Strategies for Improving Biodiversity Conservation in the Netherlands: Enlarging Conservation Areas vs. Constructing Ecological Corridors

Otso Ovaskainen

Professor of Mathematical Ecology

Department of Biosciences, Helsinki University, Finland

Contents

Structure of the report

As described in *Aims of the study* below, this report addresses a problem defined by Council for the Environment and Infrastructure, the Netherlands. In start by describing the *Material and Methods* used to produce this report and by defining the *Key concepts* providing the vocabulary for reading this report. I then summarize scientific literature on topics that are directly relevant to the scope of this report in two sections: *The links between connectivity, population viability and persistence of biodiversity* and *Do ecological corridors work in practice: does structural connectivity ensure functional connectivity?* After these preliminaries, I address the problem setting in the section *Designing a cost-effective strategy for improving biodiversity conservation in the Netherlands.* Finally, I discuss how the interplay between conservation planning and scientific research could be strengthened in the section *Recommendation for the future: an evidence-based conservation strategy*.

Aim of the study

In an email to Otso Ovaskainen in 3rd April 2012, Bart Thorborg (Council for the Environment and Infrastructure, the Netherlands) formulated the problem setting as follows.

The Dutch Council for the environment and infrastructure is preparing an advisory report to the government on future nature policy. The development of biodiversity will be a key aspect of this report. In order to stop further biodiversity decline the Dutch government aims at extending the area available for natural habitats and enhancing their interconnectivity. This has to be achieved with rather limited financial resources.

A key problem in the Netherlands regarding to habitats is that areas where natural development takes place are highly fragmented, through road infrastructure, build up area's and arable land. Exceptions are the Veluwe area, the Oostvaardersplassen, the freshwater lake IJsselmeer and the intertidal Waddenzee area. In order to support the development of robust metapopulations a defragmentation programme is in place, aiming to spend about 400 million Euro until 2018 on the construction of migration zones and road and waterway crossings (ecoducts) optimized for various specific species. Construction of an ecoduct for road crossing typically requires 3-4 [million; correction added by Ovaskainen] Euro.

An alternative strategy to promote robust populations would be the enlargement of existing areas for natural development by acquiring more area. Thus more development space comes available to all species in a particular area and favourable environmental conditions can better be maintained. On the other hand exchange between populations in different areas is not facilitated. Typical prices for land acquisition in the Netherlands are around 40.000 euro per ha. Additional investment is required for reconstruction and maintaining favourable conditions.

The Council would like to ask your expert opinion on the relative effectiveness of both strategies for supporting biodiversity in a country as the Netherlands. This opinion may take the form of a qualitative advise, discussing the pros and cons of building corridors and buying land, and how the pros and cons depend on the circumstances as discussed with professor Frank Berendse. More specific information that would be required for a more thorough quantitative analysis is unfortunately not available on short notice.

Material and Methods

This report is based on a review of scientific literature on spatial ecology and conservation biology (see below for references), and background material received from prof. Frank Berendse and Bart Thorborg (Lawton et al. 2010, Reijnen et al. 2012, Thorborg 2012a, b), which include data on the state of the current protected area network in the Netherlands.

Much of my own research has focused on topics that are related to the scope of this report. In particular, I have examined how the structure of a conservation network influences the long-term persistence of species (Hanski and Ovaskainen 2000, Ovaskainen and Hanski 2001, Ovaskainen 2002, Ovaskainen et al. 2002, Ovaskainen and Hanski 2003a, 2004b), how the properties of an individual protected area (say, area and connectivity to other sites) determine its value as part of an ecological network (Ovaskainen 2003, Ovaskainen and Hanski 2003b), how a transient (time delay) in species response to fragmentation may generate an extinction debt (number of species that will eventually go extinct but have not yet had time to do so) at the community level (Hanski and Ovaskainen 2002, Ovaskainen and Hanski 2002), the link between individual-level and population-level processes (Ovaskainen and Hanski 2004a, Harrison et al. 2012), how different stochastic processes influence population dynamics (Ovaskainen and Cornell 2006b, a, North and Ovaskainen 2007), and the link between species-level and community-level processes (Ovaskainen et al. 2010, Ovaskainen and Soininen 2011). Another line of my research has focused on the influence of landscape structure on animal movement behaviour (Ovaskainen 2004, 2008, Ovaskainen et al. 2008b, Ovaskainen et al. 2008c, Patterson et al. 2008, Ovaskainen and Crone 2010). These studies address the link between structural connectivity and functional connectivity, e.g. asking under what kind of circumstances the construction of a movement corridor actually increases movements between protected areas (Ovaskainen et al. 2008a).

In addition to scientific research, I have experience on more practical aspects of nature conservation by being the vice-chair of the Finnish Natural Heritage Foundation, which acquires forest land for protection with the help of private donations (http://www.luonnonperintosaatio.fi/english/index).

Key concepts

Habitat loss is globally one of the greatest threats to biodiversity (World Resources Institute 2005). However, it is often difficult to assess which component of habitat loss eventually drives populations to extinction – loss of habitat area, quality, connectivity or continuity (Hanski 2005) – and at which spatial and temporal scales. In particular, habitat loss and fragmentation typically appear simultaneously and it can be difficult to disentangle whether the isolation of the habitat fragments has any effect on top of the negative effect due to loss of habitats (St-Laurent et al. 2009). Loss of connectivity has often a negative effect (Loebel et al. 2009), but it may have no effect (Trzcinski et al. 1999) or even be beneficial for part of the species community (Spanhove et al. 2009).

Many of the central concepts in conservation biology have multiple definitions and uses. This is in particular the case with concepts relating to habitat fragmentation and the concept of connectivity, both of which have a central role in this report. I will next define these key terms as they are used in this report.

Habitat and ecological networks

The concept of habitat is one of the most central concepts in ecology and conservation biology. Briefly, habitat is the range of environmental conditions under which a species may occur. Habitat can be defined at several hierarchical levels. For example, the habitat of the wood-decaying fungal species *Amylocystis lapponica* can be defined to be (from general to specific; macrohabitat to microhabitat) "forest", "spruce forest", "natural spruce forest with abundance of dead wood", "a dead spruce log", or "a naturally downed large spruce log of intermediate decay stage". All these definitions are equally valid. Importantly, habitat is not equal to species occurrence. Habitats which are perfectly suitable for the focal species may vary greatly in the abundance of the focal species, including the case in which the species is not present at all (e.g. Hanski 2005).

Often the suitable habitats are distributed over space in a fragmented manner, i.e. as a network of habitat patches. If the populations inhabiting the individual habitat patches interact with each other, the capacity of such an ecological network (Lawton et al. 2010) to promote the persistence of biodiversity may be greater than simply the sum of those of the individual fragments.

Below, I will use the term habitat to refer to the main macrohabitats involved in the network of conservation areas in the Netherlands: forests, heaths, and wetlands. From the species perspective, the conservation status of a fragment that provides suitable habitat is not relevant. However, I will start from the assumption that the habitat fragments outside the network of protected sites will not remain accessible for the species in the long term due to competing land use pressures. Thus I refer with the term ecological network to the network of protected areas, i.e. the Dutch National Ecological Network (Reijnen et al. 2012).

Habitat loss and fragmentation and the concept of connectivity

The concepts of habitat loss and fragmentation are illustrated in Fig. 1. Habitat loss refers to the loss of habitat area or habitat quality. Loss or deterioration in habitat quality includes processes such as loss of natural structures, e.g. abundance of dead wood in forested habitats. In the case of Netherlands, especially relevant aspects of habitat deterioration include eutrophication and acidification (Reijnen et al. 2012).

Habitat fragmentation *per se* refers to loss of connectivity, i.e. the division of continuous habitat into small and isolated fragments without decreasing habitat area or habitat quality. In reality, habitat loss and fragmentation occur together, and in this sense habitat fragmentation *per se* can be considered as a theoretical concept. While the total area that can be protected depends much on economical constrains (funding available for conservation) and political will, the spatial configuration (where to allocate the conservation funds) can be adjusted more easily, and thus in this sense it is of great practical value to understand the consequences of habitat fragmentation *per se*.

Structural connectivity of a habitat fragment refers to the proximity of other habitat fragments and the existence of corridor-like structures. Population-dynamic connectivity of a habitat fragment refers to the proximity of those habitat fragments that are inhabited by the focal species, and here proximity should be measured in terms of the movement capacity of the focal species. The term isolation is used as an inverse of connectivity.

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Figure 1: Concepts of habitat loss and fragmentation.
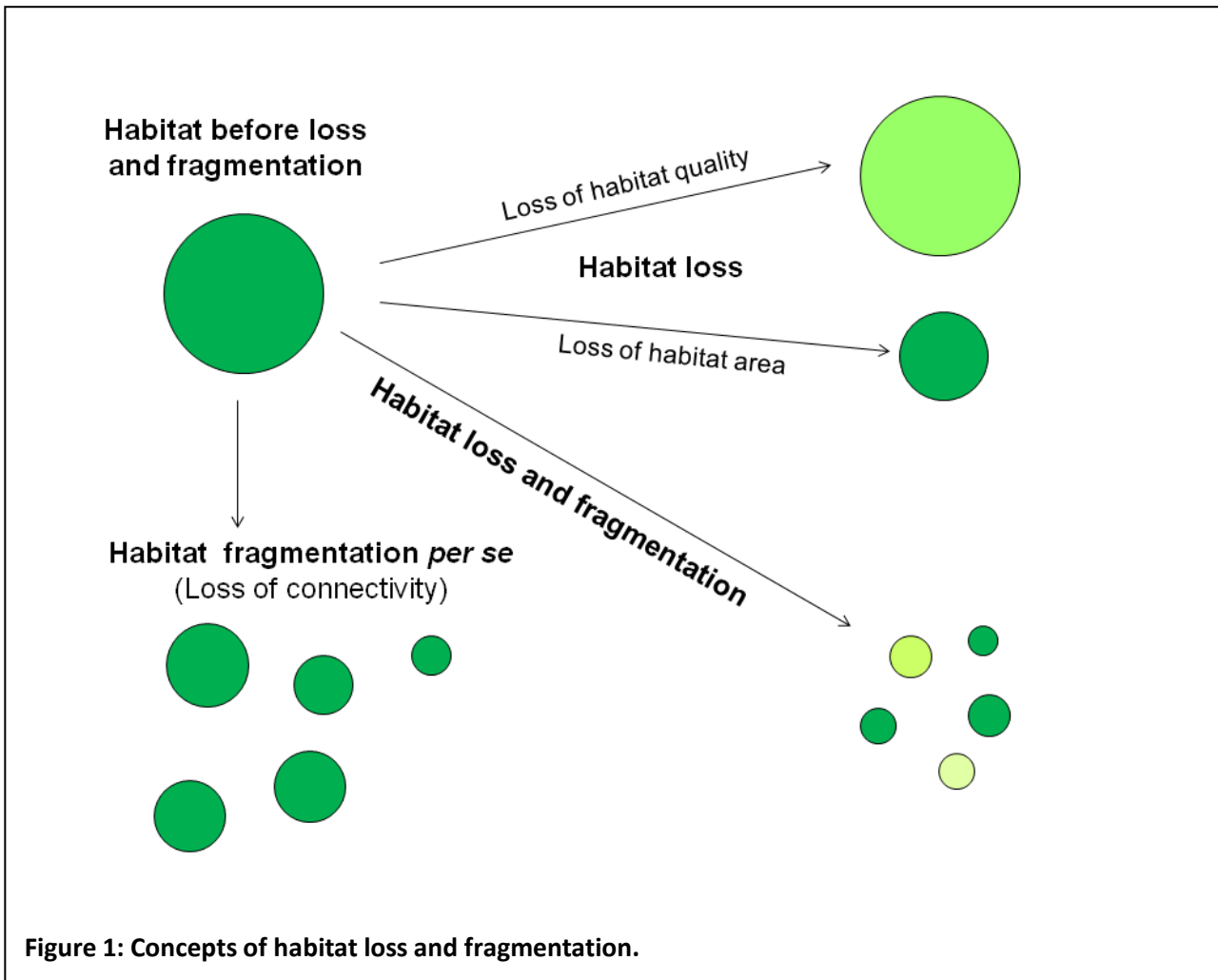
One central topic of this report deals with the role of connectivity. In simple terms, given two ecological networks with the same total amount of habitat, is it better for biodiversity conservation if the habitat occurs in a continuous manner (low level of habitat fragmentation *per se*, high level of connectivity) or if the habitat occurs as a set of more or less isolated habitat fragments (high level of habitat fragmentation *per se*, low level of connectivity)? As neither of the extremes is likely to the optimal solution (see below), thus it is important to understand which factors influence the optimal level of connectivity.

Ecological corridors

Ecological corridors are one mean of increasing connectivity among habitat fragments. Ecological corridors may be natural or they may be man-made, such as ecoducts and other road crossing structures aimed at enabling animal movement across highways and other dispersal barriers (Taylor and Goldingay 2010). In the context of ecological corridors, it is especially important to separate structural connectivity from functional connectivity. Structural connectivity refers to the mere existence of a corridor as a physical structure, whereas a corridor provides functional connectivity only if it actually increases movements between the populations.
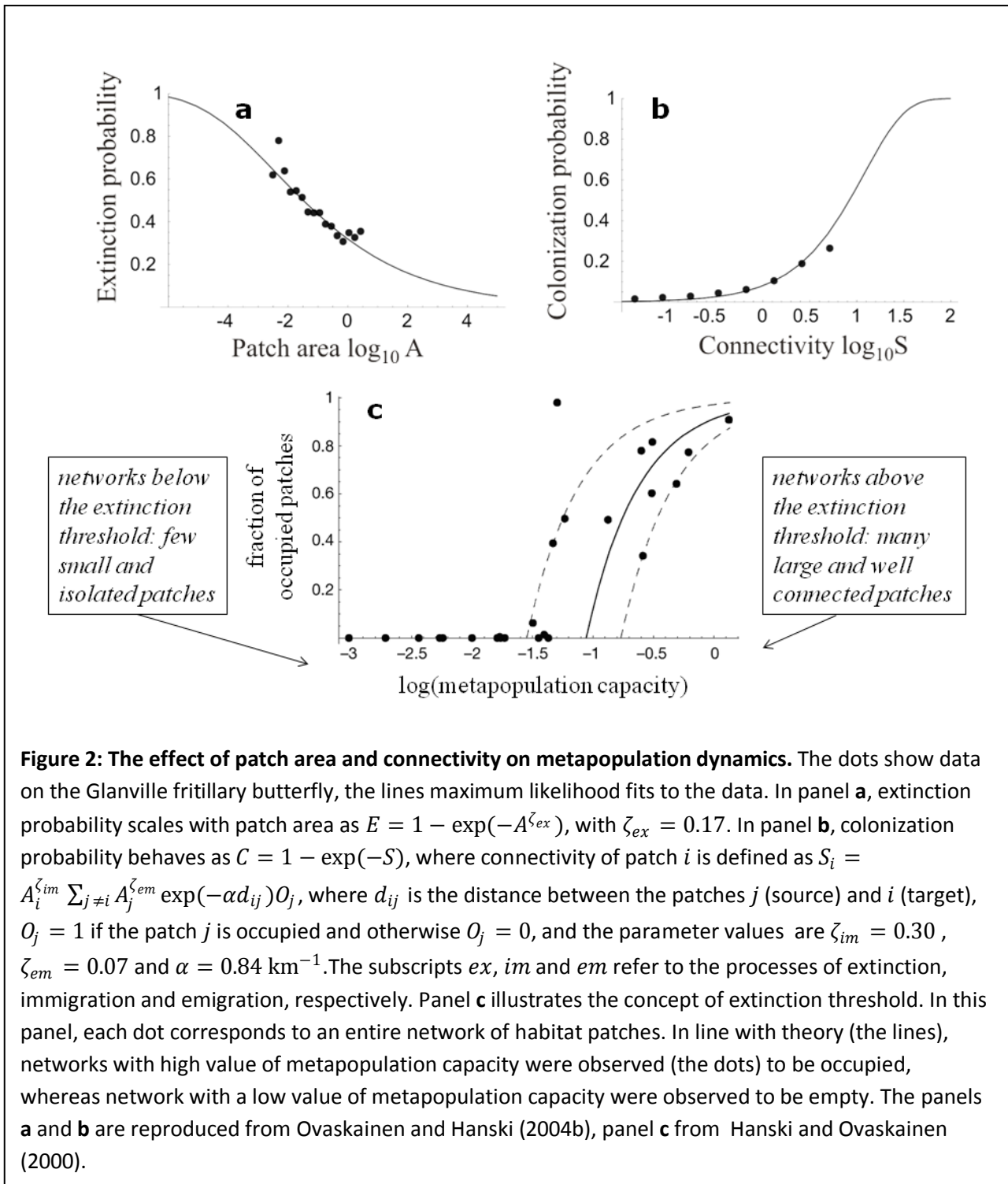
The links between connectivity, population viability and persistence of biodiversity

I will next briefly review the influence of habitat loss and fragmentation, and especially of connectivity, on processes that play a central role in the conservation of biological diversity. These considerations provide the scientific basis for the practical recommendations made in the forthcoming sections.

How habitat fragmentation influences population dynamics and persistence?

Species inhabiting highly fragmented landscapes, such as the Dutch National Ecological Network, often work as a metapopulation, i.e. a population of interacting populations (Hanski 1999, Hanski and Gaggiotti 2004). I will illustrate metapopulation theory in the context of the well studied Glanville fritillary butterfly metapopulation (Hanski and Ovaskainen 2000, Ovaskainen and Hanski 2001, 2004b). In the Åland Islands, within an area of ca. 70 km x 50 km, this species inhabits a network of ca. 4,000 habitat patches (dry meadows with larval host plants). These meadows are mostly very small (<1 ha in area), so this network resembles some parts of the fragmented protection area network in the Netherlands. In the butterfly system, none of the habitat fragments is large enough to support the long-term persistence of a local population. Extinction probability is much influenced by patch area, so that populations inhabiting large habitat fragments have a smaller extinction risk than populations inhabiting small habitat fragments (the parameter $\zeta_{ex} > 0$ in Fig. 2), mainly because populations inhabiting small fragments are themselves small, and because small patches may suffer from various kinds of edge-effects. Extinctions are compensated by colonizations, i.e. the establishment of new populations by migrants originating from the extant populations. The colonization probability increases with the area of the focal habitat fragment because larger fragments are easier to find and they provide more resources (the parameter $\zeta_{im} > 0$ in Fig. 2). Colonization probability also increases with population-dynamic connectivity to the extant populations. Connectivity depends on distances between the source patches and the target patch, and the areas of the source patches. Large source patches have large populations and thus a greater rate of production of potential colonizers, but this is partly compensated by the fact that the per-capita emigration rate is lower in large patches than in small patches. As a result, there is only a mild positive dependency between the area of the source patch and the colonization probability of the target patch (the parameter $\zeta_{em} > 0$ in Fig. 2).

A metapopulation (regional collection of local populations) will persist in the long term only if the local extinctions are compensated by colonization of empty habitat patches. Based on the dependency of extinction and colonization rates on patch area and connectivity (Fig. 2ab), metapopulation persistence increases with increasing number of habitat patches in the network, with increasing areas and qualities of the habitat patches, and with increasing connectivity among the patches within the network. The relevant combination of these factors has been termed the metapopulation capacity of the fragmented landscape (Hanski and Ovaskainen 2000). If the metapopulation capacity of the network is below a threshold value, the species will not persist in the long-term, even though the network contains patches of perfectly suitable habitat (Fig. 2c).

Figure 2: The effect of patch area and connectivity on metapopulation dynamics. The dots show data on the Glanville fritillary butterfly, the lines maximum likelihood fits to the data. In panel **a**, extinction probability scales with patch area as $E = 1 - \exp(-A^{\zeta_{ex}})$, with $\zeta_{ex} = 0.17$. In panel **b**, colonization probability behaves as $C = 1 - \exp(-S)$, where connectivity of patch i is defined as $S_i = A_i^{\zeta_{im}} \sum_{j \neq i} A_j^{\zeta_{em}} \exp(-\alpha d_{ij}) O_j$, where d_{ij} is the distance between the patches j (source) and i (target), $O_j = 1$ if the patch j is occupied and otherwise $O_j = 0$, and the parameter values are $\zeta_{im} = 0.30$, $\zeta_{em} = 0.07$ and $\alpha = 0.84$ km^{-1}. The subscripts ex, im and em refer to the processes of extinction, immigration and emigration, respectively. Panel **c** illustrates the concept of extinction threshold. In this panel, each dot corresponds to an entire network of habitat patches. In line with theory (the lines), networks with high value of metapopulation capacity were observed (the dots) to be occupied, whereas network with a low value of metapopulation capacity were observed to be empty. The panels **a** and **b** are reproduced from Ovaskainen and Hanski (2004b), panel **c** from Hanski and Ovaskainen (2000).

Patterns predicted by metapopulation theory have been tested with species belonging to several taxonomical groups, including e.g. a woodpecker (Pakkala et al. 2002) and species of wood-decaying fungi (Hottola 2009). While the details (e.g. parameter values and best fitting functional forms) will vary from case to case, the link from spatial configuration of an ecological network to the dynamics and persistence of species is likely to be robust and general for species inhabiting fragmented landscapes.

The above theory leads to three take-home messages that are relevant in the context of developing conservation strategies for the Netherlands.

First, if a network of conservation areas is too fragmented, a species of conservation interest may not be able to persist in the network. As a consequence, the network of conservation areas is not cost-effective. The biodiversity benefits per hectare of protected area (and thus per euro) are greater if the individual sites are large, and if they are well connected to each other. As a numerical example, our study of wood-decaying fungi showed that the same amount of resources can yield five times as many occurrences of red-listed species if the resources are concentrated than if they are spread sparsely within a landscape (Hottola 2009). For species with low conservation priority, typically species with generalized resource requirements, connectivity within and among the reserves is much less of an issue (Henle et al. 2004, Hottola 2009).

Second, as a direct consequence of the above, efforts of conserving new areas should be focused on enlarging existing areas and improving their quality rather than protecting new sites far away from the existing sites (Lawton et al. 2010). Following this strategy, additions to the network of protected areas increase not only total area, but also connectivity. Metapopulation theory provides quantitative means of assessing the trade-off between area and connectivity (Ovaskainen 2003, Ovaskainen and Hanski 2003b), but the application of these tool call for species-specific data that were not available for the production of this report.

Third, the optimal balance between many small vs. few large reserves depends on how the processes of local extinction, emigration and immigration scale with patch area. If these depend strongly on patch area ($\zeta = \zeta_{ex} + \zeta_{em} + \zeta_{im} > 1$), few large reserves is an optimal solution, whereas in the opposite case ($\zeta < 1$), many small reserves (with the same total area) is a better solution (Ovaskainen 2002). In the case of the Glanville fritillary butterfly, the parameter ζ that describes the total dependency of population dynamics on patch area can be estimated to be ca. $\zeta = 0.54$ (Figure 2), suggesting that for this species maximizing connectivity (by bringing all habitat into a single large conservation area) would not be an optimal solution. Thus, some level of fragmentation *per se* may actually be beneficial for this (and many other) species. One reason here is environmental stochasticity, i.e. spatial and temporal random variation between beneficial and adverse environmental conditions. For example, in the case of the Glanville fritillary butterfly, variation in rainfall influences patch quality through the condition of the host plants. A network of several patches buffers better against environmental stochasticity than a single large patch, as it avoids the risk of all populations being simultaneously hampered by adverse conditions. This consideration may be especially relevant in the context of climate change, which may lead to shifts in habitat suitability over space and time (Lawton et al. 2010).

Population genetics and evolutionary processes

Genetic diversity is one important aspect of biological diversity. Like population dynamic processes, also population genetic and evolutionary processes can be greatly modified by habitat loss and fragmentation (Hanski and Gaggiotti 2004). The interaction between genetic diversity and ecological dynamics is illustrated by the concept of extinction vortex: decreased population size can lead to inbreeding (mating between relatives), which can lead to inbreeding depression (lower reproductive potential of the individuals), which can lead to reduced population growth rate, which can lead to increased extinction risk (Saccheri et al. 1998). To avoid such a negative feed-back loop, populations (and hence protected areas) should be large enough and well enough connected, thus reinforcing the points discussed above in the context of ecological dynamics.

As habitat fragmentation reduces connectivity among populations, it is likely to reduce the amount of genetic variation within populations but increase the amount of genetic differentiation among populations. Thus some level of fragmentation *per se* can actually help sustain genetic diversity at the large scale. Some level of fragmentation *per se* can also be beneficial for the process of local adaptation, which may be counteracted by too much gene flow among the local populations (North et al. 2011). However, in systems such as the Dutch Ecological Network, the current high level of fragmentation *per se* makes it obvious that also from the point of view of genetic and evolutionary considerations, the benefits of increasing connectivity will greatly outweigh the potential negative effects of too high level of connectivity. However, the risk of mixing individuals with different genetic backgrounds needs to be considered in potential translocation measures.

Species interactions and community-level dynamics

Much of the theory reviewed above is derived from the single-species point of view, whereas the aim of biodiversity conservation is at the level of species communities, ecosystems and ecosystem services. If the dynamics of species communities would simply be the sum of the dynamics of the individual species, the single-species theory would generalize directly to the community level. However, direct and indirect interactions among species complicate the picture considerably. As an example, in the community of wood-decaying fungi, species interact through a number of competitive and facilitative mechanisms, leading to positive and negative co-occurrence patterns in the field (Ovaskainen et al. 2010). As in most other species communities (Henle et al. 2004, Lawton et al. 2010), also in this species community the species that are specialized in their resource use (Hottola 2009, Hottola et al. 2009) are most fragmentation-sensitive. As the fragmentation-sensitive red-listed species are the first ones to be lost from the small and isolated habitat fragments, the competitive pressure in such fragments becomes released, and as a consequence the common generalist species may become more abundant in isolated fragments than in well-connected fragments. Thus while isolated sites may actually harbour many species, they often lack the species of major conservation interest.

The task of predicting how an entire species community responds to a perturbation in landscape structure (and thus to different conservation strategies) is overwhelmingly complex given the network of all possible direct and indirect interactions among the species. As a great simplification, the species-area relationship $S = kA^z$, first suggested by the Swedish ecologist Arrhenius (1921), provides a robust starting point. Here A refers to the size of a habitat fragment, and S is the number of species that are expected to persist on that fragment. The parameter k relates to the overall diversity of species in the taxonomic group under consideration, whereas the parameter z describes how strongly the number of species depends on habitat area.

The species-area relationship has been empirically verified for a large number of taxonomical groups, with the value of z typically varying in the range of $0.1 < z < 0.5$. As a default value, $z = 0.25$ is often used, resulting in the rule of thumb that losing 90% of the habitat area leads to the extinction of ca. half of the species. The main explanations behind the species-are relationship include the influence of habitat heterogeneity (Connor and Simberloff 1979), i.e. larger areas involve a greater diversity of habitat types and thus a greater number of different ecological niches, and the influence of habitat area per se, i.e. larger areas have lower extinction rates and higher colonization rates (Hanski and Gyllenberg 1997). The species-

area relationship can be viewed to build up from the responses of the individual species to habitat area (Ovaskainen and Hanski 2003c).

In the context of the ecological network of protected areas in the Netherlands, it is relevant to ask how the entire network supports the viability of species communities, i.e. how the communities that inhabit different sites sum up. The species-area relationship cannot be extended in any simple way, as the link from local diversity to total diversity depends on patterns of nestedness and beta-diversity, i.e. how dissimilar the communities inhabiting the different parts of the network are. Community similarity typically decreases with distance (Nekola and White 1999, Morlon et al. 2008), and thus conservation areas far from each other are likely to support a higher amount of biodiversity than conservation areas close to each other. Thus, community-level considerations imply that it is beneficial to spread conservation efforts across the landscape, whereas species-level considerations imply that it is beneficial to concentrate the conservation efforts. I will return to this apparent contradiction below in the section *Spatial prioritization of conservation efforts*.

Do ecological corridors work in practice: does structural connectivity ensure functional connectivity?

Ecological corridors are designed to improve connectivity among habitat fragments and thus the effectiveness of a conservation area network. But do they work in practice, i.e. do they provide a cost-effective conservation measure? The first critical question to ask is whether ecological corridors actually result in increasing level of movements and gene flow, i.e. whether structural connectivity is translated into functional connectivity. If this is the case, the second critical question to ask is whether increased functional connectivity results into increased population viability. As the latter question was addressed in the previous section (*The links between connectivity, population viability and persistence of biodiversity*), I will focus here on the first question.

The most obvious way in which an ecological corridor can provide functional connectivity is that it works as a movement corridor along which an individual moves within its lifetime from habitat fragment A to habitat fragment B. If it leaves offspring to fragment B, the corridor has increased the population-dynamic connectivity between these two fragments, with consequences for population dynamics and genetics. For passively moving organisms, such as seeds and pollen of plants; spores of fungi; or aphids or spiders drifting with wind, an ecological corridor is unlikely to make a big difference for individual movements. Thus a corridor has the potential to make a difference mainly for actively moving organisms, mainly animals such as mammals, birds and many insects.

Whether a corridor increases movements between habitat fragments even for actively moving animals depends critically on the interplay between landscape structure and the movement behaviour of the species. To illustrate this non-trivial link, I consider a case study in which the aim was to increase the population-dynamic connectivity between two Clouded Apollo populations in Southern Finland (Ovaskainen et al. 2008a). The main motivation here was to avoid the problems related to small population size in this endangered species of butterfly, such as that of inbreeding depression. The regional Environmental Centre connected two populations by cutting a semi-open movement corridor through forest. Next summer the corridor area was abundant in nectar plants that the butterflies use during their

adult life-stage, and consequently a lot of individuals moved to the corridor area. Based on this observation, the corridor was considered successful. However, mark recapture studies conducted both before and after the construction of the corridor showed that the number of individuals that actually moved between the two populations did not increase, and thus the corridor did not provide functional connectivity. The reason for this seemingly counterintuitive result is actually very simple. The individuals preferred the corridor area so much that they moved there slowly, and were thus unlikely to reach the other end of the corridor within their lifetime. Without the corridor, the individuals emigrated out of the habitat patches much less frequently, but they moved faster in the unsuitable matrix (mainly closed forest or cultivated field), and consequently had a greater possibility of reaching the other habitat patch. The corridor would have provided functional connectivity if the distance between the patches would have been shorter, or if the patches would have been smaller in their area. In the opposite cases, the construction of the movement corridor could have actually decreased the movements between the populations (for more details, see Ovaskainen et al. 2008a). The above example makes the point that even data on the presence of animals in a corridor does not ensure that the corridor increases functional connectivity among habitat fragments.

Another way in which an ecological corridor can provide functional connectivity is that the corridor consists of suitable breeding habitat for the focal species. In this case, the corridor may connect two populations not only through individual movement but also by allowing the species to reproduce in the corridor. Assume for example that in the above case study of the Clouded Apollo, the larval host plant *Corydalis solida* will inhabit the corridor area. If this will be the case, the corridor is likely to provide functional connectivity between the two populations even if it does not increase the probability by which the individuals move between the two fragments. Note that ecological corridors that consist of breeding habitat can increase functional connectivity also for passively moving organisms.

Ecoducts and other man-made crossing structures

A number of studies have considered the role of ecoducts in land-use planning processes (Bissonette 2002, Grau 2005, Gurrutxaga et al. 2010, Beben 2012, Reijnen et al. 2012) and modelling methods have been developed for optimizing the distribution of ecoducts within a landscape (Downs and Horner 2012).

As with any ecological corridors, the critical question is whether ecoducts actually work. A large body of literature is available for examining to which extent animals use of such crossing structures. Taylor and Goldingay (2010) conducted a comprehensive literature review of 244 published studies. More than half (51%) of these studies were conducted in North America, one fourth (25%) in Europe, 17% in Australia and 7% across several other countries. While a taxonomic bias was evident towards mammals (53%), studies have been conducted also on birds (10%), amphibians (9%) and reptiles (8%). Many of the studies (20%) included multiple taxonomic groups. The review shows that the installation of road-crossing structures for wildlife has become commonplace worldwide, and road crossing structures appear to be an important generic mitigation tool against fragmentation because a wide range of taxa indeed use them for their movements.

However, as discussed above, the fact that animals use ecoducts for their movements does not necessarily indicate that these are effective for achieving the goals of biodiversity conservation, such as viability of endangered species. As emphasized by several authors, very little is known about how beneficial these

measures actually are for conservation (Corlatti et al. 2009, Clevenger and Sawaya 2010, Lawton et al. 2010, Taylor and Goldingay 2010). For example, intuitively ecoducts enable gene flow and thus mitigate genetic problems associated with small population size, such as inbreeding depression. However, a review of scientific literature on population genetic consequences of crossing structures simply concluded that there is no evidence that wildlife overpasses do or do not efficiently address genetic issues (Corlatti et al. 2009).

Designing a cost-effective strategy for improving biodiversity conservation in the Netherlands

The present state of the protected area network in the Netherlands

Based on data by Thorborg (2012a), the current nature conservation network in the Netherlands is very fragmented. The total area of the protected area network is ca. 416,000 ha (equivalent to a square of 65 km x 65 km), consisting of 360,000 ha of forests, 37,000 ha of heaths and 19,000 ha of wetlands. Out of these, the proportion of habitat area that is located in large protected areas (>1000 ha) is 6% for forests, 24% for heaths and 20% for wetlands. These large protected areas can be considered as "mainlands" that form the core of the network, and are likely to enable the persistence of a large part of the extant biological diversity even if isolated from the other sites. The proportion of habitat area that is located in small protected areas (<10 ha) is 28% for forests, 9% for heaths and 12% for wetlands. It is very unlikely that these sites can sustain a high number of species (excluding the common generalists) if isolated from the remaining part of the conservation network, or if not active management measures (such as restoration or translocation) are carried on in a continuous basis.

Cost-effectiveness of construction of ecological corridors vs. protection of more area

Based on information from Bart Thorborg (see *Aim of the study*) the Dutch government is able to spend ca. 400 million euro for nature conservation until 2018. Two most important possibilities are acquisition of land to enlarge the current network of protected areas (ca. 40,000 € / ha) or improvement the connectivity between existing protected areas by constructing ecological corridors (ca. 4 million euro per ecoduct).

If the funding would be used solely for acquisition of land, it would make it possible to add to the present network ca. 10,000 ha of new protected areas, i.e. increase the area protected from 416,000 ha to 426,000 ha (proportional increase of 2.3%). If the funding would be used solely for construction of ecological corridors, it would make it possible to construct ca. 100 ecoducts.

The above numbers are not fully consistent with Reijnen et al. (2012), who state that "The terrestrial part comprises 450,000 ha of existing nature areas (based on the 1990 situation) and 275,000 ha of newly created habitats, including robust ecological corridors that are intended to link nature areas". However, as the purpose of this report is to compare the cost-effectiveness of different methods, the total amount of

resources available for conservation will not influence the conclusions. The main assumption below is that the cost of constructing an ecoduct equals that of acquiring ca. 100 ha of land.

As the mechanisms through which land acquisition (increase in area) and construction of ecoducts (increase in connectivity) result in biodiversity benefits operate at different units, a quantitative comparison of these two options is not straightforward, and would require additional data (see *Recommendation for the future: an evidence-based conservation strategy*). As a very simplistic starting point, consider a landscape consisting of two habitat fragments (Fig. 3). The question here is whether it is more cost-effective to increase the areas of these two fragments or to connect them by a corridor. The reasoning in Fig. 3 shows that the relative cost-effectiveness of a corridor depends on the sizes of habitat fragments to be connected, and in particular the extent c by which the corridor provides functional connectivity from the viewpoint of the focal species community. The estimation of the parameter c is challenging. In addition to the distance to be covered by the corridor, the value of the parameter c is likely to depend on a number of other factors related to landscape structure, such as the sizes of the fragments to be connected, and the habitat types of the fragments to be connected (forest, heath, or wetland). Most importantly, the effectiveness of a habitat corridor will vary greatly among species, ranging from virtually no effect (most passively moving organisms) to potentially a large effect (some actively moving organisms). In the absence of the necessary data, we may assume that in the case of ecoducts, a realistic value for the parameter c for the species of conservation interest would be in the range $0.01 < c < 0.1$. This would suggest that constructing an ecoduct becomes more cost-effective than increasing the sizes of the existing protected areas only if it the ecoduct connects conservation areas larger than 500-5,000 hectares.

Spatial prioritization of conservation efforts

Based on fundamental principles of spatial population dynamics, which are supported much by theory and data (see the review above), a highly connected network consisting of large protection areas will support the long-term persistence of a given focal species better than if the same conservation effort is spread more evenly through the landscape. While some level of fragmentation *per se* can be beneficial (see *The links between connectivity, population viability and persistence of biodiversity*), the current network of protected areas in the Netherlands is so highly fragmented that surely the goal will be in increasing rather than decreasing connectivity among the sites.

However, due to distance decay in similarity among species communities (see *Species interactions and community-level dynamics*), it is necessary to spread the conservation efforts across the entire country. Thus, and optimal national-level ecological network will consist of a number of regional-level conservation networks. Within any region, the conservation funds should be allocated in such a way that connectivity within and among the sites is maximized (i.e. large conservation areas close to each other). In this case, the regional-level networks will enable the persistence of local species communities. The presence of several regional-level networks enables the representation of different aspects of biodiversity at the national-level. Administrative boundaries are not visible to natural ecosystems, thus the above consideration is independent of administrative regions. For the same reason, the conservation priorities should be planned in a way that accounts for proximity to networks of protected habitats in the neighbouring countries.
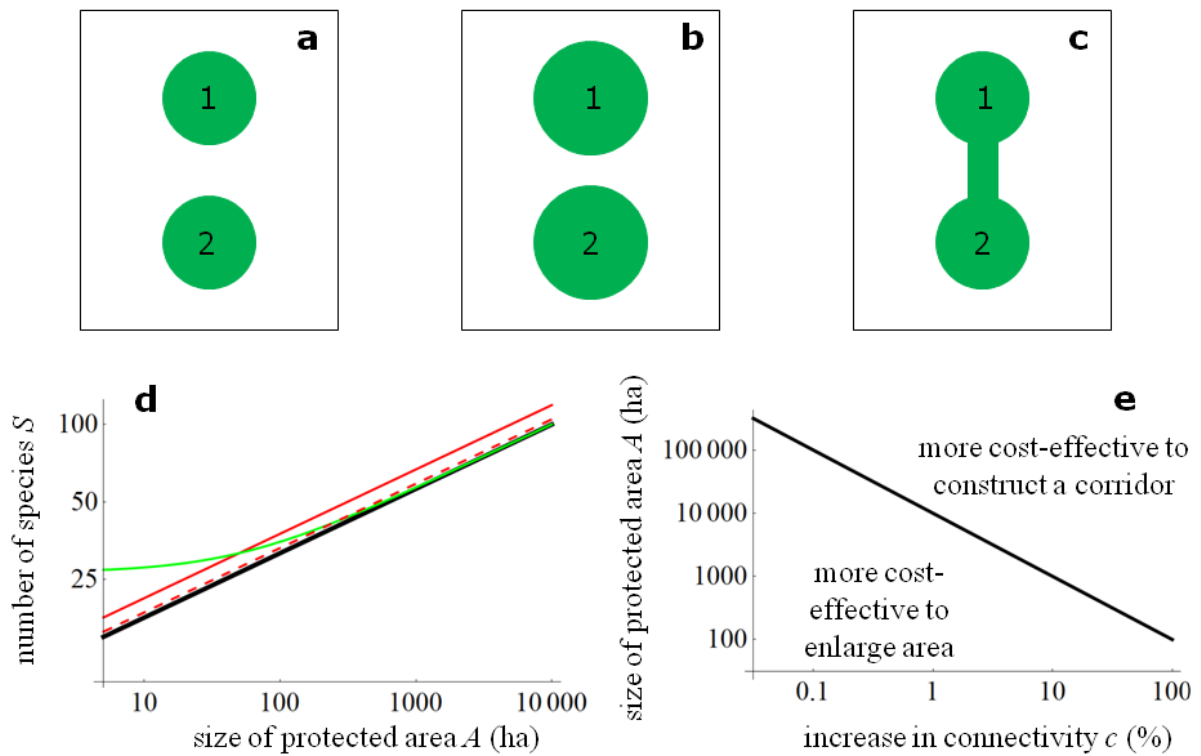
Figure 3: Cost-benefit analysis of increasing area vs. connectivity. Panel **a** depicts the starting point consisting of two habitat patches, each of area A ha. We may either allocate funds to acquire 100 ha of land, thus increasing the area of both sites by 50 ha (panel **b**) or by connecting the two sites by a corridor (panel **c**). Panel **d** shows the prediction of the species-area curve for the number of species that are expected to persist in habitat patch 1 (the situation is symmetric with respect to patch 2). The continuous black line corresponds to the original situation (panel **a**), i.e. $S = kA^z$. The green line corresponds to the scenario of panel **b**, i.e. $S = k(A + 50)^z$. The value of the corridor (the scenario of panel **c**) depends on how much of habitat patch 2 becomes accessible for the focal species community potentially inhabiting patch 1. I denote the proportion of patch 2 that becomes accessible in patch 1 by $0 \leq c \leq 1$, where c stands for the effect of connectivity. By the species-area curve, the number of species expected to persist in patch 1 is $S = k(A + cA)^z$. The continuous red line depicts the ideal case in which the corridor fully connects the two fragments into a single large reserve ($c = 1$), whereas the dashed line corresponds to a lower (yet still very high) level of functional connectivity ($c = 0.2$). Under this model, the construction of a corridor becomes more cost-effective than enlarging habitat area if $A > 50/c$ (panel **e**). The above reasoning and thus the threshold value of $A = 50/c$ is independent of the parameter values k and z of the species-area curve.

In practical terms, the above considerations suggest that land acquisition and restoration actions should be concentrated at the core areas of the present conservation network. The first priority should be in enlarging the present conservation areas and by improving their quality, the second in acquiring new protected areas nearby the existing areas. With these measures, the two goals of increasing habitat area

and increasing habitat connectivity will be achieved simultaneously. This recommendation is in line with that of Reijnen et al. (2012). It is also in line with Lawton et al. (2010) who outline the pathway for the creation of a coherent and resilient nature conservation network for England.

The construction of ecoducts is a more risky strategy, as hard evidence for their role in increasing functional connectivity is very limited, or at least was not available for the preparation of this report. What is clear from the above analyses is that if ecoducts are to be constructed, they should be used to connect large and high-quality sites that are already close to each other. As stated by Lawton et al. (2010), increasing connectivity helps, but first there needs to be high quality sites with thriving wildlife populations to connect. Due to lack of scientific evidence for the effectiveness on corridors in increasing the survival of populations, Lawton et al. (2010) set the priority of conservation actions for England as "Better management of existing sites > Bigger sites > More sites > Enhance connectivity > Create new corridors". With the reasoning given above, I agree. However, I would like to note that in addition to potentially providing benefits for species conservation, crossing structures can also increase road safety for humans. In some environments, the savings in property damage alone can outweigh the construction costs of the crossing structures (Donaldson 2007). Under such a scenario, the construction of crossing structures can be well justified even if their benefits for biodiversity conservation remain uncertain, but in this case their funding should not compromise funding used for the protection of biodiversity.

Recommendation for the future: an evidence-based conservation strategy

The above considerations are of qualitative nature and thus the recommendation should be interpreted with much caution. A quantitative analysis would require quantitative data in particular related to the biodiversity benefits that may result from the construction of ecoducts. Given the relatively high amount of financial resources to be invested, the development of an evidence-based conservation strategy (Sutherland et al. 2004, Lawton et al. 2010) and an adaptive management plan seems a priority. A central component of such a strategy is a monitoring programme that evaluates the effectiveness of the conservation measures that have already been taken and that are to be taken in the near future.

I will next outline what kind of data could be informative for assessing the optimal balance between enlarging habitat area vs. constructing ecoducts. I outline a very specific plan for the sake of making it concrete. Of course, this plan should be considered not more than an illustrative example that requires much further development if to be implemented.

The role of patch area and connectivity can be rather reliably assessed already from snapshot data, i.e. data without a temporal component. To collect such data, one should select, using an appropriate randomization scheme, a number of conservation sites (say, 50 areas of each of the three habitat types, representing full variation in area, and within each size class variation in connectivity to other conservation areas). These sites are to be surveyed for a focal species group of interest, e.g. birds, insects, or vascular plants, depending on the species groups of conservation interest and on the available expertise and other resources. At least two kinds of data are needed: data on species presence (the list of all species present in the site) and data on population abundance (the number of individuals counted on standardized study plots / transects).

The role of ecoducts is more difficult to judge from snapshot data, e.g. for the reason that the decision of constructing an ecoduct is likely to be correlated with habitat area, quality, and proximity to other sites. Thus, there is a need for data with a temporal dimension. Assume e.g. that 20 ecoducts will be constructed in the near future, so that they will connect 40 protected areas. Select as control sites, using an appropriate randomization scheme, another 40 protected areas which are similar in their areas, habitat types, qualities and their proximities to other sites. These 80 sites are to be surveyed for key biodiversity indicators such as species presence and abundance. Standardized survey plots / transects should be located both near and far from the ecoduct for those sites that are to be connected. The surveys should start before the ecoducts are constructed, and they should be repeated e.g. annually. From these data, the ecological benefits obtained by constructing an ecoduct can be inferred by examining if sites that are connected by an ecoduct perform better (in terms of biodiversity indicators such as species presence and abundance) than sites which are not connected by an ecoduct. The control sites are needed to separate the effect of the ecoduct from overall trends. For example, if biodiversity indicators decrease in all sites, but less in sites connected by ecoducts, the construction of ecoducts has been beneficial. If the sites that are connected by ecoducts do not perform better than sites without ecoducts, the conclusion will be that even if ecoducts may provide functional connectivity (as partially evidenced by the fact that animals use them), the population-dynamic consequences are so small that they are masked by other sorts of variation (e.g. random fluctuations in environmental conditions), and thus their construction is not ecologically cost-effective.

Availability of the kind of data outlined above would have made it possible to perform quantitative instead of qualitative analyses, and thus to provide more direct support for the decision process. Possibly such data are at least partially available given the high level of ecological research in the Netherlands. Indeed, the analyses of Reijnen et al. (2012) indicate that much of the data required to analyze the effects of patch area and connectivity may actually exist. The availability of key data needed for evidence-based conservation should be discussed with local stakeholders such as biodiversity researchers, protected area managers and environmental NGOs. If the relevant data are available, they should be incorporated into the planning process. If the relevant data are not available, as I expect to be largely the case for the ecoducts, allocating part of the funding to a monitoring programme may be very cost-effective. If 5% of the funds are used to a highly targeted monitoring scheme that helps to increase the effectiveness of future conservation actions by 20%, the monitoring scheme will be a good investment.

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