

How to develop the nature conservation strategies for The Netherlands?

still is suitable habitat for that species (e.g. Hanski & Ovaskainen, 2000). As a consequence, a highly fragmented network of conservation areas is not likely to be cost-effective. For species with low conservation priority, typically species with generalized resource requirements, connectivity within and among the reserves is much less of an issue than for species with high conservation priority (e.g. Henle et al., 2004).

The task of predicting how an entire species community responds to a change 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 main explanations behind the species-area relationship include the influence of habitat heterogeneity (Connor & 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 & Gyllenberg, 1997). The species-area relationship is important, because it can be used to predict what happens when habitat is lost. As a rule of thumb, losing 90% of the habitat area leads to the extinction of ca. half of the species. However, this does not take place immediately, as habitat loss is followed by a transient during which a number of species that will eventually go extinct are still present. The number of such 'living dead' species is termed the extinction debt (Tilman et al., 1994). The species-area relationship refers to the equilibrium situation after such a transient.

Ecological corridors are aimed at improving connectivity among sites. They may be natural or man-made, such as 'ecoducts' (photo 1) and other road crossing structures. A number of studies have considered the role of ecoducts in the context of land-use planning processes (e.g. Reijnen et al., 2012). The main critical question with ecological corridors is whether they actually work, i.e. do they increase movements among the populations they connect, or even more importantly, do they increase the viability of the populations. Taylor & Goldingay (2010) conducted a comprehensive literature review of 244 published studies on ecological corridors. The review shows that the installation of road-crossing structures for wildlife has become commonplace worldwide, and that a wide range of taxa indeed use them for their movements. However, 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. Surprisingly little is known about how beneficial ecological corridors actually are from the nature conservation point of view. 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).

Habitat loss is globally one of the greatest threats to biodiversity (Hanski, 2005). In the case of The Netherlands, the vast majority of land area has been converted from natural habitats to urban developments and intensive agriculture. Especially relevant aspects of habitat deterioration include eutrophication and acidification (Reijnen et al., 2012). In this situation, well planned conservation measures are needed to ensure the persistence of the remaining biodiversity and to restore part of the biodiversity that has been lost already. Two central tools for achieving such aims are the enlargement of the present network of protected areas and improving the quality of existing protected areas. Given the cost of acquiring land and the pressures for alternative forms of land use, cost-effective conservation measures are needed; this calls for a combination of scientific knowledge and of local expertise.

I was asked by the Dutch Council for the environment and infrastructure (Rli) to provide an expert opinion on the future development of the Dutch National Ecological Network. In particular, the task was to assess the relative cost-effectiveness of enlarging the existing network of protected areas versus the construction of ecological corridors. The idea behind ecological corridors is that they can help populations inhabiting individual conservation areas interact with each other, in which case the capacity of the ecological network to promote the persistence of biodiversity may be greater than simply the sum of those of the individual fragments (Lawton et al., 2010).

Let me start by confessing that I am not an expert in nature protection in The Netherlands, so my assessment is based on some basic statistics on the state of the network of protected areas, reflected against a review of scientific literature on spatial ecology and conservation biology. In my own research, I have studied some themes that are relevant in this context, e.g. how landscape structure influences animal movements (e.g. Ovaskainen et al., 2008; Patterson et al., 2008) and how the structure of a conservation network influences the long-term persistence of species (e.g. Hanski & Ovaskainen, 2000). The full report for the Dutch Council is available online (Ovaskainen, 2012).

A brief review of ecological theory

Before addressing the aims of this study, I will set the background by briefly reviewing relevant ecological theory. To start with, I note that if a network of conservation areas is too fragmented, a species of conservation interest may not be able to persist even if there

The present state of the Dutch National Ecological Network

The current nature conservation network in The Netherlands is very fragmented. The total protected area 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 that is located in large protected sites (>1,000 ha) is 6% for forests, 24% for heaths and 20% for wetlands. These key areas can be considered as 'mainlands' that form the core of the network. They are likely to facilitate the persistence of a substantial part of the extant biological diversity even if isolated from the other sites. The proportion of habitat area that is located in very small protected sites (<10 ha) is 28% for forests, 9% for heaths and 12% for wetlands. It is unlikely that these sites can sustain a high number of species (excluding the common generalists and species with small area requirements) 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.

Which is better: construction of ecological corridors or protection of more area?

The Dutch government plans to invest ca. 400 million euros for construction of ecoducts to improve connectivity among the conservation areas due to the highly fragmented nature of the conservation area network. A relevant question in this context is the cost-efficiency of ecoducts as a conservation measure, compared e.g. to the acquisition of land for enlarging the current network of protected areas. As a quantitative cost-benefit analysis would call for data that was not available, I conducted a qualitative analysis based on a number of simplified assumptions, the validity of each of which may be questioned. To start with, I assume that acquisition of land costs ca. 40,000 € per ha, whereas the construction of ecological corridors costs ca. 4 million € per ecoduct. Thus, the cost of constructing a single ecoduct equals that of acquiring ca. 100 ha of land. The present plan in The Netherlands is to include in the ecological network of protected sites ca. 450,000 ha of terrestrial area, out of which at this moment ca. 416,000 ha have been protected. If the funding planned for ecoducts would be used solely for acquisition of land, it would make it possible to add to these plans ca. 10,000 ha of new protected areas. If the funding would be used solely for construction of ecological corridors, it would make it possible to construct ca. 100 ecoducts.

The mechanisms through which land acquisition (increase in area) and construction of ecoducts (increase in connectivity) result in biodiversity benefits operate at different units. As a very simplistic starting point, consider a landscape consisting of two habitat fragments (fig. 1) that are identical in their habitat type.



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 figure 1 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.

In addition to the length of the corridor vs. the movement ability of the focal species, 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 to moderate or potentially a large effect. In the absence of the necessary data, I make the rough assumption that $0 \leq c < 0.01$ for most passively moving organisms such as those fungal and vascular plant species that are dispersed by wind and for which the ecoduct does not provide breeding habitat. We may further assume that $0.001 < c < 0.01$ for many insects, and that $0.01 < c < 0.1$ for many birds and mammals. Those fungi or plants that are dispersed by a vector (e.g. insect or bird) have the c value of their vector. For such species for which the ecoduct provides breeding habitat the value of the parameter c can be substantially higher than expected



Photo 1. Do ecoducts provide a cost-effective conservation measure? The ecoduct in the photo was constructed in the year 2003 to connect two protected areas in the so called Groenewoud region in the province Noord-Brabant (photo: Rijkswaterstaat / Joop van Houdt)

solely from the effect of the corridor on their movement behaviour. Importantly, there is no reason to assume that ecoducts would be especially effective in providing connectivity for those highly specialized species for which the lack of connectivity is the greatest problem; actually it is more likely that ecoducts are mostly used by common species. In summary, we may assume that a realistic value of the parameter c for the species of conservation interest is in the range $0.01 < c < 0.1$. This would suggest that construction of ecoducts becomes more cost-effective than increasing the sizes of existing protected areas only, if the ecoduct connects conservation areas larger than 500-5,000 hectares (fig. 1).

Concluding remarks

An optimal national-level ecological network is likely to 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. to enlarge the existing areas or create new conservation areas close

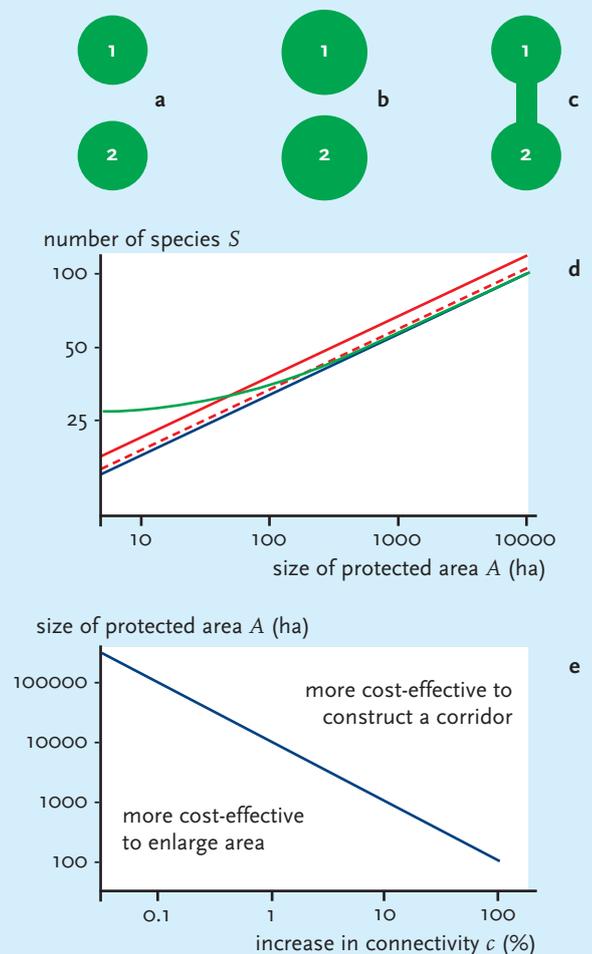


Fig. 1. Cost-benefit analysis of increasing area vs. connectivity.

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.

to the existing ones. Such high quality regional-level conservation networks will facilitate 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. In practical terms, land acquisition and restoration actions should be concentrated at the core areas of the present conservation network. The first priority should be in enlarging existing conservation areas and by improving their quality, and 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), and it is also in line with Lawton et al. (2010) who outlined 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 my assessment. 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. 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". I agree.

The above considerations are of qualitative nature and thus these recommendations should be interpreted with much caution. A quantitative analysis would require quantitative data 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 program that evaluates the effectiveness of the conservation measures that have already been taken and that are to be taken in the near future. For concrete suggestions relating to such a monitoring program, see Ovaskainen (2012).

Literature

- Arrhenius, O., 1921. Species and area. *Journal of Ecology* 9: 95-99.
Connor, E.F. & D. Simberloff, 1979. The assembly of species communities; chance or competition. *Ecology* 60: 1132-1140.
Corlatti, L., K. Hacklaender & F. Frey-Roos, 2009. Ability of wildlife

overpasses to provide connectivity and prevent genetic isolation. *Conservation Biology* 23: 548-556.

Hanski, I., 2005. The shrinking world: ecological consequences of habitat loss. International Ecology Institute, Oldendorf.

Hanski, I. & M. Gyllenberg, 1997. Uniting two general patterns in the distribution of species. *Science* 275: 397-400.

Hanski, I. & O. Ovaskainen, 2000. The metapopulation capacity of a fragmented landscape. *Nature* 404: 755-758.

Henle, K., K.F. Davies, M. Kleyer, C. Margules & J. Settele, 2004. Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation* 13: 207-251.

Lawton, J.H., P.N.M. Brotherton, V.K. Brown, C. Elphick, A.H. Fitter, J. Forshaw, R.W. Haddow, S. Hilborne, R.N. Leafe, G.M. Mace, M.P. Southgate, W.J. Sutherland, T.E. Tew, J. Varley & G.R. Wynne, 2010. Making space for nature: A review of England's wildlife sites and ecological network. Report to Defra.

Ovaskainen, O., 2012. Strategies for Improving Biodiversity Conservation in the Netherlands: Enlarging Conservation Areas vs. Constructing Ecological Corridors. An expert report submitted to the Dutch Council for the environment and infrastructure. http://www.rli.nl/sites/default/files/u61/otso_ovaskainen_strategies_for_improving_biodiversity_conservation_in_the_netherlands.pdf.

Ovaskainen, O., M. Luoto, H. Rekola, E. Meyke & M. Kuussaari, 2008. An empirical test of a diffusion model: predicting clouded apollo movements in a novel environment. *American Naturalist*: 610-619.

Patterson, T.A., L. Thomas, C. Wilcox, O. Ovaskainen & J. Matthiopoulos, 2008. State-space models of individual animal movement. *Trends in Ecology & Evolution* 23: 87-94.

Reijnen, R., A. van Hinsberg, W. Lammers, M. Sanders & W. Loonen, 2012. Optimising the Dutch national ecological network. Spatial and environmental conditions for a sustainable conservation of biodiversity. In: T. M. De Jong, R. Posthoorn & J. Dekker (eds). *Landscape ecology, town and infrastructure*.

Sutherland, W.J., A.S. Pullin, P.M. Dolman & T.M. Knight, 2004. The need for evidence-based conservation. *Trends in Ecology & Evolution* 19: 305-308.

Taylor, B.D. & R.L. Goldingay, 2010. Roads and wildlife: impacts, mitigation and implications for wildlife management in Australia. *Wildlife Research* 37: 320-331.

Tilman, D., R.M. May, C.L. Lehman & M.A. Nowak, 1994. Habitat destruction and the extinction debt. *Nature* 371: 65-66.

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