REVIEW ARTICLE

Metapopulation and its applications in conservation biology

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Abstract

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Metapopulation, originally pioneered by Levins, refers to a series or set of local populations, each existing on a patch of suitable habitat that is separated from other occupied patches by unsuitable terrain. Each population has its own relatively independent dynamics. The long-term persistence and stability of the metapopulation arise from a balance between population extinction and recolonisation. Although metapopulation concepts are not commonly fit to real world conditions and there are still questions about the generality of metapopulation dynamics and the applicability of metapopulation models to specific problems in conservation, they have contributed significant insights into conservation and have inspired field studies focused on collecting key data on demography and movement. Moreover, metapopulation concepts have had positive effects in conservation research, especially, as interest in metapopulation dynamics has prompted renewed research concerning dispersal capacities that is extremely valuable in understanding population structure. Therefore, metapopulation concepts replace the island biogeography concepts that have been used in the past for decades.

Key words : metapopulation, ecogogical modeling, conservation,
minimum viable metapopulation

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บทคัดย่อ

โกศล ยุทธรรม มัลลิกา เจริญสุธาสินี และ กฤษณะเดช เจริญสุธาสินี

ประชากรแบบเมต้าและการนำไปใช้ในด้านชีววิทยาการอนุรักษ์

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ประชากรแบบเมต้าได้มีการเริ่มต้นศึกษาโดย Levins หมายถึง อนุกรมหรือเซ็ทของประชากรที่อาศัยอยู่กันเป็นกลุ่ม ประชากรกลุ่มนี่แยกออกจากประชากรกลุ่มอื่น ๆ โดยสภาพพื้นที่ที่ไม่เหมาะสม ประชากรแต่ละกลุ่มมีพลวัตรของมันเองอย่างอิสระไม่ขึ้นกับประชากรอื่น ประชากรแบบเมต้าจะอยู่ได้และมีความเสถียรสูงหรือไม่ขึ้นอยู่กับความสมดุลระหว่างการสูญพันธุ์และกลับมายึดเป็นอาณานิคมของประชากรโดยมีการอพยพเป็นตัวกลางในการทำหน้าที่นี้ ถึงแม้ว่าแนวคิดของประชากรแบบเมต้าไม่ค่อยจะเหมาะสมกับสถานการณ์จริงและยังคงมีคำถามเกี่ยวกับพลวัตรของประชากรแบบเมต้าและการจะนำเอาผลของแบบจำลองทางคณิตศาสตร์ไปใช้ในการแก้ปัญหาทางด้านการอนุรักษ์ได้หรือ แต่ประชากรแบบเมต้ายังคงมีความสำคัญมากในด้านการอนุรักษ์เพราะสามารถทำให้เข้าใจและเป็นแรงจูงใจในการศึกษาภาคสนาม ทำให้โฟกัสการเก็บข้อมูลที่สำคัญเกี่ยวกับการศึกษาด้านประชากร และการอพยพของประชากร นอกจากนี้แนวคิดของประชากรแบบเมต้ายังมีผลเชิงบวกกับการทำวิจัยด้านการอนุรักษ์ โดยเฉพาะอย่างยิ่งพลวัตรของประชากรแบบเมต้าที่เกี่ยวกับความสามารถในการกระจายทำให้สามารถเข้าใจเกี่ยวกับโครงสร้างของประชากรมากขึ้น ดังนั้นแนวคิดประชากรแบบเมต้าจะเข้ามาทดแทนแนวคิดการศึกษาด้านประชากรเกาะ (island biogeography) ที่เคยใช้กันมาหลายสิบปี

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The term metapopulation was first introduced by Levins (1969). Studies using metapopulation generally subdivide the general population into a series of local populations with a balance between extinctions and recolonisations of local populations that facilitates long-term persistence of the metapopulation. The key process is the interpatch connection functions by migration (Figure 1) (Hanski and Gilpin, 1997). Metapopulation models have been widely used in the biological field including in population ecology, conservation biology, and pest control (for details see Wu, 1993; Harrison, 1994; Hanski and Gilpin, 1997; Takagi, 1999; Fagan *et al.*, 2002).

Modelling has become an important tool in population and conservation biology as evidenced by many books that provide excellent advice on model construction, that have recently published by such authors as: Cappuccino and Price, 1995; Haefner, 1996; Hanski and Gilpin, 1997; Hilborn and Mangel, 1997; Roughgarden, 1998; Shugart, (1998).

What is a model? A model is a representation of a particular thing, idea, or condition (Jackson *et al.*, 2000). Models can be very simple, such as a logistic growth model for a single species, or extremely complex, such as an individual based model. Model can be categorised into two classes: qualitative (expressed in words or diagrams) and quantitative (expressed in mathematical equations or computer languages) (Wu, 1993). Many ecological theories today are represented in largely mathematical terms because mathematics provides the most precise language to describe complex ecological systems and is also an ideal tool for prediction in ecological systems (Tilman *et al.*, 1994; Jansen, 1995; Gyllenberg and Hanski, 1997; Hanski and Ovaskainen, 2000; Keymer *et al.*, 2000; Casagrandi and Gatto, 2002). However, mathematical formulations have limitation in that they usually force ecologists to make clear and unambiguous assumptions. There are many models used in population ecology including metapopulation models. Metapopulation models are useful

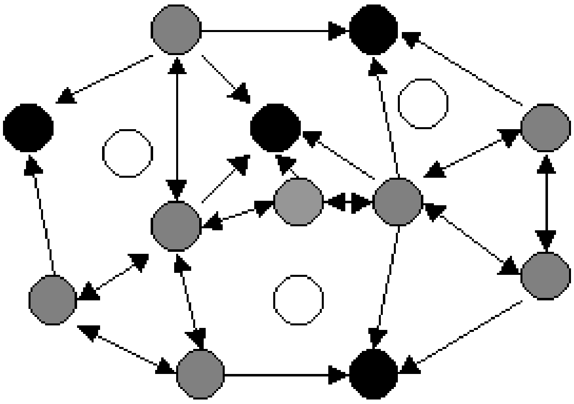

Figure 1. The ideal metapopulation is a set of local populations in which the interpatch connection functions by migration facilitate long-term persistence with the balance between colonisation and extinction. The empty habitat patches (in white) are susceptible to colonisation from nearby local population. Local populations whose persistence depends on immigration from nearby local populations (sink populations) are shown in black, while the sources of immigrants (source populations) are shown in grey (Marquet, 2002).

and popular models that fall into the quantitative type and are always represented as analytical or simulation models.

There are three types of modelling approaches used in metapopulation studies assuming many habitat patches and local population (Hanski and Gilpin, 1997): (1) spatially implicit approaches, often based on a critical simplification of what at first appears as a hopelessly complex problem, in which the habitat patches and local populations are discrete (and are generally assumed to have independent dynamics) but are assumed to be all equally connected to each other, (2) spatially explicit approaches in which it is assumed that local populations are arranged as cells on a regular grid (lattice), with population sizes modelled as either discrete or continuous variables and where local populations are assumed to interact only with local populations in the nearby cells, and (3) spatially realistic approaches in which the models allow one to include in the model the specific geometry of particular patch networks, such as how many patches there are in the network, how large they are, and where exactly they are located. For more details see Table 1.

In this review article, we will briefly describe the metapopulation concepts and how metapopulation concepts are applied in conservation (for excellent detail see Hanski and Gilpin, 1997). Finally, we will give some ideas about the use and misuse of metapopulation studies, especially concerning rules for both theoreticians and conservationists which have been argued by Doak and Mills (1994).

Mathematical Modelling

The pioneer metapopulation model was first proposed by Levins (1969) (for detail see Box 1). This model has been modified and widely used in population studies because the habitats used by most species are becoming fragmented; therefore the populations fall into metapopulation concepts (Box 2).

From the box 1, at equilibrium, $\frac{dP}{dt} = 0$, the proportion of occupied sites can be investigated by,

$$P^* = 1 - \frac{e}{\beta} \qquad (1)$$

Table 1. Three types of modelling approaches used in metapopulation studies. The table provides definitions, examples, advantages, and disadvantages of each type of modelling approach.

Modelling Approaches	Definition	Examples	Advantages	Disadvantages
Spatially Implicit Models	Model in which all local populations are equally connected.	Classical Levins model, and all patch models and structured models	It greatly facilitates the mathematical and conceptual analysis.	It can be used to study only a subset of all interesting questions, such as, what if migration rate is high enough to rescue local population?
Spatially Explicit Models	Model in which migration is distance-dependent, often restricted to the nearest habitat patches; the patches are typically identical cells on a regular grid, and only presence or absence of the species in a cell is considered.	Cellular automata models, interacting particle systems, and couple map lattice models	The mathematical rules that govern local behaviour are the same from cell to cell and it is easy to write a computer program to model the dynamics.	The state of the metapopulation cannot be described simply by the fraction of cells occupied; an entire vector of presences and absences is needed.
Spatially Realistic Models	Model that assigns particular areas, spatial locations, and possibly other attributes to habitat patches, in agreement with real patch networks; spatially realistic models.	Simulation models and the incidence function model	The model is closely linked with empirical field studies.	Meaningful application of the model assumes much data.

In the classical Levins metapopulation model, the lifetime of a local population is exponentially distributed with parameter e because the extinction is modelled by assigning a constant rate e, that is to say the expected lifetime of a local population is $1/e$. The empty suitable patches are colonised with the colonisation rate β. Therefore, the expected number of local populations that have been colonised by one local population during its lifetime equals

$$R_0 = \frac{\beta}{e} \qquad (2)$$

The threshold condition of metapopulation persistence is represented as the following condition:

$$R_0 > 1 \qquad (3)$$

In a metapopulation context, this threshold condition determines when a landscape composed of a set of empty patches is successfully colonised, and also determines its long-term persistence (Marquet and Velasco-Hernandez, 1997).

Metapopulation Conservation Biology

In the past, conservation biology emphasised habitat relationships of individual species to a focus on refuge design, guided by the dynamic theory of island biogeography and the genetic deterioration owing to drift and inbreeding. This theory dealt with species richness of communities. For new conservation biology we aim at studying the population level, since the older concept, island biogeography, has been replaced by the new concept, metapopulation, which describes the population level (Figure 2). However, the island biogeographic theory shares key underpinnings

Box 1. The classical Levins metapopulation model

The classical Levins metapopulation model assumes that *N*, the large number of available discrete habitat patches, is constant and that all patches have the same size and quality. All patches are connected with each other via migration. In Levins model, habitat patches are scored only as occupied or unoccupied, and actual sizes of the local population are ignored. Denote the number of occupied and unoccupied patches by *O* and *U*, respectively. At equilibrium, we assume that each individual in the patch produces a total of β propagules per time unit and these propagules find unoccupied patches at a rate *U*/*N*. We assume that the occupied patches become extinct at a rate *e*. The equations that represent this system are (Marquet, 2002):

$$\begin{aligned}\frac{dO}{dt} &= \beta O\frac{U}{N} - eO\\ \frac{dU}{dt} &= -\beta O\frac{U}{N} + eO\end{aligned} \qquad (1)$$

Dividing the Eq. 1 by *N*, defining $O/N = P$ (the fraction of occupied habitat patches) and $U/N = 1 - P$ (the fraction of patches available for colonisation), then Eq. 1 can be written as the classic Levins metapopulation model.

$$\frac{dP}{dt} = \beta P(1-P) - eP \qquad (2)$$

Box 2. The concept of Levins metapopulation model

The concept of an ideal metapopulation model consists of four main assumptions that are (Hanski and Gilpin, 1997):

1) Space is discrete, therefore, it is possible and useful to distinguish between habitat patches that are suitable for focal species and the rest of the environment.
2) Habitat patches have equal area, isolation, and quality.
3) The dynamics of all local populations are assumed to be asynchronous events containing independent dynamics of each local population.
4) The exchange rate of individuals among local populations is so low that migration has no real effect on local dynamics in the existing populations (local dynamics occur on a fast time scale in comparison with metapopulation dynamics). This feature facilitates the long-term persistence of the metapopulation with the balance of extinction followed by colonisation.

Note that the habitat patches of the metapopulation are large enough to accommodate panmictic local populations, but not larger.

with metapopulation models that are by nature discrete entities, with movement of individuals among relatively unstable local populations. There is also an obvious difference between these theories which is that the island biogeographic theory treats communities, not individual species.

According to the definition of metapopulation, we will describe how metapopulation can be

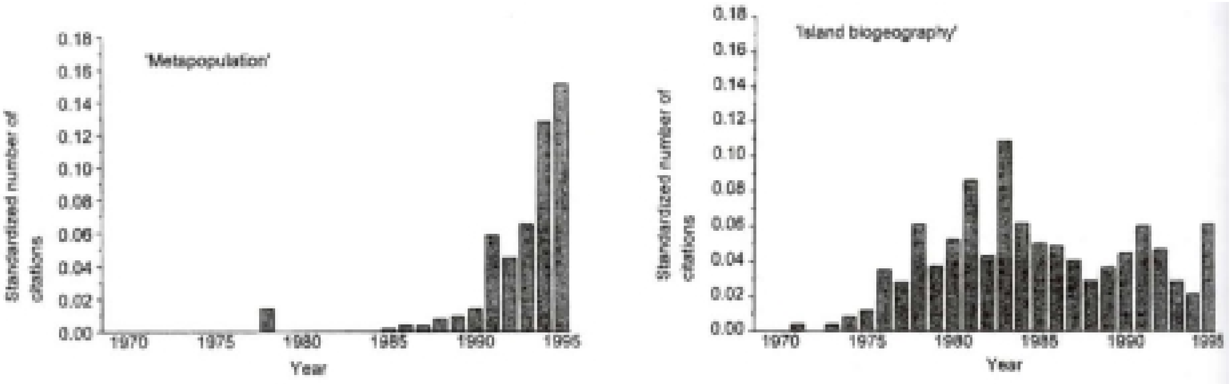

Figure 2. Number of citation to keyword "island biogeography" and "metapopulation" in the BIOSIS database in 1970-1995, standardised by the respective total number of papers in the data base (Hanski and Gilpin, 1997).

applied in conservation biology to answer these frequently asked questions: Does it follow that most species persist in a balance between extinction and recolonisation? Are all species truly metapopulations, if a long enough time scale is considered? What is the minimum amount of suitable habitat necessary for metapopulation survival? Can we apply metapopulation concepts to conservation? What has been modified from the classical Levins model?

For the question of whether or not most species in the real world persist in the balance between extinction and colonisation, we argue that such a situation may not always be occurring. This is supported because: (a) Landscape fragmentation is the major cause for extinction of local population as stress by many authors who work on empirical field studies (Beier, 1995; Lenihan and Peterson, 1998; Kurki *et al.*, 2000; Lindenmayer *et al.*, 2001) as well as those working on the theoretical studies (Gyllenberg and Hanski, 1997; Bascompte and Sole, 1998; Casagrandi and Gatto, 1999; Hanski and Ovaskainen, 2000; Casagrandi and Gatto, 2002). Therefore, local extinctions may occur in the course of a species' decline to regional extinction with recolonisation occurring infrequently or not at all due to the fact that the species' habitats are undergoing reduction and fragmentation naturally or caused by humans. (b) The population in nature is not usually represented by local populations with the same size and quality, but persist as the mainland-island metapopulation (Harrison, 1994) in which the mainland may be a single large or high-quality habitat patch, and it seems difficult or unlikely to go extinct. The island, in contrast, has colonisation and extinction events occurring more frequently. Therefore, in examining the persistence of the population in mainland-island metapopulation, the population viability of the mainland population is more appropriate. The island populations are also important in some events, especially the migration of the juvenile state to colonise island patches in which island patches persist as breeding patches for juvenile states of some organisms (Peacock and Smith, 1997). According to the empirical work on voles metapopulation, Crone *et al.* (2001) argued that it is not clear that voles would persist on larger islands (mainland patches) in the archipelago in the absence of recolonisation from smaller islands (island patches). Similarly, it is quite unlikely that voles could persist on tiny skerries in the absence of occasional colonisation from more persistent subpopulations on larger islands.

However, Hanski *et al.* (1995) examined the persistence of an endangered butterfly species (*Melitaea cinxia*) in a fragmented landscape in Finland (Figure 3). They surveyed the entire Finnish distribution of this endangered species within an area of 50 by 70 km^2, in a network of 1502 dis-

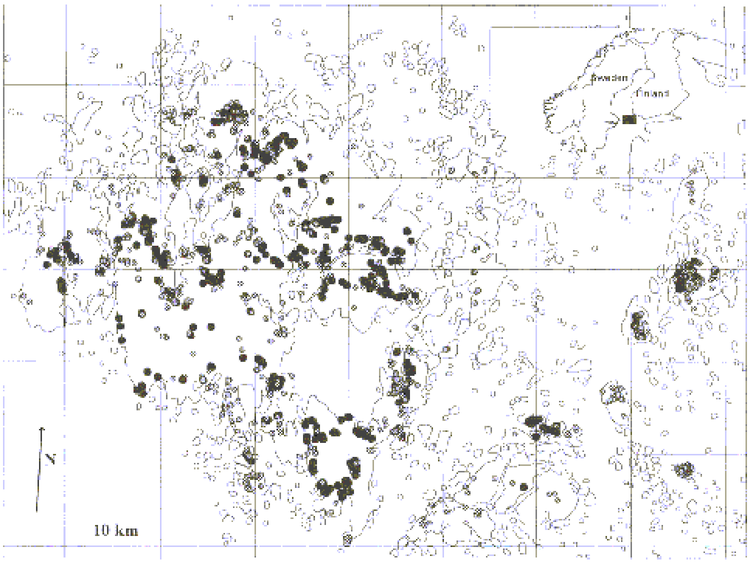

Figure 3. Map of Åland islands in southwestern Finland, showing the locations of the habitat patches (dry meadows) suitable for the Glanville fritillary *Melitaea cinxia* (dots). Patches that were occupied in late summer 1993 are shown by black dots. The size of the grid is 100 km^2 (Hanski and Gilpin, 1997).

crete habitat patches (dry meadows). They argued that the system of this butterfly species satisfied the four necessary conditions for a species to persist in a balance between stochastic local extinction and recolonisation: (1) the habitat patches support local breeding populations, (2) no single population is large enough to ensure long-term survival, (3) the patches are not so isolated as to prevent recolonisation, and (4) local dynamics are sufficiently asynchronous to make simultaneous extinction of all local populations unlikely. Furthermore, they also demonstrated that the occurrence of this butterfly in its naturally fragmented environment is consistent with two qualitative predictions and one quantitative prediction stemming from metapopulation models (see Hanski *et al.*, 1995 for details). Moreover, the empirical data provided by Biedermann (2000) also demonstrated that the froghopper *Neophilaenus albipennis* metapopulation falls into the conditions of classical metapopulation (see Box 3 for detail).

Are all species truly metapopulations, if a long enough time scale is considered? It is perhaps true in a limited sense. A large population must eventually go extinct. Organisms with long-life-span, such as large mammals simply have slower metapopulation dynamics than do insects (Harrison, 1994). It may, however, be true that all species are going to persist as metapopulations in a long-time scale consideration. There are many factors affecting this, for example, the ability of such organisms to disperse, the distance between patches that allows interpatch connection functions by migration, and the asynchronous dynamics of any local populations that seem to be true for patchy landscapes.

To answer the question of what the minimum amount of suitable habitat necessary for metapopulation survival is, we must examine the current research. However, most available studies are theoretical (Etienne and Heesterbeek, 2000; Bascompte *et al.,* 2002). The important factors relating to the minimum amount of suitable habitat necessary for metapopulation survival are the viability of local populations and the size of local populations. When the size or quality of habitat

Box 3. An example using mathematical model-fitting field data.

An excellent example of using a mathematical model to fit field observation data is the study of Biedermann (2000) who studied the occupancy pattern of the froghopper *Neophilaenus albipennis*, surveyed in a network of 506 patches of its host plant *Brachypodium pinnatum*, in the porphyry landscape north of Halle in Eastern Germany. The study area covered about 17 km^2 and is characterised by more than 200 porphyry and limestone outcrops with dry grassland, all within agricultural land. The size of the patches ranged from 1 to over 7000 m^2, the mean size being 118 m^2. The distribution according to area shows a high number of small patches.

In order to simulate the dynamics of the metapopulation the incidence function model (IF) was used. The model was successfully fitted to the field data. The model is spatially explicit and requires only a minimum of empirical data. This model is based on a linear first-order Markov chain in which each habitat patch has constant transition probabilities between the state of being empty or occupied. The IF used in this study is shown as,

$$j_i = \frac{1}{1+e'/(S_i^2 \cdot A_i^x)} . \qquad (1)$$

J_i denotes the stationary probability of patch *i* being occupied (the incidence of the species in patch *i*), *e*' includes the extinction risk (*e*) and *y*' with $e' = e \cdot y'^2$ when *y*' is the combination of two parameters (the steepness of recolonising probability by increasing the number of immigrants, *y*, and the density and the emigration characteristics of the species, β, with $y' = y/\beta$), S_i the expression $p_j \cdot \exp(-\alpha \cdot d_{ij}) \cdot A_j^b$ (β represents the density and the emigration characteristics of the species, α states the effect of distance on dispersal success, d_{ij} the distance between patch *i* and *j*, A_j the area size of patch *j*, *b* the dependency of emigration on patch size, and p_j equals 1 for occupied and 0 for empty patches), *x* the environment stochasticity, and A_i the patch area.

The IF can be fitted to the empirical data on spatial arrangement and patch occupancy of *N. albipennis* by using maximum likelihood (*ML*) regression to obtain the value of *a*, *e*', and *x*. The model was iterated until the minimum value of *ML* was found. The total number of turnover of patch occupancy, which is required in order to get the values of *y*' and *e*, can be obtained from the following equation:

$$T = \sum \frac{1}{S_i^2+y'^2} \cdot \left(S_i^2 \cdot (1-p_i) + \frac{e' \cdot p_i}{A_i^x}\right) \qquad (2)$$

The values of the parameter estimation of the incidence function model of the metapopulation of *N. albipennis* are: $\alpha = 2.58$, $e' = 1.88$, $x = 0.839$, $ML = 148.2$, $T = 45$, $y' = 17.9$, and $e = 0.00587$.

A sensitivity analysis on the parameters extinction rate *e* and environmental stochasticity *x* was performed by analysing the model result with varying parameter values. The model result is the minimum number of patches for the survival of the metapopulation for 100 years. The extinction varied from 0.002 to 0.010. The minimum number of patches required for a survival probability of 95% in the patch size class 101-1,000 m^2 strongly depends on the extinction rate. An alteration in *e* by 10% results in a decrease or increase in the model result by three patches (Figure 1a). The environmental stochasticity varied from 0.2 to 1.6. The relationship between the minimum number of patches required for a survival probability of 95% in the patch size class 101-1,000 m^2 and the environmental stochasticity *x* is less steep than in the extinction rate. An alteration in *x* by 10% results in a decrease or increase by two patches (Figure 1b).

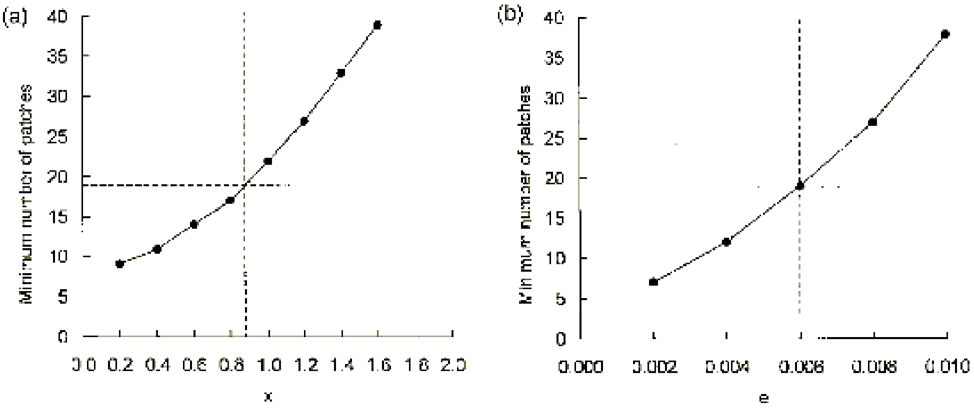

Figure 1. Sensitivity analysis: minimum number of patches (size class 101-1,000 m^2) required for a survival probability of 95% (100 years) for the metapopulation with varying parameter values of (a) the environmental stochasticity x and (b) the extinction rate e.

In conservation, the concept of the minimum viable metapopulation (MVM) size was used. For the metapopulation of *N. albipennis* a minimum number of 93 patches for a period of 100 years is derived from the simulation results. Reducing the patch number to this value, the simulation yields a survival probability of 95%, if the remaining patches in the study area are 118.0 m^2, that is 93 patches covering 10,974 m^2. A metapopulation solely built up of patches of 101-1,000 or 1,001-7,233 m^2 would require a total area of suitable habitat of 6,089 or 11,711 m^2, respectively. If the mean density is 2.1 individuals per m^2 and the fraction occupied is 17.8%, the population size of this species will be about 2,300-4,400 individuals. In conservation practice individual stands of the host plant are seldom a target of protection efforts. In the study area those efforts would focus on patches of dry grassland. The host plant of *N. albipennis* covers an average of 3.8% of the dry grassland. Therefore, a total area of 0.16-0.31 km^2 of dry grassland would be required to preserve the minimum number of patches for the long-term persistence of the metapopulation. This is 0.9-1.8% of the study area. The total amount of dry grassland in the study area is about 5%, so that finally, between one-fifth and one-third of the dry grassland of the porphyry landscape would be required for the long-term persistence (100 years) of the metapopulation of *N. albipennis*.

patches decreases, the extinction of local populations is increased as has been argued by many authors (Akcakaya, 2000; Biedermann, 2000; Etienne and Heesterbeek, 2000; Horino and Miura, 2000). Biedermann (2000) used the minimum viable population (MVM) to predict long-term persistence of the metapopulation *N. albipennis* by using the incidence function model with an examination of the effect of patch size and of patch number (for details see Box 3).

An excellent example in using metapopulation model to fit the empirical data is shown in Box 3. In this example the authors also stress the application of the model to predict the future trend of the metapopulation and to conserve this metapopulation species using the concept of the minimum viable metapopulation (MVM) size. Doak and Mills (1994) argued that in cases where metapopulation concepts are applied to conservation problems, we must recognise both the practical and political limitations we face. Both modelers and conservationists have to be concerned about the following points:

1. More work is needed on methods for estimating population and community parameters from incomplete data sets. The lack of data is the root cause of the prevalence of theory in conservation arguments; using theory to make the most of what data are available is an obvious but often criticised application of theory.
2. Theoreticians should clearly state how data could be productively and cheaply collected to assess the essence of their favorite phenomena. Because a model cannot be built with incomplete data, the theoreticians have to be concerned that if data are complete, then modelling can use them to make reliable predictions for management. If data are partially complete, then modelling may be useful in making qualitative predictions. Finally, if data are poor, modelling may not be useful at all.
3. Field workers should pay attention to the recommendations of the theoreticians and try to collect data that will be useful when parameterising models, and otherwise testing the importance of plausible theoretical concerns.
4. Modellers of real species or communities should seek to formulate the simplest models necessary to capture the relevant biological details of their systems.
5. Both theoreticians and field workers have to recognise that the primary purpose of building models is to make predictions because if you want to represent a realistic scenario, factual evidence is required.
6. Theoreticians have to be concerned that the idea of a large, multipurpose model is incompatible with the idea of a model as a focused problem-solving tool. If a different question is asked, it is likely that different model will be needed because simplifying assumptions will be different.

From the rules stressed by Doak and Mill (1994) above, there are many authors using mathematical models of metapopulation to fit the field data and to test the validation of these models (for detail see Table 2).

According to the assumption of the classical Levins metapopulation model (Box 2), the metapopulation consist of a series of local habitat patches which are roughly the same in quality and size. The patches are classified only by the presence or absence of interested organisms. Each of the local population dynamics is independent from each other. Furthermore, the dynamics of all local populations is assumed to be asynchronous events. The interconnection between patches, equally for all patches, functions by migration in which it is assumed that the migration from the source patches does not affect the dynamics of the sink patches and the long-term persistence is incorporated by the balance of extinction and recolonisation. Finally, the metapopulation is assumed to be in the infinite world. In the real world, the population usually does not support these criteria, since there are some modifications of Levins metapopulation model evident (for details see Table 3).

Discussions

Although metapopulation concepts are not commonly fit to real word conditions and there still may be questions regarding the generality of metapopulation dynamics and the applicability of metapopulation models to specific problems in conservation, they have contributed important insights to conservation and have inspired field studies focused on collecting key data on demographics and movement (Hanski and Gilpin, 1997). Furthermore, as stressed by Doak and Mills (1994), metapopulation concepts have had positive effects in conservation research. In particular, interest in metapopulation dynamics has prompted renewed research concerning dispersal capacities that is extremely valuable in understanding population structure. Moreover, metapopulation models investigating the effects of correlation in extinction risks and dispersal probabilities have also led to greater concern about these phenomena among field researchers. For all of the reasons stated above, in cases considering metapopulation-like

Table 2. Examples of using metapopulation mathematical models to fit the field data. The table provides the species, model/methodology that was used, and whether or not these species characterise the metapopulation according to the assumptions described in Box 2 (1, 2, 3, and 4). - represents none of details provided in the studies.

Empirical Species	Model/Methodology	References	Assumptions
Measles	Generalised Linear Models (GLMs)	Finkenstädt and Grenfell, 1998.	1
Dingy skipper butterfly (*Erynnis tages*)	Mark-Release-Recapture Technicqes (MMR)	Gutierrez *et al*., 1999.	1, 3, 4
Ringlet butterfly (*Aphantopus Hyperantus*)	Mark-Release-Recapture Techniques (MMR)	Sutcliffe *et al*., 1997.	1 (partially patchy system)
Glanville fritillary butterfly (*Melitaea cinxia*)	(1) Logistic Regression Model (2) Levins model, Core-Satellite hypothesis, and Incidence Function (IF) Model	Hanski and Singer, 2001. Hanski *et al*., 1995.	1, 3, 4 1, 3, 4
Froghopper (*Neophilaenus albipennis*)	Incidence Function Model	Biedermann, 2000.	1, 3, 4
Mountain pygmypossums (*Burramys parvus*)	Population Viability Analysis (PVA) Hetergeneity Model (Program CAPTURE)	McCarthy and Broome, 2000. Broome, 2001.	1, 3, 4 (female) 1, 3, 4
Weevil (*Hadramphus spinipennis*) and its host plant (*Aciphylla dieffenbachia*)	Spatially Explicit Model (determined spatial pattern of host plant and dynamics of weevil)	Johst and Schöps 2003.	1, 3, 4
Laughing kookaburra (*Dacelo novaeguineae*) and sacred kingfisher (*Todiramphus sanctus*)	Analysis the Likelihood of Extinction (ALEX)	Lindenmayr *et al*., 2001.	-
Yellow legged herring gull (*Larus cachinnans*)	Multi-Site Matrix	Brooks and Lebreton, 2001.	-
Helmeted honeyeater (*Lichenostomus melanops cassidix*)	Population Viability Analysis (PVA)	Akcakaya *et al*., 1995.	-
Piping plover (*Charadrius melodus*)	Population Viability Analysis (VORTEX version 7)	Plissner and Haig, 2000.	1, 3, 4
White-backed Woodpecker (*Dendrocopos leucotos*)	Metapopulation Model	Carlson, 2000.	-
Steller sea lions (*Eumetopias jubatus*)	Multi-Scaled Metapopulation Model Population Viability Analysis (PVA)	York *et al*., 1996. Gerber and VanBlaricom, 2001.	1, 4 1, 4
Japanese black bear (*Ursus thibetanus japonicus*)	Population Viability Analysis (PVA)	Horino and Miura, 2000.	1, 3, 4
Vole (*Microtus agrestis*)	Levins Model and Incidence Function (IF) Model	Crone *et al*., 2001.	1, 3, 4

Table 3. Examples of modifications of the classical Levins metapopulation model.

Modifications	Results	References
Spatially Structured Metapopulation Models		
• The model includes demographic stochasticity in which the model used is specified Markov process, and then the simulation results were compared with the field data.	The model is realistic as it was designed to fit the field data of three species: *Pterostichus lepidus, Pterostichus niger,* and *Bolitotherus cornutus*, and so it effectively presents it.	Casagrandi and Gatto, 2002.
• The models incorporate spatial and temporal variation in patch quality and the rescue effect.	The correlation between the fractions of suitable patches and empty patches is positive if and only if the average value of the resource decreases as the number of patches increase, while the rescue effect and change in patch number have the opposite effect.	Gyllenberg and Hanski, 1997.
• Patch areas varied according to real population systems and human landscape modification.	*Aphantopus hyperantus* is more likely to leave small rather than large patches and more likely to arrive in large rather than small patches.	Sutcliffe *et al.*, 1997.
• The model includes the consideration of habitat destruction.	Habitat destruction is the important factor affecting the persistence of organisms. As habitat destruction increases the probability of persistence of organisms is decreased.	Bascompte and Sole, 1998.
• The mesoscale approach in which it is subjected to demographic stochasticity, environmental catastrophes and habitat loss.	The good disperser species are affected more by habitat destruction than by environmental disasters.	Casagrandi and Gatto, 1999.
• The model includes the rescue effect.	The model does not fit with field data.	Hanski *et al.*, 1995.
• The incidence function model allows one to make quantitative prediction about patch occupancy in particular patch networks.	The model successfully predicted patch occupancy for some of the field data collected.	Hanski *et al.*, 1995.
• The model includes the variation of matrix quality.	A higher-quality matrix generally buffers against extinction. However, it depends on exact conditions of the metapopulation.	Vandermeer and Carvajal, 2001.
Cellular Automata Models		
• Each local population only interacts with the nearby local populations.	The rescue effect has its most importance influence when the topological structure is the same in which self-organised spatio-temporal patterns appear.	Keymer *et al.*, 1998.

(to be continued)

Table 3. (continued)

Modifications	Results	References
• Applied pair approximation to metapopulation.	The spatial correlations of habitat types completely determine equilibrium population density on suitable sites. The amount of suitable habitat has no effect, precisely the opposite of what the mean-field approximation predicts.	Hiebeler, 2000.
• The model includes the consideration of habitat destruction. Each local population only interacts with the nearby local populations.	Habitat destruction is the most important factor affecting the persistence of organisms. As habitat destruction increases the probability of persistence of organisms is decreased.	Bascompte and Sole, 1998.
• The lattice metapopulation model that is based on the interacting particle systems in which they incorporate explicitly both metapopulation and patch dynamics.	Metapopulation persistence and extinction are strongly influenced by the rate at which the landscape changes, in addition to the amount of habitat destroyed.	Keymer *et al*., 2000.
• Applies the two analytical approaches, metapopulation capacity and pair approximation, to study the metapopulation dynamics and the pattern of habitat loss.	An increasing correlation in the spatial arrangement of the remaining habitat increases patch occupancy. This increase is more evident for species with short-range than long-range dispersal. To be most beneficial for metapopulation size, the range of spatial correlation in landscape structure should be at least a few times greater than the dispersal range of the species.	Ovaskainen *et al*., 2002.

populations, we need to be careful to consider how underlying ecological and behavioural mechanisms can shape the rules by which metapopulation dynamics operate.

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