Developing and Testing Methods to Assess Species Extinction Risk and Ecosystem Degeneration

by

Xiaofeng Ruan

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Department of Renewable Resources
University of Alberta

Abstract

Species worldwide are becoming increasingly threatened due to the rapid changes in climate and land use induced by human activities. The loss of species threatens the provision of food, goods and many other ecosystem services essential to the sustainability and well-being of human society. It is therefore important to monitor, assess and predict the loss of biodiversity at both the species and ecosystem levels so the need for any intervention can be determined. A major challenge to this task is a lack of consistent and scale-independent evaluation methods. My thesis strives to address this gap by testing some currently available methods and proposing improved ones to assess the endangerment status of species and the degeneration of ecosystems.

In chapter two, I derived a model to estimate the loss of species abundance based on both the area of occupancy and spatial autocorrelation of occupied cells. This new model performed generally better in predictive power than an existing area-based model. In chapter three, I tested a spatial analysis tool, called a scalogram, for assessing the impact of disturbance on species extinction. Scalograms describe how the value of a metric changes with spatial scale (e.g., grain size) following some simple relationship, such as a power-law or a simple linear equation. I showed that it is feasible to estimate species extinction risk by analyzing the change in landscape metrics over spatial scales. In chapter four, I tested the hypothesis that the collapse of the power-law patch-size distribution could signal an early warning for ecosystem degeneration (i.e., desertification of grassland). I found that a power-law patch-size distribution was dependent on a species' abundance, spatial

aggregation and the spatial scale of analysis. All three factors could cause the patch-size distribution to deflect from the power-law model. Thus, I concluded that the power-law model was not suitable for indicating ecosystem degeneration.

Understanding status of endangered-species and ecosystem degeneration is profoundly important in biological conservation. Methods developed in my thesis provide potentially useful tools for assessing extinction risk in the real world. The applications of these methods are expected to contribute to the study, legislation and practice in landscape management and biological conservation.

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Chapter 1: Introduction

1.1 Research background

Species extinction is probably one of the few ecological terms ingrained in our minds since childhood. When a kid is staring at the skeleton of a dinosaur in a museum, or watching the movie *Jurassic Park* in the theatre, they are already touched by species extinction. In the scientific field, the extinction of species has been attracting ecologists' attention for centuries. In the late 1850s, Charles Darwin (1859) stated his view of species extinction: "species and groups of species gradually disappear, one after another, first from one spot, then from another, and finally from the world."

1.1.1 Why species extinction matters

Species extinction inevitably leads to the abatement of biodiversity, which is integral to human civilization. Loss of species usually have detrimental impacts on productivity, reducing the basic supply of crops, domestic animals, fibers, medicines, and other daily necessities for human societies (Tilman 2000; Cardinale et al. 2012). It also affects many other essential ecosystem services, such as biogeochemical cycles (Ewel et al. 1991; Hooper and Vitousek 1998), air and water purification (Bolund and Hunhammar 1999; Boulton et al. 2008), climate regulation (Lovelock and Kump 1994; Harding and Lovelock 1996), pest and disease control (Roelfs 1988; Altieri 1999), barriers to biological invasion (Kennedy et al. 2002; Tilman 1997), and resistance and resilience to perturbation (Naeem and Li 1997; McCann 2000).

Furthermore, loss of species severs our connection to nature and history: species inspire songs, stories, dances, poetry, and festivals (Alonso et al. 2001; Wheeler et al. 2012). Certain rare species, such as the pandas in China, are the treasures of these nations, and their extinction would hurt the national prides of these countries.

1.1.2 Major topics in studying species extinction

There are numerous studies addressing issue of species extinction. By choosing ‘species extinction’ as a key word in the ‘Web of Science’ database, one can find more than 113,200 articles that had been published by the end of 2015. In this introduction, I provide a broad context by illustrating three relevant topics.

Identifying the causes of species extinction

Based on the fossil record, it is generally accepted that five mass extinctions have occurred since the Cambrian Period (~540 million years ago). These rapid and worldwide decreases in the number of life forms on the planet happened during the End Ordovician, Late Devonian, End Permian, End Triassic and End Cretaceous periods (Raup and Sepkoski 1982; Labandeira and Sepkoski 1993; Macleod et al. 1997; McElwain and Punyasena 2007; Alroy 2008). The natural events associated with causing these mass extinctions include climate warming, sea-level falls associate with glaciations and asteroid impacts (Grieve and Cintala 1993; Wignall 2001; Morgan et al. 2006; Peters 2008; Barnosky et al. 2011).

The rate of species extinction today is much higher than the average extinction rate over evolutionary time, and the major causes documented in the literature include climate change, habitat loss, pollution, over-hunting/egg collecting, species invasion, and interactions between these (Diamond 1989; Tilman et al. 1994; Vitousek et al. 1997, Mace et al. 2008).

Estimating species extinction rates

Although over 99.9 % of species that ever existed are thought to be already extinct, the background extinction rate is relatively even, at 0.0001-0.00001% per year or 1-10 species per year based on fossil records (Raup 1991). Surprisingly, the near-term extinction rate is estimated to be 1,000 to 10,000 times higher than the background rate (Primm et al 1995; Dirzo and Raven 2003; MEA 2005). Some scientists, therefore, believe that we are currently in the midst of a human-caused mass extinction that differs from the previous five natural mass extinctions (Dirzo and Raven 2003; Barnosky et al. 2011).

However, precise contemporary extinction rates are unknown and there are many methodological difficulties in their estimation. For example, the number of species extinctions predicted from the power-law species-area relationship are often higher than the ones being actually observed (May and Lawton 1995; Rosenzweig 1995). The concept of the extinction debt has been a common explanation for this overestimation, stating that the fewer individuals still alive after the habitat is destroyed do not form a viable population, and that a time lag occurs between species extinction and habitat loss (Tilman et al. 1994). Recently, He and Hubbell (2011) showed that the discrepancy between the predicted and observed extinctions actually arises mathematically from the use of the power-law species-area curve when species are not randomly distributed in nature. By comparing estimated extinctions using the species- and endemics-area curves and testing in 10 datasets across the world, they found that the resulting overestimation of species extinctions could be higher than 160%.

Assessing species extinction risk

Globally the International Union for Conservation of Nature (IUCN) Red List of Threatened Species is the most widely adopted and comprehensive system for the assessment of species extinction risk (IUCN-SSC 2004; Mace et al. 2008). The outline of the system was proposed by Mace and Lande (1991), and through a continuing process of review, redevelopment, and further review, the Red List system has become more reliable and widely accepted since 2001 (Mace et al. 2008). At the heart of the IUCN Red List system is the five endangerment assessment criteria that determine the risk category based on the reduction in population size and the spatial extent of species occurrence. A species that meets at least one of the five criteria is placed in a threatened category. For example, according to Criterion A, a species is considered as Vulnerable, Endangered, or Critically Endangered if its population size decreases, respectively, by 30, 50 or 80% within 10 years or three generations, whichever is longer (IUCN-SSC 2010). By Criterion B, the endangerment status of a species is determined by the reduction in the area of its occupancy.

The IUCN criteria have been adopted for assessing a diverse range of taxonomic groups over different temporal and spatial scales. Both population- and range-size based methods are well-suited for the studies of birds, marine and freshwater species (Knapp et al. 2011; Verreycken et al. 2014); population-size-based methods are the primary criterion for the vast majority of mammal species (Clausnitzer et al. 2009; Molnar et al. 2010; Rozylowicz and Dobre 2010; Tyler 2010; Wittmer et al. 2010; Wittemyer et al. 2013; Mosnier et al. 2015; Srivathsa et al. 2015); while range-size-based methods are more suitable for insects (Adriaens et al. 2014), amphibians, reptiles, and plants (Clausnitzer et al. 2009; Rakotoarinivo et al. 2014; Rossi et al. 2014; Brummitt et al. 2015; Garavito et al. 2015). For different spatial scales, range-size based methods are more suitable to national, continental or global distribution of species (La Sorte and Jetz 2010; Comeros-Raynal et al 2012; Brace et al. 2014; Puri et al. 2015), while population-size-based methods are widely considered in relatively small sample plots (Lewis and Senior 2011; Song et al. 2013; Nourani et al. 2015). Also, range-size-based methods are the predominant approach for assessing long-term data, especially deriving from fossil records (Grund et al. 2012; Tietje and Kiessling 2013; Dunhill and Wills 2015; Saupe et al. 2015).

The IUCN criteria have fuelled the expansion of the knowledge of species endangerment status for a wide array of taxonomic groups. Hoffman et al. (2010) reviewed the current endangerment status of the world’s vertebrates, and found that 13%, 21%, and 30% of birds, mammals, and amphibians were assigned as threatened, respectively. Collen et al. (2014) showed that approximately 20% of freshwater species were purportedly at risk. Davies and Baum (2012) found that 13.5% of assessed marine species were placed in the category of threatened species.

1.1.3 Gaps and issues in current methods

The discrepancy between population- and range-size-based methods

Although population-size-based methods are biologically more justifiable, long-term data on population size at biogeographic scales are rarely available for many, if not most, species. In contrast, data on the area of occupancy are relatively easy to obtain but range-size-based criteria are more arbitrary and lack biotic justification. Also, there is a wealth of empirical evidence that the endangerment status result based on one criterion may contrast strikingly with that using others. For instance, Fox et al. (2011) found that distribution data may underestimate the extinction risk of butterflies at 10×10 km scale. The authors recommended that the appropriate grain size for studying the spatial patterns of butterflies was 2×2 km. However, in a case study on plant species, Abeli et al. (2009) found to the contrary, showing that range-size-based methods overestimated endangerment status because of the restricted distribution of the target plant species.

Two main issues emerging from the above examples are: 1) discrepancy between the population-size based and the range-size based methods, and 2) dependence of the result on the scale of measurement. A solution to the first issue is introduced in the following paragraph, and the scale-dependence issue is discussed below this.

To address the discrepancy between the two major endangerment criteria, He (2012) derived a model making explicit the link between the area of a species' occurrence map and the loss of abundance. The model assumes that the spatial distribution of the study species remains unchanged before and after disturbance. This assumption is an approximation. In reality, the spatial patterns may vary due to the nature of different disturbances, and therefore, additional parameters are needed to take account of the changes in spatial patterns. Thus, in this thesis, I derived a new model to assess a species extinction risk by integrating the criteria A and B in the IUCN system and also considering the autocorrelation in species' spatial distribution.

The scale dependence of the measurement

The range size criteria of the IUCN system, along with a number of other landscape metrics, have been widely accepted in biodiversity assessments (reviewed in Uuemaa et al. 2009). Particular to the group of organisms on which my thesis mainly focuses, Burton and Samuelson (2008) and Hernandez-Stefanoni and Dupuy (2008) found that woody species richness and abundance were closely associated with high proportion of forest cover. Additionally, Moser et al. (2002) and Kumar et al. (2006) showed that forest edge length and edge density enhanced vascular plant species richness, and that forest fragmentation promoted the establishment of pioneer species. However, as shown in the case of butterflies by Fox et al. (2011), spatial patterns are largely subject to the scale of observation, which is one of the major concerns in landscape ecology (Gardner et al. 1987; Wiens 1989; Levin 1992; Wu and Loucks 1995). The scale-dependence issue leaves ecologists needing to use a great deal of personal discretion concerning how they interpret and compare patterns obtained at different spatial scales.

In a series of systematic studies, landscape ecologists found that the behavior of some commonly used landscape metrics (i.e., number of patches, edge length, and mean patch size) showed predictable patterns when presented in scalograms—plots that reveal the dependence of landscape metrics on the grid size of measurement. Moreover, these patterns could be described by simple linear, power-law or exponential functions (Wu et al. 2002; Wu 2004; Shen et al. 2004). Following this line of research, I extended these scaling relationships by linking changes in scalograms with species extinction risk. My approach is more general and scale-independent than other multiscale analyses, which can lead to controversial results as shown in the aforementioned case study on butterflies (Fox et al. 2011).

Methods for assessing the degeneration of ecosystem

The elevated current species extinction rate may lead to the loss of biodiversity at both species and ecosystem level. Rodriguez. et al. (2011) and Keith et al. (2013) independently modified and redeveloped the IUCN's criteria for assessing the degeneration of ecosystems based mainly on the distribution range of ecosystems. In one related but distinct research field—bifurcation and chaos—many indices have been put forward to predict the onset of ecosystem degeneration, including recovery time and length, spatial and temporal correlation and variance of species abundance/coverage (Wilssel 1984; Verarrt et al. 2012; Carpenter et al. 2011; Drake et al. 2010; Dai et al. 2013; also see review papers in Scheffer et al. 2009; Scheffer et al. 2013). However, one disadvantage of these quantities is that they are time and labor-intensive measures. As a more practical alternative, Kefi et al. (2007) hypothesized that any deviation in the empirical patch-size distribution of vegetation from the power-law model was indicative of ecosystem degeneration.

Many researchers have however, been critical of Kefi et al.'s (2007) method. For instance, Maestre and Escudero (2009) and Weerman et al. (2012) showed that a truncated power-law model was a better alternative to the power-law in describing patch-size distributions of perennial vegetation and diatom biofilms with no recent disturbance. The ongoing debate indicates that power-law behaviour is unlikely to be universal but is dependent on the circumstances from which the data arise. One unanswered question likely to be crucial to the debate is whether the power-law is robust to changes in abundance, spatial aggregation and spatial scales.

1. 2 Research Objectives

The rate at which humans have been altering the global ecosystem makes the loss of biodiversity one of the world's most pressing crises. Thus, understanding the endangerment status of species and ecosystems is central to conservation planning and sustainable development. Although much effort has been devoted to developing practical methods for assessing species extinction risk and ecosystem degeneration, important issues remain unsolved including (though not limited to) discrepancies in implied endangerment status among different criteria; and, uncertainties in the scale dependence of different measures used to assess landscape condition.

A desirable method to replace existing approaches would be adequately simple and consistent for use in assessing a wide array of taxonomic groups over different spatial and temporal scales. The central theme of my thesis is to test existing methods for this potential and to develop new approaches for assessing species extinction risk and ecosystem degeneration. The remainder of my thesis is organized as follows.

In chapter two, the species' endangerment status is assessed based on the use of occurrence maps. I derived a model by incorporating the changes in range sizes and spatial autocorrelation. This newly derived model was compared with He's (2012) area-based model at multiple scales by both simulation and empirical data and showed improved performance.

In chapter three, the endangerment status of species is assessed by the use of scalograms of landscape metrics, which are formed by progressively computing the values of each metric over a spectrum of scales. The results indicated that the use of scalograms is a promising avenue to address the scale-dependence issue in assessing species extinction risk based on occurrence maps. Particularly, the scalograms of number of patches and edge length had the strongest predictive power among all the selected landscape metrics.

In chapter four, the use of the power-law model for predicting ecosystem degeneration was carefully examined. I comprehensively tested the effects of scale, abundance and spatial aggregation on the spatial patterns observed. The results showed that the power-law distribution was sensitive to all the three factors, and that the deviation of patch-size distribution from the power-law could be triggered by intrinsic characteristics of spatial patterns (i.e., abundance and spatial aggregation) as well as changing spatial scales.

The augmented methods developed in my thesis are practical in application, and provide promising tools to assess species extinction risk in disturbed environments. These methods can also lead to considerable savings in labor, cost and time required to achieve biological conservation and can inform interventions designed to prevent further loss of biodiversity at both species and ecosystem level. The applications of these methods together with the criteria of the IUCN system are expected to significantly contribute to both the study and practice of conservation planning and landscape management.

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Chapter 2: Assessing species extinction risk based on occupancy and spatial autocorrelation of species

2.1 Abstract

One of the most important yet challenging tasks in biological conservation is to assess the extinction risk of species. Most of the currently available methods evaluate extinction risk based on changes in either population size or distribution range over a given period of time. Although population-size-based methods are biologically more justifiable, data on the change in population size are seldom available for most species. To solve this issue, an area-based model was recently derived based on maps of species occupancy and was shown to be effective in predicting extinction risk at any given spatial scale. However, it is as yet unknown how different spatial distributions of species affect model performance. In this paper, I generalized this method by incorporating spatial autocorrelation using joint counts of neighboring cells in an occurrence map. I assessed the performance of this generalized model using both simulated and empirical data at multiple spatial scales. The results showed that the generalized model had better predictions than the original area-based model, particularly when species are of high abundance, strongly aggregated in distribution, or mapped at coarse scales. In the case of less abundant species, differences in the two model predictions are minimal.

2.2 Introduction

It is recognized that simple and efficient ways of assessing extinction risk are important for conservation biologists (Lamoreux et al. 2003; Mace et al. 2008). Most of the currently available methods, including the five quantitative criteria proposed by the International Union for Conservation of Nature (IUCN) Red List system, evaluate extinction risk based on the change of species population size or their distribution ranges over a given period of time (IUCN-SSC 2004). Although population-size-based methods are biologically more justifiable, their implementation in practice is often restricted because accurate population size estimates and long-term dynamics on the landscape to regional scales required are rarely available (Possingham et al. 2002; Lamoreux et al. 2003; Robbirt et al. 2006; Mace et al. 2008). However, the alternative area-based criterion (i.e., Criterion B in IUCN's Red List system), which assigns a species to an endangerment category if the extent (or area) of occupancy is lower than a threshold value, is arguably more arbitrary and less biologically justifiable.

To circumvent the need for species abundance data and make an explicit link between species occupancy and extinction risk, He (2012) developed a model based on the area of species occurrence:

$$P_c = 1 - (1 - P)^{(1-c)}, \tag{1}$$

or $$c = 1 - \frac{\ln(1-P_c)}{\ln(1-P)}, \tag{2}$$

where P is the original occupancy of a species and P_c is the resulting occupancy after a certain proportion (c) of the population is removed. This model effectively combines the IUCN Red List Criteria A and B within a single method. It is based on

Criterion A, which is biological more justifiable, but uses data on occupancy rather than population size, which is more easily attainable than abundance data and has been widely used as a proxy measure of species abundance (Wilson et al. 2004; Cardillo et al. 2008, Mace et al. 2008).

The model has its origins in extinction theory derived from population genetics and ecology (Mace and Lande 1991, Lande 1993, Caughley 1994). Although originally based on an assumption of random species distributions, it is also consistent with non-random (negative binomial) occupancy-abundance distributions (He 2012). This area-based model, for the first time, makes explicit the relationship between the area of distribution and species extinction risk and provides a useful tool for conservation and management planning. It answers the question of how much loss in population size will result from a given loss in area of occurrence.

Although this model is simple, robust to changes in scale and free of parameters, it assumes that the spatial distribution pattern of the study species remains unchanged before and after disturbance (Johnson et al. 1993; He 2012). This assumption is reasonable for many species as shown by He (2012), but different types of disturbance could lead to different spatial patterns in the post-change landscape. For example, selective logging and retention-patch harvesting create different spatial patterns of distribution, while insect/pathogen infection and wind disturbance could result in changes to species distributions (Sousa 1984; He et al. 2002; Scheller and Mladenoff 2005; Karst et al. 2014). The area-based model can be improved to incorporate the possibility of a change in spatial pattern before and after disturbance through the introduction of new parameters to equation 1.

To account for the possibility of changes in spatial patterns of species distribution before and after disturbance requires explicit consideration of spatial autocorrelation in occupancy. The objective of this study was to account for spatial autocorrelation in the model proposed by He (2012) and thereby improve its accuracy and reliability in predicting species' extinction risk. I tested and compared the performance of the extended and original models under various combinations of abundance and spatial distributions at multiple scales using both simulations and empirical data. The significance and limitations of the model in risk assessment applications are discussed.

2.3 Methods

2.3.1 Model

Several authors have proposed methods to quantify spatial autocorrelation in distribution patterns (Conlisk et al. 2009, Solow and Smith 2010, Yin and He 2014). In this study, I adopted the method of Yin and He (2014) to quantify spatial autocorrelation by joint statistics between empty versus occupied neighboring cells in an occurrence map. This is a simple yet germane measurement for spatial autocorrelation of a binary map (Cliff and Ord 1973). Compared with He's (2012) area-based model, the new model takes account of spatial autocorrelation in species distribution by introducing two new model parameters:

$$P_c = 1 - (1 - P)^{\frac{I_c}{I}(1-c)}, \tag{3}$$

or

$$c = 1 - \frac{I}{I_c} \times \frac{\ln(1-P_c)}{\ln(1-P)}, \tag{4}$$

where c is the percentage loss of population size, P and P_c are proportions of occupied area over the total area of a study for a target species before and after disturbance, I and I_c are measures of spatial autocorrelation of the distributions of the species before and after disturbance, respectively.

To derive Eq. 3 and Eq. 4, I firstly recognized the following relationship derived from the binomial distribution for random distribution of species (He and Gaston 2000).

$$P = 1 - (1 - \frac{a}{A})^{N_0} \tag{5}$$

$$N_0 = \frac{\ln(1-P)}{\ln(1-\frac{a}{A})} \tag{6}$$

where N_0 is species abundance, A is total study area, a is cell size (mapping resolution) and P is occupancy of the species.

Eq. 6 can be used to estimate species abundance from the occurrence map for randomly distributed species (He and Gaston 2000). In reality, most species are aggregated resulting in the underestimation of abundance if a random assumption is used (Conlisk et al. 2009; Hwang and He 2011; Azaele, et al. 2012). The real species abundance (N) can be corrected by multiplying the estimated abundance (N_0) by an autocorrelation index (I):

$$N = N_0 \times I \tag{7}$$

where I = 1 for randomly distributed species (I will be defined in next subsection). Substituting Eq. 7 in Eq. 5 gives:

$$P = 1 - (1 - \frac{a}{A})^{\frac{N}{I}} \quad (8)$$

Similarly, one can establish a relationship between species abundance and area of occupancy after disturbance (N_c and P_c, respectively) as

$$P_c = 1 - (1 - \frac{a}{A})^{\frac{N_c}{I_c}} \quad (9)$$

where N_c is species abundance after disturbance, P_c is the resultant area of occupancy for the target species after disturbance, and I_c is an autocorrelation index after disturbance (see the definition of I_c in next subsection). Given the loss of population (c), species abundance before and after disturbance (N and N_c, respectively) follows a simple function:

$$N_c = (1 - c) \times N \quad (10)$$

Solving Eq. 8, Eq. 9, and Eq. 10 together leads to Eq. 3 and Eq. 4

2.3.2 Measuring spatial autocorrelation in the model

Eq. 8 was derived by Yin and He (2014) to estimate species abundance from a given occurrence map. Here, I adopted the approach of Yin and He (2014) to compute the two spatial autocorrelation parameters (I and I_c) by counting the number of joints between adjacent black (occupied) and white (unoccupied) cells based on the distribution maps before and after disturbance, respectively. It is a simple yet germane measurement for the spatial autocorrelation of a binary map (Cliff and Ord 1973). Two types of joints are considered in this analysis. The first one is the black and white joints in the first-order neighborhood, which represents the number of joints by neighboring black and white cells sharing the same edge (Figure 2-1, left). These are denoted as BW joints. The degree of spatial autocorrelation associated with BW joints is defined as

$$I_{BW} = \frac{E(BW)}{O(BW)}, \tag{11}$$

where $E(BW)$ is the expected number of BW joints under random distribution and $O(BW)$ is the observed number of BW joints (Figure 2-1, left).

The second joint type is black and white joints of the second-order neighborhood (Figure 2-1, right), which defines the number of joints by neighboring black and white cells sharing the same edge or diagonal vertex and is denoted as DBW joints. Similarly, the spatial autocorrelation associated with DBW joints can be measured as

$$I_{DBW} = \frac{E(DBW)}{O(DBW)}, \tag{12}$$

where $E(DBW)$ is the expected number of vertex joint under random distribution and $O(DBW)$ is the observed number of vertex joint (Figure 2-1, right). These two I indices measure the degree of spatial aggregation for binary distribution maps. If a species is randomly distributed, I is expected to be 1. $I > 1$ indicates aggregation, while $I < 1$ indicates regular distribution.

2.3.3 Testing the model

I tested and compared the performance of Models (2) and (4) using both simulated and empirical data. In both studies a 50-ha (1000×500 m) plot was used to define the study extent. I varied species abundances from 1000 to 5000, in increments of 1000 and manipulated the amount of spatial aggregation in four scenarios from random to highly aggregated distributions. For each scenario I simulated 1000 replicates. Therefore, there are 20000 samples in total (5 abundance × 4 spatial distributions × 1000 replicates).

Spatial clustering distributions were generated using the rThomas function in the package ‘spatstat’ of R 3.0.3 (R Development Core Team, 2014). This program does not generate exactly the same number of pre-fixed trees. To account for this I only retained a species if its simulated number of individuals was no more than 105 % or less than 95 % of the pre-fixed abundance. Three parameters in rThomas determine a cluster distribution: number of clusters (Ƙ), number of individuals within each cluster (μ), and radius of a cluster (RC). In this analysis, I made the following two assumptions: 1) Ƙ and μ were equivalent to $\sqrt{N}$, where N was species abundance; 2) maximum radius of a cluster (MRC) equaled $\sqrt{\frac{A}{\pi\sqrt{N}}}$, where A is the area of the study plot. I simulated three different RC, representing different degrees of spatial aggregations described above, which equal 1/4 MRC, 1/3 MRC, and 1/2 MRC, respectively. The examples of a simulated species with 1000 individuals under the four different spatial distributions are given in Figure 2-2. The R code for the simulation is provided in Appendix 1.

For obtaining an occupancy map, the entire 50-ha plot was converted into a lattice system at a given cell size (i.e., 10×10 m). A cell is defined as occupied if it contains at least one individual, otherwise it is empty. To assess the impact of disturbance, I randomly removed c (= 30, 50 and 80%) of individuals of a target species to represent the reduction in population size due to the disturbance. These three values, respectively, represent vulnerable, endangered and critical endangered criteria of the IUCN Red List. Species occupancy (P) and spatial autocorrelation index (I) were calculated from the occurrence map before the disturbance, while reduced species occupancy (P_c) and reduced spatial autocorrelation index (I_c) were computed from the occurrence map after the disturbance. Models (2) and (4) were applied to estimate c (the extinction risk as defined by the IUCN Criterion A) based on occurrence maps before and after disturbance (the IUCN Criterion B). The R code for the computation of occupancy and spatial spatial autocorrelation index is provided in Appendix 2.

The mean predicted values of extinction risk and their standard errors of 1000 replicates were compared across various scenarios. The agreement between the predicted values of extinction risk and the known risk (as defined by the 30, 50 and 80% reduction in population size in the simulation) was measured by the relative root mean squared error (rRMSE) as follows:

$$rRMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(\frac{x_i - o_i}{o_i})^2} \tag{13}$$

where x_i is the predicted extinction risk for species i, and o_i is the known extinction risk of the species, and n is the total number of replicates for each scenario. To examine the impact of cell size on the performance of the two models, I repeated the above work at three different spatial scales: a=10×10, 20×20, and 25×25 m.

I further tested the two models using an empirical set of data consisting of 302 tree species distributed in a 50 ha stem-mapping plot from Barro Colorado Island (BCI), Panama (Condit et al. 1996). Species with more than 10000 individuals were excluded since they fully saturated the occurrence map. Species with very low abundance (< 10 individuals) were also excluded because those species do not have enough population size for implementing 50% or 80% reduction. In total, 240 species were analyzed. As previously stated, different types of disturbance may result in different spatial patterns. Because the diameter at breast height (DBH) is available for every tree in the BCI plot, I implemented selective logging by removing c = 30, 50 and 80 % of individuals with larger DBH for each species. Following the procedures described in the above, the predicted values of extinction risk by the two models were compared at the three scales.

2.4 Results

As shown in Figures 2-3 – 2-5, the rRMSEs for model (4) with either BW or DBW joints were almost always smaller than that of model (2), indicating the superiority of model (4). There was little difference between the BW joints and DBW joints for model (4) in predicting extinction risk, suggesting that both the first-order and second-order joints could effectively describe spatial autocorrelation in species distribution.

The performance of all models became progressively worse with increasing of abundance, spatial aggregation and mapping resolution (Tables 2-1 – 2-15; Figures 2-3 – 2-5). For instance, the rRMSEs of the model (2) and model (4) with BW joints and DBW joints raised considerably from 0.174 to 0.469 (model 2), 0.109 to 0.476 (model 4 with BW joints), and 0.108 to 0.476 (model 4 with DBW joint), respectively, when the abundance increased from 1000 to 5000 while the spatial distribution was slightly aggregated and the cell size equaled 25 m (Figure 2-3b – 2-3r). Also, the estimated values of extinction risk of the models were 0.300 (same as the true value) under random distribution, but dropped to 0.218 (model 2), 0.249 (model 4 with BW joints) and 0.249 (model 4 with DBW joints) under the slightly aggregated distribution at 25 m scale (Table 2-1, last column). Similarly, the mapping scale could affect the performance of both models. When the cell size increased from 10 to 25 m, while abundance equaled 5000 and spatial distribution was at high aggregation, the rRMSEs changed sharply from 0.436 to 0.684 (model 2), 0.145 to 0.617 (model 4 with BW joints), and 0.147 to 0.617 (model 4 with DBW joints), respectively (Figure 2-3d). Although both models performed worse when abundance was high, large scale and high intensity of aggregation, model (4) clearly outperformed model (2) with closer predicted values. There was little difference however between the two joints structures in model (4).

Results for the empirical BCI data were similar to the simulations and show that both models were scale dependent (Table 2-16). For instance, the predicted values of extinction risk by model (2) and model (4) with BW joints dropped from 0.483 and 0.493 to 0.459 and 0.474, respectively, when population reduction c=0.5 was implemented and the cell size increased from 10 to 25 m. In general, consistent with the simulation results, model (4) performed better than model (2).

2.5 Discussion

The IUCN's Red List of Threatened Species is perhaps the most widely adopted system for evaluating species' extinction risk (Eken et al. 2004, Miller et al. 2007, Mace et al. 2008). At the core of the IUCN Red List system is the five endangerment assessment criteria. Criterion A makes use of population size as a measurement. It is biologically justifiable but its application is hampered due largely to the paucity of abundance data for most species. Criterion B determines species endangerment status according to the size of occupied area. Although occupancy data are relatively easy to acquire, this criterion does not have much biological support and is less accurate because factors other than abundance can alter a species' occupancy, such as the change in spatial distribution of species patterns. He's (2012) method integrates the IUCN's criteria A and B based on the justifiable criterion A but using the more easily obtained occupancy data. In this study, I further improved this method by taking into account of spatial autocorrelation.

Equipped with models (2) and (4), one can estimate the loss of abundance of a species given the change in the occurrence map of this species over a certain period of time. My results showed that model (4), that accounts for spatial autocorrelation in species distribution, performed better than model (2). The trade-off of model (4) is that there are two extra parameters (I and I_c) to estimate. This means model (4) can only be applied to situations where occurrence maps are available, while model (2) is equally applicable to occurrence maps or data of site occurrence (i.e., presence/absence across spatially discontinuous sites). Given an occurrence map, the estimation of I or I_c is straightforward.

Simulation results showed that high abundance, intensive aggregation, and coarse scale affected both models (Tables 2-1– 2-15 and Figures 2-3 – 2-5). As expected, under random distribution, both models performed equally well irrespective of the abundance and mapping resolutions, because the reduction in occupancy and the loss of abundance is precisely captured by model (2). This relationship deteriorated progressively with increasing spatial aggregation, becoming worse with increasing abundance and mapping resolution (Figures 2-3 – 2-5). Model (4) improves on model (2) by introducing spatial autocorrelation to assess and consider spatial aggregation. It thus ameliorates the effects of abundance, scale, and spatial aggregation and improves its performance.

The predictions of model (2) were always smaller than the true extinction risk when the spatial distribution was aggregated (Tables 2-1 – 2-15). The logic behind this is simple: the random assumption underestimated the degree of spatial aggregation. When the parameters of spatial autocorrelation were considered, the predictions of model (4) could be biased high or low, indicating that this method was scale dependent and the appropriate grid cell was determined by both abundance and spatial aggregation. For example, the appropriate grid size should be between 10 and 20 m when the abundance was 1000 because the predictions of model (4) were biased high when grid cell was 20, while the predictions were biased low when grid cell was 10 (Table 2-1). However, the appropriate grid size should be smaller than 10 m, when the abundance was 5000 since the predictions were always biased low (Table 2-13), indicating the parameters adopted in the model still underestimated the degree of real spatial aggregation. The BW/DBW joints considered in model (4) were first nearest neighbors, and the model could be further improved by incorporating high-order nearest neighbors.

It is notable that the difference between the predicted values of the two models in the empirical data set was less evident than that in the simulation (Figure 2-3 and Table 2-16). This is because the densities of most empirical species are not as high as those in the simulation tests. There are only 44 species that have abundance larger than 1000, let alone 5000 in the 50 ha BCI plot. Another reason is that very few species in the BCI plot show such aggregated distributions as those of "highly aggregated" pattern (Figure 2-2d; see also Condit et al. 2000). Nevertheless, it is true that the model (4) almost always performed as good as or better than model (2). Although we recommend the use of model (4), the difference between model (4) and (2) is likely to be insignificant for most empirical datasets unless highly abundant species are present such as those in the simulation.

Understanding the endangerment status of species is profoundly important to biological conservation and management decision making. With the increasing documentation of species' distributions worldwide (Gaston 2000; Guralnick and Hill 2009), methods such as the one developed in this study, together with other criteria of the IUCN system, provide useful tools to assess species extinction risk. in the real world. These methods have application in research, policy development and practical biological management and conservation.

2.6 Conclusions

Population size-based and area-based methods are two major criteria for assessing species extinction risk. Although population size-based methods are more biologically justifiable in assessing species, the paucity of long-term data restricts its application. Area-based methods are easy to implement but more arbitrary and lacking in biological meaning. In this study, a novel extinction risk model was developed by incorporating spatial autocorrelation indices into a recently derived area-model based on occupancy.

This new model was compared with the area-based one at multiple spatial scales with both simulated and empirical data sets. A random disturbance was applied in simulations, while selective logging was implemented in empirical testing. This analysis yields the following main results: 1) the newly derived model outperformed the original area-based model in both the simulation and empirical testing; and 2) both models were subjected to high abundance, large scale and intensive spatial aggregation. However, predictive performance in the original area-based model declined faster than with the new model under these conditions and it provides an improved means to estimate extinction risk over a broader range of conditions.

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Table 2-1. Predicted extinction risk by models (2) and (4) with 1000 initial individuals when *c*=30% of population reduction. Values in the parenthesis are standard errors for 1000 replications.

Models	Spatial distribution	Cell size (m)		
		10	20	25
Model (2)	Random	0.300 (0.006)	0.300 (0.013)	0.300 (0.018)
	Slightly aggregated	0.291 (0.007)	0.267 (0.016)	0.252 (0.020)
	Moderately aggregated	0.281 (0.008)	0.235 (0.017)	0.210 (0.021)
	Highly aggregated	0.259 (0.010)	0.187 (0.018)	0.159 (0.020)
Model (4) with BW joints	Random	0.300 (0.008)	0.300 (0.018)	0.300 (0.024)
	Slightly aggregated	0.306 (0.010)	0.299 (0.023)	0.288 (0.030)
	Moderately aggregated	0.312 (0.011)	0.300 (0.027)	0.276 (0.036)
	Highly aggregated	0.320 (0.015)	0.272 (0.032)	0.228 (0.037)
Model (4) with DBW joints	Random	0.300 (0.008)	0.300 (0.017)	0.300 (0.024)
	Slightly aggregated	0.306 (0.010)	0.299 (0.022)	0.287 (0.030)
	Moderately aggregated	0.312 (0.011)	0.300 (0.027)	0.276 (0.035)
	Highly aggregated	0.320 (0.015)	0.272 (0.032)	0.228 (0.037)

Table 2-2. Predicted extinction risk by models (2) and (4) with 1000 initial individuals when *c*=50% of population reduction. Values in the parenthesis are standard errors for 1000 replications.

Models	Spatial distribution	Cell size (m)		
		10	20	25
Model (2)	Random	0.500 (0.005)	0.500 (0.012)	0.500 (0.016)
	Slightly aggregated	0.490 (0.007)	0.461 (0.016)	0.441 (0.021)
	Moderately aggregated	0.477 (0.008)	0.417 (0.019)	0.382 (0.024)
	Highly aggregated	0.449 (0.010)	0.348 (0.020)	0.304 (0.025)
Model (4) with BW joints	Random	0.500 (0.007)	0.500 (0.016)	0.499 (0.022)
	Slightly aggregated	0.506 (0.009)	0.503 (0.020)	0.489 (0.029)
	Moderately aggregated	0.515 (0.010)	0.504 (0.024)	0.477 (0.034)
	Highly aggregated	0.526 (0.013)	0.476 (0.031)	0.418 (0.038)
Model (4) with DBW joints	Random	0.500 (0.007)	0.500 (0.016)	0.500 (0.022)
	Slightly aggregated	0.506 (0.009)	0.503 (0.020)	0.489 (0.028)
	Moderately aggregated	0.515 (0.010)	0.504 (0.024)	0.476 (0.034)
	Highly aggregated	0.526 (0.013)	0.475 (0.031)	0.417 (0.037)

Table 2-3. Predicted extinction risk by models (2) and (4) with 1000 initial individuals when *c*=80% of population reduction. Values in the parenthesis are standard errors for 1000 replications.

Models	Spatial distribution	Cell size (m)		
		10	20	25
Model (2)	Random	0.800 (0.003)	0.800 (0.006)	0.800 (0.008)
	Slightly aggregated	0.793 (0.003)	0.774 (0.009)	0.760 (0.014)
	Moderately aggregated	0.785 (0.004)	0.742 (0.012)	0.713 (0.017)
	Highly aggregated	0.766 (0.006)	0.680 (0.016)	0.632 (0.021)
Model (4) with BW joints	Random	0.800 (0.004)	0.800 (0.008)	0.800 (0.010)
	Slightly aggregated	0.805 (0.005)	0.805 (0.010)	0.799 (0.014)
	Moderately aggregated	0.810 (0.005)	0.809 (0.011)	0.796 (0.016)
	Highly aggregated	0.819 (0.007)	0.797 (0.015)	0.760 (0.021)
Model (4) with DBW joints	Random	0.800 (0.003)	0.800 (0.007)	0.800 (0.010)
	Slightly aggregated	0.805 (0.004)	0.805 (0.010)	0.799 (0.014)
	Moderately aggregated	0.810 (0.005)	0.809 (0.011)	0.796 (0.015)
	Highly aggregated	0.819 (0.007)	0.796 (0.015)	0.759 (0.021)

Table 2-4. Predicted extinction risk by models (2) and (4) with 2000 initial individuals when *c*=30% of population reduction. Values in the parenthesis are standard errors for 1000 replications.

Models	Spatial distribution	Cell size (m)		
		10	20	25
Model (2)	Random	0.300 (0.006)	0.300 (0.016)	0.300 (0.025)
	Slightly aggregated	0.283 (0.007)	0.241 (0.018)	0.218 (0.024)
	Moderately aggregated	0.263 (0.009)	0.193 (0.017)	0.166 (0.020)
	Highly aggregated	0.227 (0.010)	0.144 (0.016)	0.125 (0.018)
Model (4) with BW joints	Random	0.300 (0.008)	0.300 (0.021)	0.300 (0.032)
	Slightly aggregated	0.307 (0.011)	0.277 (0.028)	0.249 (0.038)
	Moderately aggregated	0.314 (0.013)	0.260 (0.030)	0.220 (0.037)
	Highly aggregated	0.315 (0.017)	0.208 (0.031)	0.167 (0.034)
Model (4) with DBW joints	Random	0.300 (0.008)	0.300 (0.020)	0.300 (0.032)
	Slightly aggregated	0.307 (0.010)	0.277 (0.028)	0.249 (0.038)
	Moderately aggregated	0.314 (0.013)	0.259 (0.030)	0.219 (0.037)
	Highly aggregated	0.314 (0.016)	0.207 (0.031)	0.167 (0.034)

Table 2-5. Predicted extinction risk by models (2) and (4) with 2000 initial individuals when *c*=50% of population reduction. Values in the parenthesis are standard errors for 1000 replications.

Models	Spatial distribution	Cell size (m)		
		10	20	25
Model (2)	Random	0.500 (0.005)	0.500 (0.014)	0.500 (0.021)
	Slightly aggregated	0.479 (0.008)	0.426 (0.020)	0.394 (0.026)
	Moderately aggregated	0.454 (0.009)	0.358 (0.021)	0.315 (0.026)
	Highly aggregated	0.407 (0.012)	0.278 (0.019)	0.242 (0.024)
Model (4) with BW joints	Random	0.500 (0.007)	0.501 (0.019)	0.500 (0.027)
	Slightly aggregated	0.508 (0.010)	0.478 (0.026)	0.442 (0.038)
	Moderately aggregated	0.518 (0.012)	0.459 (0.029)	0.401 (0.042)
	Highly aggregated	0.523 (0.015)	0.390 (0.030)	0.322 (0.039)
Model (4) with DBW joints	Random	0.500 (0.007)	0.501 (0.018)	0.500 (0.026)
	Slightly aggregated	0.509 (0.009)	0.478 (0.025)	0.442 (0.037)
	Moderately aggregated	0.517 (0.012)	0.459 (0.029)	0.400 (0.042)
	Highly aggregated	0.522 (0.014)	0.389 (0.030)	0.321 (0.039)

Table 2-6. Predicted extinction risk by models (2) and (4) with 2000 initial individuals when *c*=80% of population reduction. Values in the parenthesis are standard errors for 1000 replications.

Models	Spatial distribution	Cell size (m)		
		10	20	25
Model (2)	Random	0.800 (0.003)	0.800 (0.006)	0.800 (0.009)
	Slightly aggregated	0.787 (0.004)	0.748 (0.013)	0.722 (0.019)
	Moderately aggregated	0.769 (0.006)	0.690 (0.016)	0.645 (0.021)
	Highly aggregated	0.734 (0.008)	0.600 (0.019)	0.545 (0.023)
Model (4) with BW joints	Random	0.800 (0.004)	0.800 (0.008)	0.800 (0.012)
	Slightly aggregated	0.807 (0.005)	0.793 (0.012)	0.772 (0.018)
	Moderately aggregated	0.814 (0.006)	0.786 (0.015)	0.747 (0.021)
	Highly aggregated	0.821 (0.007)	0.741 (0.018)	0.675 (0.025)
Model (4) with DBW joints	Random	0.800 (0.004)	0.800 (0.008)	0.800 (0.012)
	Slightly aggregated	0.807 (0.005)	0.793 (0.012)	0.772 (0.018)
	Moderately aggregated	0.814 (0.006)	0.785 (0.015)	0.746 (0.021)
	Highly aggregated	0.820 (0.007)	0.740 (0.018)	0.674 (0.025)

Table 2-7. Predicted extinction risk by models (2) and (4) with 3000 initial individuals when *c*=30% of population reduction. Values in the parenthesis are standard errors for 1000 replications.

Models	Spatial distribution	Cell size (m)		
		10	20	25
Model (2)	Random	0.300 (0.006)	0.301 (0.019)	0.302 (0.036)
	Slightly aggregated	0.275 (0.008)	0.220 (0.021)	0.193 (0.026)
	Moderately aggregated	0.247 (0.009)	0.166 (0.017)	0.141 (0.021)
	Highly aggregated	0.202 (0.010)	0.125 (0.015)	0.109 (0.018)
Model (4) with BW joints	Random	0.299 (0.008)	0.300 (0.025)	0.301 (0.045)
	Slightly aggregated	0.304 (0.011)	0.254 (0.032)	0.216 (0.046)
	Moderately aggregated	0.309 (0.014)	0.222 (0.032)	0.177 (0.040)
	Highly aggregated	0.299 (0.018)	0.173 (0.030)	0.141 (0.032)
Model (4) with DBW joints	Random	0.299 (0.008)	0.300 (0.024)	0.301 (0.045)
	Slightly aggregated	0.304 (0.011)	0.253 (0.031)	0.215 (0.046)
	Moderately aggregated	0.309 (0.014)	0.222 (0.031)	0.176 (0.039)
	Highly aggregated	0.298 (0.018)	0.172 (0.029)	0.141 (0.032)

Table 2-8. Predicted extinction risk by models (2) and (4) with 3000 initial individuals when *c*=50% of population reduction. Values in the parenthesis are standard errors for 1000 replications.

Models	Spatial distribution	Cell size (m)		
		10	20	25
Model (2)	Random	0.500 (0.006)	0.500 (0.017)	0.502 (0.030)
	Slightly aggregated	0.470 (0.008)	0.397 (0.022)	0.358 (0.031)
	Moderately aggregated	0.434 (0.010)	0.317 (0.020)	0.274 (0.025)
	Highly aggregated	0.372 (0.012)	0.242 (0.019)	0.213 (0.022)
Model (4) with BW joints	Random	0.500 (0.008)	0.500 (0.021)	0.502 (0.036)
	Slightly aggregated	0.508 (0.010)	0.449 (0.030)	0.398 (0.046)
	Moderately aggregated	0.515 (0.013)	0.411 (0.031)	0.342 (0.041)
	Highly aggregated	0.507 (0.016)	0.331 (0.033)	0.274 (0.037)
Model (4) with DBW joints	Random	0.500 (0.007)	0.500 (0.021)	0.502 (0.036)
	Slightly aggregated	0.508 (0.010)	0.449 (0.030)	0.397 (0.046)
	Moderately aggregated	0.515 (0.012)	0.411 (0.031)	0.341 (0.040)
	Highly aggregated	0.506 (0.016)	0.330 (0.033)	0.273 (0.036)

Table 2-9. Predicted extinction risk by models (2) and (4) with 3000 initial individuals when *c*=80% of population reduction. Values in the parenthesis are standard errors for 1000 replications.

Models	Spatial distribution	Cell size (m)		
		10	20	25
Model (2)	Random	0.800 (0.003)	0.800 (0.007)	0.801 (0.013)
	Slightly aggregated	0.780 (0.005)	0.725 (0.016)	0.690 (0.023)
	Moderately aggregated	0.754 (0.006)	0.648 (0.017)	0.594 (0.023)
	Highly aggregated	0.703 (0.009)	0.545 (0.019)	0.489 (0.023)
Model (4) with BW joints	Random	0.800 (0.004)	0.800 (0.009)	0.801 (0.015)
	Slightly aggregated	0.807 (0.005)	0.776 (0.015)	0.741 (0.024)
	Moderately aggregated	0.814 (0.006)	0.755 (0.017)	0.697 (0.025)
	Highly aggregated	0.816 (0.008)	0.685 (0.022)	0.606 (0.029)
Model (4) with DBW joints	Random	0.800 (0.004)	0.800 (0.009)	0.801 (0.015)
	Slightly aggregated	0.807 (0.005)	0.776 (0.015)	0.740 (0.024)
	Moderately aggregated	0.814 (0.006)	0.754 (0.017)	0.696 (0.025)
	Highly aggregated	0.815 (0.007)	0.683 (0.022)	0.605 (0.029)

Table 2-10. Predicted extinction risk by models (2) and (4) with 4000 initial individuals when *c*=30% of population reduction. Values in the parenthesis are standard errors for 1000 replications.

Models	Spatial distribution	Cell size (m)		
		10	20	25
Model (2)	Random	0.300 (0.007)	0.301 (0.025)	0.304 (0.058)
	Slightly aggregated	0.267 (0.009)	0.201 (0.021)	0.174 (0.028)
	Moderately aggregated	0.233 (0.010)	0.150 (0.017)	0.129 (0.020)
	Highly aggregated	0.184 (0.010)	0.114 (0.014)	0.101 (0.017)
Model (4) with BW joints	Random	0.300 (0.009)	0.300 (0.029)	0.304 (0.069)
	Slightly aggregated	0.302 (0.012)	0.231 (0.034)	0.190 (0.053)
	Moderately aggregated	0.302 (0.014)	0.196 (0.034)	0.154 (0.042)
	Highly aggregated	0.280 (0.018)	0.154 (0.028)	0.124 (0.029)
Model (4) with DBW joints	Random	0.300 (0.009)	0.300 (0.029)	0.304 (0.075)
	Slightly aggregated	0.302 (0.011)	0.231 (0.034)	0.189 (0.052)
	Moderately aggregated	0.302 (0.014)	0.196 (0.033)	0.154 (0.041)
	Highly aggregated	0.279 (0.018)	0.153 (0.027)	0.125 (0.029)

Table 2-11. Predicted extinction risk by models (2) and (4) with 4000 initial individuals when *c*=50% of population reduction. Values in the parenthesis are standard errors for 1000 replications.

Models	Spatial distribution	Cell size (m)		
		10	20	25
Model (2)	Random	0.500 (0.006)	0.502 (0.020)	0.504 (0.045)
	Slightly aggregated	0.460 (0.009)	0.371 (0.024)	0.329 (0.033)
	Moderately aggregated	0.415 (0.011)	0.287 (0.022)	0.249 (0.026)
	Highly aggregated	0.345 (0.011)	0.221 (0.018)	0.197 (0.022)
Model (4) with BW joints	Random	0.500 (0.008)	0.502 (0.025)	0.503 (0.054)
	Slightly aggregated	0.505 (0.011)	0.421 (0.034)	0.361 (0.053)
	Moderately aggregated	0.509 (0.013)	0.370 (0.034)	0.298 (0.044)
	Highly aggregated	0.487 (0.017)	0.295 (0.031)	0.246 (0.037)
Model (4) with DBW joints	Random	0.500 (0.008)	0.502 (0.025)	0.503 (0.058)
	Slightly aggregated	0.505 (0.011)	0.420 (0.034)	0.361 (0.052)
	Moderately aggregated	0.508 (0.013)	0.370 (0.034)	0.298 (0.043)
	Highly aggregated	0.486 (0.017)	0.295 (0.030)	0.246 (0.037)

Table 2-12. Predicted extinction risk by models (2) and (4) with 4000 initial individuals when *c*=80% of population reduction. Values in the parenthesis are standard errors for 1000 replications.

Models	Spatial distribution	Cell size (m)		
		10	20	25
Model (2)	Random	0.800 (0.003)	0.800 (0.009)	0.801 (0.019)
	Slightly aggregated	0.773 (0.006)	0.701 (0.019)	0.659 (0.027)
	Moderately aggregated	0.740 (0.008)	0.613 (0.020)	0.555 (0.025)
	Highly aggregated	0.677 (0.009)	0.507 (0.020)	0.455 (0.024)
Model (4) with BW joints	Random	0.800 (0.004)	0.800 (0.011)	0.801 (0.022)
	Slightly aggregated	0.806 (0.005)	0.757 (0.018)	0.710 (0.030)
	Moderately aggregated	0.812 (0.006)	0.724 (0.020)	0.652 (0.028)
	Highly aggregated	0.806 (0.008)	0.639 (0.023)	0.558 (0.031)
Model (4) with DBW joints	Random	0.800 (0.004)	0.800 (0.011)	0.801 (0.024)
	Slightly aggregated	0.806 (0.005)	0.757 (0.018)	0.710 (0.029)
	Moderately aggregated	0.812 (0.006)	0.723 (0.020)	0.651 (0.028)
	Highly aggregated	0.805 (0.008)	0.638 (0.023)	0.557 (0.030)

Table 2-13. Predicted extinction risk by models (2) and (4) with 5000 initial individuals when *c*=30% of population reduction. Values in the parenthesis are standard errors for 1000 replications.

Models	Spatial distribution	Cell size (m)		
		10	20	25
Model (2)	Random	0.300 (0.007)	0.303 (0.033)	0.285 (0.065)
	Slightly aggregated	0.259 (0.009)	0.187 (0.022)	0.162 (0.030)
	Moderately aggregated	0.221 (0.010)	0.138 (0.016)	0.119 (0.020)
	Highly aggregated	0.170 (0.009)	0.107 (0.014)	0.095 (0.016)
Model (4) with BW joints	Random	0.300 (0.009)	0.304 (0.038)	0.286 (0.079)
	Slightly aggregated	0.297 (0.012)	0.213 (0.040)	0.169 (0.057)
	Moderately aggregated	0.296 (0.016)	0.175 (0.033)	0.137 (0.039)
	Highly aggregated	0.261 (0.018)	0.140 (0.027)	0.117 (0.030)
Model (4) with DBW joints	Random	0.300 (0.009)	0.304 (0.038)	0.287 (0.096)
	Slightly aggregated	0.296 (0.012)	0.212 (0.039)	0.169 (0.056)
	Moderately aggregated	0.295 (0.015)	0.175 (0.032)	0.137 (0.038)
	Highly aggregated	0.260 (0.018)	0.140 (0.026)	0.117 (0.029)

Table 2-14. Predicted extinction risk by models (2) and (4) with 5000 initial individuals when *c*=50% of population reduction. Values in the parenthesis are standard errors for 1000 replications.

Models	Spatial distribution	Cell size (m)		
		10	20	25
Model (2)	Random	0.500 (0.006)	0.502 (0.025)	0.488 (0.045)
	Slightly aggregated	0.450 (0.010)	0.349 (0.026)	0.306 (0.036)
	Moderately aggregated	0.399 (0.011)	0.266 (0.021)	0.233 (0.026)
	Highly aggregated	0.321 (0.011)	0.207 (0.017)	0.184 (0.021)
Model (4) with BW joints	Random	0.500 (0.009)	0.502 (0.030)	0.488 (0.060)
	Slightly aggregated	0.500 (0.011)	0.393 (0.041)	0.325 (0.061)
	Moderately aggregated	0.500 (0.014)	0.337 (0.036)	0.272 (0.045)
	Highly aggregated	0.463 (0.018)	0.270 (0.031)	0.226 (0.036)
Model (4) with DBW joints	Random	0.500 (0.008)	0.502 (0.030)	0.489 (0.073)
	Slightly aggregated	0.500 (0.011)	0.393 (0.040)	0.325 (0.060)
	Moderately aggregated	0.500 (0.014)	0.336 (0.035)	0.271 (0.045)
	Highly aggregated	0.462 (0.018)	0.269 (0.030)	0.226 (0.036)

Table 2-15. Predicted extinction risk by models (2) and (4) with 5000 initial individuals when *c*=80% of population reduction. Values in the parenthesis are standard errors for 1000 replications.

Models	Spatial distribution	Cell size (m)		
		10	20	25
Model (2)	Random	0.800 (0.003)	0.801 (0.011)	0.795 (0.018)
	Slightly aggregated	0.766 (0.006)	0.681 (0.020)	0.633 (0.030)
	Moderately aggregated	0.726 (0.009)	0.583 (0.020)	0.525 (0.026)
	Highly aggregated	0.653 (0.010)	0.479 (0.019)	0.430 (0.024)
Model (4) with BW joints	Random	0.800 (0.004)	0.801 (0.013)	0.795 (0.024)
	Slightly aggregated	0.804 (0.006)	0.737 (0.021)	0.678 (0.036)
	Moderately aggregated	0.809 (0.007)	0.693 (0.023)	0.613 (0.034)
	Highly aggregated	0.794 (0.009)	0.602 (0.024)	0.523 (0.033)
Model (4) with DBW joints	Random	0.800 (0.004)	0.801 (0.013)	0.796 (0.030)
	Slightly aggregated	0.804 (0.005)	0.737 (0.021)	0.678 (0.036)
	Moderately aggregated	0.808 (0.007)	0.692 (0.023)	0.612 (0.033)
	Highly aggregated	0.793 (0.008)	0.600 (0.024)	0.522 (0.032)

Table 2-16. Predicted extinction risk by models (2) and (4) for BCI plot data. Values in the parenthesis are standard errors for 240 species.

Implemented extinction risk	Cell size (m)	Predicted extinction risk		
		Model (2)	Model (4) with BW joints	Model (4) with DBW joints
c = 30%	10	0.293 (0.046)	0.300 (0.052)	0.300 (0.050)
	20	0.282 (0.053)	0.291 (0.057)	0.291 (0.055)
	25	0.279 (0.058)	0.290 (0.060)	0.288 (0.059)
c = 50%	10	0.483 (0.061)	0.493 (0.061)	0.493 (0.063)
	20	0.465 (0.073)	0.479 (0.077)	0.477 (0.076)
	25	0.459 (0.076)	0.474 (0.075)	0.472 (0.075)
c = 80%	10	0.783 (0.053)	0.793 (0.048)	0.792 (0.047)
	20	0.769 (0.065)	0.779 (0.074)	0.777 (0.074)
	25	0.761 (0.073)	0.768 (0.086)	0.766 (0.083)

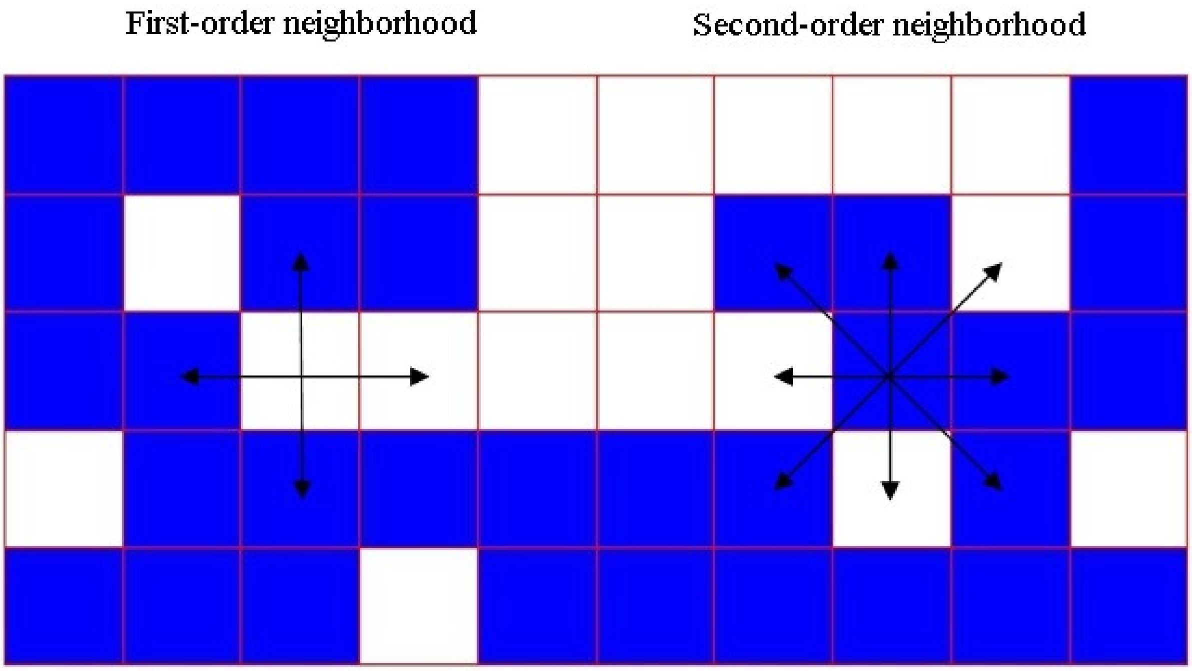

Figure 2-1. Illustration of the black and white joints for the first-order neighborhood and second-order neighborhood. The occupied and empty cells are denoted as black (B) and white (W), respectively.

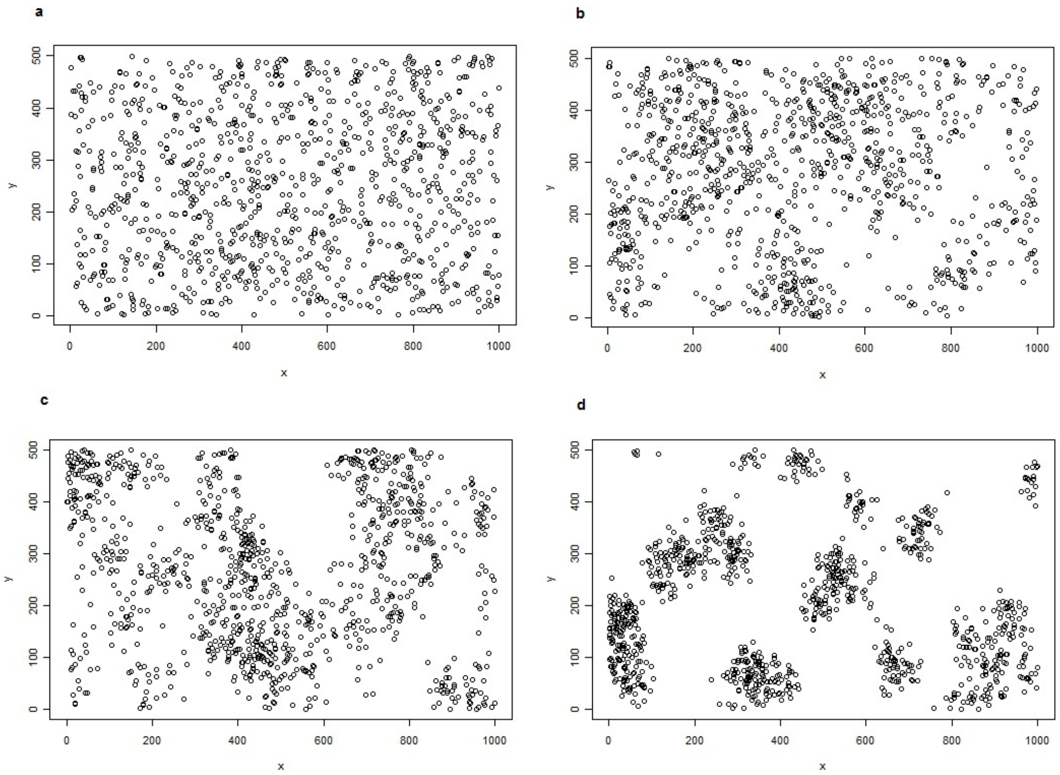

Figure 2-2. Distributions of a simulated species with 1000 individuals under random (a), slightly aggregated (b), moderately aggregated (c), and highly aggregated (d) patterns in a 1000×500 m plot.

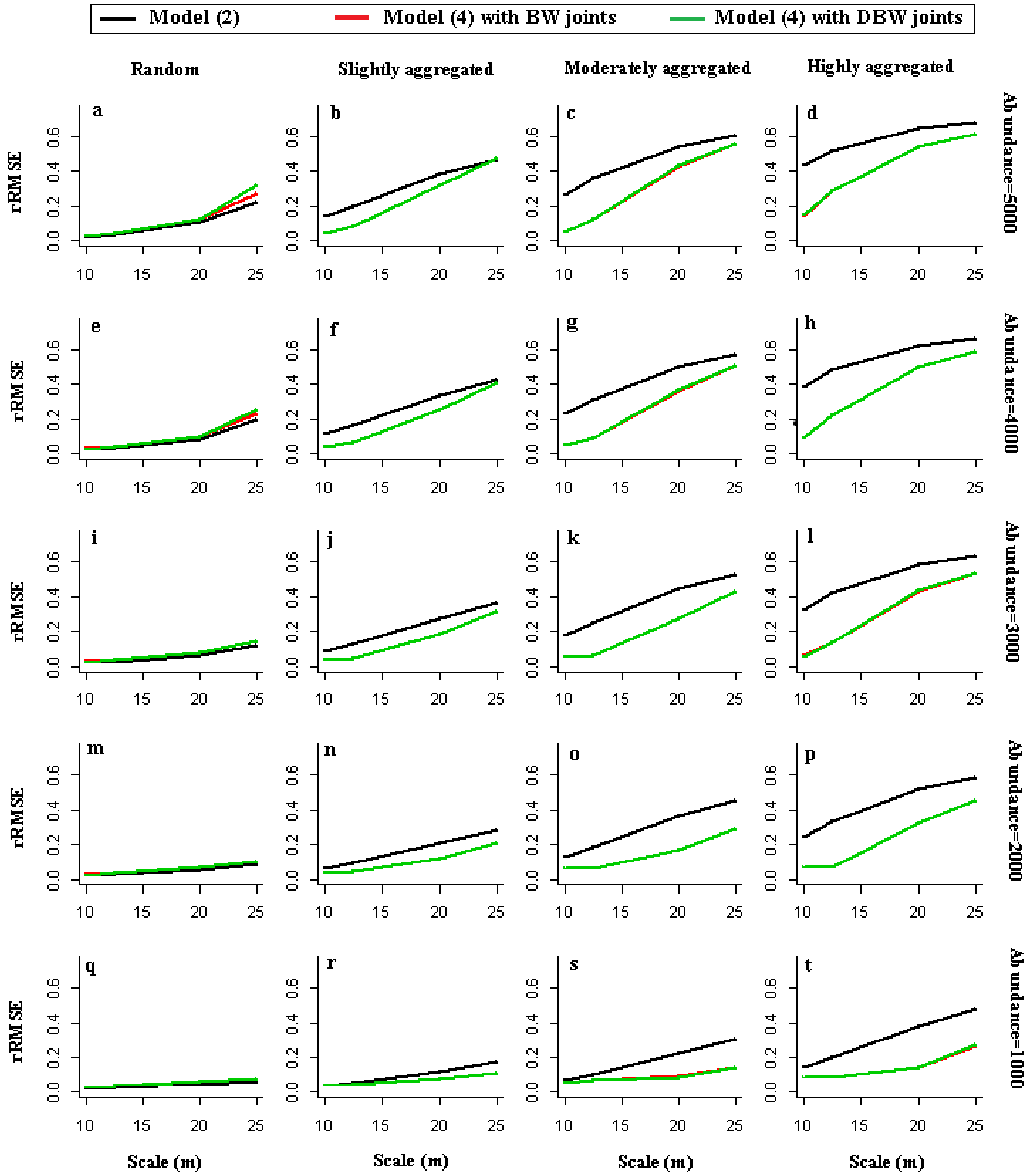

Figure 2-3. rRMSEs for model (2) (black lines), model (4) with BW joints (red lines) and with DBW joints (green lines) for different combinations of abundance and spatial aggregation when disturbance intensity *c* = 0.3 was implemented. Red lines and green lines overlap in most cases.

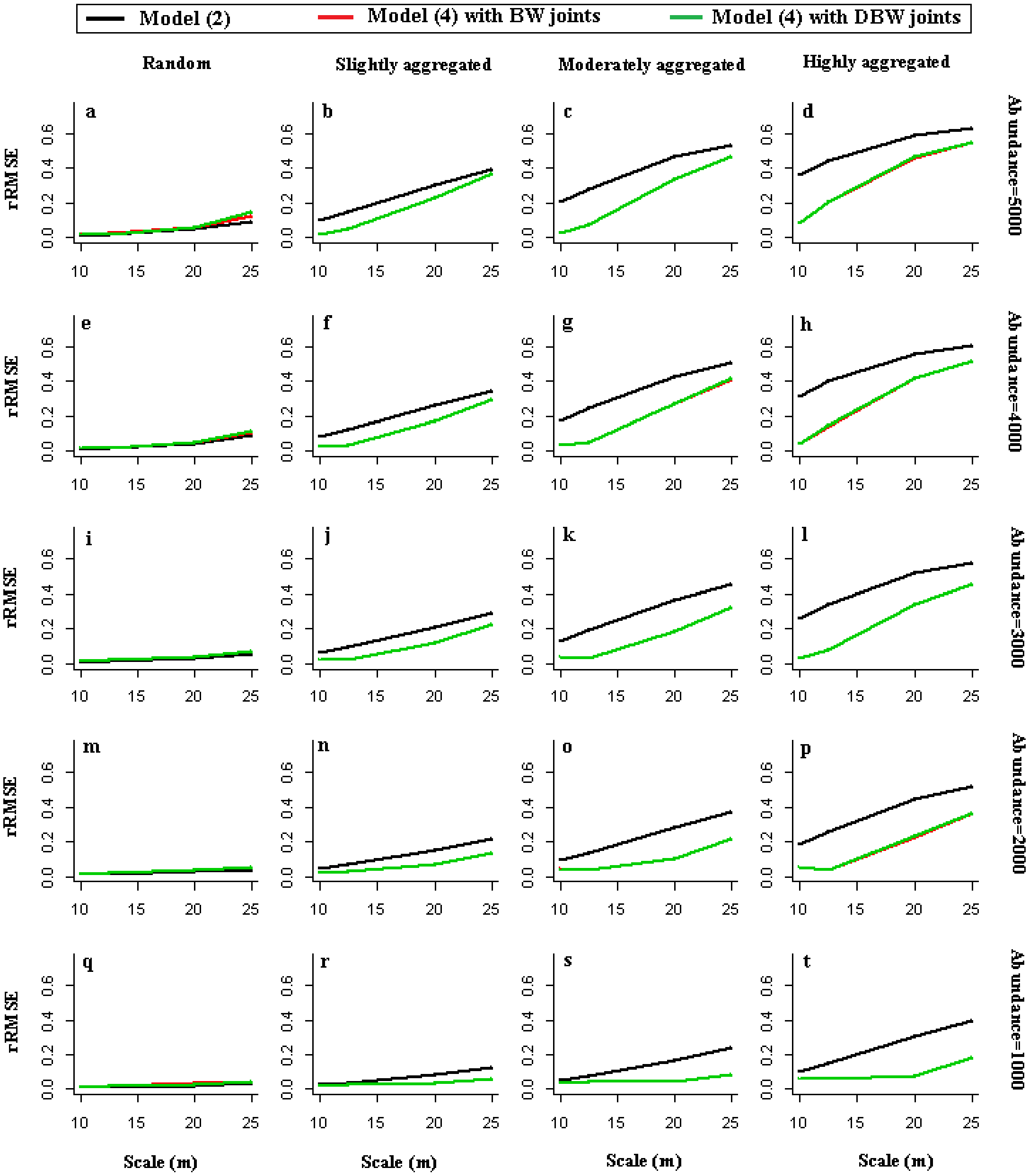

Figure 2-4. rRMSEs for the area-based model (black lines), the spatial-area model with BW joints (red lines), and the spatial-area model with DBW joints (green lines) in multiple scenarios when disturbance intensity c=0.5 was implemented.

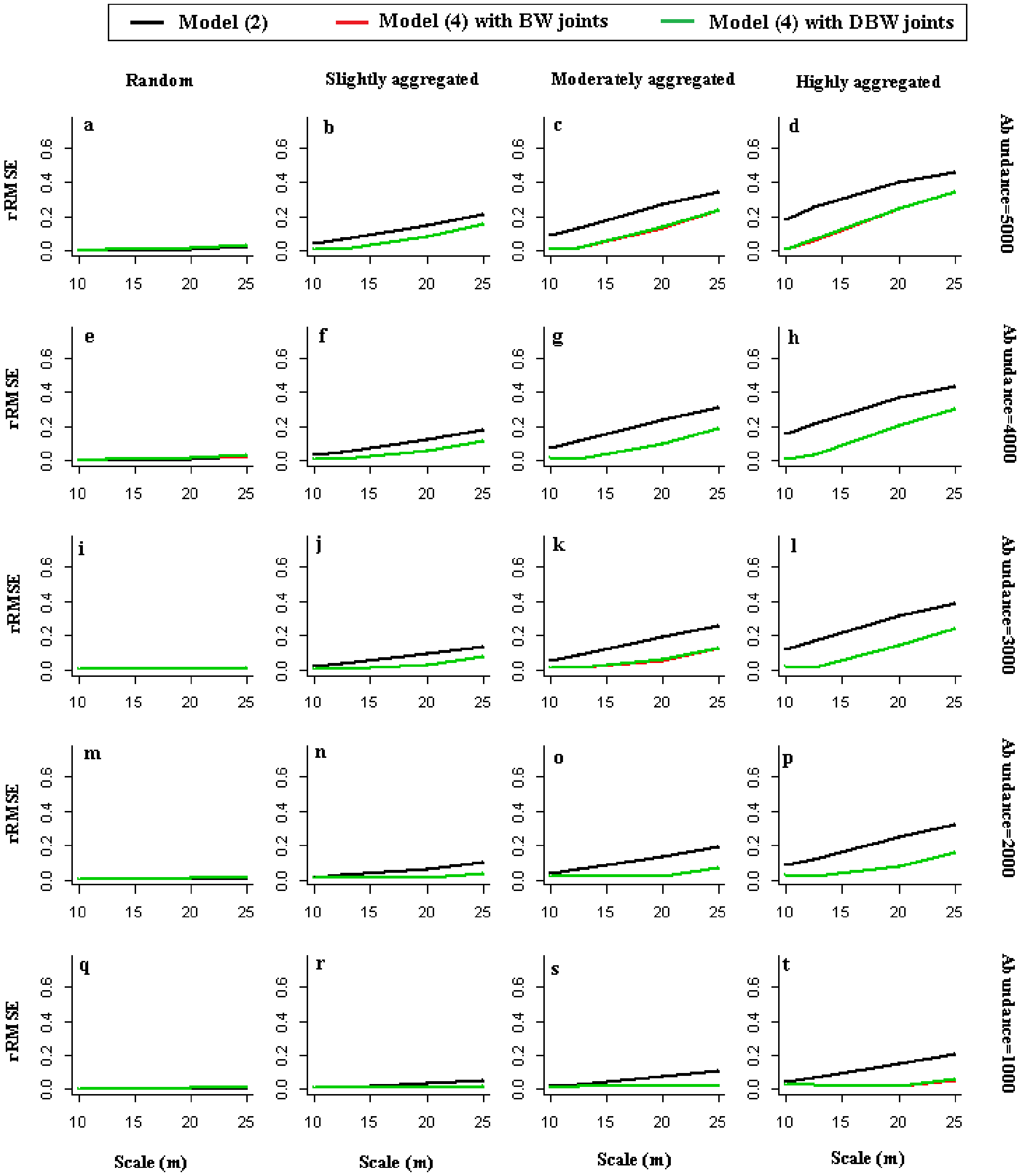

Figure 2-5. rRMSEs for the area-based model (black lines), the spatial-area model with BW joints (red lines), and the spatial-area model with DBW joints (green lines) in multiple scenarios when disturbance intensity c=0.8 was implemented.

Chapter 3: Testing the robustness of scalograms of landscape metrics and their application to the assessment of extinction risk

3.1 Abstract

The scale dependence of ecological patterns is a major impediment to depicting spatially structured landscapes. A widely adopted solution is to investigate the changes in landscape metrics over a spectrum of spatial scales, using so-called scalograms. Despite of the importance of scalograms for understanding the behavior of landscape metrics, their application in landscape management and biological conservation has not been explored. This chapter examines changes in the scalograms of six commonly used landscape metrics responding to various disturbance intensities. The predictive power of this method was tested through both simulated and empirical data. The results indicated that the scalograms of the number of patches (NP), mean patch size (MPS), patch size standard deviation (PSSD) and largest patch index (LPI) were robust to changes in abundance and spatial distributions; while for the predictive power, the scalograms of the number of patches (NP), edge length (EL), and mean patch size (MPS) performed well in both simulation and empirical testing. The results show the scalograms tested in this chapter could be useful for assessing species extinction risk in highly structured landscapes.

3.2 Introduction

The measurement and interpretation of spatially structured landscapes is necessary for understanding ecological processes and has received much research attention (Turner 1989; Levin 1992; Wu and Levin 1994; Wu et al. 2002). A major impediment to quantifying and monitoring a landscape is the scale multiplicity of heterogeneity. That is, landscape patterns depend on the scale at which they arise (Gardner et al. 1987; Wiens 1989; Levin 1992; Wu and Loucks 1995). A well-known example is the coastline paradox, which implies that a landmass has no single well-defined perimeter, and that the length highly depends on the observed spatial scale (Mandelbrot 1983; Peitgen 2004).

In the last three decades, many studies have improved our understanding of the effect of scale by using both simulated and empirical tests (Gardner et al. 1987; Delcourt and Delcourt 1996; Hargis et al. 1998; Saura and Martinez-Millan 2001; Baldwin et al. 2004; Saura 2004; Saura and Castro 2007). In a series of studies, Wu et al. (2002), Wu (2004) and Shen et al. (2004) investigated scalograms of landscape metrics by progressively computing the values of the metrics over a spectrum of scales. These researchers divided about 20 commonly used landscape metrics into three categories: simple scaling function (type 1), staircase-like scaling behavior (type 2), and unpredictable (type 3). In the type 1 category, metrics are predictable by changes in scale and these relationships can be fitted by either the linear, logarithmic or power-law function. Examples of type 1 landscape metrics include the number of patches (NP), patch density (PD), and total edge (TE). Type 2 includes metrics, such as patch richness (PR) and patch richness density (PRD), which exhibit stair-case behavior across scales. In type 3 metrics, scale response is unpredictable, showing erratic patterns in response to changing scales. Mean patch fractal dimension (MPFD) and contagion (CONT) fall into this type.

Although these analyses on the scalogram are interesting and have received much attention in the literature (Wu 2013), the application of predictable scalograms is limited to downscaling the values of landscape metrics from coarse scales to fine scales (e.g., Pablo and Entraigas 2014). Researchers studying the consequences of biophysical processes and human activities often undertake tedious, potentially redundant computations and comparisons of landscape metrics over both grain sizes and study extents (e.g., Hudak et al. 2004, Cayuela et al. 2006 and Wu et al. 2011). The use of scalograms would avoid this necessity, but their applications in landscape management and biological conservation have not been evaluated.

To make scalograms useful requires a better understanding of how these scaling relations respond to various intensities of external disturbances. The intent of this analysis is to model the relationship between the changes in scalograms and the levels of disturbance intensities. In previous studies, Leimgruber et al. (2002) and Frate (2014) showed clear effects of disturbance on scalograms, but these studies did not test the generality of their findings due largely to the lack of spatial patterns affected by different levels of disturbance intensities in real landscapes. In this study, I use simulation to solve this problem. The advantage of simulation is that we can easily test the robustness of scalograms to the change in species abundance and other key determinants of spatial patterns (i.e., spatial distribution).

The specific objectives of this chapter are twofold. First, I modeled the scalograms of six selected landscape metrics and tested the robustness of these models to the change in abundance and spatial distributions of species. Second, I studied the variation in the scalograms of landscape metrics in response to changing disturbance intensities. I used both simulated and empirical data to conduct this analysis. It is noteworthy that in the literature the term 'scale' could refer to extent, grain size, spatial lag, or cartographic rate (Wiens 1989; Lam and Quattrochi 1992; Schneider 2001; Dungan et al. 2002; Wu et al. 2006). In this study, I restrict the term 'scale' to refer only to grid size or cell size unless specified otherwise.

3.3 Methods

3.3.1 Constructing scalograms of landscape metrics

Six landscape metrics belonging to type 1 category were adopted in this study, including the Number of Patches, Edge Length, Mean Patch Size, patch size standard deviation (PSSD), patch size coefficient of variation (PSCV), and large patch index (LPI). A brief summary of these metrics is presented in Table 3-1. The scalograms of the landscape metrics were obtained by progressively computing the values of the metrics over a spectrum of grid sizes. The formation of one single large patch should not be allowed when selecting suitable grid sizes. In this study, the scalograms were based on the following grid sizes: a = 5×5, 6.25×6.25, 8×8, 10×10, 12.5×12.5, 15.625×15.625, 20×20, and 25×25 m. After comprehensively comparing the behavior of the scalograms with various abundance and spatial distributions, the scalogram of NP was found to be best fitted by the exponential model, and the scalograms of the other five landscape metrics were best fitted by the power-law model (Table 3-1).

3.3.2 Simulation test

Testing the robustness of scalograms to changing abundance and spatial distributions

In simulations, I fixed the study extent to a 100-ha (1000×1000 m) area and in scenarios I varied species abundance from 1000 to 5000 by increments of 1000 individuals, and spatial distributions from random, slightly aggregated, moderately aggregated, to highly aggregated. 1000 replications were repeated for each scenario, and there were 20000 samples in total (5 abundance × 4 spatial distributions × 1000 repetitions).

The aggregated distributions were generated by using rThomas in the package of 'spatstat' in R 3.0.3 (R Core Development Team 2014). This program does not generate exactly the same number of pre-fixed trees. To account for this I only retained a species if its simulated number of individuals was no more than 105 % or less than 95 % of the pre-fixed abundance. Three main factors determine a cluster distribution: number of clusters (Ƙ), number of individuals within each cluster (μ), and radius of a cluster (RC). In this chapter, I made the following two assumptions: 1) Ƙ and μ were equal to $\sqrt{N}$, where N was the given species abundance; 2) the maximum radius of a cluster (MRC) equaled $\sqrt{\frac{A}{\pi\sqrt{N}}}$, where A was the area of extent, and *N* was the abundance for a given species. I simulated four different radii to represent different degrees of clustering, equaling to 1/4 MRC, 1/3 MRC, and 1/2 MRC, respectively. Figure 3-1 gives an example of a simulated species with 1000 individuals under four different spatial distributions. The R code for the simulation is provided in Appendix 1.

To obtain the occupancy data, the entire 100-ha plot was gridded by a given grid size (i.e., 10×10 m). A cell was defined as being occupied if it contains at least one individual, otherwise it is defined as empty. A patch is defined by rook neighbors—adjacent occupied cells shared with the same edge. The values of the six selected metrics (NP, EL, MPS, PSSD, PSCV and LPI; Table 3-2) were calculated by the program R 3.0.3 (R Core Development Team 2014) at this given grid size. R code was provided in Appendix 3. The scalograms of the metrics were then computed based on the eight aforementioned grid sizes (5 to 25 m). Since the scalograms of the six metrics followed simple linear functions after transformation, the coefficient of determination (R^2) was used to determine the goodness-of-fit of the scalograms under different scenarios.

Assessing extinction risk by scalograms

To implement an artificial disturbance resulting in increased extinction risk, I randomly removed the c = 5, 10, 20, 30, 40, 50, 60, 70, and 80% of individuals of a target species. There were a total of 10 disturbance intensity levels including the original pattern without a disturbance (c = 0). Eight disturbance intensities were applied for modeling the changes in the scalograms (which were captured by the changes in both the intercept and slope) responding to different disturbance intensities, with the remaining two (c = 50 and 80%) being retained for the interpolation and extrapolation of the resultant abundance (1- c), respectively.

The mean predicted values of the resultant abundance and standard errors of 1000 repetitions were compared across various scenarios. The agreement between the predictions and the true abundance (1-c) was measured by the relative root mean squared error (rRMSE) as follows:

$$rRMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(\frac{x_i - o_i}{o_i})^2}\ , \qquad (1)$$

where x_i is the predicted resultant abundance for species i, o_i is the real extinction risk implemented for this species, and n is the total number of repetitions for each scenario. The predictions of models fitted to scalograms for patch size standard deviation (PSSD), patch size coefficient of variance (PSCV) and largest patch index (LPI) were poor, and therefore, I only report the predictions for the number of patches (NP), edge length (EL) and mean patch size (MPS).

3.3.3 Empirical test

The empirical data was obtained from a 50-ha (1000×500 m) tropical rain forest plot on Barro Colorado Island (BCI), Panama. Every individual of tree and shrub species with a diameter at breast height (DBH) larger than 1 cm was measured and identified to species, and its' spatial coordinates were recorded. The plot was resurveyed every five years since 1980. The detailed description of the BCI plot was provided in Condit et al. (1996). In this analysis, I used the 1980 census, which contains 302 tree species, but I investigated only 31 of them because they satisfied the requirement that one large patch should not be formed at any selected grid size (from 5 to 25 m).

Following the same procedures as in the simulation (Section 3.3.2), I constructed the scalograms for the six landscape metrics for each species and examined the changes in the parameters of the scalograms in response to different disturbance intensities. Since DBH was recorded for each individual in the BCI plot, I applied selective logging as the external disturbance: c = 5, 10, 20, 30, 40, 50, 60, 70 or 80 % of the individuals of a target species with larger DBH were removed. Two disturbance intensities (c = 50 and 80%) were retained for interpolation and extrapolation, respectively, while others were used to model the changes in the scalograms with the disturbance intensities. The rRMSEs (Eq. 1) were used to measure the agreement between the predicted and the real disturbance intensities.

3.4 Results

3.4.1 Robustness of scalograms to changing abundance and spatial distributions

A brief summary of the six selected landscape metrics and their simple mathematic forms are presented in Table 3-1. The mean R^2 and the standard deviation for 1000 replicates of the scalograms with varied abundance and spatial distributions are reported in Table 3-2.

The results from the simulations showed that the scalograms of the number of patches (NP), mean patch size (MPS), patch size standard deviation (PSSD), and largest patch index (LPI) were comparatively robust to changes in abundance and spatial distribution, with the mean R^2 greater than 0.9 in all scenarios. In contrast the scalograms of edge length (EL) and patch size coefficient of variance (PSCV) were sensitive to both abundance and spatial aggregation. The mean R^2 of the scalogram of PSCV was 0.979 when the abundance was 1000 and spatial distribution was random, but the power law distribution of PSCV collapsed when the abundance was 5000 and spatial distribution was aggregated ($R^2 < 0.15$; Table 3-2). The behavior of the scalogram of Edge Length differed between scenarios of increasing abundance and spatial aggregation. When the abundance was 1000, the scalogram of EL collapsed with increased spatial aggregation, whereas the R^2 of the scalogram increased with spatial aggregation when the abundance was larger than 2000.

The results from the BCI plot were consistent with those from the simulation. The scalograms of the number of patches (NP), mean patch size (MPS), patch size standard deviation (PSSD), and largest patch index (LPI) were robust over the spectrum of grid sizes; whereas the power law distributions of edge length (EL) and patch size coefficient of variance (PSCV) were poor models ($R^2 = 0.514$ and 0.351, respectively; Table 3-3). The results from the simulation and the empirical data implied that the scalograms of EL and PSCV may follow other non-linear functions (see Discussion).

3.4.2 Estimating species extinction risk by scalograms

As mentioned in Section 3.3.2, the predictions of patch size standard deviation (PSSD), patch size coefficient of variance (PSCV) and largest patch index (LPI) were poor. Thus, I only report the predictions of the number of patches (NP), edge length (EL) and mean patch size (MPS) (Tables 3-4, 3-5 and 3-6, respectively) and their rRMSEs (Figure 3-2). The intercept and the slope of the scalogram of NP, and the intercept of the scalogram of EL were fitted by the power law function; while the slope of the scalogram of EL, and the intercept and the slope of MPS were fitted by the simple linear function.

The predicted values of the resultant abundance (1-*c,* which is 0.5 in the interpolation) were relatively constant and close to the true values no matter what the abundance and spatial distributions were used (Tables 3-4, 3-5 and 3-6). The rRMSES of the intercept and slope of the scalogram of edge length (EL) were always smaller than 0.133, while the rRMSES of the intercept and slope of the scalogram of the number of patches (NP) and mean patch size (MPS) were smaller than 0.15 and 0.3 respectively in most scenarios (Figure 3-2). The predictions of the three metrics became progressively worse in the extrapolation (c=0.8) with increased abundance and spatial aggregation. Among the three metrics, NP worked comparatively well with the rRMSES smaller than 0.3 in most cases. The extrapolation of EL and MPS were unacceptable, with rRMSES values that were up to or larger than 1 (Figure 3-2).

The empirical results conform to those from simulations. The intercept of the scalograms of the number of patches (NP) and of edge length (EL) performed best, with the rRMSEs being 0.042 and 0.008 in the interpolation (*c*=0.5), and 0.106 and 0.137 in the extrapolation (*c*=0.8), respectively (Table 3-7). The slope of the scalogram of mean patch size (MPS) worked well in the interpolation (*c*=0.5) with rRMSES being 0.090, but it became worse in the extrapolation (*c*=0.8) with rRMSES increasing to be 0.653.

3.5 Discussion

Landscape metrics have been widely used in biodiversity assessment (see the review of Uuemaa et al. 2009). Particularly, for plant species on which this chapter focuses, coverage, edge length, and edge density of forest are all positively associated with species richness and abundance (Moser et al. 2002; Kumar et al 2006; Samuelson 2008; Hernandez-Stefanoni and Dupuy 2008). However, the scale of observation is the major impediment to description of spatial patterns in hierarchically structured landscapes, thereby hindering the interpretation and comparison of results from different studies (Wiens 1989; Levin 1992; Wu and Loucks 1995). In this chapter, I extended the use of scalograms in assessing species extinction risk, and showed that it was a promising avenue to overcome the scale-dependence issues in landscape management and biological conservation.

In the previous study on scalograms, Wu (2004) found that 12 landscape metrics can be classified as type 1 metrics, which have simple scale relations. In this study, I examined only six of them, including the number of patches (NP), edge length (EL), mean patch size (MPS), patch size standard deviation (PSSD), patch size coefficient of variance (PSCV) and largest patch index (LPI). I focused on class-level landscapes and excluded the landscape-level metrics in Wu's (2004) study (e.g., Shannon's Diversity Index). Additionally, some metrics are numerically related. For instance, over a fixed extent patch density (PD) is mathematically related to NP. Although the parameters in their scalograms differed considerably, their predictions were identical and PD was thereby excluded from this analysis.

The results indicated that abundance and spatial aggregation had little effect on the scalograms of the number of patches (NP), mean patch size (MPS), patch size standard deviation (PSSD), and largest patch index (LPI) (R^2 larger than 0.96 in most scenarios; Figure 3-2), which is a critical premise for their application in assessing species extinction risk. The scale relations of edge length (EL) and patch size coefficient of variance (PSCV) were vulnerable to changing abundance and spatial aggregation (R^2 became lower with increased abundance and spatial aggregation; Figure 3-2), implying that their scalograms may follow some non-linear relations. As He and Hubbell (2003) showed, the relationship between Edge Length and grid size is a bell-shaped curve. One can imagine that EL increases first with the increased grid size due to the enlargement of the contour of each occupied grid; meanwhile, NP decreases consistently with the grid size because of many small patches merging into a few large ones. When NP decreases by a more than off-setting amount relative to the growing contour, EL then decreases. The grid size where the maximum value of EL occurs is determined by both the abundance and spatial distribution. The R^2

for EL in Table 3-2 implied that the grid size at which the threshold value occurs was comparatively large (close to 25 m) when the abundance was low and the spatial distribution was random but relatively small (close to 5 m) when abundance was high and the spatial distribution was aggregated. The robustness of a polynomial distribution for EL was outside the scope of this chapter, and its application to assessing extinction risk still awaits further study.

Given the robustness of the scalograms and their predictive power, the number of patches (NP) and mean patch size (MPS) are recommended for estimating the loss of species abundance (which is the extinction risk as defined by the IUCN Criterion A) based on distribution maps (the IUCN Criterion B). Particularly, when the abundance was 1000 in the simulation, the rRMSES of NP and MPS were smaller than 0.08 and 0.14 in the interpolation (c=0.5), respectively (Figure 3-2). This feature of model performance is important because conservation biologists are more concerned about species of low abundance. In extrapolations NP also provided a better prediction when the abundance was low, with rRMSES smaller than 0.14 even in highly aggregated spatial distributions. Extrapolations for both NP and MPS became worse with increased abundance and spatial aggregation, and the rRMSES of MPS could be as high as 3.6.

The application of this method requires detailed stem-mapping data for the first census of a plot, but only needs occupancy data for subsequent surveys. One can apply artificial disturbance intensities on the original landscape patterns, and construct a relationship between the changes in the scalograms and different disturbance intensity levels. The true risk of extinction risk can be estimated by the scalograms of the number of patches (NP) or mean patch size (MPS) obtained from the occurrence map for spatial patterns after the disturbance.

It has been widely recognized that landscape metrics are scale dependent, forming so-called scalograms (Wu et al. 2002; Wu 2004; Shen et al. 2004). Despite the importance of the scalogram for investigating the behavior of landscape metrics over spatial scales, its application in conservation biology is not well explored. This study explored the changes in scalograms in responding to different levels of disturbance intensity. The results showed that it was likely to be a new and promising avenue for estimating species extinction risk. A nontrivial feature of the use of scalograms is that it circumvents the scale-dependence issue, which is a major concern in landscape ecology. The method developed in this chapter is expected to facilitate assessing the endangerment status of species in spatially structured landscapes, thereby contributing to the study and practice in landscape management and biological conservation.

3.6 Conclusion

Scalograms are important for understanding behaviors of landscape metrics over spatial scales, but their applications in landscape management and biological conservation are not well studied. This present paper developed a new framework to fill this gap by exploring the changes in scalograms in responding to disturbance intensities. The performance of this new method was thoroughly tested by using both simulated and empirical data sets.

The results revealed that the scalograms of the number of patches (NP), mean patch size (MPS), patch size standard deviation (PSSD), and largest patch index (LPI) were robust to changing abundance and spatial distribution. The predictions of the number of patches (NP), edge length (EL), and mean patch size (MPS) were relatively accurate, especially for interpolation. Given the robustness of the scalograms and their excellent predictive power, I recommend that NP and MPS are the most useful for the assessment of species extinction risk.

3. 7 Literature cited

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Table 3-1. Summary of the six commonly used landscape metrics

Landscape metrics	Abbreviation	Description and Formula	Scalogram Models
Number of Patches	NP	Total number of patches in the landscape	Exponential: $lny = a + bx$
Edge Length	EL	Sum of the lengths of all edge segments (m)	Power law: $y = ax^b$
Mean Patch Size	MPS	The average area of patches (m^2)	Power law: $y = ax^b$
Patch Size Standard Deviation	PSSD	The standard deviation of patch size in the landscape (m^2)	Power law: $y = ax^b$
Patch Size Coefficient of Variance	PSCV	The ration of standard deviation of patch size to mean patch size	Power law: $y = ax^b$
Largest Patch Index	LPI	The ration of the area of the largest patches to the total area of the landscape	Power law: $y = ax^b$

Table 3-2. R^2 for the scalogram models of the six landscape metrics in the simulation

Abundance	Spatial distribution*	NP	EL	PSCV	MPS	PSSD	LPI
1000	Random	0.936	0.986	0.991	0.984	0.988	0.978
		(0.008)	(0.001)	(0.007)	(0.002)	(0.003)	(0.009)
	Slight	0.959	0.975	0.971	0.983	0.981	0.970
		(0.008)	(0.004)	(0.015)	(0.002)	(0.005)	(0.011)
	Moderate	0.973	0.954	0.984	0.982	0.986	0.981
		(0.007)	(0.008)	(0.009)	(0.003)	(0.005)	(0.009)
	High	0.989	0.883	0.963	0.983	0.994	0.991
		(0.004)	(0.021)	(0.026)	(0.003)	(0.003)	(0.005)
2000	Random	0.905	0.922	0.945	0.929	0.935	0.928
		(0.011)	(0.004)	(0.012)	(0.007)	(0.005)	(0.010)
	Slight	0.972	0.869	0.975	0.969	0.975	0.976
		(0.008)	(0.018)	(0.011)	(0.005)	(0.007)	(0.010)
	Moderate	0.989	0.770	0.971	0.977	0.990	0.989
		(0.004)	(0.034)	(0.021)	(0.004)	(0.004)	(0.005)
	High	0.996	0.491	0.860	0.986	0.996	0.988
		(0.002)	(0.064)	(0.006)	(0.003)	(0.001)	(0.007)
3000	Random	0.923	0.747	0.867	0.897	0.929	0.933
		(0.011)	(0.009)	(0.034)	(0.012)	(0.004)	(0.008)
	Slight	0.982	0.630	0.967	0.964	0.982	0.985
		(0.006)	(0.041)	(0.015)	(0.006)	(0.006)	(0.006)
	Moderate	0.995	0.428	0.935	0.979	0.993	0.989
		(0.002)	(0.060)	(0.035)	(0.004)	(0.002)	(0.005)
	High	0.992	0.082	0.769	0.990	0.995	0.983
		(0.004)	(0.042)	(0.0839)	(0.002)	(0.003)	(0.010)
4000	Random	0.944	0.423	0.883	0.900	0.936	0.950
		(0.003)	(0.016)	(0.029)	(0.005)	(0.003)	(0.007)
	Slight	0.990	0.293	0.926	0.966	0.988	0.987
		(0.004)	(0.054)	(0.025)	(0.007)	(0.004)	(0.004)
	Moderate	0.997	0.104	0.899	0.981	0.994	0.989
		(0.002)	(0.044)	(0.041)	(0.004)	(0.001)	(0.006)
	High	0.986	0.027	0.698	0.993	0.994	0.978
		(0.005)	(0.024)	(0.111)	(0.002)	(0.003)	(0.012)
5000	Random	0.947	0.104	0.855	0.907	0.949	0.967
		(0.014)	(0.011)	(0.032)	(0.008)	(0.004)	(0.006)
	Slight	0.994	0.054	0.865	0.969	0.991	0.984
		(0.003)	(0.028)	(0.029)	(0.006)	(0.002)	(0.005)
	Moderate	0.996	0.005	0.845	0.984	0.994	0.984
		(0.003)	(0.007)	(0.055)	(0.004)	(0.002)	(0.009)
	High	0.982	0.182	0.603	0.994	0.994	0.973
		(0.006)	(0.043)	(0.141)	(0.001)	(0.004)	(0.014)

Note: values in the parenthesis are standard errors for 1000 repetitions.

Table 3-3. R^2 for the scalogram models of the six landscape metrics in the BCI plot

	NP	EL	PSCV	MPS	PSSD	LPI
R^2	0.981 (0.027)	0.779 (0.224)	0.920 (0.163)	0.979 (0.010)	0.983 (0.010)	0.979 (0.013)

Table 3-4. Predictions of the resultant abundance (1-*c*) by the scalograms of NP in the simulation

	Parameters	Spatial distribution	Abundance				
			1000	2000	3000	4000	5000
c=0.5	intercept	Random	49.49 (0.70)	48.75 (0.48)	48.34 (0.69)	49.98 (1.07)	52.60 (2.15)
		Slight	50.21 (0.61)	50.26 (0.73)	50.71 (0.91)	51.30 (1.21)	51.91 (1.35)
		Moderate	50.45 (0.70)	50.92 (0.91)	51.56 (1.17)	52.07 (1.35)	52.51 (1.62)
		High	50.86 (0.99)	51.80 (1.30)	52.50 (1.54)	52.81 (1.82)	52.94 (2.36)
	Slope	Random	49.75 (2.50)	48.85 (1.20)	49.65 (1.18)	52.38 (1.59)	55.20 (2.77)
		Slight	50.23 (2.72)	50.97 (1.89)	51.73 (1.78)	52.42 (2.15)	52.85 (2.32)
		Moderate	50.94 (2.66)	51.86 (2.20)	52.58 (2.48)	52.95 (2.55)	53.12 (2.81)
		High	51.72 (2.99)	52.89 (2.88)	53.35 (3.10)	53.35 (3.44)	52.98 (4.23)
c=0.8	Intercept	Random	19.62 (0.28)	21.79 (0.37)	22.58 (0.51)	21.44 (0.44)	19.52 (0.51)
		Slight	19.41 (0.37)	19.59 (0.48)	19.18 (0.57)	18.50 (0.70)	17.81 (0.71)
		Moderate	19.24 (0.43)	18.79 (0.54)	18.10 (0.60)	17.26 (0.73)	16.56 (0.90)
		High	18.72 (0.57)	17.53 (0.72)	16.58 (0.83)	15.85 (0.95)	15.33 (1.05)
	Slope	Random	20.86 (2.82)	21.83 (1.36)	21.14 (0.93)	19.11 (0.82)	16.80 (0.87)
		Slight	19.88 (2.83)	18.94 (1.69)	17.91 (1.35)	17.06 (1.34)	16.36 (1.23)
		Moderate	19.34 (2.76)	17.74 (1.73)	16.69 (1.51)	15.99 (1.51)	15.23 (1.71)
		High	18.13 (2.57)	16.34 (2.05)	15.35 (1.93)	14.98 (1.94)	14.63 (2.00)

Note: values in the parenthesis are standard errors for 1000 repetitions.

Table 3-5. Predictions of the resultant abundance (1-*c*) by the scalograms of EL in the simulation

	Parameters	Spatial distribution	Abundance				
			1000	2000	3000	4000	5000
c=0.5	intercept	Random	50.39 (0.21)	50.13 (0.19)	49.95 (0.18)	49.80 (0.16)	49.71 (0.16)
		Slight	50.35 (0.25)	50.16 (0.23)	50.07 (0.23)	50.06 (0.66)	50.08 (0.24)
		Moderate	50.33 (0.30)	50.22 (0.29)	50.21 (0.28)	50.27 (0.28)	50.35 (0.26)
		High	50.32 (0.35)	50.35 (0.34)	50.49 (0.33)	50.68 (0.31)	50.82 (0.33)
	Slope	Random	50.38 (3.40)	50.03 (1.59)	50.12 (1.02)	50.16 (0.70)	50.29 (0.57)
		Slight	50.46 (3.15)	50.58 (1.66)	50.82 (1.15)	51.15 (0.95)	51.34 (0.81)
		Moderate	50.63 (3.06)	51.07 (1.70)	51.48 (1.20)	51.87 (1.04)	52.22 (0.91)
		High	51.11 (2.43)	51.86 (1.56)	52.48 (1.26)	53.12 (1.06)	53.46 (1.03)
c=0.8	Intercept	Random	19.20 (0.14)	19.61 (0.13)	19.92 (0.12)	20.17 (0.12)	20.39 (0.11)
		Slight	19.25 (0.17)	19.59 (0.16)	19.75 (0.15)	19.84 (0.16)	19.86 (0.17)
		Moderate	19.32 (0.20)	19.55 (0.18)	19.61 (0.18)	19.56 (0.18)	19.47 (0.19)
		High	19.37 (0.24)	19.43 (0.23)	19.23 (0.22)	18.99 (0.22)	18.76 (0.66)
	Slope	Random	20.40 (4.64)	19.73 (2.22)	19.55 (1.47)	19.27 (1.10)	19.27 (0.84)
		Slight	19.12 (4.26)	17.95 (2.37)	16.85 (1.74)	16.05 (1.42)	15.20 (1.29)
		Moderate	18.31 (4.12)	16.24 (2.39)	14.83 (1.79)	13.54 (1.26)	12.22 (1.49)
		High	16.78 (3.66)	14.06 (2.47)	11.35 (2.04)	9.62 (1.74)	7.98 (1.61)

Note: values in the parenthesis are standard errors for 1000 repetitions.

Table 3-6. Predictions of the resultant abundance (1-*c*) by the scalograms of MPS in the simulation

	Parameters	Spatial distribution	Abundance				
			1000	2000	3000	4000	5000
c=0.5	intercept	Random	49.31 (3.06)	48.38 (1.40)	48.34 (1.39)	51.24 (1.99)	55.74 (3.67)
		Slight	50.30 (3.83)	51.61 (2.93)	53.31 (3.15)	55.28 (4.02)	57.43 (4.60)
		Moderate	51.60 (4.05)	54.13 (4.14)	57.20 (5.23)	60.51 (6.57)	64.93 (8.41)
		High	53.67 (5.46)	59.95 (7.51)	69.21 (0.99)	69.89 (13.3)	57.47 (18.8)
	Slope	Random	49.50 (2.44)	48.54 (1.13)	48.46 (1.12)	50.69 (1.60)	53.96 (2.82)
		Slight	50.20 (2.88)	51.14 (2.06)	52.21 (2.00)	53.31 (2.37)	54.17 (2.53)
		Moderate	51.13 (2.84)	52.65 (2.51)	54.01 (2.84)	54.99 (2.96)	55.72 (3.25)
		High	52.42 (3.40)	54.78 (3.42)	56.27 (3.77)	57.05 (4.26)	57.19 (5.51)
c=0.8	Intercept	Random	23.19 (3.59)	27.19 (1.72)	25.08 (1.68)	19.62 (1.49)	13.22 (2.03)
		Slight	19.41 (4.56)	15.67 (3.84)	11.28 (4.05)	6.82 (4.48)	3.65 (3.27)
		Moderate	16.55 (5.05)	9.33 (5.01)	3.82 (4.07)	1.50 (3.00)	1.19 (2.77)
		High	10.89 (6.20)	2.84 (4.62)	5.60 (15.03)	49.75 (45.8)	95.38 (35.6)
	Slope	Random	22.69 (2.88)	26.26 (1.45)	24.74 (1.42)	20.07 (1.22)	14.74 (1.61)
		Slight	19.51 (3.54)	16.71 (2.78)	13.56 (2.73)	10.43 (3.03)	7.66 (2.98)
		Moderate	17.24 (3.81)	12.16 (3.29)	7.98 (3.31)	4.76 (3.37)	2.47 (2.89)
		High	13.10 (4.36)	6.03 (4.13)	2.37 (3.04)	1.01 (2.10)	0.62 (1.81)

Note: values in the parenthesis are standard errors for 1000 repetitions.

Table 3-7. Predictions of the resultant abundance (1-*c*) by the scalograms of NP, EL and MPS in the BCI plot.

Disturbance intensity	Landscape metrics	Parameter	Predictions	rRMSE
c = 50 %	NP	Intercept	50.40 (2.11)	0.042
		Slope	49.89 (2.17)	0.043
	EL	Intercept	50.25 (0.34)	0.008
		Slope	51.40 (6.02)	0.122
	MPS	Intercept	51.12 (6.64)	0.133
		Slope	51.59 (4.27)	0.090
c = 80 %	NP	Intercept	19.75 (2.14)	0.106
		Slope	25.81 (8.36)	0.504
	EL	Intercept	19.61 (0.63)	0.037
		Slope	19.78 (9.36)	0.462
	MPS	Intercept	30.96 (19.2)	1.097
		Slope	24.10 (12.6)	0.653

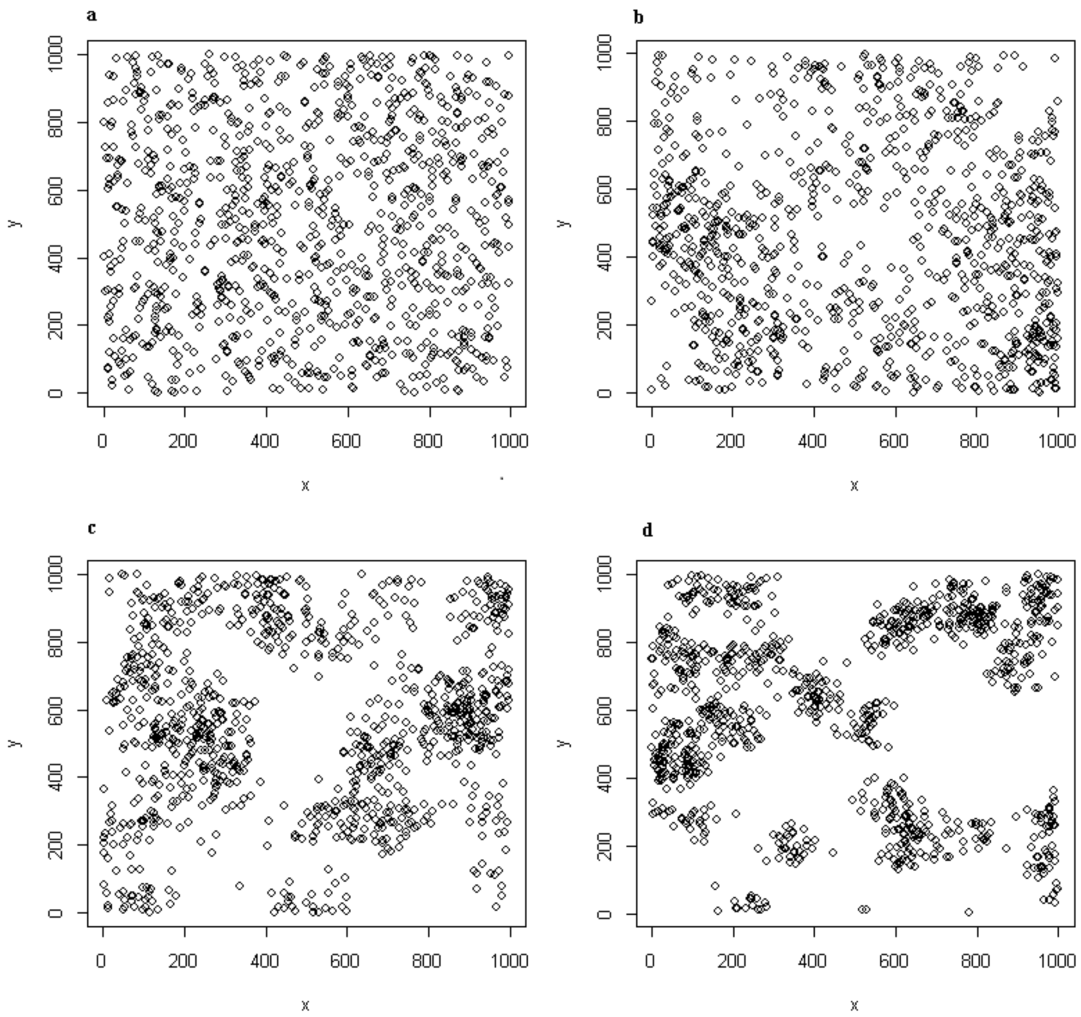
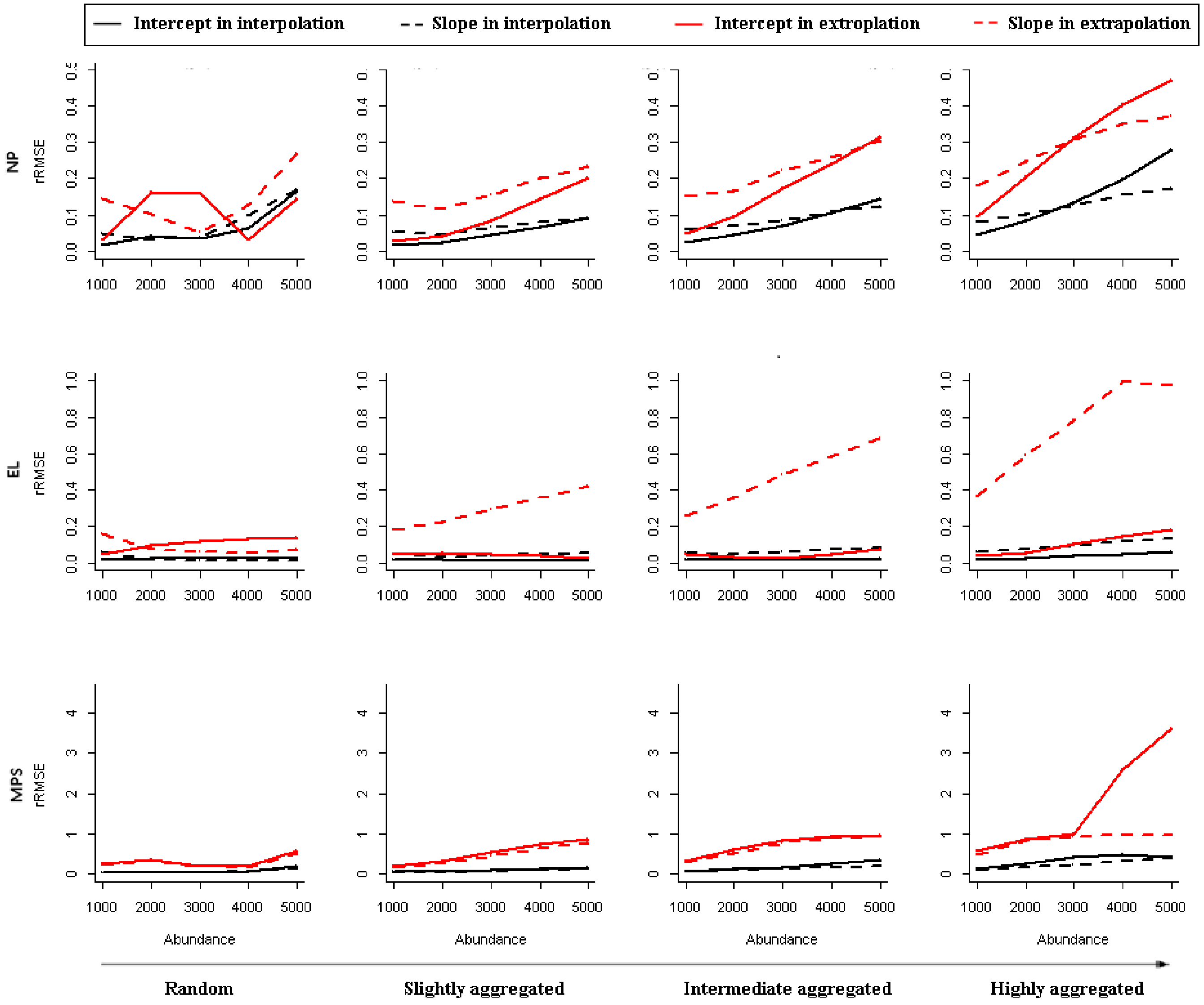


Figure 3-1. Example simulated species distributions with 1000 individuals under four different spatial patterns: (a) random distribution; (b) slightly aggregated distribution; (c) moderately aggregated distribution; (d) highly aggregated distribution.


Intercept in interpolation
Slope in interpolation
Intercept in extroplation
Slope in extrapolation
NP
EL
MPS
rRMSE
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.8
1.0
0
1
2
3
4
1000
2000
3000
4000
5000
Abundance
Random
Slightly aggregated
Intermediate aggregated
Highly aggregated

(Figure on the previous page)

Figure 3-2 . rRMSEs for the predictions of the scalograms of NP, EL and MPS in different scenarios with various abundance and spatial distributions. Black solid lines: the interpolation of the intercept of the scalograms (c = 50 %); black dashed lines: the interpolation of the slope of the scalograms (c = 50 %); red solid lines: the extrapolation of the intercept of the scalograms (c = 80 %); red dashed lines: the extrapolation of the slope of the scalograms (c = 80 %).

Chapter 4: Could the power-law signal an early warning for ecosystem degeneration caused by external disturbance?

4.1 Abstract

The power-law function has long been used to model the spatial distribution of species. A recent study has shown that failing to fit to the power-law could be an early warning of ecosystem degeneration. The generality of this finding has been widely discussed, but a question critical to the debate has been overlooked: whether the power-law model is subject only to the effect of disturbance or whether it can be affected by other factors? To answer this question, I compared the power-law model with a truncated power-law model, analyzing the possible effects of spatial scale, species abundance and spatial distribution on these two models. The results of both simulation and empirical analysis showed that the two models were sensitive to the effects of abundance, spatial aggregation and scale, and that the power-law model was inferior to the truncated model. The results suggest that power-law model is of little use for signaling early warning of ecosystem degeneration as a result of disturbance.

4.2 Introduction

With few exceptions, the distribution of species in landscapes is often heterogeneous, forming spatially patchy patterns (Roth 1976; Niemela et al. 1992; Brown 1995). Among the many methods and models used to describe the geometric and statistical properties of species distribution, the power-law model is particularly prominent. It predicts that the majority of species in nature have many small patches with a few large ones – the number of patches along patch size forms a log-log linear relationship. This relationship has been widely studied both in theory and application. In theory, random walks (Sneppen et al. 1995), phase transitions and critical phenomena (Reynolds et al. 1977; He and Hubbell 2003), self-organized criticality (Bak et al. 1987; Drossel and Schwabl 1992), combinations of exponentials (Miller 1957) and Yule's birth and death stochastic process can give rise to a power-law distribution.

In applications, Kefi et al. (2007) hypothesized that the power-law model could be used to indicate the degeneration of ecosystem caused by external disturbance. The rationale behind Kefi et al.'s work is the argument that under catastrophic regime shifts, many complex systems contain critical thresholds (or so-called 'tipping points'), at which highly stable systems shift abruptly to a low stable state (see reviews in Scheffer et al. 2009 and Scheffer et al. 2012). Examples of catastrophic regime shifts in ecology include lake eutrophication, desertification of arid/semi-arid ecosystems, and collapse of fish stocks (Beisner et al. 2003; Scheffer et al. 2003; Rietkerk et al. 2004; Hsieh et al. 2006; Litzow 2008). Recent studies have shown that systems close to a tipping point would release early warning signals.

For instance, when a tipping point is approaching, the recovery time and length, spatial correlation and variance of abundance or coverage, and autocorrelation between adjacent neighbors will increase dramatically (Wilssel 1984; Verarrt et al. 2012; Carpenter et al. 2011; Drake et al. 2010; Dai et al. 2013). Thus, it seems reasonable to use those measures (i.e., recovery time, spatial correlation, variance and autocorrelation, etc.) to indicate the approach of a critical state transition in a study system.

However, a major disadvantage of these measures is that they are all time- and labor-intensive to measure. Alternatively, the power-law model provides a simple tool potentially useful for predicting ecosystem degeneration. Kefi et al. (2007) showed in the absence of grazing that patch-size patterns of vegetation cover follow a power-law distribution, while the power-law model failed to fit the patch-size distribution when there was intensive grazing leading to the onset of desertification.

Maestre and Escudero (2009) and Weerman et al. (2012), however, questioned the generality of Kefi et al.'s finding and showed that a truncated power-law model was a better alternative to describing patch-size distributions of perennial vegetation and diatom biofilms with no recent disturbance history. Also, in a case study of oak woodland in Southern Portugal, Costa et al. (2014) found that the truncated power-law gave a better fit to patch-size distributions before the occurrence of wildfire. The discrepancy of the patch-size distribution suggests that the power-law model is unlikely to apply universally but is contingent on the circumstances from which data arise.

There are many factors other than disturbance that could result in non-power-law distributions such as the spatial scale of observation and the abundance and spatial distribution of species. First, scale is without doubt the prime issue affecting spatial patterns (Wien 1989; Levin 1992). He and Hubbell's percolation theory (2003) showed that the number of patches decreases with increasing grain size, indicating that spatial pattern may be sensitive to the scale at which the pattern is mapped. Second, spatial distributions can take many forms and result in various patch size distributions. For example, Scanlon et al. (2007) showed that random spatial distribution of patches could derail the power-law model. Third, species of different abundance can also have different patch size distribution that may cause the failure of the power-law distribution. Percolation theory (Stauffer and Ahorany 1992; He and Hubbell 2003) predicts that a large patch forms when the proportion of occupied patches reaches a threshold of 0.59 for random distribution, thereby leading to the abrupt reduction of the number of patches, which may also derail the power-law model.

An important premise of the use of power-law model is that the patch size distribution should be robust to factors other than disturbance. But as previously mentioned, any observed lack of fit of the model could be simply due to the scale of observation, or spatial distribution rather than disturbance. Moreover, the possible effects of those factors other than disturbance on the power-law model are little examined. In this chapter, I tested whether the power-law model was robust to changes in scale, abundance, and spatial distribution. I used both simulations and empirical data to compare the power-law model and a truncated power-law model by varying spatial scale, abundance and spatial distribution of species.

4.3 Methods

4.3.1 Simulation scenarios and empirical data

I firstly simulated species distributions in a 50-ha area (1000×500 m) that defines the study extent. In the simulation, I varied abundance (400, 1000, 2000, 3000, 4000 and 5000 individuals), scale (5, 10 and 20 m) and spatial distribution (regular, random and four different degrees of aggregated distribution). In total there were 108 different scenarios (6 abundance × 3 scales × 6 spatial distributions). I did 1000 replicates for each scenario.

To generate regular and clustered distributions, I used the functions rStrauss and rThomas in the 'spatstat' package of R 3.0.3 (R Development Core Team 2014), respectively. The two programs do not generate exactly the same number of pre-fixed trees. To account for this I retained only a species if its simulated number of individuals was no more than 105 % or less than 95 % of the pre-fixed abundance. To generate the clustered distributions, I made the following assumptions: 1) Number of parent trees are equal to $\sqrt{N}$ (round to integer), where N was the total number of individuals; 2) the maximum distance between a parent tree and offspring (MD) equaled $\sqrt{\frac{A}{\pi\sqrt{N}}}$, where A is study area (50 ha). I simulated four different distances between parent trees and offspring (DPO), representing different degree of aggregation, which are 1/4 MD, 1/3 MD, 1/2 MD and 3/4 MD, respectively (see

Figure 4-1). The R code for the simulation of aggregated distribution is provided in Appendix 1.

I also used empirical data to evaluate the effects of spatial scale, species abundance and spatial aggregation on the performance of the power-law and truncated power-law models. I used the first census data of 50 ha (1000×500 m) plot on the Barro Colorado Island (BCI), Panama, which was established in 1980-1982. Most of the island, including 48 ha of the 50-ha plot, has seen no human disturbance other than research activities for over 500 years (Condit et al. 1996). There are 302 species, with the most abundant species having 31,934 stems.

4.3.2 Generating patch-size distributions

Given a real or a simulated species, I divided the whole plot (1000×500 m) into small grid cells according to the grain size (e.g., 20 m). If there was at least one individual located in the cell, the cell was occupied, otherwise it was considered to be empty. I then clustered the occupied cells sharing an edge into a patch (Figure 4-2a), and plotted the number of patches ($N(S)$) against the patch size (S) to draw the patch-size distribution (Figure 4-2b). This is equivalent to the patch-size distribution of vegetation cover in Kefi et al. (2007). The patch size distributions for three different grain sizes (5×5, 10×10 or 20×20 m) were analyzed in this study. The R code for the calculation of the number of patches is provided in Appendix 3.

4.3.4 Statistical analysis

I used the power-law model ($N(S) = CS^{-\gamma}$, where $N(S)$ represents the number of patches, S represents patch size and C and γ are two parameters to be estimated) and a truncated power-law model ($\mathrm{N(S)} = \mathrm{CS}^{-\gamma}\exp\left(-\frac{\mathrm{S_x}}{\mathrm{S}}\right)$, where S_x is a parameter to make the model more flexible) to fit patch-size distributions obtained from the simulated and empirical species data at three scales. Because there were two parameters in the power-law model and three in the truncated power-law model, at least four patch-size classes were required for estimating model coefficients. To make the fitting more reliable, I only considered the simulated species that had six patch-size classes. I used Akaike's Information Criterion (AIC) to judge which model had the most support, which is determined by both the residue and the number of parameters in the model. A lower AIC value indicates the superiority of a model.

4.4 Results

4.4.1 Simulation test

Of the 108 simulated scenarios, 67 met the model fitting requirement that species that had six patch-size classes or better. The number of patch-size distributions where the power-law had a superior model fit (lower AIC value) never exceeded 550 patch-size distributions (Figure 4-3). For the total of 1000 simulations this represents around half of the data and is broadly consistent with a random expectation: neither the power law-model nor the truncated model had clear superiority over each other.

The *y* value in Figure 4-3 represents the number of patch-size distributions fitted well by the power-law model in 1000 simulations, hence one can easily obtain the number of patch-size distributions where the truncated power-law was superior through a simple calculation (1000 – the *y* value in Figure 4-3). Although the truncated power-law did work significantly well in some scenarios, e.g., when the abundance equal to 5000 and the distribution being aggregated distribution at 10 m, better performance of either model showed no systematic pattern (Figure 4-3f). A superior fit for the truncated power-law was not restricted to specific conditions of abundance, scale or spatial distribution and any of the three factors could alter the patch-size distribution and best fitting model.

4.4.2 Empirical test

I fitted the power-law and truncated power-law model to 35 BCI tree species that had at least six patch-size classes and had abundances that ranged from 358 to 2899. The patch-size distribution of the each species at three different scales (5, 10, and 20 m) was fitted by both the power-law and the truncated power-law (Table 4-1).

When the grain size was 5 m (first two columns in Table 4-1), the power-law model provided a better fit to patch-size distributions of 12 species (with lower AIC value), whose abundances were not significantly different from the remaining 23 species ($p = 0.147$ in the t-test). When scaling up from 5 to 10 m (middle two columns in Table 4-1), 15 species' patch-size distributions changed significantly: eight of which then deviated from the power-law to the truncated power-law, while seven of which changed in the opposite direction. In total, the power-law provided a better fit to patch-size distributions of 11 species, whose abundances again did not differ from the remaining 24 species ($p = 0.233$, the data were log-transformed to meet the assumption of normality in the t-test). When scaling up from 10 to 20 m (last two columns in Table 4-1), 14 species' patch-size distributions changed significantly: eight of which shifted from the power-law to the truncated power-law, while the remaining six changed in the opposite. The power-law provided a better fit to patch-size distributions of nine species (with lower AIC value), whose abundances were not significantly different from the remaining 26 species ($p = 0.175$, the data were log-transformed to meet the assumption of normality in the *t*-test).

Overall, the results in the BCI plot conformed to those in the simulation, indicating that neither the power-law nor the truncated power-law model showed clear superiority in fitting patch-size distributions for species. However, unlike the simulations, the power-law model fit to a species' distribution depended on its' specific characteristic (i.e., abundance and spatial pattern) as well as the scale at which the spatial pattern was mapped.

4.5 Discussion

It has been recognized that power-laws occur in a wide variety of phenomena (Bak 1996, Brown et al. 2002, Newman 2005), and two major types of power laws are commonly studied in ecology (White et al. 2008), including the bivariate relationship between two variables (i.e., species-area relationship and body-size allometries) and frequency distribution of some event (i.e., the sizes of earthquakes and the numbers of species within certain biological taxa). The focus of this chapter—patch size distribution of vegetation cover—belongs to the second type, and the application of the power-law distribution is based on the argument of the catastrophic regime shift (Scheffer and Carpenter 2003), which has been observed to occur in many complex systems, including financial markets (May et al. 2008), climate change (Lenton et al. 2008), and water and rangeland ecosystems (Scheffer et al. 2001; Scheffer and Carpenter 2003). Unlike other data-demanding warning signals, the use of power-law model is shown to be simple and efficient in predicting the desertification of dryland ecosystem caused by grazing pressure (Kefi et al. 2007; Kefi et al. 2011).

Although the generality and robustness of this method have been questioned (Maestre and Escudero 2009; Maestre and Escudero 2010; Weerman et al. 2012; Costa et al. 2014), the power-law model is considered to be a useful indicator of changes in spatial patterns (Carpenter et al. 2011; Scheffer et al. 2012). For example, Schoelynck et al. (2012) and Khalyani et al. (2013) found that the power-law model gave a better fit to the cumulative patch-size distributions in real case studies.

However, the results of this chapter show that power-law model is sensitive to the effect of spatial scale, species abundance and spatial distribution of species, suggesting that Kefi et al.'s (2007) conclusion that power-law model is useful to indicate the effect of disturbance is not reliable. Interestingly, I also found the truncated power-law is not superior to the power-law model, which has previously been suggested (Maestre and Escudero 2009; Weerman et al. 2012). My analysis clearly showed that neither of the tested methods was immune to the effects of scale, abundance and spatial distribution of species which can seriously confound the power-law or truncated power-law patterns. Thus, the deviation in patch-size distribution from power-law behavior is not a reliable pattern to predict ecosystem degeneration.

Lin et al. (2010) found that with an appropriate binning method, the deviation of patch-size distributions from the power-law model was indicative of the degeneration of rangeland in Inner Mongolia, China, whereas the truncated power-law gave a better fit to all the patch-size distributions when the original data were adopted. White et al. (2008) also showed that uncorrected simple logarithmic binning would cause bias of the power law distributions. Therefore, it is noteworthy that binning method could be another determinant affecting the performance of the power-law model. Options for binning data are also highly dependent on the study extent and mapping resolution, thereby compromising the universality of the use of the power-law for describing patch-size distributions. In this chapter, each bin in x-axis represents a single patch-size value, and no evidence was found in support of Kefi et al.'s work (2007).

Alternatives to the power-law model should be explored to signal early warning in the change of ecosystems. For instance, Corrado et al. (2014) proposed that percolation—the formation of one single large patch—could serve as an indicator of desertification transitions. Las Heras et al. (2011) suggested a focus on the fragmentation and the loss of large vegetation patches when assessing landscape structure in semi-arid ecosystems. Finding appropriate warning signals is an important task to forecast the occurrence of degeneration and prevent the collapse of ecosystems. However, the use of the power-law distribution to indicate or predict ecosystem degeneration is unreliable because specific landscape characteristics (i.e., abundance and spatial distribution) and methodological issues (i.e., scale and binning method) can all cause patch-size distributions to deviate from the power-law model.

4.6 Conclusion

The power-law model which describes that spatial distribution of species typically consists of a few large patches with many small ones. The model has been used to predict the occurrence of disturbance. However, the application of this method in ecology remains controversial because the sensitivity of the power-law model to factors other than disturbance has not been thoroughly evaluated.

In this study, I used simulation and empirical data to evaluate the effects of abundance, scale and spatial distribution of species on the performance of the power-law model and truncated power-law model. These results showed that neither the power law-model nor the truncated model had clear superiority over each other. Both models were sensitive to abundance, scale and spatial distribution. The failure of power-law to fit patch size distribution could be caused by improper scale or specific abundance and spatial distribution rather than disturbance. I therefore conclude that power-law model or the truncated model has little use to predict ecosystem degeneration.

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Table 4-1. Performances of the power-law and the truncated power-law for the patch-size distributions of 35 species in the BCI plot

Species	abundance	5 m		10 m		20 m	
		AIC$_{PL}$	AIC$_{TPL}$	AIC$_{PL}$	AIC$_{TPL}$	AIC$_{PL}$	AIC$_{TPL}$
Beilshmiedia pendula	2318*	44.62	35.06	48.49	45.50	0.93	-2.77
Calophyllum longifolium	1130	**14.68**	**15.08**	3.75	1.77	27.17	20.77
Cassipourea elliptica	1007	**0.10**	**1.81**	37.62	21.05	1.76	-0.18
Cecropia insignis	716*	23.67	21.24	28.87	25.72	17.28	16.45
Cordia bicolor	765*	23.67	4.90	37.83	34.22	10.31	7.32
Cordia lasiocalyx	1282*	18.37	2.04	33.62	17.10	0.64	-19.19
Coussarea curvigemia	2079	**30.99**	**32.39**	**17.16**	**19.13**	20.09	17.44
Croton billbergianus	358	12.83	6.99	**17.39**	**17.50**	9.63	8.36
Cupania seemannii	1212	15.49	13.18	**41.37**	**43.27**	**1.27**	**3.18**
Eugenia galalonensis	1581*	10.90	9.00	54.62	41.62	-4.91	-5.04
Eugenia oerstediana	1926	39.21	25.52	**31.34**	**33.29**	7.51	-7.18
Guarea Guidonia	1838*	37.10	36.18	54.92	43.90	-2.88	-4.68
Guarea dumetorum	1038	12.79	5.85	**12.94**	**14.42**	**10.44**	**12.19**
Lacistema aggregatum	1404*	8.21	8.17	31.14	25.12	6.30	-17.55
Maquira guianensis	1460	**24.19**	**25.84**	41.96	25.46	12.54	5.48
Miconia argentea	600*	11.75	4.71	23.40	15.87	17.09	12.54
Ocotea whitei	429	22.96	19.39	**5.42**	**5.81**	8.73	3.02
Oenocarpus mapora	1830	**24.98**	**26.37**	**71.13**	**72.19**	9.09	5.68
Ouratea lucens	1193	**23.99**	**24.25**	42.55	40.17	25.49	12.88
Palicourea guianensis	867*	**7.075**	**9.02**	**21.12**	**22.20**	**-5.76**	**-3.84**
Picramnia latifolia	1047	23.63	6.63	41.36	39.03	**-4.26**	**-3.80**
Poulsenia armata	1404*	34.73	29.43	12.44	6.40	2.24	-13.12
Prioria copaifera	1382*	49.75	39.01	35.49	17.51	1.46	-13.59
Protium panamense	2899	**30.09**	**31.33**	21.20	15.64	**-2.36**	**-2.34**
Protium tenuifolium	2853*	53.11	42.36	41.35	39.63	5.25	1.71
Psychotria marginata	554*	7.76	5.34	8.57	7.98	7.71	5.94
Pterocarpus rohrii	1462	27.83	8.06	**50.06**	**51.92**	7.65	6.82
Quararibea asterolepis	2200*	35.39	22.83	30.18	17.72	8.54	-3.01
Rinorea sylvatica	2314	**27.60**	**29.59**	12.84	9.86	**7.28**	**7.40**
Simarouba amara	1230	24.97	14.08	**27.46**	**28.97**	7.35	-4.88
Socratea exorrhiza	622*	38.67	34.81	15.20	5.27	16.02	7.46
Swartzia simplex_var.grandiflora	2662	**65.24**	**67.23**	42.33	40.36	**-6.45**	**-5.26**
Talisia nervosa	747	**11.11**	**12.40**	**2.23**	**29.39**	19.75	12.16
Virola sebifera	1615	**21.57**	**23.40**	36.76	28.91	**-2.41**	**-0.44**
Ouratea lucens	1193	**23.99**	**24.25**	42.55	40.17	25.49	12.88

(*Table is on the previous page*)

Note: The AIC value of the power-law model is denoted by AIC_{PL} and the AIC value of the truncated power-law model is denoted by AIC_{TPL}; bold figure means the power-law model works better than the truncated power-law model; '*' indicates that either the power-law or the truncated power consistently provides a better fit to the patch-size distribution of the species across the three scales.

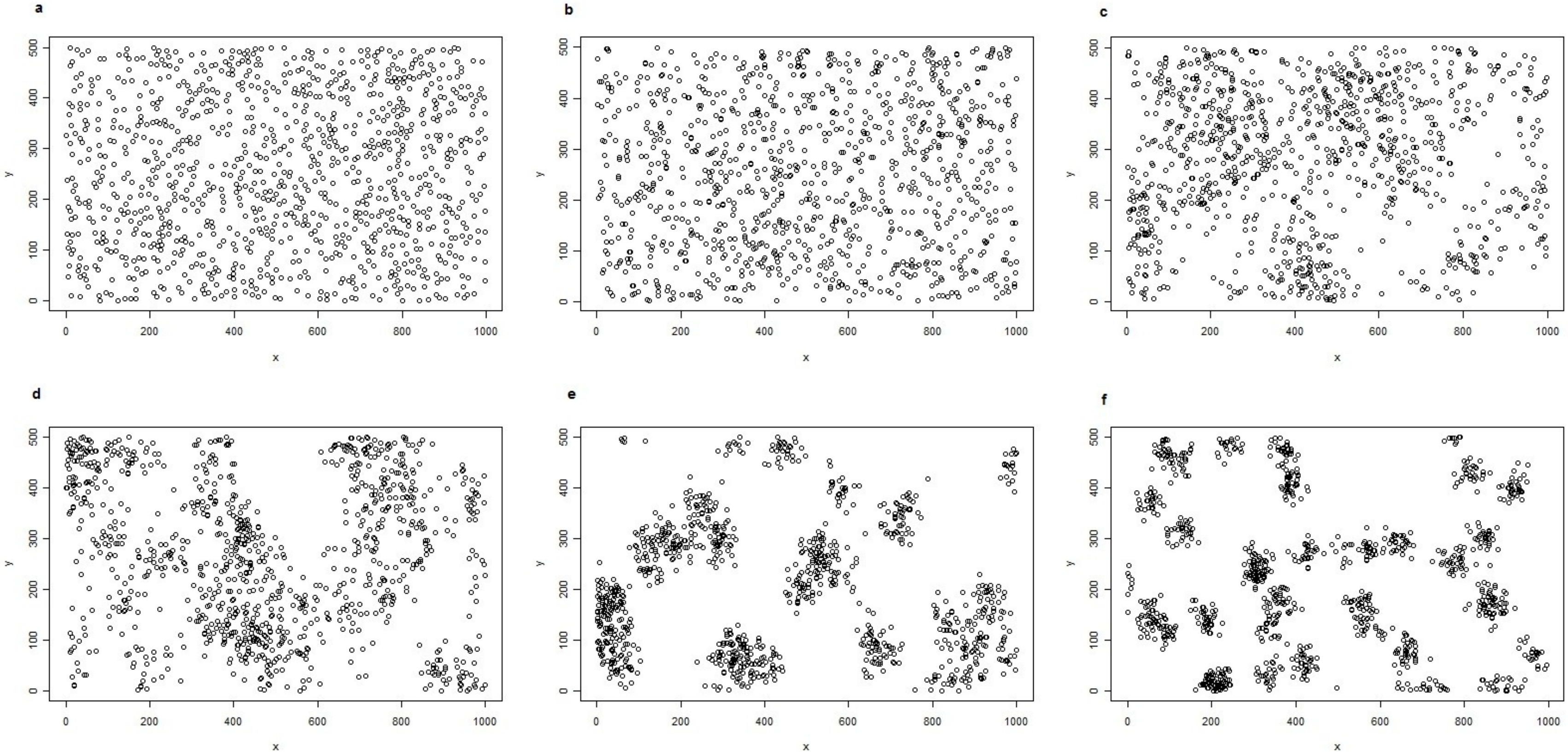

Figure 4-1. Illustrations of a simulated species with 1000 individuals in a 50-ha plot under different spatial distributions. (**a**)**.** regular distribution; (**b**)**.** random distribution; (**c**)**.** slightly aggregated distribution (distance between parent trees and offspring (DPO) equal to 3/4 maximum distance (MD)); (**d**)**.** moderately aggregated distribution (DPO equal to 1/2 MD); (**e**)**.** more aggregated distribution (DPO equal to 1/3 MD); (**f**)**.** highly aggregated distribution (DPO equal to 1/4 MD).

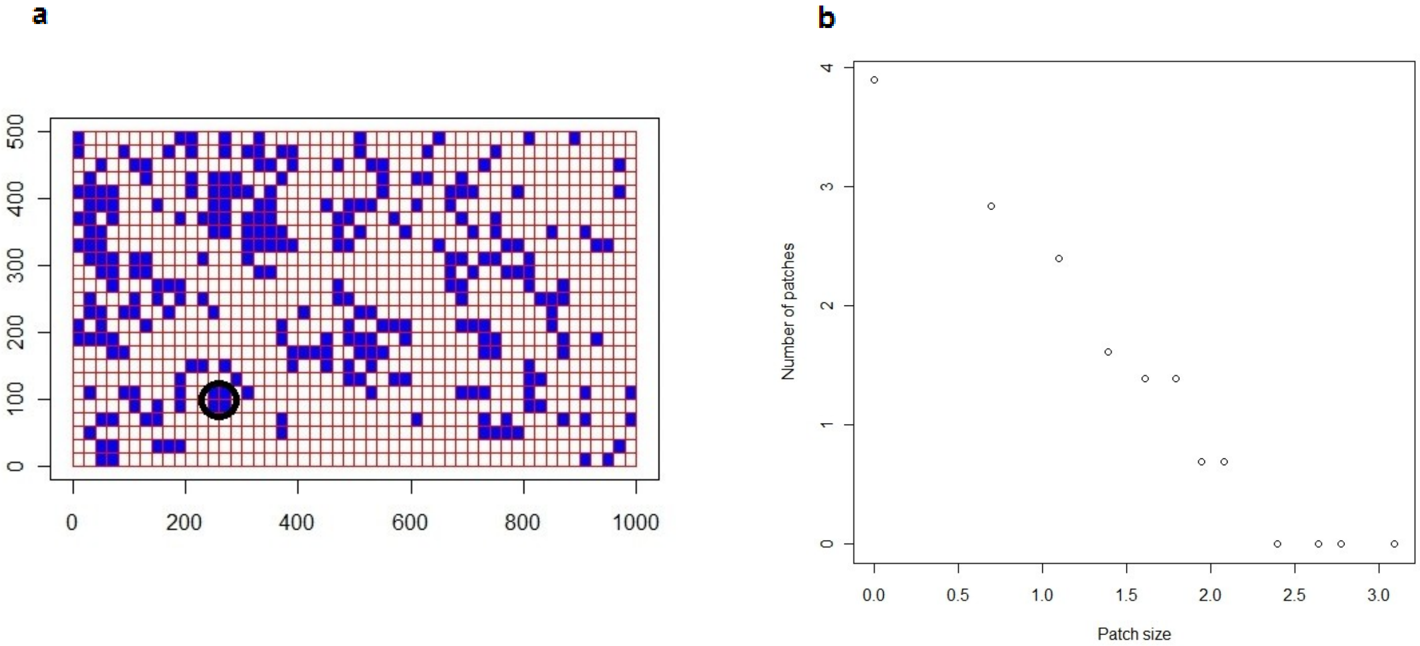

Figure 4-2 Spatial distribution of *P. guianensis* with 867 individuals in the BCI plot when the grain size equal to 20×20 m. **(a).** the occupancy map of *P. guianensis*; (**b**)**.** the patch-size distribution of *P. guianensis*.

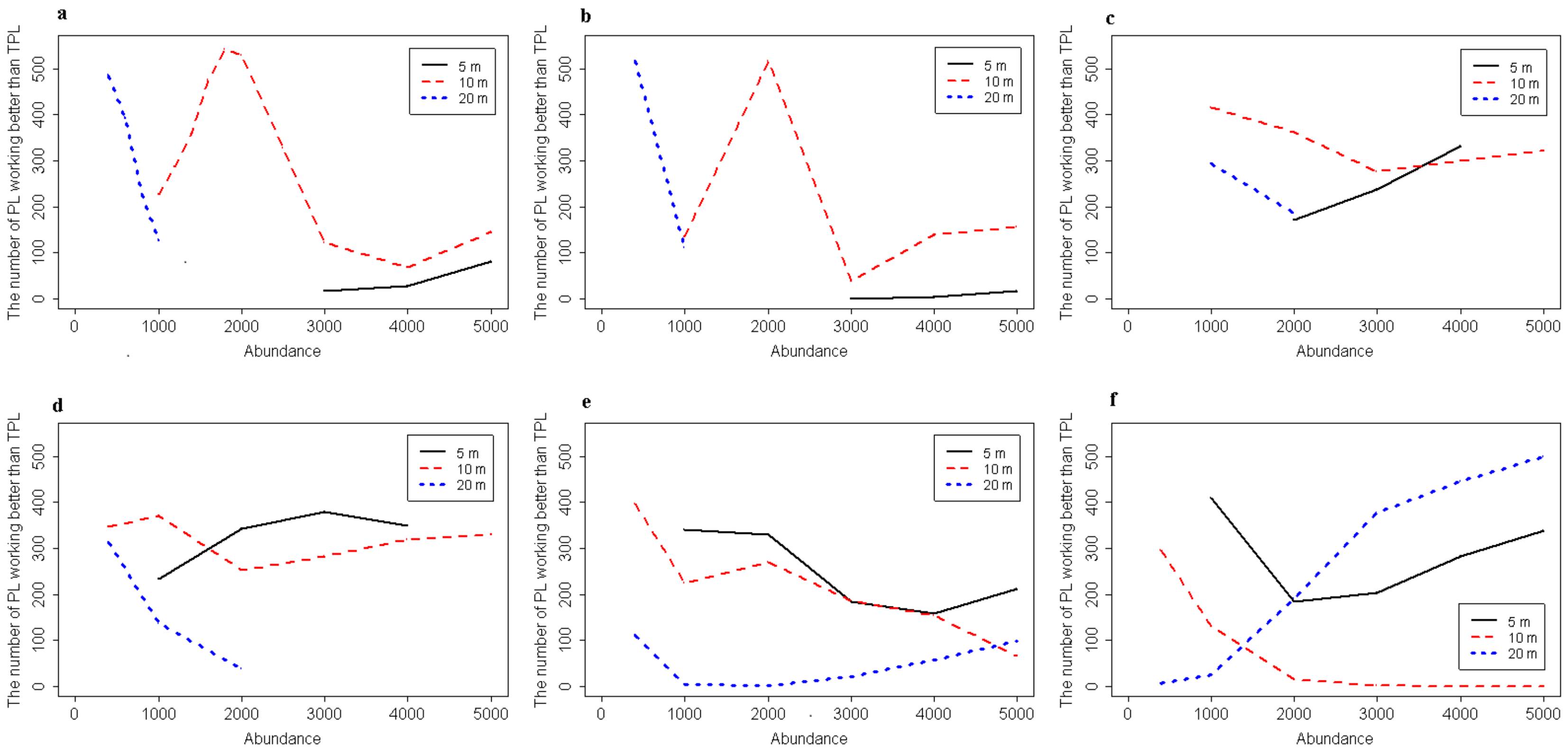

Figure 4-3. Number of species patch-size distributions fitted well by the power-law model in 1000 simulations of different scenarios. Note that each panel corresponds to the respective spatial distribution shown in Figure 4-1. (a). regular distribution; (b). random distribution; (c). slightly aggregated distribution; (d). moderately aggregated distribution; (e). more aggregated distribution; (f). highly aggregated distribution.

Chapter 5: Conclusion remarks

The ongoing and projected changes in climate and land-use are expected to jeopardize survival of many species and disrupt the functioning of otherwise healthy ecosystems (Tilman 2000; Cardinale 2012). Simple and practical methods are urgently needed for assessing the endangerment status of many affected species and quantifying the impact of natural and man-made disturbances on ecosystem integrity. However, there is a wealth of empirical evidence that discrepancy among different criteria and scale-dependence of the measurements are prevalent, rendering it difficult to interpret and compare results obtained at different spatial and temporal scales (e.g., Abeli et al. 2009; Fox et al. 2011).

5.1 Major findings and contributions of the study

The main objective of my thesis was to test the robustness of existing methods to variations in the scale of observation, abundance and spatial aggregation and to develop improved methods for understanding the endangerment status of species and ecosystems in spatially structured landscapes.

In chapter two, I started with the discussion on the pros and cons of an area-based model, which was derived by He (2012) and solely based on the occupancy of a species to assess the extinction risk. I extended this model to incorporate spatial autocorrelation. Both the necessary parameters to incorporate occupancy and spatial autocorrelation are easily obtained from species' occurrence maps. The newly derived model performed generally better than He’s (2012) model particularly when the abundance was high and spatial distribution was aggregated.

In chapter three, I extended the use of scalograms in assessing extinction risk by linking the changes in scalograms with disturbance intensity levels. By testing the robustness of scalograms to changing abundance and spatial aggregation and comparing the predictive power, I found that the scalograms of both NP and MPS were useful in estimating species extinction risk. The use of this method overcomes the scale-variant property when interpreting and comparing landscape metrics at a single spatial scale.

In chapter four, the use of deviations from power-law distributions for predicting ecosystem degeneration was carefully examined by changing abundance, spatial aggregation, and spatial scales. The results indicated that the power-law of patch-size distribution of vegetation covers was vulnerable to all three factors. Thus, I concluded that the deviation of patch-size distribution from power-law could not be used as an early signal for indicating ecosystem degeneration because the failure of power-law may be triggered by intrinsic characteristics of spatial patterns (i.e., abundance and spatial aggregation) as well as changing spatial scales, which confounds any effect of disturbance.

5.2 Limitations of the study

First of all, the methods developed in this thesis can only be used to unsaturated maps. At coarse scales (i.e., a=50×50 and 100×100 m in the BCI plot), percolation happens – a single large patch forms or the map is fully saturated, which causes the number of patches to reduce to one. The indices for spatial autocorrelation in chapter 2 and the landscape metrics (i.e., patch size standard deviation and mean patch size) in chapter 3 cannot be calculated when all the occupied cells are connected, leading to the failure of these methods.

Second, there is always a trade-off between simplicity and efficiency of any empirical method. To improve the performance of the area-based models, two extra parameters to capture the spatial autocorrelation have to be introduced into the model. Moreover, all the methods in this thesis require lattice data to compute landscape metrics and patch-size distribution of vegetation covers. These methods are not as parsimonious and flexible as He's (2012) model, which can be applied for presence/absence data across spatially discontinuous sites.

Third, my thesis mainly focuses on modelling observed spatial patterns to estimating extinction risk. However, in real landscapes, the underlying mechanisms and the ongoing processes are also central questions to researchers (Wiens et al. 1993; Wu and Hobbs 2002). Species interaction and different types of disturbance may cause a dynamical system to respond differently to environmental changes (Dai et al. 2013; Lever et al. 2014; Dai et al. 2015). For instance, Dai et al. (2015) showed that stability and resilience of a system could reduce at different rates when two types of disturbance (the direct reduction in abundance representing hunting in nature, and decreases in nutrient addition representing progressive deterioration of the environment) were applied separately. This line of interesting research begets the attention of further studies on the relationship between ecological processes and spatial patterns.

5.3 Future research

There is a dire need to determine the endangerment status of species and to predict the collapse of ecosystems in advance. Powerful tools for researchers to accomplish this task are still lacking in practice. Simplicity, efficiency, and scale-independence are three desirable features of a useful evaluation criterion for assessing extinction risk. Further studies should aim to develop new methods to meet these requirements. Also, the methods developed in this study are well tested by simulation, but their applications for the vast array of species groups in heterogeneous environments await further exploration.

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Appendix

Appendix 1. R code for the simulation of species with aggregated distribution

```
library(spatstat)
generate.clu=function(sp,ka,sig,mu){
#####################################################################################
# Simulating spatial clustering distribution
# sp: abundance of the simulated species
# ka: intensity of the clusters; k in chapter 2
# sig: the maximum distances of the offspring to the parent tree; RC in chapter 2
# mu: expected number of offspring per cluster; u in chapter 2
#####################################################################################
sp=sp
ka=ka
sig=sig
mu=mu

num=1000 # num is the number of simulations
for (i in 1:num){
repeat{
clu=rThomas(ka,sig,mu,win = owin(c(0,1000),c(0,500))) #
cluster=as.data.frame(clu)
m=length(clu$x)
if(m>(sp-0.05*sp)&m<(sp+0.05*sp))break
}
write.csv(cluster,file=paste('clusp',sp,'_',i,'_',sig,'.csv',sep="))
print(i)
}
}

## abundance = 1000
```

```
# slightly aggregation
ka=0.00003162278
sig=80.26293
mu =31.62278
sp=1000
generate.clu(sp,ka,sig,mu)

# intermediate aggregation
ka=0.00003162278
sig=50.16433
mu =31.62278
sp=1000
generate.clu(sp,ka,sig,mu)

# highly aggregation
ka=0.00003162278
sig=33.44289
mu =31.62278
sp=1000
generate.clu(sp,ka,sig,mu)

## abundance = 2000
# slightly aggregation
ka=0.00004472136
sig=63.27451
mu =44.72136
sp=2000
generate.clu(sp,ka,sig,mu)

# intermediate aggregation
ka=0.00004472136
```

```
sig=42.18301
mu =44.72136
sp=2000
generate.clu(sp,ka,sig,mu)

# highly aggregation
ka=0.00004472136
sig=28.12201
mu =44.72136
sp=2000
generate.clu(sp,ka,sig,mu)

## abundance = 3000
# slightly aggregation
ka=0.00005477226
sig=57.17498
mu =54.77226
sp=3000
generate.clu(sp,ka,sig,mu)

# intermediate aggregation
ka=0.00005477226
sig=38.11665
mu =54.77226
sp=3000
generate.clu(sp,ka,sig,mu)

# highly aggregation
ka=0.00005477226
sig=25.4111
mu =54.77226
```

```
sp=3000
generate.clu(sp,ka,sig,mu)

## abundance = 4000
# slightly aggregation
ka=0.00006324555
sig=53.20731
mu =63.24555
sp=4000
generate.clu(sp,ka,sig,mu)

# intermediate aggregation
ka=0.00006324555
sig=35.47154
mu =63.24555
sp=4000
generate.clu(sp,ka,sig,mu)

# highly aggregation
ka=0.00006324555
sig=23.64769
mu =63.24555
sp=4000
generate.clu(sp,ka,sig,mu)

## abundance = 5000
# slightly aggregation
ka=0.00007071068
sig=50.23037
mu =70.71068
sp=5000
```

```
generate.clu(sp,ka,sig,mu)

# intermediate aggregation
ka=0.00007071068
sig=33.54691
mu =70.71068
sp=5000
generate.clu(sp,ka,sig,mu)

# highly aggregation
ka=0.00007071068
sig=22.36461
mu =70.71068
sp=5000
generate.clu(sp,ka,sig,mu)
```

Appendix 2. R code for computing occupancy and spatial autocorrelation in Chapter 2

```
library(SDMTools)
result.loop=function(cell,sp,sig,plotdim=c(1000,500)){
###########################################################################
# Calculate the Occupancy and Parameters of spatial autocorrelation for Chapter 2
# cell: a linear size, not area
# sp: abundance of the data
# sig: spatial aggregation of the data
# sp & sig are in the name of the data
# plotdim: the maximum size of the plot in x and y direction
############################################################################
plotdim=plotdim
cell=cell
sp=sp
sig=sig

for (i in 1:length(cell)){
 cellsize=cell[i]
 result_loop=result.main(cellsize,sp,sig,plotdim)
 print(i)
 }
}

result.main=function(cellsize,sp,sig,plotdim){
######################################################################
# Output and save the results
# cellsize = a linear size, not area
# sp: abundance of the data
# sig: spatial aggregation of the data
# sp & sig are in the name of the data
# plotdim = the maximum size of the plot in x and y direction
```

```
######################################################################
cellsize=cellsize
plotdim=plotdim
abund=sp
aggreg=sig

nu=5 # the number of simulated data
res=lapply(1:nu, function(x){data=read.csv(file=paste('clusp',abund,'_',x,'_',aggreg,'.csv',sep=''),header=T)
                    occup.bci.main(data,cellsize,plotdim)})

result=matrix(unlist(res),nrow=nu,byrow=T)
colnames(result)=c('BW','DBW','occupancy','exp_BW','exp_DBW')
write.csv(result,file=paste('clusp',abund,'_',aggreg,'_c',0,'_',cellsize,'.csv',sep=''))
}

occup.bci.main=function(data,cellsize,plotdim){
######################################################################
# Calculate occupancy and spatial autocorelation for a target species
# cellsize = a linear size, not area
# plotdim = the maximum size of the plot in x and y direction
######################################################################
xmax=plotdim[1]
ymax=plotdim[2]
nxcell=xmax/cellsize          # No. of cells along x-axis
nycell=ymax/cellsize          # No. of cells along y-axis
x=data$x
y=data$y

codex = x%/%cellsize + 1
codey = y%/%cellsize + 1
code = codey + codex * 10000
```

```
comp = tapply(rep(1, length(code)), code, sum)
code = rep(1:nxcell,nycell)*10000 + rep(1:nycell, each=nxcell)
comp1 = rep(0,length(code))
names(comp1)=code
comp1[names(comp)]=comp  # comp1 is abundance map

z=matrix(comp1,nr=nxcell,byrow=F)
z[which(z>0)]=1   # convert the point data into a binary map
z1=z
# calculate the length of occupied contour
z[2:(nxcell-1),2:(nycell-1)]=0
if (z[1,1]==1){z[1,1]=2}
if (z[1,nycell]==1){z[1,nycell]=2}
if (z[nxcell,1]==1){z[nxcell,1]=2}
if (z[nxcell,nycell]==1){z[nxcell,nycell]=2}
sedge=sum(z)

# calculate the diagnol pair of black/white joints
# moving the matrix to the up right
z2=z1[-1,]
z2=z2[,-nycell]
z2=cbind(rep(0,nxcell-1),z2)
z2=rbind(z2,rep(0,nycell))
z12=z1+z2
z12=z12[,-1]
z12=z12[-nxcell,]
z12[which(z12!=1)]=0

# moving the matrix to the low right
z3=z1[-nxcell,]
z3=z3[,-nycell]
```

```
z3=cbind(rep(0,nxcell-1),z3)
z3=rbind(rep(0,nycell),z3)
z13=z1+z3
z13=z13[-1,]
z13=z13[,-1]
z13[which(z13!=1)]=0
corn=sum(z12)+sum(z13)

ccl.mat= ConnCompLabel(z1)
ps.data=ClassStat(z1)

BW=ps.data$total.edge[2]-sedge
DBW=corn
occupancy=ps.data$prop.landscape[2]
exp_BW=2*occupancy*(1-occupancy)*(2*nxcell*nycell-nxcell-nycell)
exp_DBW=4*occupancy*(1-occupancy)*(nxcell-1)*(nycell-1)

res=cbind(BW,DBW,occupancy,exp_BW,exp_DBW)
return(res)
}
```

Appendix 3. R code for computing the number of patches and other landscape metrics in Chapters 3 and 4

```
result.main=function(sp,num,sig,cellsize,plotdim=c(1000,1000)){
######################################################################
# Calculate landscape metrics for chapters 3 and 4
# sp: abundance of the species
# num: the number of simulated data
# sig: spatial aggregation
# num & sig are in the name of the data
# cellsize: a linear size, not area
# plotdim: the maximum size of the plot in x and y direction
######################################################################
sp=sp
num=num
sig=sig
cellsize=cellsize
plotdim=plotdim

numpatch=numeric() # Number of Patches in chapters 3 and 4
msize=numeric() # Mean Patch Size in chapter 3
occup_area=numeric()
shared_edge=numeric()
elen=numeric()
noccupied=numeric()
larg=numeric() # Largest Patch Index in chapter 3 (need to be divided by the total area)
el_nocontour=numeric()  # Edge Length in chapter 3
corner=numeric()
exp_edge=numeric()
```

```
exp_corn=numeric()
patch_sd=numeric() # Patch Size Standard Deviation in chapter 3
patch_cv=numeric() # Patch Size Coefficient of Variance in chapter 3

for (i in 1:num){
dat=read.csv(file=paste('clusp',sp,'_',i,'_',sig,'.csv',sep=''),header=T)
occup.bci=occup.bci.main(dat,cellsize,plotdim)

numpatch[i]=occup.bci[[2]]
msize[i]=occup.bci[[4]]
occup_area[i]=occup.bci[[3]]
shared_edge[i]=occup.bci[[5]]
elen[i]=occup.bci[[6]]
noccupied[i]=occup.bci[[1]]
larg[i]=occup.bci[[7]]
el_nocontour[i]=occup.bci[[8]]
corner[i]=occup.bci[[9]]
exp_edge[i]=occup.bci[[10]]
exp_corn[i]=occup.bci[[11]]
patch_sd[i]=occup.bci[[12]]
patch_cv[i]=occup.bci[[13]]
print(i)
}

result=cbind(numpatch,msize,noccupied,occup_area,shared_edge,elen,larg,el_nocontour,corner,exp_edge
,exp_corn,patch_sd,patch_cv)
write.csv(result,file=paste('result',sp,'_',sig,'_c0','_',cellsize,'.csv',sep=''))
}
```

```
occup.bci.main=function(data,cellsize,plotdim){
#####################################################################
# Calculate occupancy for random distribution of trees
# cellsize: a linear size, not area
# plotdim: the maximum size of the plot in x and y direction
#####################################################################
noccup=numeric()                # no of occupied cells for a species
xmax=plotdim[1]
ymax=plotdim[2]
nxcell=xmax/cellsize            # no of cells along x-axis
nycell=ymax/cellsize            # no of cells along y-axis

npatch=numeric()
msize=numeric()
lsize=numeric()
x=data$x
y=data$y

# call program presence.fn which converts the points into
# presence/absence data
occup.out=presence.fn(cellsize,nxcell,nycell,x,y,xmax,ymax)
npt=occup.out[[3]]
noccup=occup.out[[2]]           # no of occupied cells

# call program patch.size.fn which generize the patch size graph
patch.size=patch.size.fn(nxcell,nycell,x,y,npt,noccup,cellsize)

occup.bci=list()
occup.bci[[1]]=noccup
```

```
occup.bci[[2]]=patch.size[[1]]
occup.bci[[3]]=patch.size[[3]]
occup.bci[[4]]=patch.size[[2]]
occup.bci[[5]]=patch.size[[4]]
occup.bci[[6]]=patch.size[[5]]
occup.bci[[7]]=patch.size[[6]]
occup.bci[[8]]=patch.size[[7]]
occup.bci[[9]]=patch.size[[8]]
occup.bci[[10]]=patch.size[[9]]
occup.bci[[11]]=patch.size[[10]]
occup.bci[[12]]=patch.size[[11]]
occup.bci[[13]]=patch.size[[12]]
return(occup.bci)
}

##################################################
# convert cell count into presence/absence data
# count the number of occupied cells and occupied area
###################################################
presence.fn=function(cellsize,nxcell,nycell,x,y,xmax,ymax){

xx=seq(0,xmax,len=nxcell+1)
yy=seq(0,ymax,len=nycell+1)

npt=count.fn(cellsize,nxcell,nycell,x,y)   #call function count.fn for observed pattern

occup=ifelse(npt>0,1,0)                    #convert abundance npt into presence/absence

noccup=0
```

```
noccup=sum(occup)

occup=matrix(occup,ncol=nxcell)

occup.out=list()
occup.out[[1]]=occup
occup.out[[2]]=noccup
occup.out[[3]]=npt
return(occup.out)
}

############################################
# count the no of points (trees) in a cell
############################################
count.fn=function(cellsize,nxcell,nycell,x,y){

# Divide the plot into a grid system with cell size = cellsize
npt=numeric()                    # no of points in each cell
occup=numeric()                  # presence in each cell

ncell=0                  # total no of cells
xlo=-cellsize
for (i in 1:nxcell){
xlo=xlo+cellsize
xup=xlo+cellsize
ylo=-cellsize
 for (j in 1:nycell){
 ylo=ylo+cellsize
 yup=ylo+cellsize
```

```
 ncell=ncell+1
 npt[ncell]=length(x[(x>xlo&x<xup)&(y>ylo&y<yup)])
 }
}
return(npt)
}

##################################
# generize the patch size distribution
##################################
patch.size.fn=function(nxcell,nycell,x,y,npt,noccup,cellsize){
zz=npt
# build up a buffer outside the data
# add two rows and two columns to the data
dim(zz)=c(nycell,nxcell)
z=rep(0,(nycell+1))
for (i in 1:nxcell){
 z=c(z,0,0,zz[,i])
}
z=c(z,rep(0,(nycell+3)))
dim(z)=c((nycell+2),(nxcell+2))

# give a unique number to each occupied cell
row=dim(z)[1]
col=dim(z)[2]
lab=1

for (i in 1:row){
 for (j in 1:col){
```

```
  if (z[i,j]>0){
    z[i,j]=lab
    lab=lab+1
  }
 }
}

# define patches
repeat{
stop=0
for (i in 2:(row-1)){
 for (j in 2:(col-1)){
  if (z[i,j]>0){
   z5=c(z[i,j],z[(i+1),j],z[(i-1),j],z[i,(j+1)],z[i,(j-1)])
   small=min(subset(z5,z5>0))
   if (z[i,j]>small){z[i,j]=small;stop=1}
   if (z[(i+1),j]>0&z[(i+1),j]>small){z[(i+1),j]=small;stop=1}
   if (z[(i-1),j]>0&z[(i-1),j]>small){z[(i-1),j]=small;stop=1}
   if (z[i,(j+1)]>0&z[i,(j+1)]>small){z[i,(j+1)]=small;stop=1}
   if (z[i,(j-1)]>0&z[i,(j-1)]>small){z[i,(j-1)]=small;stop=1}
  }
 }
}
if(stop==0)break
}

# count the number of patch and the size
zzz=as.vector(z)
number=unique(zzz)
```

```
npatch=subset(number,number>0)
numberpatch=0
numberpatch=length(npatch)     ## calculate the number of patch
zzz=subset(zzz,zzz>0)
s=min(zzz)
l=max(zzz)
n=rep(0,1000000)
for (i in s:l){
 n[i]=length(zzz[zzz==i])
}
n=subset(n,n>0)
meansize=(sum(n)/length(unique(zzz)))*cellsize*cellsize # calculate the mean patch size
sm=min(n)
la=max(n)*cellsize*cellsize  # calculate the maximum patch size
pssd=sd(n)*cellsize*cellsize # calculate the standard deviation
pscv=pssd/meansize # calculate the coefficient of the variance
nu=unique(n)
len=length(nu)
xxx=0
yyy=0
for(i in 1:len){
xxx[i]=nu[i]   # size of patch
yyy[i]=length(n[n==nu[i]])   # number of patch
}

sedge=0  # number of shared edge
for (i in 2:(row-1)){
 for (j in 2:(col-1)){
  if (z[i,j]>0&z[i+1,j]>0&z[i,j+1]==0){sedge=sedge+1}
```

```
  if (z[i,j]>0&z[i+1,j]==0&z[i,j+1]>0){sedge=sedge+1}
  if (z[i,j]>0&z[i+1,j]>0&z[i,j+1]>0){sedge=sedge+2}
 }
}
occupany=noccup/(nxcell*nycell)
el=4*noccup*cellsize-2*sedge*cellsize
contou=0
for (i in 2:(row-1)){
 if (z[i,2]>0){contou=contou+1}
 if (z[i,col-1]>0){contou=contou+1}
}

for (i in 2:(col-1)){
 if (z[2,i]>0){contou=contou+1}
 if (z[row-1,i]>0){contou=contou+1}
}

el2=4*noccup*cellsize-2*sedge*cellsize-contou*cellsize

# calculate the joint corner
corn=0
for (i in 2:(row)){
 for (j in 2:(col)){
  if (z[i-1,j-1]>0){
  if (z[i,j]>0){corn=corn+1}
   }else{if (z[i,j-1]>0&z[i-1,j]>0) {corn=corn+1}
   }
 }
}
```

```
exp.edge=occupany*occupany*(2*nxcell*nycell-nxcell-nycell)
exp.corn=(occupany*occupany+(1-occupany)*occupany*occupany)*(nxcell-1)*(nycell-1)


patch.size=list()
patch.size[[1]]=numberpatch
patch.size[[2]]=meansize
patch.size[[3]]=occupany
patch.size[[4]]=sedge
patch.size[[5]]=el
patch.size[[6]]=la
patch.size[[7]]=el2
patch.size[[8]]=corn
patch.size[[9]]=exp.edge
patch.size[[10]]=exp.corn
patch.size[[11]]=pssd
patch.size[[12]]=pscv

return(patch.size)
}
```