics which incorporated density dependent re-colonization of sub-habitats and delayed colonization by predators after the prey populations have colonized a sub-habitat (Karsai and Kampis 2011). The agents in the model were devoid of any abilities to sense the presence of surrounding prey – predator populations, producers, or the reflecting border walls within the system. The movements of the agents have been simplified to random walk. Foraging and probability that an agent would travel through the connecting portals has been randomized as well (Karsai and Kampis 2011). On one hand, this type of simplification allowed us to concentrate on the individual agents and their interactions at the basic level which produced the emergent dynamics, and on the other, prevented the model from being unnecessarily complicated. Nevertheless, we obtained results which were the emergent outcomes of the model system mediated by experimental parameter settings per the necessities of various studies conducted and extensive parameter sweeps.

Effects of Habitat Types, Varying Regeneration Times of Producers and Quality Levels of Predators on Coexistence Dynamics of Prey – Predator Population

The simple agent-based model we built produced some interesting predictions on the prey – predator coexistence dynamics within the model system. Findings from this study show that coexistence dynamics (determined in terms of prey and predator population size) is influenced significantly by varying regeneration times of the producers, the combination of connectivity and fragmentation levels of different habitat types and quality levels of predators within the habitats. Statistical analyses of our results proved (Table 3 – 6; Figure 11 -14) that these three factors are indeed significantly responsible for prey and predator population size. We will evaluate the effects of each of these three factors in detail below.

Effects of Varying Regeneration Times of Producers

The findings from our study show that varying regeneration times of producers significantly influences the coexistence dynamics. The producers found in the model systems were as simple as the rest of the model parameters and were devoid of any morphological adaptations such as spines and thick cuticles or chemical defenses known as secondary compounds (Krohne 2001, 252 – 254 p). To control the negative sides as well as positive sides of herbivory such as overexploitation of photosynthetic parts of plant system or increase in production of seeds respectively (Krohne 2001, 256 p), the regeneration times of producers ($Time_{regeneration}$) was implemented or controlled externally (Figure 1) and the foraging by prey population was completely randomized (Figure 2) within the model system.

Habitats with producers which took shorter time interval to regenerate ($Time_{regeneration} = 1 – 59$) or high productive environment supported a robust prey-predator population in comparison to the habitats with producers which took a longer time interval to regenerate ($Time_{regeneration}$ = 60 – 100) or low productive environment. High productive environment ($Time_{regeneration}$ = 10 – 59) helped maintain a steady supply of food sources for prey population. This made optimal foraging per time – step more probable for prey populations which helped them meet their energy needs continuously enhancing their probability for reproduction (Figure 2) and maintained higher population size (Figure 15a and 19a) as well as higher survival times (Figure 17a and 19a). This had a significant positive impact upon the predator populations also as prey populations were their only food source. Thus, readily available food sources made optimal foraging per time – step more probable even for predator populations enhancing their probability for reproduction (Figure 3) which improved their functional and numerical response (Krohne 2001, 261 p) resulting in larger predator population size (Figure 15b and 19b) and predator survival time (Figure 17b and 19b) also.

On the contrary, in low productive environment ($Time_{regeneration}$ = 60 – 100), the probability for optimal foraging per time-step declined. Both prey and predator populations now spent more energy and time foraging which exhausted their limited energy reserves. Unless they find food sources to replenish declining energy levels vital to carry normal life processes, the chances that they could successfully forage and reproduce further declines. Hence, eventually the populations died out resulting in smaller prey population size (Figure 15a and 19a) and smaller prey survival time (Figure 17a and 19a) followed by smaller predator population size (Figure 15b and 19b) and smaller predator survival time (Figure 17b and 19b).

Effects of Fragmented and Connected Habitats

The findings from our study show that both habitat types i.e., fragmented habitats and connected habitats significantly influence the coexistence dynamics. Bender et al. (1998), Fischer and Lindenmayer (2007) and Blackburn et al. (2011) reported that habitat fragmentation leads to population decline akin to our study predictions which show that fragmented habitats (W1C0, W2C0, W3C0; Figure 5-7) leads to lower prey population size (Figure 15a) and prey survival times (Figure 17a) as well as lower predator population size (Figure 15b) and lower predator survival time (Figure 17b). Inducing fragmentation leads to mosaic landscapes of habitat patches. This may affect the population through reduction in total area of suitable habitats (Krohne 2001, 137 p). Within such patchy habitats, the predator – prey population tend to fluctuate heavily often leading to extinction of one of the species followed by the other resulting in habitats where just prey food survives as in (Karsai and Kampis, 2011) (Figure 5 – 7). The degree to which habitable area was lost depended upon the intensity of fragmentation. Higher the level of fragmentation, greater the lost in habitat area which had more negative consequences resulting in smaller population size (Figure 15a and 15b) and population survival time (Figure 17a and 17b).

Karsai and Kampis (2011) reported implementing connectivity between fragmented habitats to be advantageous as it ensured the coexistence of prey - predator populations similar to our study predictions which show that connected habitats (W1C1, W2C2, W3C3; Figure 8 - 10) lead to higher prey population size (Figure 19a) and prey survival time (Figure 21a) as well as higher predator population size (Figure 19b) and higher predator survival time (Figure 21b). Implementing connectivity between the habitat patches basically allows for movements between such patches and hence, establishes connectivity (Brudvig et al. 2012). This allows for dispersal of predator – prey populations across the habitats (Holyoak and Lawler 1996; Ament et al. 2014). This implied that the prey populations were now capable to find temporal refuges by escaping into neighboring sub habitats with the help of connecting portals which not only helped to reduce overexploitation by highly efficient predators but also allowed for reproduction (Karsai and Kampis, 2011). As prey populations escaped from point of extinction and stabilized, successful foraging per unit time step became more probable for predator populations also. It ensured higher predator population size as well as higher survival time. This process facilitated by corridors repeated in cycle hence, larger prey - predator population size (Figure 19a and 19b) was maintained along with higher survival times (Figure 21a and 21b).

Effects of Quality Levels of Predators

The findings from our study show that quality levels of predators significantly influence the coexistence dynamics. High quality predators ($\text{Gain}_{\text{predator}} > 30$) overexploited the prey populations reducing their overall population size and survival time in fragmented habitats (W1C0, W2C0 and W3C0). This in return led to decline and extinction of predator populations in subsequent generations. Karsai and Kampis (2011) reported prey - predator population dynamics like our study predictions which show that within fragmented habitats, high quality predators overexploited the prey population and reduced their overall population size (Figure 16a) and survival times (Figure 18a). This decrease in prey population and survival time eventually led to decrease in predator population size (Figure 16b) and survival time (Figure 18b) (Karsai and Kampis 2011). Since, high quality predators obtained high amount of energy from food, they could possibly utilize it to travel farther distances for foraging. This increased the chances of them encountering a potential prey if available in the habitat. These dynamics occurred in each sub - habitats and its magnitude increased with increase in level of fragmentation (W). This led to potential over-exploitation of prey population without a chance for relief.

High quality predators ($Gain_{predator} > 30$) on the other hand, reduced the prey population size but maintained its own population in larger numbers in connected habitats (W1C1, W2C2 and W3C3). Karsai and Kampis (2011) reported increase in predator populations after implementation of connectivity between the habitats akin to our study predictions which shows that implementing connectivity leads to larger population size of high quality predators (Figure 20b) and survival time (Figure 22b). Connectivity allowed for movement between the habitats and thus, prey populations often found temporal refuges in neighboring sub-habitats. This provided prey populations an opportunity to recuperate from ongoing over-exploitation by high quality predators in new habitats which might also provide for reproduction (Karsai and Kampis, 2011; Karsai et al. 2016). Hence, it resulted in larger prey population size in subsequent generations as compared to fragmented habitats. This cycle continued over subsequent generations.

It is noteworthy that low quality predators ($Gain_{predator} = 10 – 30$) were not able to gain as much energy from food as high quality predators which led to early deaths of such predators due to hunger. This resulted in smaller population size for low quality or less efficient predators. Hence, in presence of low quality predators, prey population was maintained in larger number (Figure 20a) with higher survival time (Figure 22a).

Effects of Quality Levels of Predators in Coexistence of Identical Prey Population in High Production Environment

The findings from our study show that implementation of non-biased low quality or less efficient predators ($Gain_{predator} = 10 – 30$) in the model system with two identical prey populations ensures higher survivability of both prey populations thus, enhancing coexistence dynamics whereas implementation of non – biased high quality or highly efficient predators ($Gain_{predator} > 30$) effectively reduces their population size to the point of extinction. The results reveal that prey population size flourished when the habitats were comprised of less efficient predators whereas the prey population size decreased as the predators became more efficient (Figure 28). Our observations differed from that of Paine (1964) and Hall et al. (1970) findings that predicted predation solely promotes coexistence by reducing probability for one monopolizing species to out-perform another species. One possible reason for such differences could be that their studies do not take the varying levels of quality or efficiency of predators within the habitats into considerations as we did while we conducted our studies. Also, the difference could result from the fact that we have implemented prey populations with identical life history parameters whereas in their studies there might have been differences between the prey populations.

For this case, our result seems to be similar in some part to Karsai et al. (2016) findings on effects of implementation of non-biased predators on competition. It reported that highly efficient predator populations overexploited the prey populations like our study predictions (Figure 28) where it showed that high quality predators overexploited the prey population resulting in low prey population size. Meanwhile, low quality predators which were weak foragers and not as efficient struggled to forage (Figure 3). Their inability to forage better prevented them from consuming more prey population which in turn further declined their chances to obtain enough energy to reproduce as well (Karsai et al. 2016). This in turn resulted in both identical prey populations coexisting for subsequent generations in larger numbers owing to less efficient predator population whereas the less efficient predator population sustained in smaller size.

Effects of Habitat Patterns in Survival Time of Identical Prey Population in Both High and Low Production Environment

Dynamics Within High Production Environment

The findings from our study show that in high production environment, implementation of fragmented habitats (W3C0) results in higher survival time of both identical prey populations compared to implementation of unfragmented (W0C0) or connected habitats (W3C3). The results we obtained show higher survival times for both prey populations within fragmented habitats (Figure 29) in high production environment. However, those results also suggest that effects of fragmented habitats are influenced by high productivity levels of environment or fast regeneration of producers ($\text{Time}_{\text{regeneration}} = 10$) as well to regulate survival time dynamics.

One of the prominent effects of fragmentation is that there is reduction in size of the habitat patches (Fahrig 2003). This leads to formation of regional metapopulations (Krohne 1997) acting as independent network of small habitat patches (Harrison and Bruna 1999). Hence, the newly formed habitat patches or sub-habitats start to play independent dynamics. The prey and predator population fluctuates heavily within such sub-habitats (Karsai and Kampis 2011). When the prey population in such sub – habitats was exposed to overexploitation by means of predation, it went extinct first. This resulted in predator population going extinct as well. Similarly, there is probability that predator population becomes extinct first owing to the random nature of the model execution process combined with initialization state of the model (Table 2). This became true in case of high quality predators and when this happened, the chances were highly likely that the surviving prey population would utilize the benefits of high production environment in absence of natural predators. With ample food resources and absence of predators, more prey populations could forage and reproduce successfully in subsequent generations as their probability of successful foraging per time step increases (Figure 2). This resulted in high prey survival time for both prey populations (Prey I and Prey II) in fragmented habitats as shown in (Figure 29). In addition to this, it is also possible that fragmentation compounded the effects of this survival time dynamics by discouraging migration of other prey populations from surrounding sub-habitats through lack of dispersal thus, creating stable dynamics where population survival time stayed higher throughout the experiment.

Dynamics Within Low Production Environment

The findings from our study show that in low production environment, implementation of fragmented habitats (W3C0) results in lower survival time of both identical prey populations compared to implementation of unfragmented (W0C0) or connected habitats (W3C3). Fragmented habitats will result in lower survival time for not only prey populations, but for predator populations also. The results we obtained show lower survival times for both prey population and predator population within fragmented habitats (Figure 32; compared to higher production environment, Figure 28) in low production environment. However, those results also suggest that effects of fragmented habitats are influenced by low productivity level of environment or slow regeneration of producers ($\text{Time}_{\text{regeneration}} = 50$) as well to regulate survival time dynamics.

Similar sub-habitat dynamics occurred as explained for high production environment above. However, in this case the prey populations which survived the overexploitation were devoid of opportunities to utilize the benefits of high production environment as the regeneration of producers would take five times as longer compared to high production environment. This reduced the probability for successful foraging per time step (Figure 2). However, during this time, the prey population still had to forage at a cost of their limited energy reserves. As it took longer for them to replenish the energy level, they eventually died out due to hunger (Figure 2) resulting in low survival time for both prey populations (Prey I and Prey II) as shown in (Figure 32). In addition to this, it is also possible that fragmentation in the case of low productivity compounded the effects of this survival time dynamics by discouraging possible escape of prey populations to neighboring habitat patches with probability of more resources thus, creating stable dynamics where the prey survival time stayed lower throughout the experiment.

Real World Implications

One of the previous agent-based model study conducted on connected fragmented habitats facilitating coexistence dynamics between prey – predator populations by (Karsai and Kampis 2011) inspired the experimental study conducted by (Cooper et al. 2012) in simple but real ecosystems with real prey – predator system (*Paramecium – Didinium*). This protozoan prey – predator study even relates to the one performed by Gause (1934) but the interesting fact here is that not only its authors were inspired by the theoretical model work by Karsai and Kampis (2011), but also the experimental real ecosystem by Cooper et al. (2012) behaved as predicted by the model of Karsai and Kampis (2011). For example, some of the results of the real ecosystem study conducted by Cooper et al. (2012) showed that reduced habitat size through increased level of fragmentation or increased patchiness of the habitats increased extinction probability which meant that smaller fragments hosted smaller populations which became more prone to stochastic extinctions. It also showed that predator populations became more asynchronous as the level of fragmentation of the habitats were increased like the study performed by Karsai and Kampis (2011).

The findings of our research work express coexistence of prey – predator populations as combined function of regeneration time of producers, type of habitats and quality levels of predators. Our work points towards corridor connectivity as a possible method to mitigate the negative effects of fragmentation of wildlife populations caused by constructions of roads, highways, ditches and fences which could be beneficial for overall prey – predator populations; especially for highly efficient predator populations. Importance of wildlife crossing structures has been emphasized in the past studies such as usage of open crossing structures or overpass by Grizzly Bears (Sawaya et al. 2013) and wildlife crossing structures enhancing the viability of wildlife populations in Banff National Park (Clevenger and Sawaya 2010). Similarly, Damschen et al. (2014) showed habitat corridors affecting wind dynamics and seed dispersal; thus, positively impacting the species richness of wind-dispersed plants in such habitats. Our agent-based model study not only relates to these experimental studies but also adds to the idea that connectivity could further lead to successful coexistence of prey – predator populations.

CHAPTER 5

CONCLUSIONS

We have presented a novel approach to predict several emergent coexistence dynamics occurring between prey – predator populations within connected and fragmented habitats under various productivity levels of the environment by using simplistic and abstract agent-based model. By varying levels of studied parameters such as regeneration times of producers, different habitat types and quality levels of predators, our model revealed the significant impacts of such parameters in prey – predators' population size and survivorship. Increasing level of connectivity stabilized prey – predator populations and led to increased survivorship. Establishing connectivity also helped to maintain high-quality predator population in larger numbers. In absence of predation, the coexistence of two types of prey populations with identical life history parameters was more probable in connected habitats. The interactions between competition and predation was such that low-quality predators helped maintain both competing prey populations in larger numbers whereas high-quality predators overexploited the competing prey populations unlike the popular notion that overall predation helps in coexistence dynamics by limiting the population of better competitors. Similarly, fragmented habitats supported larger competing prey population size in high-productive environment whereas unfragmented and connected habitats supported larger competing prey population size in low-productive environment. It was also observed that connected habitats were better than fragmented habitats in supporting robust predator population across entire levels of productivity of environment.

Our goals here, besides informing about possible environmental significance of our work, is also to acknowledge the contribution that agent-based modeling could make as a unique and strong platform to facilitate study of complex ecological phenomena by assisting the experimental and theoretical ecological studies while seeking possibilities of informatics in ecology owing to myriad of data that can be generated using such agent-based models. It must be borne in mind that this study comprises of very simple agents, environments and their interactions and we acknowledge the fact that the model has been ideally kept very simple to achieve our goal of studying the patterns of bottom – up emergent dynamics of coexistence in-silico. Further research could incorporate the use of evolutionary algorithms to make agents capable of learning from previous experiences enhancing their sensing and predictions abilities of their surroundings which could reveal more about the coexistence dynamics.

REFERENCES

Abrahamson, D, Wilensky, U. (2004). NetLogo Random Basic model. Center for Connected Learning and Computer-Based Modeling, Northwestern Institute on Complex Systems, Northwestern University, Evanston, IL.

Aguirre A, Dirzo R. 2008. Effects of fragmentation on pollinator abundance and fruit set of an abundant understory palm in a Mexican tropical forest. Biol. Conserv. 141:375–384.

Ament R, Callahan R, McClure M, Reuling M, Tabor G. 2014. Wildlife Connectivity: Fundamentals for Conservation Action. :41.

Andrieu E, Dornier A, Rouifed S, Schatz B, Cheptou PO. 2009. The town Crepis and the country Crepis: How does fragmentation affect a plant-pollinator interaction? Acta Oecologica 35:1–7.

Armstrong RA, McGehee R. 1980. Competitive Exclusion. Am. Nat. 115:151–170.

Auyang SY. 1998.Foundatioins of Complex-system Theories in Economics, Evolutionary Biology, and Statistical Physics.Cambridge University Press. 2 - 174 p.

Ayala FJ. 1970. Competition, Coexistence, and Evolution. :130–136.

Bacaer, Nicholas. 2011. A Short History of Mathematical Population Dynamics.Spring-Verlag London.31-41 p.

Bayne EM, Boutin S, Moses RA. 2008. Ecological factors influencing the spatial pattern of Canada lynx relative to its southern range edge in Alberta, Canada. Can. J. Zool. 86:1189–1197.

Beier P. 1993. Determining Minimum Habitat Areas and Habitat Corridors for Cougars.

Conserv. Biol. 7:94–108.

Beier P, Noss RF. 1998. Do Habitat Corridors Provide Connectivity? Conserv. Biol. 12:1241–1252.

Bender DJ, Contreras TA, Fahrig L. 1998. Habitat loss and population decline: A meta-analysis of the patch size effect. Ecology 79:517–533.

Blackburn HB, Hobbs NT, Detling JK. 2011. Nonlinear responses to food availability shape effects of habitat fragmentation on consumers. Ecol. Soc. Am. 92:98–107.

Borshchev A, Filippov A. 2004. From System Dynamics to Agent Based Modeling. Simulation 66:25–29.

Brudvig LA, Damschen EI, Haddad NM, Levey DJ, Tewksbury JJ. 2015. The influence of habitat fragmentation on multiple plant-animal interactions and plant reproduction. Ecology 96:2669–2678.

Brudvig LA, Wagner SA, Damschen EI. 2012. Corridors promote fire via connectivity and edge effects. Ecol. Appl. 22:937–946.

Castiglione, F.2006.Agent Based Modeling.Scholarpedia, 1(10):1562.

Caswell H. 1978. Predator-Mediated Coexistence : A Nonequilibrium Model. Am. Nat. 112:127–154.

Chase JM, Abrams PA, Grover JP, Diehl S, Chesson P, Holt RD, Richards SA, Nisbet RM, Case TJ. 2002. The interaction between predation and competition: A review and synthesis. Ecol. Lett. 5:302–315.

Clevenger, Sawaya M. 2010. Piloting a non invasive genetic sampling method for evaluating population level benefits of wildlife crossing structures. Ecol. Soc. 15

Cooper JK, Li J, Montagnes DJS. 2012. Intermediate fragmentation per se provides stable predator-prey metapopulation dynamics. Ecol. Lett. 15:856–863.

Damschen EI, Baker DV, Bohrer G, Nathan R, Orrock JL, Turner JR, Brudvig LA, Haddad NM, Levey DJ, Tewksbury JJ. 2014. How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. Proc. Natl. Acad. Sci. 111:3484–3489.

DeAngelis DL, Grimm V. 2014. Individual-based models in ecology after four decades. F1000Prime Rep. 6:39.

DeAngelis DL, Mooij WM. 2005. Individual-Based Modeling of Ecological and Evolutionary Processes. Annu. Rev. Ecol. Evol. Syst. 36:147–168.

Dmowski K, Kozakiewicz M. 1990. Influence of a shrub corridor on movements of passerine birds to a lake littoral zone. Landsc. Ecol. 4:99–108.

Epstein JM, Axtell R. 1996. Growing Artificial Societies. Brookings Institution Press (D.C). 2 - 26 p.

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. Annu Rev Ecol Evol Syst 34:487–515.

Fahrig L. 2014. Relative Effects of Habitat Loss and Fragmentation on Population. 61:603–610.

Fahrig L, Merriam G. 1985. Habitat Patch Connectivity and Population Survival Author. Ecol. Soc. Am. 66:1762–1768.

Fahrig L, Merriam G. 1994. Conservation of fragmented populations. Conserv. Biol. 8:50–59.

Fargione J, Tilman DG. 2002. Competition and coexistence in terrestrial plants. Compet. coexistence:165–206.

Fischer J, Lindenmayer DB. 2007. Landscape modification and habitat fragmentation: a synthesis. Glob. Ecol. Biogeogr. 16:265–280.

Franklin AB, Noon BR, George TL. 2002. What is habitat fragmentation? Stud. Avian Biol. 25:20–29.

Garcia EA, Mittelbach GG. 2008. Regional Coexistence and Local Dominance in Chaoborus : Species Sorting along a Predation Gradient. Ecol. Soc. Am. 89:1703–1713.

Gliwicz ZM, Wrzosek D. 2008. Predation-Mediated Coexistence of Large- and Small-Bodied Daphnia at Different Food Levels. Am. Nat. 172:358–374.

Grimm V, Berger U, DeAngelis DL, Polhill JG, Giske J, Railsback SF. 2010. The ODD protocol: A review and first update. Ecol. Modell. 221:2760–2768.

Grimm V, Revilla E, Berger U, Jeltsch F, Mooij WM, Railsback SF, Thulke H-H, Weiner J, Wiegand T, DeAngelis DL. 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. Science (80-.). 310:987–991.

Gurevitch J, Morrison JA, Hedges L V. 2000. The Interaction between Competition and Predation: A Meta-analysis of Field Experiments. Am. Nat. 155:435–453.

Haddad NM. 1999. Corridor and Distance Effects on Interpatch Movements: A Landscape Experiment with Butterflies. Ecological Applications, Vol. 9, No.2 (May,1999), pp. 612-622

Hall DJ, Cooper E, Werner EE. 1970. LIMNOLOGY AND OCEANOGRAPHY

Hardin G. 1960. The Competitive Exclusion Principle. 131.

Harrison S, Bruna E. 1999. Habitat fragmentation and large-scale conservation: what do we know for sure? Ecography (Cop.). 22:225–232.

Holyoak M, Lawler SP. 1996. The Role of Dispersal in Predator--Prey Metapopulation Dynamics. J. Anim. Ecol. 65:640–652.

Jungck J. 1997. Ten equations that changed biology. Bioscene 23:11–36.

Kalmykov L V, Kalmykov VL. 2012. A mechanistic verification of the competitive exclusion principle. :1–31.

Karsai I, Kampis G. 2011. Connected fragmented habitats facilitate stable coexistence dynamics. Ecol. Modell. 222:447–455.

Karsai I, Montano E, Schmickl T. 2016. Bottom-up ecology: an agent-based model on the interactions between competition and predation. Http://Dx.Doi.Org/10.1080/23737867.2016.1217756 3:1–20.

Krohne DT. 1997. Dynamics of metapopulations of small mammals. Am. Soc. Mammal. 78:1014–1026.

Krohne DT. 2001. General Ecology. Second Edition. Pacific Grove (CA). 137 - 139 p.

Krohne DT. 2001. General Ecology. Second Edition. Pacific Grove (CA). 228 - 232 p.

Krohne DT. 2001. General Ecology. Second Edition. Pacific Grove (CA). 245 p.

Krohne DT. 2001. General Ecology. Second Edition. Pacific Grove (CA). 252 - 254 p.

Krohne DT. 2001. General Ecology. Second Edition. Pacific Grove (CA). 256 p.

Krohne DT. 2001. General Ecology. Second Edition. Pacific Grove (CA). 261 p.

Krohne DT. 2001. General Ecology. Second Edition. Pacific Grove (CA). 420 p.

Levey DJ, Bolker BM, Tewksbury JJ, Sargent S, Haddad NM. 2005. Effects of landscape corridors on seed dispersal by birds. Science 309:146–8.

Levin SA. 1970. Community Equilibria and Stability, and an Extension of the Competitive Exclusion Principle. Am. Nat. 104:413–423.

MacArthur RH. 1958. Population Ecology of Some Warblers of Northeastern Coniferous Forests. Ecology 39:599–619.

MacArthur RH, Wilson EO. 1967. The Theory of Island Biogeography. Princeton, NJ: Princeton Univ. Press

Moilanen A, Hanski I. 2001. On the use of connectivity measures in spatial ecology. Oikos 95:147–151.

Murcia C. 1995. Edge effects in fragmented forests: implications for conservation. Trends Ecol. Evol. 10:58–62.

Neill C, Daufresne T, Jones CG. 2009. A competitive coexistence principle? Oikos 118:1570–1578.

Paine RT. 1966. Food Web Complexity and Species Diversity. Am. Nat. 100:65–75.

Pierce JE, Larsen RT, Flinders JT, Whiting JC. 2011. Fragmentation of sagebrush communities: Does an increase in habitat edge impact pygmy rabbits? Anim. Conserv. 14:314–321.

Polhill JG, Parker DC, Brown DG, Grimm V. 2008. Using the ODD protocol for comparing three agent-based social simulation models of land use change. JASSS - J. Artif. Soc. Soc. Simul. 11:Article Number 3.

La Polla VN, Barrett GW. 1993. Effects of corridor width and presenece on the population dynamics of the meadow vole (Microtus pennsylvanicus). Landsc. Ecol. 8:25–37.

Powell AH, Powell GVN. 1987. Population Dynamics of Male Euglossine Bees in Amazonian Forest Fragments Published by : The Association for Tropical Biology and Conservation Stable URL : http://www.jstor.org/stable/2388742. Biotropica 19:176–179.

Prugh LR. 2017. An Evaluation of Patch Connectivity Measures Author (s): Laura R . Prugh Published by : Wiley on behalf of the Ecological Society of America Stable URL : http://www.jstor.org/stable/40347271 REFERENCES Linked references are available on JSTOR for this a. 19:1300–1310.

Rathcke B, Jules ES. 1993. Habitat Fragmentation and Plant Pollinator Interactions. Curr. Sci. 65:273–277.

Rayfield B, Pelletier D, Dumitru M, Cardille JA, Gonzalez A. 2016. Multipurpose habitat networks for short-range and long-range connectivity: A new method combining graph and circuit connectivity. Methods Ecol. Evol. 7:222–231.

Resasco J, Haddad NM, Orrock JL, Shoemaker D, Brudvig LA, Damschen EI, Tewksbury JJ, Levey DJ. 2014. Landscape corridors can increase invasion by an exotic species and reduce diversity of native species. Ecology 95:2033–2039.

Rosenberg DK, Noon BR, Meslow CE. 1997. Biological Corridors : Form, Function, and Efficacy - Linear conservation areas may function as biological corridors, but they may not mitigate against additional habitat loss. Bioscience 47:677–687.

Rosenberg DK, Noon BR, Meslow EC. 1997. Biological Corridors: Form, Function, and Efficacy. Bioscience 47:677–687.

Salau K, Schoon ML, Baggio JA, Janssen MA. 2012. Varying effects of connectivity and dispersal on interacting species dynamics. Ecol. Modell. 242:81–91.

Sawaya MA, Clevenger AP, Kalinowski ST. 2013. Demographic connectivity for ursid populations at wildlife crossing structures in banff national park. Conserv. Biol. 27:721–730.

Schmickl T, Karsai I. 2010. The interplay of sex ratio, male success and density-independent mortality affects population dynamics. Ecol. Modell. 221:1089–1097.

Schweiger EW, Diffendorfer JE, Holt RD, Pierotti R, Michael S. 2000. The Interaction of Habitat Fragmentation , Plant , and Small Mammal Succession in an Old Field Ecol. Monogr. 70:383–400.

Shurin JB, Allen EG. 2001. Effects of competition, predation, and dispersal on species richness at local and regional scales. Am. Nat. 158:624–637.

Squires JR, DeCesare NJ, Olson LE, Kolbe JA, Hebblewhite M, Parks SA. 2013. Combining resource selection and movement behavior to predict corridors for Canada lynx at their southern range periphery. Biol. Conserv. 157:187–195.

Taylor PPD, Fahrig L, With KK a. 2006. Landscape connectivity: a return to the basics. Connect. Conserv.:29–43.

Tilman D. 1980. Resources: A Graphical-Mechanistic Approach to Competition and Predation.

Am. Nat. 116:362–393.

Tischendorf L, Fahrig L. 2000. On the usage and measurement of landscape connectivity. Oikos 90:7–19.

Vance RR. 1984. The Effect of Dispersal on Population Stability in One-Species , Discrete-Space Population Growth Models.The American Naturalist, Vol.12, No.2 (Feb, 1984), pp. 230-254 Published by : The University of C. Am. Nat. 123:230–254.

Vasudev D, Fletcher RJ, Goswami VR, Krishnadas M. 2015. From dispersal constraints to landscape connectivity: Lessons from species distribution modeling. Ecography (Cop.). 38:967–978.

Wangersky PJ. 1978. Lotka-Volterra Population Models. 9:189–218.

Watkins A, Noble J, Doncaster CP. 2011. An agent-based model of jaguar movement through conservation corridors. Adv. Artif. Life, ECAL 2011 Proc. 11th Eur. Conf. Synth. Simul. Living Syst.:846–853.

Wilensky, U. (1999). NetLogo. Center for Connected Learning and Computer-Based Modeling, Northwestern University, Evanston, IL. http://ccl.northwestern.edu/netlogo/

Wu J. 2009. Ecological Dynamics in Fragmented Landscapes. Pricet. Guid. to Ecol.:438–444.

Xu W, Ouyang Z, Vina A, Zheng H, Liu J, Xiao Y. 2006. Designing a conservation plan for protecting the habitat for giant pandas in the Qionglai mountain range, China. Divers. Distrib. 12:610–619.

APPENDICES

APPENDIX A

3D Surface plots of Prey populations as a function of varying regeneration times, habitat types and quality levels of predator populations

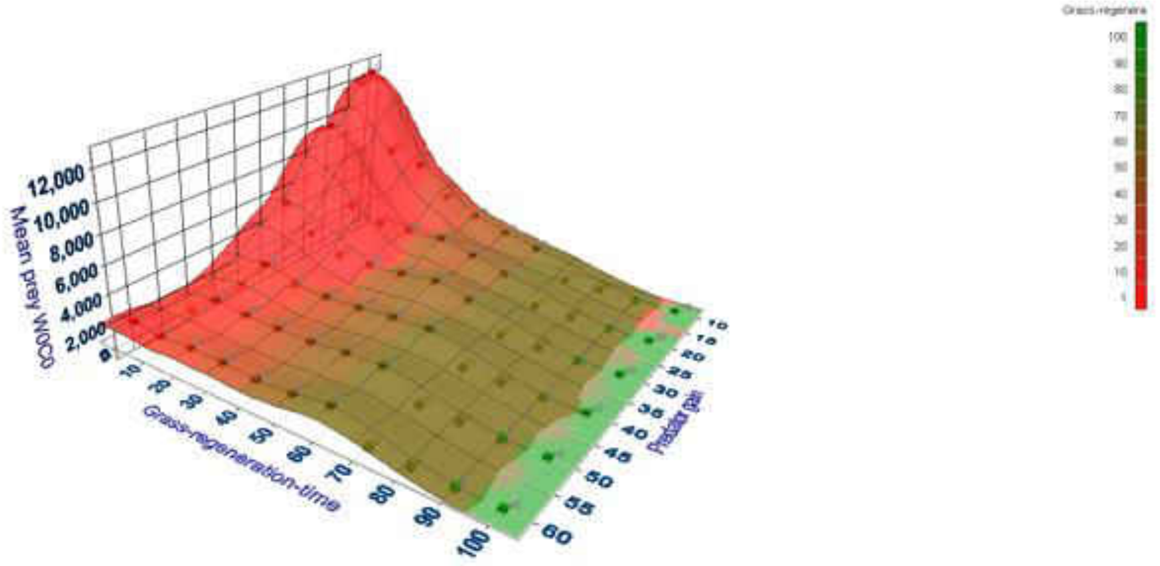

Figure 33. A 3D surface plot showing the Prey populations at varying regeneration times and predator quality levels in an unfragmented habitat (W0C0); fragmentation level (W) = 0 and connectivity (C) = 0.

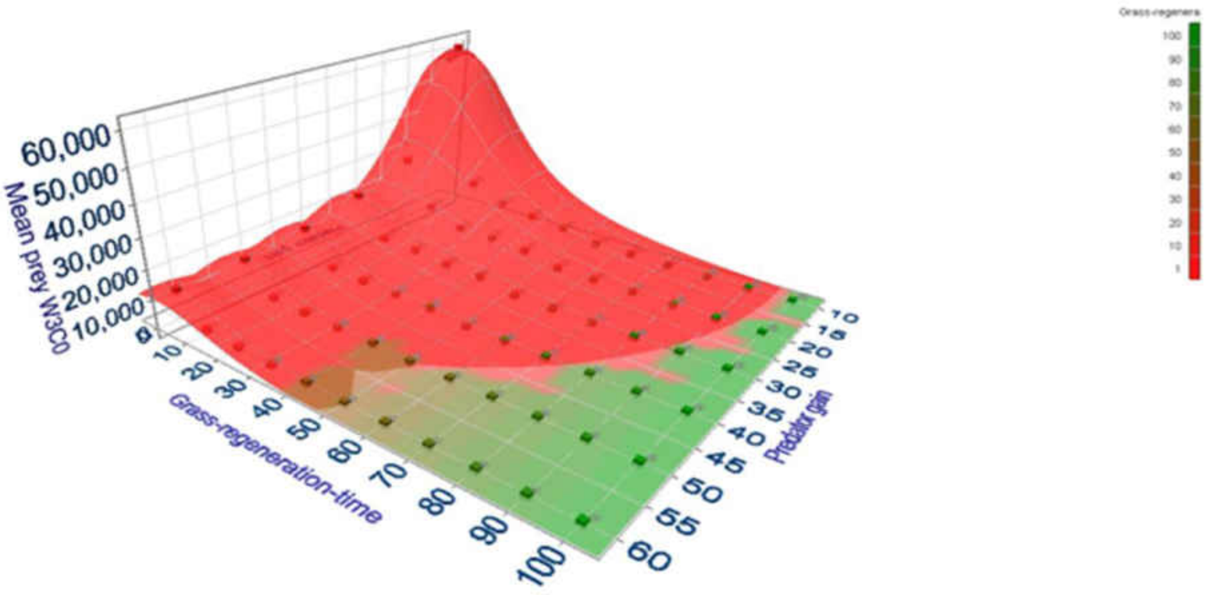

Figure 34. A 3D surface plot showing the Prey populations at varying regeneration times and predator quality levels in a fragmented habitat without connectivity (W3C0); fragmentation level (W) = 3 and connectivity (C) = 0.

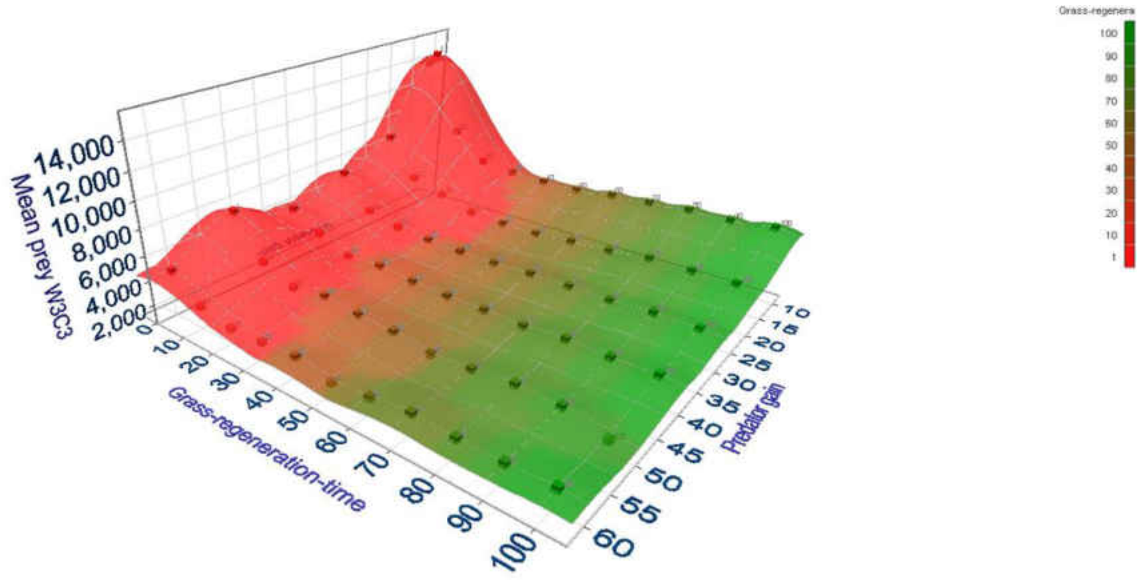

Figure 35. A 3D surface plot showing the Prey populations at varying regeneration times and predator quality levels in a fragmented and connected habitat (W3C3); fragmentation level (W) = 3 and connectivity (C) = 3.

APPENDIX B

3D Surface plots of Predator populations as a function of varying regeneration times, habitat types and their quality levels

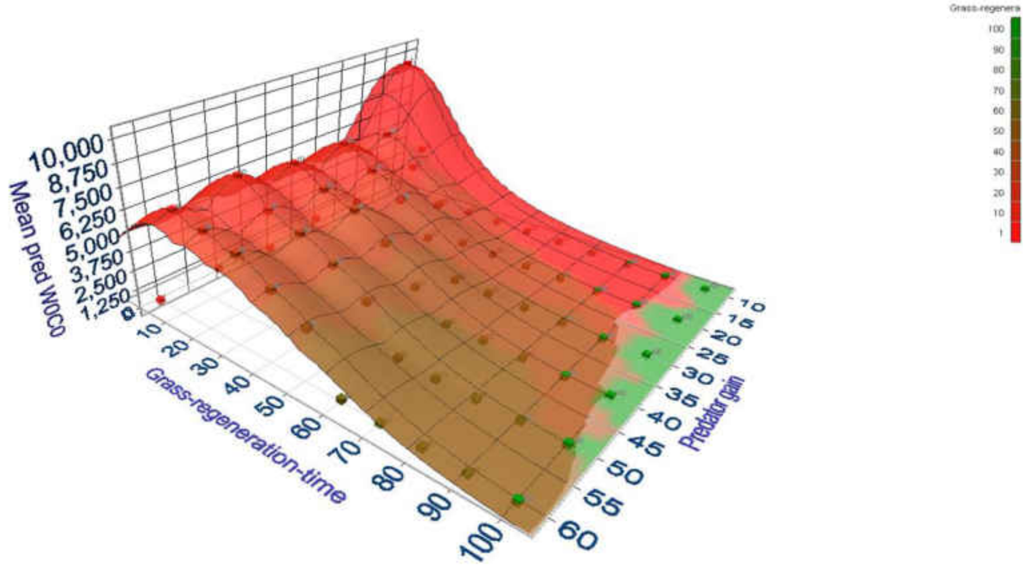

Figure 36. A 3D surface plot showing the Predator populations at varying regeneration times and their quality levels in an unfragmented habitat (W0C0); fragmentation level (W) = 0 and connectivity (C) = 0.

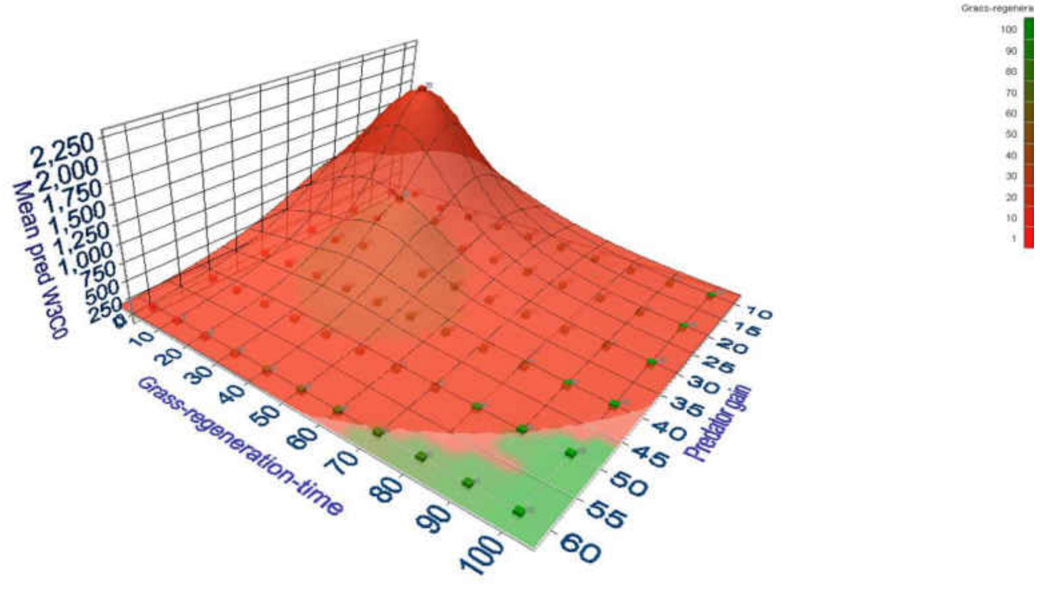

Figure 37. A 3D surface plot showing the Predator populations at varying regeneration times and their quality levels in a fragmented habitat without connectivity (W3C0); fragmentation level (W) = 3 and connectivity (C) = 0.

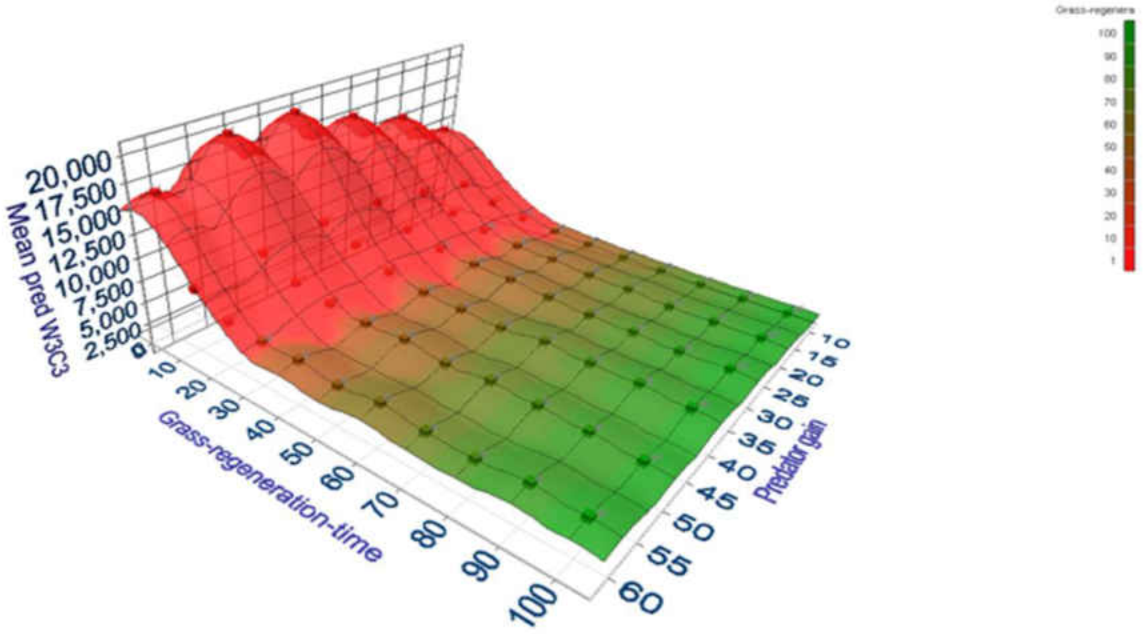

Figure 38. A 3D surface plot showing the Predator population at varying regeneration times and their quality levels in a fragmented and connected habitat (W3C3); fragmentation level (W) = 3 and connectivity (C) = 3.

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