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Master Thesis

Ecologically viable population sizes: Determining factors

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Titel
Title:
Ecologically viable population sizes: Determining factors

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Sammanfattning
Abstract:

The minimum ecologically viable population size (MEVP) of a species describes the minimum size at which the species itself or another species in the same ecosystem goes extinct as a result of the loss of inter-specific interactions. The MEVP shows a good potential for use as a tool for exploring the mechanisms behind species extinctions, but presently only a small amount of research has been done that takes advantage of this. In this study the MEVP is used to investigate what properties of species can be used as good indicators of ecological importance. 100 large computer generated food webs were created with an assembly model and the reduction in density that was necessary to induce an extinction event in the web was subsequently determined for each species within the webs. This change in density was then correlated with 28 different properties, measured for each species. The results show that properties that measure how well connected a species is, as well as measures of the species role as a prey item in the web are the ones with the greatest potential to find species with high MEVP. Further, the results put emphasis on the importance of regarding the web as a whole when working with species extinctions, while also highlighting the usefulness of the MEVP concept.

Contents

1. Abstract

The minimum ecologically viable population size (MEVP) of a species describes the minimum size at which the species itself or another species in the same ecosystem goes extinct as a result of the loss of inter-specific interactions. The MEVP shows a good potential for use as a tool for exploring the mechanisms behind species extinctions, but presently only a small amount of research has been done that takes advantage of this. In this study the MEVP is used to investigate what properties of species can be used as good indicators of ecological importance. 100 large computer generated food webs were created with an assembly model and the reduction in density that was necessary to induce an extinction event in the web was subsequently determined for each species within the webs. This change in density was then correlated with 28 different properties, measured for each species. The results show that properties that measure how well connected a species is, as well as measures of the species role as a prey item in the web are the ones with the greatest potential to find species with high MEVP. Further, the results put emphasis on the importance of regarding the web as a whole when working with species extinctions, while also highlighting the usefulness of the MEVP concept.

Keywords: assembly model, ecologically effective populations, extinction, keystone species, MEVP, MVP, species interactions.

2. Introduction

Climate change, together with the ever increasing pressure put on nature by human activities has led to the skyrocketing of recent extinction rates, estimated somewhere between 100 and 1000 times their pre-human rates; future extinction rates are predicted to be even higher than this (Pimm *et al.* 1995). Such enormous changes put pressure on conservation biology to develop ever more efficient ways to preserve and protect the biodiversity that we are so very dependent on.

An important part of conservational work is to somehow quantify the extinction risks of species, so that effective conservation policies and priorities can be formulated. To this end the concept of minimum viable population (MVP) size is often used. MVP describes a lower limit of a population's abundance below which it will be facing a specified risk of extinction within a specified time span, e.g. 10 % risk within 100 years (Shaffer 1981). MVP is generally used as a tool to make quantitative estimations of the current or future threat situation of a population; or to

evaluate what effects a specific perturbation, such as harvesting, will have on a particular population.

Species do not exist on their own in nature, however, and this is a fact that needs to be recognized and taken into consideration when making conservational decisions (Soulé *et al.* 2003). When considering this, it becomes clear that the usefulness of MVP as a tool for risk assessment is severely limited, since it does not give any information as to what happens to the rest of the community following the reduction of one of its species.

As a species' abundance declines, so does the strength with which it interacts with other species in its environment, something that can have far-reaching consequences throughout the community. Simple mechanisms arising from the fact that a population is part of a larger community, such as secondary extinction of a predator following the loss of an important prey species, are important structuring factors of the post-extinction community (Ebenman *et al.* 2004). Furthermore there are also other, less intuitive effects following from being part of a community. One such mechanism is the regulation provided by a keystone predator that is keeping competitively superior species' abundances low, allowing other, less strongly competing species to be present as well, thereby promoting a higher diversity in the community (Paine 1969).

A classic example illustrating the importance of keystone species comes from the North Pacific Ocean and southern Bering Sea, where the over-harvesting of sea otters during the 18th and 19th century resulted in whole kelp forests being laid to waste, with devastating effects on the biodiversity as a consequence, due to the loss this one important species (Estes & Palmisano 1974). Other examples of where the disturbance of a single species caused similar cascading effects are numerous. For instance, the decline in cougars led to changes in the stream fish communities in Zion National Park (Ripple & Beschta 2006) and the unsustainable cod fishing has caused poisonous algal blooms in the Baltic Sea (Casini *et al.* 2008). For further examples see Power (1990), Menge (2000) as well as Schmitz (2000), see Polis et al. (2000) for a discussion on trophic cascades.

The MVP-concept fails to detect important effects like these and has therefore been criticized for being overly reductionistic and unrealistic in its focus on one single species, lifting it out of its environmental context of the community that it is part of (Conner 1988; Soulé *et al.* 2005; Sanderson 2006). Also, to not include species interactions in a viability analysis of a

population have been shown to produce results that actually perform poorly when predicting extinction risks (Sabo 2008). For these reasons, another concept has been introduced, that of minimum ecologically viable population (MEVP) size. It takes the MVP one step further and measures how rare a species can become while at the same time keeping its ecological roles intact (Clark 2005; Ebenman & Jonsson 2005). That is, at what population size do other species that are depending on the subject species go extinct?

By increasing mortality for species in model food webs, Clark (2005) found that about a third (35.6 %) of all extinctions caused were of species other than the species subjected to the increase in mortality (non-self extinctions). This is a substantial amount and points toward the importance of including the whole community into a viability analysis. With the results of Clark (2005) in mind, MEVP might be a much more relevant tool to use compared to the MVP when making conservation policies and setting goals for species abundances. Accordingly, it has been suggested that adopting a more ecosystem-level oriented approach would enable the detection of broad patterns and strategies for use in management situations (Lindenmayer *et al.* 2007). Although, as of yet, too little is known about the MEVP for it to be easily applied in practical situations.

A better understanding of what makes species important to the integrity of the community would make conservation priorities clearer and possibly conservation work more effective. Many attempts have been made to find indices and measures that quantify the importance of species within ecological communities, and to find good such measures is currently an important goal of conservational biology (Jordan & Scheuring 2004).

In this study I explore what kind of traits, properties and species specific indices (from now on referred to as properties) will predict if a species has a high MEVP. This is done with the help of large model food webs with realistic dynamics, built with an assembly process. A number of factors thought to affect the size of the MEVP of species are then examined by perturbing communities created with this process. The aim is to determine which properties of species, if any, can be used as precursors for indicating what species are important to the system in the sense that a relatively small reduction in their abundance will lead to extinctions. As will be shown, the most important property of species in deciding its MEVP is its amount of direct or indirect links to other species; and in particular the amount of direct and indirect predators a species has.

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3. Method
3.1 The Assembly of the Model Food Webs
To construct the ecological communities, a sequential assembly approach was developed where one species was added at a time. In short, a species was added, dynamics was applied and then the stability of the system was tested. If the system was stable, another species was added, if it was unstable the added species was removed and the procedure was rerun with a new species. The software used to construct the food web assembly method was MATLAB R2007b. In the sections below I describe the details of each major step in the process, beginning with the criteria for food web stability used; followed by an explanation of the method to determine the link distribution. After that comes a description of the way dynamics was imposed on the system as well as a presentation of the allometric relationships and parameters used in the food web construction. Finally the whole assembly procedure is outlined.

3.1.1 Food Web Stability
The method to assemble the food webs used in this study was in many ways similar to that of Lewis (2008). A difference is that while Lewis utilized the permanence criterion (Hofbauer & Sigmund 1988; Law & Morton 1996) as a dynamical constraint to determine if a new species could invade or not, here local stability around an equilibrium point was used instead. The reason for not using permanence here is that for the purpose of determine the success of species addition, permanence have been shown to not perform much better than simple feasibility alone (Kristensen 2008). Another, larger difference was in the way the invasion attempts were handled. If the invasion led to loss of permanence, Lewis (2008) and others (Law & Morton 1996; Ebenman *et al.* 2004) used an algorithm that let the system collapse to a permanent, smaller sub-system; in effect allowing extinctions to occur during the assembly process. While arguably being a realistic way of simulating the build-up of ecological communities, this method has an unfortunate drawback, it involves checking the permanence of all possible subsystems of the original community after a new species introduction has rendered the community non-permanent. This is fine so long as the number of species in the community is relatively low, but as the number of species (S) increases, so does the number of calculations needed to extract the subsystems by a factor of 2^{S-2}. This becomes so computationally demanding that it is not possible to build webs containing a large number of species with existing computational resources (for 50 species the number of calculations required for determining the post-extinction community after *one* species insertion is ~$2^{48} = 2.8 * 10^{14}$).

Instead, by simply discarding all added species that made the system lose local stability, stable food webs containing as many as over 100 species could easily be constructed in a very short time, while still having a close resemblance to real food webs (see section 4.1). The reader should be aware that no claims are made that this method is a realistic way of modelling the assembly of natural ecological communities; rather it is a means to an end – to create realistic representations of said communities.

3.1.2 Link Structure: Who Eats Whom?

The distribution, and to some extent the strength, of the feeding links within the community was determined with a Gaussian function (referred to as the 'preference function' throughout this text) as defined by Lewis (2008):

$$z_{ij} = \frac{1}{\gamma\sqrt{2\pi}} \exp\left[-\frac{1}{2}\left(\frac{\log\left(\beta m_i / m_j\right)}{\gamma} \right)^2 \right] \qquad (1)$$

$$\text{for } m_i < m_j \text{ and } -\alpha\gamma \leq \log\left(\beta \frac{m_i}{m_j} \right) \leq \alpha\gamma \qquad (2)$$

The preference z_{ij} for the prey i of the predator j is controlled by three parameters: γ defines the standard deviation of the curve and so, determines diet breadth of the consumer; α also controls the breadth of the diet by defining where the tails of the function are truncated; β is the most preferred consumer to prey body mass ratio, thereby determining where, on a continuum of prey body masses, the predator has its peak preference. For predators the interval [10 – 1000] was used for β, which gives a good match with empirical data (Woodward *et al*. 2005). For herbivores, due to lack of empirical data on the preferred ratio of consumer to basal species body mass ratio, a preferred prey body mass was instead drawn from the basal species body mass interval. A β-value to be used in the preference function was then calculated as $\beta = m_j / m_{pref}$, where m_j is the mass of the herbivore and m_{pref} is the mass of the preferred prey.

The parameters α and γ was also drawn from intervals, a difference from Lewis (2008); this was done to ensure that there was good diversity of both generalists and specialists in the webs. See Table 1 for details on the parameters used. Another difference was that prior to calculating interaction strengths, a species' preferences was always normalized so that they summed to 1, according to:

$$z_{ij} = z_{ij} \frac{1}{\sum z_j} \qquad (3)$$

3.1.3 Food Web Dynamics

The dynamics within the system was described by a generalized Lotka-Volterra model:

$$\frac{dx_i}{dt} = x_i \left(r_i + \sum_{j=1}^{n} a_{ij} x_j \right) \qquad (4)$$

where x_i is the population density of species i, r_i is the intrinsic growth rate of species i if it is a producer or the mortality rate of species i if it is a consumer, a_{ij} is the per capita effect of species j on the growth rate or mortality rate of species i. When species j is a consumer and species i its prey this effect is negative and when species j is a prey species being preyed upon by i the effect is positive:

$$a_{ji} = -\varepsilon a_{ij} \qquad (5)$$

where ε is the ecological conversion efficiency which was assumed to be equal for all consumer species, as it does not follow any mass dependent allometric relationship (Peters 1983). If both i and j are basal species the element a_{ij} describes the effect of inter-specific competition from j on i and lastly, for all species a_{ii} describes the self limitation, or intra-specific competition, of species i. The actual parameter values are covered in the next section.

3.1.4 Allometric Relationships and Model Parameters

A major problem in creating realistic ecosystem models is that it often requires a substantial amount of detailed life history information on the organisms that are being modelled. Such information can be hard to come by, both because of practical difficulties with measuring some variables, such as interaction strengths; and also because of limited resources in the form of time and money available for researchers and conservationists to perform the quite extensive surveys involved (Yodzis & Innes 1992). A convenient way to parameterize ecological models would be to use a property in species that is relatively easily measured to act as a surrogate measure for the traits used as parameters in the model (Woodward *et al.* 2005). One such surrogate measure, which can be readily assessed

empirically, is the body mass of species. According to the recently formulated metabolic theory of ecology, the metabolic rate of organisms, I, scale allometrically with body mass as

$$I = I_0 M^{3/4} \qquad (6)$$

where I_0 is a normalization constant and M is the body mass of the organism (Brown $et\ al.$ 2004). As a consequence other biological rates are predicted to follow the same kind of quarter power-law scaling relationships and this has indeed been shown empirically for a number of allometries, such as feeding and defecation rates and biomass production rates, in a wide variety of organisms (Savage $et\ al.$ 2004). In this model allometric relationships were used to parameterize the growth rate of producers, r_i; mortality of consumers, b_i; intra-specific competition, a_{ii}; and predation strengths. r_i scales as $m_i^{-1/4}$ (Yodzis & Innes 1992; Brown $et\ al.$ 2004):

$$r_i = C_r m_i^{-1/4} \qquad (7)$$

where C_r is an allometric constant that controls the amount of primary production in the system and is equal for all basal species. The mortality of consumer species, b_i scales as $m_i^{1/4}$ (Yodzis & Innes 1992; Brown $et\ al.$ 2004):

$$b_i = C_b m_i^{-1/4} \qquad (8)$$

where C_b is an allometric constant controlling the amount of mortality. Intra-specific competition a_{ii} scales as $m_i^{-1/4}$ (Virgo $et\ al.$ 2006):

$$a_{ii} = C_{aii} m_i^{-1/4} \qquad (9)$$

with C_{aii} being an allometric constant controlling the amount of intra-specific competition. The predation link strength a_{ij} (Peters 1983) is:

$$a_{ij} = \frac{\delta z_{ij} m_j^{3/4}}{C_{dens} m_i^{1/4}} \qquad (10)$$

where δ is a constant controlling the strength of predation, z_{ij} is the feeding preference for species i of species j, m_j is the mass of the predator j, C_{dens} is

a constant that determines the density of the prey population at equilibrium and m_i is the mass of species i. For parameter values, see Table 1.

Constants		Intervals	
C_r	4.10×10^{-3}	α	2 - 4
C_b	1.19×10^{-5}	γ	0.2 - 1
C_{aii}	10^{-12}	β	$10^1 - 10^3$
$C_{dens.}$	10^{-2}	m_{basal}	$10^{-15} - 10^{-9}$
δ	9.6×10^{-3}	$m_{herbivore}$	$10^{-8} - 10^0$
ε	0.1	$m_{predacious}$	$10^{-7} - 10^2$
		$C_{intersp.}$	$0 - 10^{-12}$

3.1.5 Assembly

The first step of the model was to create a stable system of two basal species as a foundation to build the rest of the community upon. This was done by drawing two random body masses from a specific basal species body mass interval and assigning growth rate as well as inter-specific competition drawn from the interval $C_{intersp.}$ and intra-specific competition (for details on the dynamics see sections 3.1.3 and 3.1.4); see Table 1 for parameter values). The two-species system was then checked for positive equilibrium densities and local stability (May 1974). When stability was reached, other kinds of species were introduced. The introduced species were divided into three classes, basal species, herbivorous species and predacious species. Each class had the same probability of being picked each time a new species was introduced with one exception: at all times the fraction of basal species was never allowed to increase above 20 % of the total amount of species. After deciding class, a body mass for the new species was drawn randomly from the corresponding body mass interval and growth or mortality rate and competition strengths were derived for the species. All species had intra-specific competition, but only basal species had inter-specific competition. This inter-specific competition was drawn from the interval $C_{intersp.}$(see Table 1). If the species was a consumer the preferences for existing species were calculated (see Eq. 1, section 3.1.2). Following that, the strengths of the predatory interactions were calculated (see Eq. 10, section 3.1.4). Finally the preference functions of the predators already in the web at the time of insertion were checked to see if the newly inserted species would be preyed upon by any of them, if so appropriate links were added. When all rates and interactions had been established the system was checked for an equilibrium point where all densities were positive and for local stability around that equilibrium. If the community was stable it was kept and a new species was introduced, if it was unstable

the community was reverted to the structure before the species insertion and a completely new species was tested. When 50 species had been reached the community was considered complete. The completed communities were then filtered to remove food webs that had a connectance lower than 0.06 and a fraction of top species that was higher than 0.15.

3.2 Determining Species' Minimum Ecologically Viable Population Size

A measure of the species' MEVPs was acquired by first adding an extra mortality, E_j, to each species j until an extinction event occurred. When this extinction occurred, the density of j could be calculated; the proportional change in this density was used to quantify that species' MEVP. E_j was calculated analytically by first determining the densities at the equilibrium point:

$$\hat{X} = -A^{-1}r \qquad (11)$$

where A is a matrix containing all the interactions between species and r is a vector of intrinsic growth rates or mortality rates of the species. The equilibrium densities with the extra mortality added was:

$$\hat{X}' = -A^{-1}\left(r - E_j e_j\right) \qquad (12)$$

where e_j is a vector with 1 in row j and 0 elsewhere. For each species i the new equilibrium density $\hat{X}_i'$ with the extra mortality added to species j can then be written as:

$$\hat{X}_i' = \hat{X}_i - E_j \gamma_{ij} \qquad (13)$$

where γ_{ij} is the jth element of the ith column of A^{-1}. An extinction event is defined as when any equilibrium density is zero, so by setting $\hat{X}_i' = 0$ and then rearranging equation (13) we get the equation:

$$E_j(i) = \frac{\hat{X}_i}{\gamma_{ij}} \qquad (14)$$

by which the value of how much the mortality of j has to be increased for i to go extinct, $E_j(i)$, is obtained. By then calculating $E_j(i)$ for all i in the web and taking the smallest positive value of these, the minimum amount by which the mortality of j can be increased before any species goes extinct, E_j,

is found. With the help of E_j it is then possible to calculate the new equilibrium density of the species to which the additional mortality was applied, at the time of the extinction event by inserting it into equation (12). The relative change in density, here denoted as ΔD for the sake of simplicity, of the perturbed species compared to its unperturbed equilibrium density can now be calculated as $(\hat{x}_i - \hat{x}_i')/\hat{x}_i$. Additionally, the relative increase in mortality, ΔR for similar reasons as above, was calculated as E_j / r.

3.3 Species properties
For each of the species in all the food webs under equilibrium conditions 28 different properties were calculated. These properties were chosen for different reasons; some for their supposed capability to detect keystone species, while others were chosen because they are commonly used in the literature. A summary with brief descriptions of all the properties can be found in appendix I, here follows a more in depth explanation starting with the different measures of unweighted and weighted degree used.

If *j* is the species for which the property is measured, *degree* is the amount of different links that *j* has; *negDeg* (negative degree) is the number of predators of *j*; *posDeg* (positive degree) is the number of prey that *j* has. *w.degree.in* (weighted incoming degree) is the total *per capita* effect that all of *j*'s predators and prey have on *j*; *w.negDeg.in* (weighted negative incoming degree) is the total negative *per capita* effect of all of *j*'s predators on *j*; *w.posDeg.in* (weighted positive incoming degree) is the total positive *per capita* effect of all of *j*'s prey on *j*.
w.degree.out (weighted outgoing degree) is the total *per capita* effect that *j* has on all of its predators and prey; *w.negDeg.out* (weighted negative outgoing degree) is the total negative *per capita* effect of *j* on all of its prey; *w.posDeg.out* (weighted positive outgoing degree) is the total positive *per capita* effect of *j* on its predators.
maxLink.in (maximum incoming link) is the largest *per capita* effect that another species has on *j*. *maxNegLink.in* (maximum negative incoming link) is the largest negative *per capita* effect that a predator has on *j*.
maxPosLink.in (maximum positive incoming link) is the largest positive *per capita* effect that a prey has on *j*.
maxLink.out (maximum outgoing link) is the largest *per capita* effect that *j* has on any other species. *maxNegLink.out* (maximum negative outgoing link) is the largest negative *per capita* effect that *j* has on any of its prey.
maxPosLink.out (maximum positive outgoing link) is the largest positive *per capita* effect that *j* has on any of its predators.

Closeness centrality is the mean shortest path length between *j* and all other species in the web. *Betweenness centrality* is a measure of how often *j* appears on all the shortest paths between all species in the web. Both closeness centrality and betweenness centrality was calculated with the igraph package for R (Csa'rdi & Nepusz 2006).

Trophic level is the short-weighted trophic level of a species which is the average of prey averaged trophic level and shortest trophic level (Levine 1980; Williams & Martinez 2004).

K is the keystone index proposed by Jordan *et al.* (1999). It is the sum of a bottom-up part, K_{bu}, as well as a top-down part, K_{td}. The two directed keystone indices measure how many predators (K_{bu}) or prey (K_{td}) are directly or indirectly affected by *j*.

The *trophic uniqueness* is a measure of how unique *j* is in relation to the other species in the web with respect to its distribution of links (Petchey *et al.* 2008).

The property H_i and H_j describes the diversity of biomass flows out from and into *j*, respectively (Scotti *et al.* 2009a). It can be looked upon as a measure of *j*'s inclination towards being a generalist or a specialist. A high measure of *H* indicates many evenly distributed links – a generalist; while a low measure indicates few unevenly distributed links – a specialist.

AMI_i and AMI_j (average mutual information) are measures of the amount of constraints put on the ways biomass may exit or enter *j*, respectively (Scotti *et al.* 2009a; Scotti *et al.* 2009b).

PageRank™ is the measure used by Google™ to rate web pages on the internet. It is somewhat modified here to give a high rating to species that are prey to other species who also have a high rating (Allesina & Pascual 2009).

Finally the body mass of species measured in kg was also used as a property.

The Spearman's rank correlation coefficient between the measure of MEVP, *ΔD,* and the different species properties was then calculated for every perturbed species in all replicate webs. For comparison the same was also done for the dependent variable *ΔR*.

4. Results
4.1 Model Validation with Empirical Data
A comparison of a variety of food web measures from the 100 replicate food webs with empirical data summarized in Dunne *et al.* (2004) (Benguela, Caribbean Reef Large, Caribbean Reef Small and Northeast US Shelf) and Kristensen (2008) (Skipwith Pond, Little Rock Lake, Bridge

Brook Lake, Chesapeake Bay, Ythan Estuary) was made in order to test the validity of the model (Table 2). The comparison showed a good match for both mean trophic level and maximum trophic level when compared to Kristensen (2008). The mean trophic level was substantially lower than what was presented by Dunne *et al.* (2004), although this is probably explained by high aggregation of basal species and under-representation of invertebrates in those webs. The amount of variation in prey and predators per species, represented by the standard deviation of generality and vulnerability respectively was considerably higher in the model food webs than in empirical webs. The fractions of basal, intermediate and top species fit well with those presented in Kristensen (2008). Compared to Dunne *et al.* (2004) the model webs had, on average, a larger proportion of basal and top species and a smaller fraction of intermediate species. Again, in the webs from Dunne *et al.* (2004) basal species are highly aggregated which gives reason to believe that in fact the fractions of species groups in these webs might be closer to what the model predicts.

The connectance was generally low, although it was clearly within the range of the empirical webs.

Table 2. Food web measures of the model food webs presented in this study as well as comparative empirical data from real food webs presented in Dunne et al. 2004 and Kristensen 2008. S is number of trophic species; Max Sim. is maximum similarity; frac. omn. is fraction of species that is omnivorous; gen is generality; vul is vulnerability. All values for the present study is mean from 100 replicate food webs. * = not reported. **No value was given for Frac. Omn. for one food web in Kristensen 2008, so N = 4 for this particular case.

	Present study		Dunne et al. 2004		Kristensen 2008	
	Mean (N = 100)	Range	Mean (N = 4)	Range	Mean (N = 5)	Range
S	50	50 - 50	100,75	29 - 245	51,20	25 - 83
Max Sim.	0,87	0.76 - 0.96	0,64	0.58 - 0.70	0,61	0.34 - 0.76
Trophic Level Mean	2,06	1.88 - 2.65	3,08	2.9 - 3.2	2,19	1.59 - 2.57
Trophic Level Max	3,33	3.00 - 5.60	*	*	3,58	3.36 - 4.06
Frac. Omn.	0,09	0 - 0.30	0,82	0.76 - 0.87	0.48**	0.36 - 0.60
Gen. StDev	1,55	0.91 - 2.37	1,15	0.88 - 1.92	1,06	0.71 - 1.4
Vuln. StDev	1,81	0.79 - 2.55	0,81	0.61 - 1.18	0,83	0.54 - 1.4
Frac. Basal	0,09	0.04 - 0.20	0,05	0.02 - 0.07	0,14	0.04 - 0.32
Frac. Intermediate	0,83	0.68 - 0.94	0,95	0.93 - 0.98	0,72	0.62 - 0.92
Frac. Top	0,08	0.02 - 0.14	0,01	0 - 0.04	0,14	0 - 0.38
Connectance	0,07	0.06 - 0.11	0,18	0.05 - 0.24	0,15	0.06 - 0.32

4.2 Extinction patterns

The amount of non-self extinctions was found to be very high with 63.1% of all extinctions being non-self extinctions, which is more than what was found in a previous similar study (35.6 %, Clark 2005). The high fraction of non-self extinctions is a clear indication of the importance of adopting a

multi species perspective in conservation strategies. The largest amount of non-self extinctions followed from perturbing basal species (98 % non-self extinctions) and the smallest amount was found when perturbing intermediate species (59 % non-self extinctions). Interestingly the results also show a large amount of non-self extinctions resulting from the perturbation of top species (71 % non-self extinctions), highlighting the importance of indirect effects in the model, Figure 1A. This finding is in contrast to the results of Clark (2005), where nearly all extinctions of top species were self extinctions. It is uncertain if this is due to some difference in the way dynamics was imposed on the systems between the present study and that of Clark (2005) or because of a difference in the maximum number of species (9 vs. 50) in the webs.

Another indication of indirect effects in the webs is the amount of extinctions where the extinct species has no direct link to the disturbed species (Figure 1B). The amount of extinctions due to indirect effects was high for all species types but especially high for top species. This is to be expected since, in most cases, a reduction of a predator population would benefit its prey species; the fact that the model produced results where a species with a direct connection to the perturbed top-species sometimes went extinct is evidence for the existence of extensive indirect effects in the model communities.

The type of species most resistant to extinctions was the basal species, with only 9 extinctions out of 5000 over all replicates, top species suffered 723 extinctions and intermediate species suffered the most, 4268. This distribution might be a result of the total numbers of species represented in the web, though, and to correct for this we calculated the risk of going extinct for one species in each of the species categories (Figure 1C). This figure shows that basal species are very resistant to extinction relative to their occurrence while intermediate and especially top species are susceptible to extinction relative to their occurrence.

Basal species could suffer the highest additional mortality in relation to baseline values, but the lowest change in density before a non-self extinction occurred. The communities were more sensitive to adding mortality to species higher up in the food chains, with adding mortality to intermediate species having the largest effect; the reverse is seen for density change (Figure 1D).
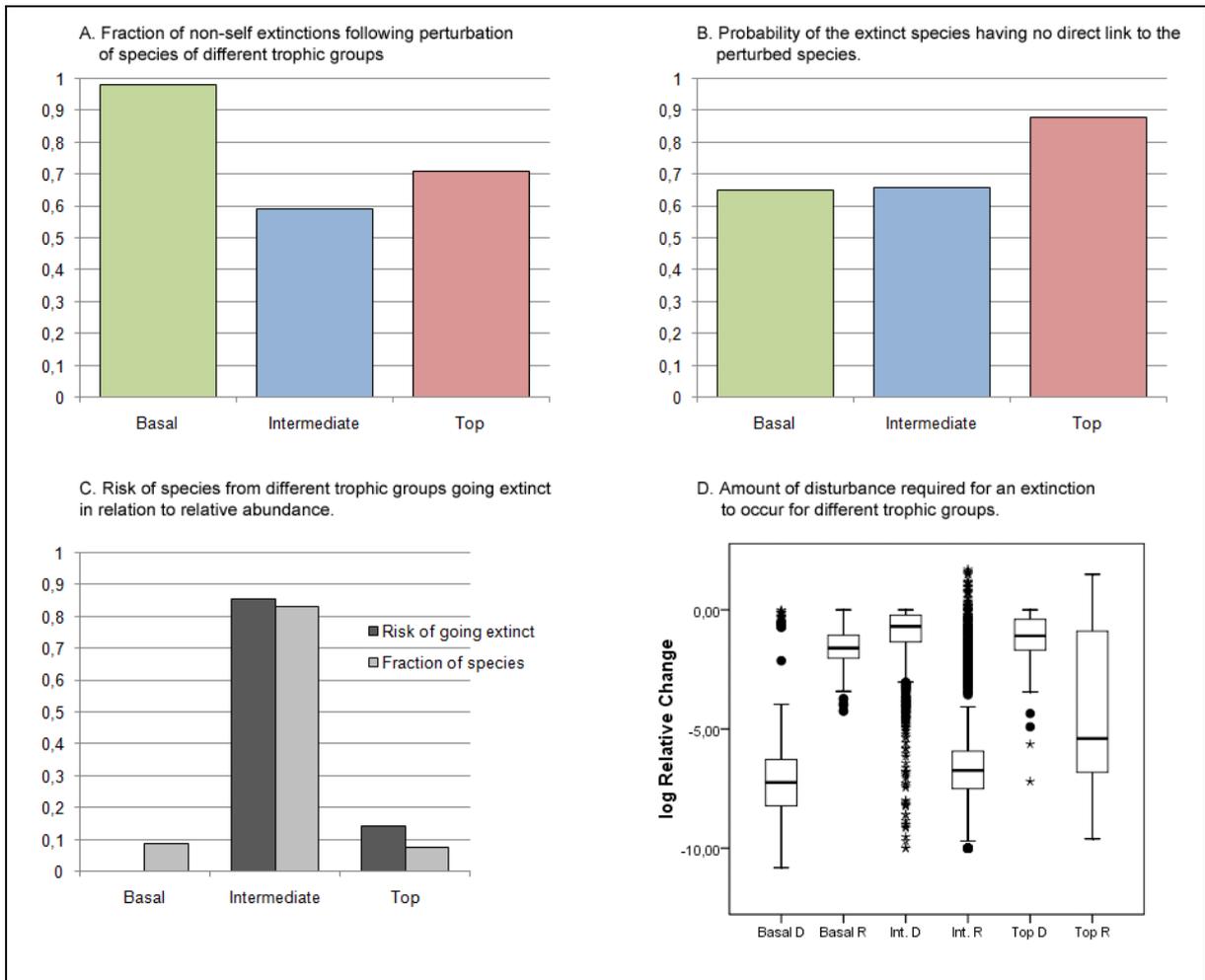
Figure 1. (A) *Fraction of times after disturbing a species from a specific trophic group that another species than the perturbed one went extinct.* **(B)** *The fraction of non-self extinctions that was of a species that had no direct link to the perturbed species (x-axis); i.e. species that are not a prey or a predator of the perturbed species.* **(C)** *The risk of going to extinction for different trophic groups; based on all extinction events in all replicates. This is set in relation to the fraction of occurrence for the same groups over all replicates.* **(D)** *The logged relative amount of disturbance that was required before a non-self extinction event occurred; either as relative change in density (D) or as relative change in mortality (R).*

4.3 Factors Influencing Minimum Ecologically Viable Population Sizes

Table 3 shows the results of the correlation analyses. Of the two dependent variables ΔD is the measure that most closely illustrates MEVP and the five best correlations found for this variable was for the properties K_{bu}, K, *PageRank*, *negDeg* and *betweenness centrality*. Interestingly all of these most important properties showed a negative correlation with ΔD meaning that the higher the property, the higher the species MEVP. These are the properties for which the highest fractions of significant results were found, but it might also be worth noting some of the less significant results. Body mass hardly showed any correlation which is interesting because there were

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so many factors in the model that was influenced by body mass. Trophic level also showed a weak correlation indicating that there were important species to be found in all heights of the webs.

For the other dependent variable, *ΔR*, which is a measure of the amount of additional mortality that can be added to the species before an extinction occurs, the largest correlations are found for the properties *K, w.degree.out, maxLink.out*, *trophic uniqueness* and *degree.* Except for *K, trophic uniqueness* and *betweenness centrality*, there is little resemblance in what properties show significant results and for the majority of the correlation coefficients the relationship is reversed. This is interesting since it indicates no agreement between the two dependent variables, and indeed a correlation analysis between the two did not show a significant correlation (*corr. coef. = 0.006; p = 0.66*).

Table 3. *List of mean correlations between measured species property and dependent variables ΔD and ΔR for non-self extinctions, as well as percent of cases where the correlation was statistically significant.*

	ΔR				ΔD		
Property	% Significant orrelations	Mean correlation	StDev of mean correlation	Property	% significant correlations	Mean correlation	StDev of mean correlation
K	84	0,54	0,17	K_{bu}	83	-0,56	0,21
w.degree.out	82	-0,58	0,21	K	71	-0,43	0,18
maxLink.out	82	-0,58	0,20	PageRank™	71	-0,46	0,18
TU	66	0,43	0,19	negDeg	67	-0,46	0,20
degree	60	0,38	0,21	Betweenness centra	62	-0,40	0,15
Betweenness centralit	55	0,38	0,17	w.posDeg.out	60	-0,39	0,27
K_{td}	55	0,40	0,32	TU	58	-0,39	0,19
maxNegLink.out	50	-0,38	0,35	maxPosLink.out	58	-0,39	0,28
w.negDeg.out	50	0,38	0,35	AMI_i	49	0,35	0,24
AMI_j	50	0,34	0,28	H_i	49	-0,44	0,27
w.negDeg.in	47	-0,32	0,29	w.posDeg.in	48	0,30	0,32
maxNegLink.in	46	0,32	0,28	w.negDeg.in	42	0,34	0,24
K_{bu}	45	0,34	0,27	maxNegLink.in	40	-0,33	0,25
AMI_i	42	-0,33	0,23	maxPosLink.in	40	0,25	0,29
w.posDeg.out	41	0,31	0,28	degree	38	-0,31	0,18
posDeg	41	0,23	0,34	Trophic level	35	0,30	0,22
maxPosLink.out	40	0,30	0,29	w.degree.out	29	0,24	0,23
w.degree.in	34	0,20	0,28	maxLink.out	28	0,24	0,23
H_j	33	0,10	0,35	w.degree.in	20	-0,16	0,25
PageRank™	30	0,21	0,25	Body mass	19	0,14	0,26
Body mass	30	-0,18	0,28	maxLink.in	19	-0,18	0,24
negDeg	29	0,25	0,29	maxNegLink.out	18	-0,15	0,26
H_i	28	0,19	0,34	w.negDeg.out	17	0,15	0,27
maxPosLink.in	26	-0,15	0,28	H_j	16	0,11	0,27
w.posDeg.in	25	-0,08	0,31	K_{td}	11	-0,06	0,24
maxLink.in	23	0,14	0,28	AMI_j	10	-0,06	0,24
Trophic level	19	-0,01	0,27	posDeg	9	0,05	0,25
Closeness centrality	13	0,10	0,21	Closeness centrality	8	-0,09	0,20

5. Discussion

The aim of the study was to find out what properties of a species can be used to predict if that species is important to the rest of the system, in the sense that a small reduction in its density will cause an extinction to occur somewhere in the web. In all, judging from the proportion of significant correlations and strength of correlations, the most promising index of this kind of importance is the bottom-up part of the keystone index (K_{bu}), originally proposed by Jordan *et al.* (1999). Together with the top-down keystone index (K_{td}) it sums to what is simply called keystone index (K). Because of this reason the relevance of K as the second most significant property can be questioned since K_{td} was not found to be significant at all (11 % significant correlations, see Table 3). K_{bu} is a measure of how many predators are directly and indirectly affected by the species under consideration and therefore it can also be thought of as a measure for how well connected a species is as a prey item supporting other species at higher trophic levels.

In line with this finding is that *PageRank™*, as well as negative degree (which is simply the number of direct predators a species has) was found to be the third and fourth most significant property measured for finding species with high MEVPs, respectively. Negative degree would be an ideal property for finding important species as it is a relatively simple thing to measure. *PageRank™*, the measure used by Google™ to rate the importance of web sites, is somewhat more complex (see Allesina & Pascual 2009 for an in-depth explanation and discussion). The variant of *PageRank™* used here is calculated in a way so that a species will get a higher rating if it supports (is a prey to) other species with a high *PageRank™*. This is somewhat similar to the bottom-up part of K in that a species that indirectly supports many predators gets a higher rating.

The fifth most significant property was betweenness centrality. It is calculated by considering all the shortest paths between all species pairs in the web; the more of these shortest paths that pass through a specific species, the higher that species' rating will be. It might be that this measure is biased toward intermediate species since basal and top species never will end up in any shortest paths except for the ones in which they are 'start' or 'end' node.

Other experimental studies have shown that the most connected species in communities generally are those whose removal leads to the greatest number of secondary extinctions, making the system sensitive to their loss (Solé & Montoya 2001; Dunne *et al.* 2002; Memmott *et al.* 2004). If we regard species with high K_{bu}, PageRank™, betweenness centrality and, to

some extent, amount of predators as highly connected, it would seem as if the same is true for the MEVP. A suggested reason for this is that the more species that are in direct or indirect contact with a disturbed species, the more opportunities there are for that disturbance to propagate through the web and cause extinctions (Dunne *et al.* 2002). Since weak interactions are known to stabilize food webs (McCann 1998), another possible explanation could be that species with many links also have weaker links. If this is true it might be hypothesized that as the highly connected species' abundance decline, so does its role as a buffer within the community. At the same time the strong links that tend to destabilize the system becomes relatively more important, ultimately leading to extinction, although this remains untested here.

An interesting point to make is that properties of species that indicate a high MEVP generally seem to require that the whole web is taken into consideration; it is a species position in relation to the rest of the species within the web that affects its importance. This puts further emphasis on the necessity of adopting community perspective within conservation biology.

An exception to this finding is that the number of predators of a species, a measure that does not require the whole community to be considered, was a good indicator of high MEVP. This, together with the fact that the other good indicators K_{bu} and *PageRank™* describe the role that the species play as a prey item in the web illustrates another major lesson to be learned from the results - that bottom-up effects are a major factor in the secondary extinction of species. Another thing that indicates the importance of bottom-up effects in these food webs is the fact that the density of basal species could only be reduced a very small amount before a non-self extinction occurred.

Of course this finding is model-specific and with the large amount of empirical evidence for the importance of top-down effects that exists (e.g. Ripple & Beschta 2006; Casini *et al.* 2008) this could be used to criticize the model. On the other hand, considering the amount of secondary extinctions that resulted from lowering the density of top-species (see Figure 1A.) there is no evidence that the model failed to produce top-down effects, it merely shows that these effects did not lead to extinctions as often as bottom-up effects did.

Including top-down effects has proven to be a challenge when constructing computer models of food webs; often realism in the form of number of species have had to be sacrificed in order to achieve realistic dynamics, or vice versa (Dunne & Williams 2009). Topological models can handle a

large amount of species, but using such a model will inevitably make it impossible to see any top-down effects (Borer *et al.* 2002). The model presented here was able to handle both a large number of species as well as realistic dynamics. In the light of the large number of non-self extinctions following the reduction in abundance of a top species, the relevance of topological studies can be questioned (Montoya *et al.* 2009). Furthermore, in line with other studies (Borrvall *et al.* 2000; Christianou & Ebenman 2005) top species faced the highest risk of extinction, at least in relation to their abundance but, importantly, not only because of direct bottom-up effects (loss of prey). In many cases following the perturbation of a top species, another top species went extinct due to some indirect effect propagating through the system. With this model 71% of the cases where a top species was perturbed, another species went extinct.

Completely different correlations were found for the measured properties and the disturbance depending on which of the two variables ΔR and ΔD that was used. Seen from a single species perspective it would be expected that an increase in mortality would lead to a decline in abundance and thus the two variables would have similar correlations. Here, when considering secondary extinctions from a community perspective this is clearly not the case; increasing a species' mortality up to the point where another species goes extinct may or may not mean that the first species' density also has changed, no correlation was found between the extra mortality added and the change in equilibrium density. This is most likely due to complex feedback mechanisms and indirect effects; and it further highlights the importance of considering the community as a whole in this kind of research. Furthermore, another important conservation implication can be found here: the measure with which a disturbance is quantified will affect what species-properties are good indicators of importance of one species to the rest of the community.

5.1 Conclusion and Future Directions
As indicated by the large amount of non-self extinctions seen in this study a community-perspective needs to be adopted in conservational work. Species with a large number of direct and indirect links to other species; as well as species with important bottom-up roles should be prioritized. Also, the best predictors for high MEVP in this study was found to require the consideration of the species' context within the food web relative to its fellow community members.

An interesting continuation of this study would be to test these findings in other models such as food web simulations or in models of real existing ecosystems. Such research could provide more robustness to the results, which is needed if they are to be of real use for conservation biology. Another rewarding line of research might be to investigate the mechanisms behind the findings here. A very large amount of complex indirect interactions was shown to exist in the model and to focus on how these interactions work to give some species a higher MEVP might indeed prove to be a fruitful endeavor, not just to conservation biology, but to our understanding of how ecosystems work in general.

6. Acknowledgements

7. References

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8. Appendix

Appendix I.List of the different species properties of species ȷ *that were measured and used in the correlation analysis. All were measured at equilibrium density.*

AMI_j	The contribution of j to the distribution of energy in the system (incoming).
AMI_i	The contribution of j to the distribution of energy in the system (outgoing).
Betweenness centrality	A measure of the amount of shortest paths between all nodes that pass through j.
Body mass	The bodymass of j in kg.
Closeness centrality	Mean length of all shortest paths within the system between j and all other species.
H_i	Diversity of biomass flows out of j (Scotti *et al.* 2009).
H_j	Diversity of biomass flows into j (Scotti *et al*. 2009).
K	Keystone index (Jordan *et al.* 1999).
K_{bu}	Keystone index, bottom up (Jordan *et al.* 1999).
K_{td}	Keystone index, top down (Jordan *et al.* 1999).
maxLink.in	Magnitude of the strongest per capita effect from another species on j.
maxLink.out	Magnitude of the strongest per capita effect from j on another species.
maxNegLink.in	Magnitude of the strongest negative per capita effect from another species on j.
maxNegLink.out	Magnitude of the strongest negative per capita effect from j on another species.
maxPosLink.in	Magnitude of the strongest positive per capita effect from another species on j.
maxPosLink.out	Magnitude of the strongest positive per capita effect from j on another species.
negDeg	The amount of predators of j.
w.negDeg.in	Total negative per capita effect of all of j's predators on j.
w.negDeg.out	Total negative per capita effect of j on its prey.
PageRank™	Google™ pagerank (Allesina & Pascual 2009).
posDeg	The amount of prey species of j.
w.posDeg.in	Total positive per capita effect of all of j's prey on j.
w.posDeg.out	Total positive per capita effect of j on its predators.
w.degree.in	Total per capita effect of all of j's predators and prey on j.
degree	Total number of links of species j.
w.degree.out	Total per capita effect of j on its predators and prey.
Trophic level	Short-weighted trophic level.
TU	Topological trophic uniqness (Petchey *et al.* 2008)