

# Habitat Loss, the Dynamics of Biodiversity, and a Perspective on Conservation

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## INTRODUCTION

Habitat loss has been, and still is, the greatest threat to biodiversity (Brooks et al. 2002; Hanski 2005; Groom et al. 2006). According to the Millennium Ecosystem Assessment (2005), more than half of several biomes, including the Mediterranean and temperate forests and tropical and sub-tropical dry broadleaf forests, had been converted by 1990; in Western Europe, only 2–3% of original forests remain in natural or natural-like condition (WWF Report 2001). Zooming into more detailed classifications of habitat does not change the picture. As an example, a recent in-depth assessment of changes in the quality and quantity of 368 habitat types in Finland (Raunio et al. 2008) classified the vast majority either as threatened (189 habitat types) or near threatened (105), while only 74 habitat types were considered to be of least concern. The conversion of natural habitats to agricultural land, pastures, plantations, built areas and infrastructure continues, propelled by increasing human population size and by accelerating demand for resources.

It is self-evident that populations and species will suffer when their habitat becomes degraded or is lost completely. Nonetheless, many issues concerning the response of biodiversity to habitat loss and fragmentation are less clear-cut or they are not widely appreciated. These issues include non-linearity in the ecological response of species to habitat loss and fragmentation at the landscape level, about which I have more to say in this article. The response of

species to habitat loss and other environmental changes is typically not instantaneous, particularly not when we consider changes at large spatial scales. Habitat loss leaves large numbers of species to gradually decline and go extinct. If we are not aware of this “extinction debt” (Tilman et al. 1994) we are prone to underestimate the level of threat to biodiversity (Hanski and Ovaskainen 2002). Habitat loss often involves deteriorating habitat quality, either due to intentional changes in land use, such as the conversion of natural boreal forests to intensively managed forests in northern Europe, or due to unintentional damage, exemplified by increasing edge effects with decreasing area and increasing fragmentation of habitat. Hundreds of studies have examined the relative roles of habitat quality, habitat fragment area and connectivity (inverse of isolation) in influencing the occurrence of species in fragmented landscapes (reviewed by Fahrig 1997, 2003; Prugh et al. 2008). Unfortunately, much of this work is of limited value as it does not adequately recognize that the relative roles of habitat quality, fragment area and connectivity depend greatly on landscape structure and heterogeneity, and hence there cannot be a universal answer to the question “which is more important” (Hanski 2005).

Habitat loss and fragmentation have genetic and evolutionary consequences. I shall touch below the question about reduced viability of small and fragmented populations due to inbreeding and random fixation of deleterious mutations. Concerning the evolutionary dynamics, habitat loss and fragmentation are likely to alter many components of natural selection and hence lead to evolutionary change. A prime example is selection on dispersal: several costs and benefits of dispersal are affected by the spatial structure of populations and hence by the physical structure of

the environment, which are modified by habitat loss and fragmentation. Whether the net effect is increased or decreased rate of dispersal has been much debated (Heino and Hanski 2001; Ronce and Olivieri 2004), and once again it is apparent that there is not a single answer (Hanski 2005). Furthermore, whatever the answer in a particular case, there is no basis to assume that the evolutionary change would necessarily increase the viability of populations and metapopulations. It is even possible that evolutionary changes increase the likelihood of population extinction (Gyllenberg et al. 2002), though luckily “evolutionary suicide” is more of academic interest than a cause for real concern, even if some convincing examples were reported.

The year 2010, the United Nations’ International Year of Biodiversity, was supposed to be the turning point in the loss of biodiversity, but a comprehensive report (Butchart et al. 2010) shows that the 2010 target was not met, biodiversity continues to decline, and the indicators reflecting the various pressures on biodiversity continue to increase. At hindsight, the 2010 target was overambitious and vague, there was no clear idea of how to reach it and how to measure success. The new target year is 2020, and we are now wiser, we have metrics and more specific measures that facilitate reaching the goal. Major subsidiary targets relate to the questions how much habitat should be protected and where.

In this article, I first discuss the consequences of habitat loss and fragmentation for the ecological viability of metapopulations at the landscape level with a focus on extinction thresholds (the critical minimum amount of habitat that is necessary for long-term persistence of metapopulations). I argue that apart from the amount of habitat, the degree of fragmentation at the landscape level makes a significant difference. The next section gives a brief synopsis of the genetic factors that threaten long-term viability of populations and metapopulations (inbreeding depression and fixation of deleterious mutations that lead to a permanent reduction of fitness). Based on these biological considerations, I put forward an option for habitat conservation that represents, in my opinion, a cost-effective and realistic approach. This approach could make an important contribution towards reaching the target for conservation agreed in the UN biodiversity summit in Nagoya in 2010 that aims to put an end to the decline of biodiversity by 2020.

## HABITAT LOSS AND EXTINCTION THRESHOLDS

Long-term viability of populations and metapopulations depends on a large number of demographic, genetic, and environmental factors (Lande 1993, 1998). At the

landscape level, the fraction of available habitat that is occupied by a species is an important indicator of its viability. Over the years, substantial theory has been developed for the dynamics of species living as metapopulations in fragmented landscapes (Hanski 1999; Hanski and Gaggiotti 2004), with the specific aim of predicting the fraction of occupied habitat fragments. These models are broadly similar to epidemiological models, which address the dynamics in the numbers of infected individuals in a host population (Anderson and May 1991). A key result of metapopulation and epidemiological models relates to the threshold at which a metapopulation in a fragmented landscape or a parasite in a host population goes extinct. The extinction threshold depends both on the traits of the organism and the characteristics of the environment (Hanski and Ovaskainen 2000). For a given species, the number of habitat fragments (or susceptible host individuals; Kermack and McKendrick 1927) must exceed a threshold value for the species to persist. Landscapes with little and fragmented habitat are likely to be below the extinction threshold, landscapes with much habitat are above the threshold. The purpose of the models is to quantify what is “little” and what is “much”, and how much habitat loss and fragmentation is compatible with viability. Figure 1a gives an example of the extinction threshold for the Glanville fritillary butterfly (*Melitaea cinxia*) that lives in a large network of ca. 4,000 small meadows in the Åland Islands in Finland. Some parts of the network are sparse and apparently below the extinction threshold as the butterfly is absent, other parts are above the extinction threshold and the butterfly is common.

The metapopulation theory applies most naturally to highly fragmented habitats, such as networks of small meadows, but the processes of local extinction and colonization occur in any kind of habitat. When the habitat is continuously distributed, movements of individuals are unrestricted and many species can be expected to occur practically everywhere. Habitat loss and fragmentation impair free movements with adverse consequences for the distribution and abundance of species, as Curtis (1956, p. 729) observed more than half a century ago: “Within the remnant forest stands, a number of changes of possible importance may take place... Various accidental happenings in any given stand over a period of years may eliminate one or more species from the community. Such a local catastrophe under natural conditions would be quickly healed by migration of new individuals from adjacent unaffected areas... In the isolated stands, however, opportunities for inward migration are small or nonexistent. As a result, the stands gradually lose some of their species, and those remaining achieve unusual positions of relative abundance.” In a paper that has become a classic with >1000 citations, Andrén (1994) reviewed empirical

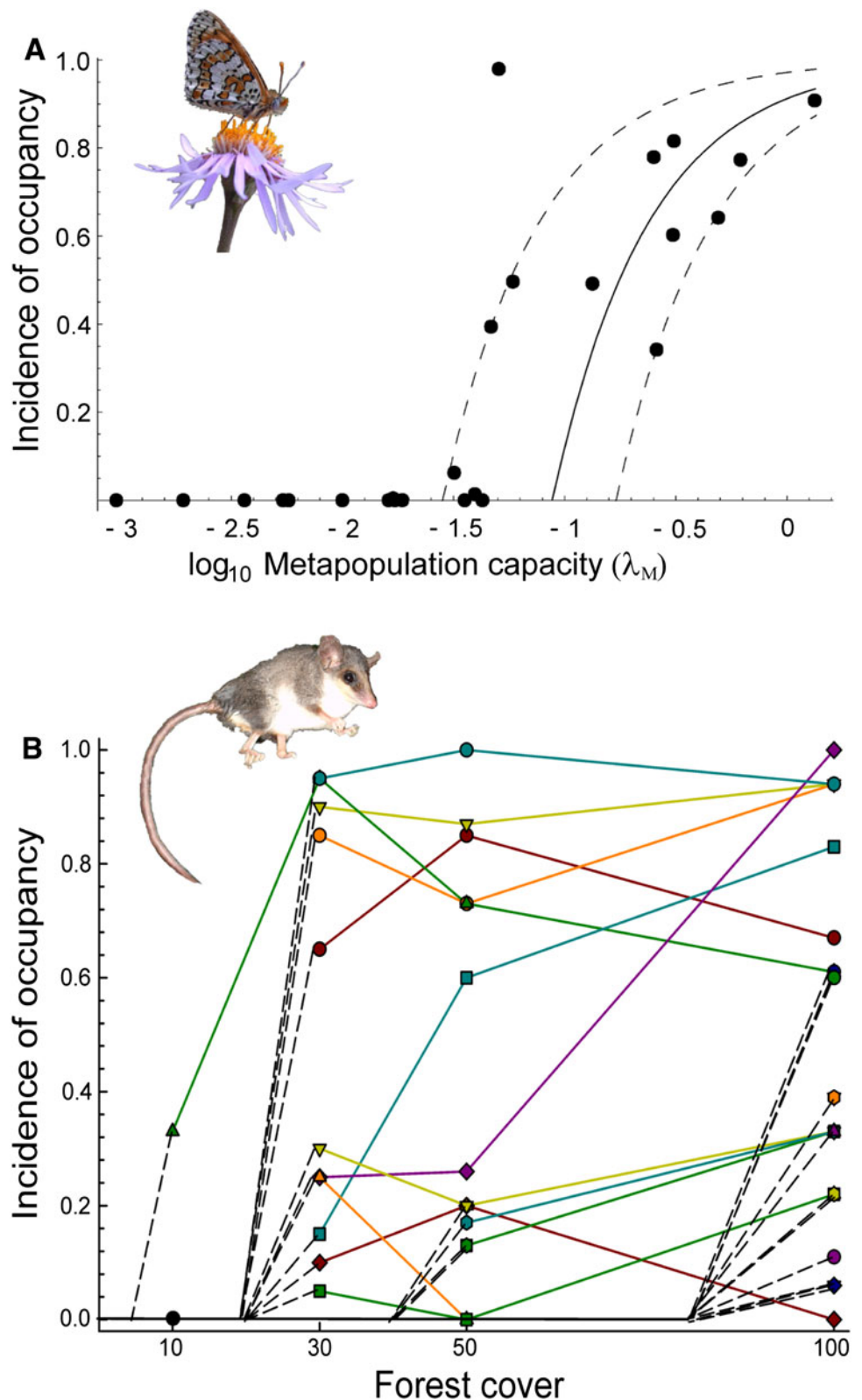
**Fig. 1 a** Metapopulation size of the Glanville fritillary *Melitaea cinxia* as a function of the metapopulation capacity ( $\lambda_M$ ) in 25 habitat patch networks in the Åland Islands in Finland (these networks represent different parts of the entire 4,000-meadow network).

Metapopulation capacity measures the amount of habitat and the level of fragmentation in the network (more habitat and less fragmented to the right). The vertical axis gives the size of the metapopulation based on a survey of habitat occupancy in 1 year. The empirical data have been fitted by a spatially realistic metapopulation model.

The result provides a clear-cut example of the extinction threshold (from Hanski and Ovaskainen 2000). **b** Incidences of occupancy in forest specialist non-volant small mammal species in fragmented landscapes in the Atlantic forest of Brazil. Data were obtained from three landscapes each ca. 100 km<sup>2</sup> in area but with dissimilar forest cover (10, 30, and 50%) and from continuous forests (100%).

Small mammals were sampled at 15 to 20 sites per landscape, widely scattered across the three fragmented landscapes and the continuous forest. The broken lines indicate that the incidence reaches zero between two levels of fragmentation that were sampled. The data are from Table S2 in Pardini et al. (2010). I have excluded three species with higher incidences in the fragments in the most fragmented landscape (10% forest cover) than in continuous forest (*Gracilinnaeus microtarsus*, *Juliomys* spp. and *Micoureus paraguayanus*) on the assumption that these species are not affected by forest fragmentation (R. Pardini, personal communication)

**b** Incidences of occupancy in forest specialist non-volant small mammal species in fragmented landscapes in the Atlantic forest of Brazil. Data were obtained from three landscapes each ca. 100 km<sup>2</sup> in area but with dissimilar forest cover (10, 30, and 50%) and from continuous forests (100%). Small mammals were sampled at 15 to 20 sites per landscape, widely scattered across the three fragmented landscapes and the continuous forest. The broken lines indicate that the incidence reaches zero between two levels of fragmentation that were sampled. The data are from Table S2 in Pardini et al. (2010). I have excluded three species with higher incidences in the fragments in the most fragmented landscape (10% forest cover) than in continuous forest (*Gracilinnaeus microtarsus*, *Juliomys* spp. and *Micoureus paraguayanus*) on the assumption that these species are not affected by forest fragmentation (R. Pardini, personal communication)



studies of birds and mammals inhabiting networks of true islands and forest fragments in farmlands to answer the question how much forest cover can be lost before

specialist forest species cross their extinction threshold. (In parentheses, I note that “forest cover” refers to forests that have the features and qualities that the species in question

requires. These qualities may not be present in managed forests and plantations, which therefore do not contribute to “forest cover” for that species.) Andrén (1994) found that an increasing fraction of studies reported an effect of habitat fragment area and/or isolation on species number or population density when the proportion of suitable habitat in the landscape was <30%, and nearly all studies reported such effects when forest cover was <10%.

The literature on thresholds involving habitat cover is somewhat confused by different researchers having addressed different, though related, questions. Andrén (1994) and many others have asked about the level of forest cover below which one may detect the effects of habitat fragment size and connectivity on species richness or population densities as indicators of adverse consequences of habitat loss and fragmentation. Reduced population densities of, e.g., top predators may have cascading effects in the community (Soulé et al. 2003) and even lead to the extinction of some species. However, the ultimate extinction threshold, the one that is treated in metapopulation theory, refers to the point along a gradient of habitat loss and fragmentation where the metapopulation loses viability because colonizations do not suffice to compensate for extinctions. Figure 1a gives an example of such a threshold for one exceptionally well-studied butterfly species. Obtaining comparable information for many other species is arduous.

One recent study that has managed the feat is due to Pardini et al. (2010) working on the occurrence of non-volant small mammal species in the Atlantic forest of Brazil. Pardini et al. (2010) sampled 39 species at 68 sites across three landscapes with dissimilar remaining forest cover, 10, 30, and 50%, as well as in the adjoining continuous forest areas. As expected, the occurrence of habitat generalist species was unaffected by forest cover, but forest specialist species showed a striking pattern. In most species, the incidence of occurrence was roughly the same in landscapes with 30, 50, and 100% forest cover, but the incidence dropped to zero in all but a single species in the landscape with 10% forest cover (Fig. 1b). Note that this pattern applies both to common species that have a high incidence in the less fragmented landscapes and to many uncommon species, though some rare species were recorded only in continuous forests. The example in Fig. 1b provides convincing support for the hypothesis that the extinction threshold for many specialist forest species is around 20% forest cover (Lande 1988; Hanski 2005 and references therein). These species are unwilling or unable to cross wide spaces outside their habitat, unlike the butterfly in Fig. 1a, which persists in a network of meadows though only a small percentage of the total area is covered by the meadows. Pardini et al.’s (2010) example is particularly important because forest loss and fragmentation

have occurred a long time ago in their study region, hence the occurrence of small mammals can be assumed to have settled down into a quasi-stationary state rather than to reflect transient dynamics following habitat loss (Metzger et al. 2009; R. Pardini, personal communication).

Figure 1 gives two clear-cut examples of extinction threshold in different kinds of fragmented landscapes. In the case of the Glanville fritillary inhabiting a network of meadows (Fig. 1a), butterflies may fly distances up to several kilometers between the meadows, and the amount of habitat and the actual spatial configuration of meadows is measured by “metapopulation capacity”, a measure that is derived from metapopulation theory (Hanski and Ovaskainen 2000). In the case of specialist forest-inhabiting small mammals in Fig. 1b, forest cover is the relevant measure, as the small mammals disperse poorly across non-forest habitats. But does habitat fragmentation matter at all in this case? Not according to Lenore Fahrig (1997, 2003), who would consider that Fig. 1b is an example of habitat loss, while fragmentation in the sense of the exact spatial configuration of the remaining habitat within the landscape makes a small difference at most. However, whether the reduced incidence of occupancy is attributed to habitat loss or fragmentation is a question of spatial scale. Consider the landscape in the Brazilian Atlantic forest that has only 10% forest cover and has lost all but one of the forest specialist small mammal species (Fig. 1b). Imagine that the forest fragments in this landscape, which extends across hundreds of km<sup>2</sup>, were relocated into one part of the landscape, in which forest cover would become 30%. There would be no forest left in the rest of the landscape, but the part with 30% cover, if large enough, would have viable populations according to Fig. 1b. Therefore, I conclude that the reason why the 10% landscape has lost the species is due to fragmentation: the total amount of habitat may be large enough, but it occurs in such a scattered pattern that specialist species remain below their extinction thresholds.

## GENETIC VIABILITY OF POPULATIONS AND METAPOPOPULATIONS

Populations living in fragmented landscapes are threatened by multiple ecological and environmental factors, but their viability can also become compromised by inbreeding, random loss of beneficial mutations (leading to loss of adaptive potential), and random fixation of deleterious mutations (increasing genetic load) (Lande 1994, 1998; Frankham et al. 2002). The Glanville fritillary in the Åland Islands has hundreds of small local populations with fast population turnover (Hanski 1999). New populations are often established by just a single dispersing female (Austin et al., in press), which means that, in the following

generation, matings among close relatives are common. Just one generation of full sib mating leads to inbreeding depression (Haikola et al. 2001) that is substantial enough to increase the risk of local extinction (Saccheri et al. 1998; Nieminen et al. 2001). The entire metapopulation, with a breeding population of a few thousand individuals at most and a history of >100 years in isolation may suffer of reduced fitness, which is indicated by crosses of butterflies from the Åland Islands with butterflies from elsewhere in northern Europe having somewhat increased egg hatching rates (A. Duplouy, personal communication). In theory, “mutational meltdown”, gradual erosion of fitness due to fixation of deleterious mutations, may threaten populations of the order of 1,000 individuals (Lande 1994; Lynch et al. 1995). Highly fragmented metapopulation structure with restricted dispersal, which the Glanville fritillary exemplifies (Hanski 1999), decreases the genetic effective population size (Whitlock and Barton 1997) and may enhance the accumulation of deleterious mutations (Higgins and Lynch 2001).

The smaller the population or the metapopulation, the greater the risk of mutational meltdown, which is therefore a serious concern in many human-dominated landscapes that harbor innumerable, completely isolated populations. The populations may be large enough to survive in the face of demographic and environmental challenges for a long time, but mutation accumulation proceeds like a cancer, first with no ill effects at all but ultimately leading to an inevitable demise. Figure 2 gives another example on the Glanville fritillary, comparing the life-time production of larvae by females from the Åland Islands and from a relatively small population that has been completely isolated on a small island in the middle of the Gulf of Finland for at least 75 years (the population had around 100 reproducing females in 2009). The life-time number of larvae produced and many other indicators of individual performance are very much reduced in this population (A. L. K. Mattila et al., in preparation), most likely due to fixation of deleterious mutations as crosses with other populations show immediate fitness recovery. The population is not yet extinct—the reduced number of offspring is still large enough to yield positive expected growth rate—but the population is vulnerable; it suffers from a permanent handicap. Reduced fitness in isolated small or relatively small populations has been reported for mammals (Hedrick 1995; Ellegren et al. 1996), birds (Westemeier et al. 1998), reptiles (Madsen et al. 1996), fish (Sato 2006), and plants (Groom and Preuninger 2001). Declining absolute fitness will ultimately reduce population size and lead to what Gilpin and Soulé (1986) called the extinction vortex, a spiral of feedbacks between demographic and genetic factors that reinforce each other and eventually lead to extinction.

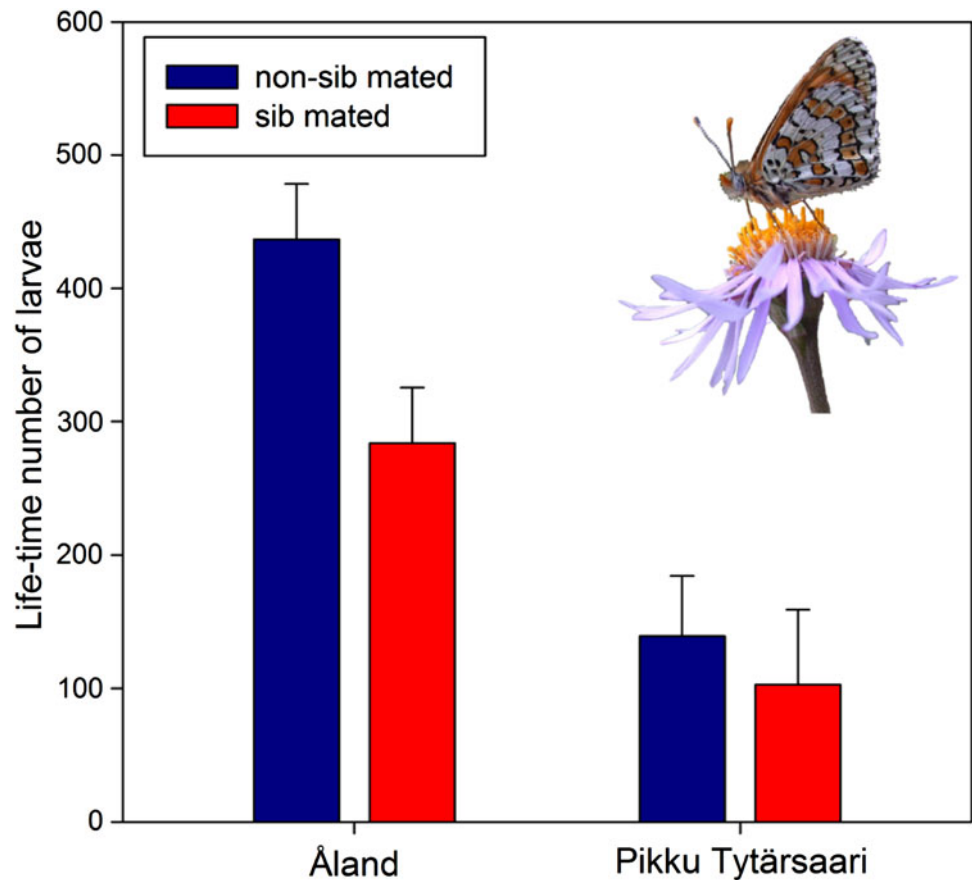
## CONSERVATION LANDSCAPES: THIRD-OF-THIRD

In the UN biodiversity summit in Nagoya in 2010, delegates from more than 190 countries agreed to increase the percentage of protected areas to 17% on land and to 10% on coastal and marine areas by 2020. These are definitely positive decisions, even if the appropriate targets for conservation continue to be debated in the literature (Jennings 2000; Rodrigues et al. 2004). However, the implementation of the Nagoya target raises two major concerns. First, a huge proportion of the current protected areas on land are located in regions with unproductive soils and severe climate at high latitudes and altitudes (Scott et al. 2001). For instance, in Finland, with the largest remaining percentage forest cover in Europe (72%), 13% of all forested land is protected, but 90% of the protected areas are located north of 66°N, and a very large fraction of these northern “forests” are so barren that they have stunted mountain birch at best. Of the 17 million ha of forested land in southern Finland, only 3% are protected, and in the case of productive forest land (annual increment >1 m<sup>3</sup>/ha) the figures are 15 million ha and 1.6% (Virkkala et al. 2000). We are fooling ourselves if the 17% agreed upon in Nagoya are located mostly on marginal lands, which is also against the letter of the agreement, to protect “especially areas of particular importance for biodiversity and ecosystem services, ... ecologically representative and well connected systems of protected areas... integrated into the wider landscapes” ([www.cbd.int/decision](http://www.cbd.int/decision), strategic goal C). The second problem is related. Even if there was political will to protect more forests and other habitats on productive lands—the kinds of habitats that really matter for biodiversity—there would be limited opportunities, in many parts of the world, to protect large continuous areas of natural or natural-like habitats. There simply are no such areas left.

Based on our knowledge about the dynamics of biodiversity outlined in the first part of this article, I propose an approach to large-scale habitat conservation that I call a third-of-third approach: a third of the land area is managed as multi-use conservation landscapes (CL), within which a third of the area is protected. This means that a third of the third, about 10% of the total area, is protected, which is less than the target set in Nagoya, but this 10% is in addition to the existing national parks and other protected areas, which are often located on marginal lands. The CLs should be located as evenly as possible across regions and countries to guarantee representativeness of the protected areas (Rodrigues et al. 2004). There are four advantages to this approach.

First, the third-of-third approach is a cost-effective way of protecting biodiversity, habitats, and ecosystems. The

**Fig. 2** Life-time production of pre-diapause larvae by Glanville fritillary females from the Åland Islands and from an old (>75 years), small (around 100 reproducing females) and completely isolated population on the island of Pikku Tytärsaari in the middle of the Gulf of Finland. The results were obtained in an experiment conducted under common garden conditions in the laboratory. Note that the fitness of females from Pikku Tytärsaari is much smaller than that of females from the large metapopulation in the Åland Islands, and in the former population one generation of full sib mating has a less adverse effect than in the metapopulation in the Åland Islands, apparently because all individuals in Pikku Tytärsaari are closely related



key rationale is the finding, illustrated in Fig. 1b, that a large fraction of specialist species persists in landscapes with 30% cover of the original vegetation. The generalist species would persist as well, and so would species that live in particular minor habitats within the broader landscape, such as the Glanville fritillary in Fig. 1a (though there is inevitably regional variation in the density of particular minor habitats with consequences for the persistence of the respective species). The example in Fig. 1b is based on forests, but I presume that the third-of-third approach would also apply to other landscape-covering habitat types. Effective protection relies on the assumption that there is no habitat degradation or other anthropogenic disturbances within individual protected fragments. In addition, these fragments should be large enough to avoid excessive edge effects and to contain small breeding populations of specialist species. To contain demographically and genetically viable metapopulations of most species, CLs as a whole should be some tens of thousands of ha in size. As a numerical example, a 20,000-ha conservation landscape could have 6,500 ha of protected habitat in some 100 fragments. Even a landscape of 20,000 ha is not large enough for large-bodied vertebrates (Gurd et al. 2001), but

such species are typically so mobile that they would persist in an archipelago of CLs if people learn to live with them.

The second advantage is practical: there are opportunities to establish CLs in regions and countries where there would be no opportunity to establish conventional national parks or other large protected areas that would exclude humans. Even then, one might not have one third of the planned CL immediately available for protection, or its habitat quality might be very low. In these cases, the 30% target can be reached, in the course of time, with appropriate restoration programs.

Third, a long-term challenge for conventional national parks and other large protected areas is changing environmental conditions with climate change. Researchers have repeatedly called for increased large-scale connectivity to allow species to move across landscapes (Heller and Zavaleta 2009). If a third of the land area was covered by CLs, they would provide the necessary connectivity.

Fourth, a disadvantage of conventional national parks and large protected areas is that they largely separate biodiversity and people. Within CLs, biodiversity and people coexist, and the ecosystem services provided by biodiversity and natural habitats, including climate

mitigation especially in the tropics (DeFries and Rosenzweig 2010), have direct benefits to local communities and to the society at large (Ostrom 1990).

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At this point, I want to make it very clear that I am not advocating downgrading or fragmenting existing national parks and other protected areas, which are essential for halting the decline of biodiversity as well as providing many other benefits. I am suggesting that we should be thinking of new ways of increasing the percentage of protected areas to reach the 17% target set in Nagoya and to stop the decline of biodiversity by 2020.

It has to be admitted that CLs are more complex for governing and management than conventional unbroken protected areas that are separated from human activity. CLs can be more vulnerable to habitat degradation, poaching and other disruptions, including road kills of vertebrates (Forman and Alexander 1998; Roger et al. 2011). A challenge in integrated conservation and management is gradual evolution of management practices. For the management practices to develop towards favoring biodiversity rather than degrading it requires institutions that support alertness, adaptation, and control (Primmer and Karppinen 2010). Local communities are more likely to have an interest in conserving nature when it supports their livelihoods (Ostrom 1990), which would be the case with many people living within CLs.

The notion of CLs is related to many other conceptual models. Harris's (1984) book outlined a long-rotation model of forest management that allocates a certain area to an old-growth fragment, around which forest stands are harvested in a rotational manner to maintain connectivity. Daily's (1997) countryside biogeography is focused on developing ways to enhance features in agricultural landscapes that would maintain biodiversity. Both models were heavily influenced by MacArthur and Wilson's (1967) island biogeographic theory. The measures of landscape cohesion presented by Opdam et al. (2003) were derived from metapopulation models and were meant to characterize the capacity of landscapes to support biodiversity. In Europe, the Natura 2000 network of protected areas aims at preserving biodiversity in human-dominated landscapes in practice, though the implementation has been focused more on individual sites rather than landscapes (Gaston et al. 2008). It would be time to upgrade the Natura 2000 network to a Natura CL network.

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