

DIMO, a plant dispersal model

Abstract

Due to human activities many natural habitats have become isolated. As a result the dispersal of many plant species is hampered. Isolated populations may become extinct and have a lower probability to become re-established in a natural way. Moreover, plant species may be forced to migrate to new areas due to climate change. Species survival in these cases may depend on increasing the connectivity of the landscape by engineering. To investigate and to predict the effects of isolation on the dispersal abilities of plant species, to increase spatial cohesion of a habitat network, to advise policy makers and spatial planners, we developed a simple GIS based dispersal model, DIMO. The model simulates dispersal and establishment of plant populations over a period of time in heterogeneous landscapes on a yearly basis. The model includes proxies for dispersal by wind, animals, water, and self-dispersal. Species establishment is based on habitat suitability maps and simulations include the effect of seed dormancy and generation time. A sensitivity analysis and validation were carried out. The model was validated with *Juncus tenuis*, an introduced species in the Netherlands. On average the difference between observed and simulated dispersal distance was 9.8 km for a distance of 155 km. The model was applied for a designed corridor in the South of the Netherlands. Model runs indicate that three of the five tested species were able to use the corridor. Two species could not, both due to lack of suitable habitat and one of them also due to lack of dispersal capacity. The results suggest that DIMO is able to evaluate the effectiveness of corridors, but also made clear that besides connectivity the present and future availability of suitable habitats in a corridor is of great importance. The model could be helpful for evaluating policy plans but also for policy making. It may be used for defining and implementation of adaptation measures to climate change on regional to continental scale.

Key-words: dispersal, germination, spatial-explicit modeling, climate change, landscape fragmentation, ecological networks

Introduction

Landscape fragmentation diminishes habitat size and connectivity of natural areas (Saunders *et al.* 1991, With & Christ 1995, Hanski & Ovaskainen 2000, Crooks *et al.* 2011). These changes are often the result of man-made activities (McDonnell *et al.* 1990, Williams *et al.* 2009). Loss of habitat leads to a direct loss of individual plants and animals but may also result in a loss of meta-population structure (Kruess & Tschardt 1994, With & Christ 1995, Hanski & Ovaskainen 2000, Debinski & Holt 2000, Crooks *et al.* 2011). The latter may, in turn, lead to the loss of locally isolated populations and eventually to the extinction of species (McDonnell *et al.* 2005, Williams *et al.* 2005, Fischer & Lindenmayer 2007).

Habitat connectivity is more important than ever now climate change may shift suitable habitat to both higher latitudes and altitudes (Araújo *et al.* 2004, Thuiller 2004). The Natura 2000 network, the European network of highly valued nature areas (under the Habitat Directive, 92/43/EEG and Bird Directive, 2009/147/EG), are designed to help to preserve species. However, when climate change 'hits' these protected areas preserving at the site may not be enough (c.f. Araújo *et al.* 2004). Species may be forced to disperse following their preferred habitat in order to survive. The alternatives are to adapt to the new circumstances or to perish. Therefore, dispersal potential of plant species may be an important trait to survive climate change (Primack & Miao 1992, Thuiller *et al.* 2008). Ozinga *et al.* 2009 showed that differences between plant species in adaptations to various dispersal vectors are important. But these adaptations are a largely

overlooked factor in explaining losses in plant diversity in Northwest Europe in the 20th century. They are as important as the more commonly accepted effects of eutrophication.

To enhance habitat connectivity and the survival of species, ecological networks have been designed on a regional scale (Jongman & Pungetti 2004, Grashof-Bokdam 2009, Noordijk *et al.* 2011) national scale (Van der Zouwen & Van Tatenhove 2002) and continental scale (Pan European Ecological Network, PEEN; Jongman *et al.*, 2010). Ecological networks are here defined as habitat networks that are connected via corridors or 'stepping stones'. The effectiveness of ecological networks on species survival should be tested with empirical data. This has been done successfully for animal species (Debinski & Holt 2000), but tests for plant species are still scarce (Bruinderink *et al.* 2003, Helm *et al.* 2006). A plant dispersal model, as described in this paper, can be used as a tool for assessing the connectivity of a fragmented landscape for plant species. Such a model should be able to work on a meta-population scale, i.e. on a regional or even continental scale, and preferably be applicable for many species.

'Up till now ecological networks have been built to preserve meta-populations of species in a certain area, whereas for the future the design has to be adapted to facilitate the migration of species' (Araújo *et al.* 2004). This calls especially for cross national networks, e.g. networks that link France with Belgium, the Netherlands and (north) Germany. A spatial planning approach for the implementation of adaptation measures to climate change in conservation planning for ecological networks is available (Vos *et al.* 2010). But for the underpinning, implementation and translation to adaptation plans such as designing a corridor, a dispersal model for plants is needed. Although there are several advanced dispersal models available (e.g. Nathan *et al.* 2011), these models are not yet easily applicable for spatial planning. This model will fill one of the knowledge gaps. Therefore, the goal of this research was to develop a model that is able to simulate dispersal of various continental plant species in a fragmented landscape on a regional to continental scale. This model deviates from species specific models that try to simulate the behavior of one species through the landscape in detail and detailed landscape planning. This model is meant to evaluate government policy and environmental planning as a part of a larger planning process on a regional or (inter) national scale including many species. Subsequently, the model was used to evaluate a designed network in the South of the Netherlands with connections in Germany and Belgium.

General introduction to the model

DIMO, short for DIspersal MOdel, simulates plant species dispersal and establishment through a (fragmented) landscape with time steps of one year. DIMO is a GIS based model. The dispersal of seeds can occur by wind, water, animals (internal and external) and all kinds of self-dispersal (e.g. explosive mechanisms). Many plant species have a high potential for long distance dispersal by more than one vector (Ozinga *et al.* 2005) and therefore it is possible for species to disperse via more than one method in the model. In that case the longest dispersal distance will be used by the model. Dispersal distances can be limited by barriers such as highways in case of dispersal by animals. In principal any form of dispersal can be limited by barriers by adding a barrier map to DIMO.

The dispersal distance of a species is based on data from the LEDA database (Knevel *et al.* 2003, Kleyer *et al.* 2008, www.leda-traitbase.org/LEDAportal), or on expert judgment (Wamelink *et al.* 2011) in case of lack of measurements. 'The LEDA Trait database provides information on plant traits that describe three key features of plant dynamics: persistence, regeneration and dispersal'. LEDA stores information per species observation combination.

Species establishment can be limited due to 'germination delay' which includes effects of seed dormancy and after establishment the expansion of a local population can be delayed by the years till the next generation is produced after establishment. When habitat conditions of a particular species are met this species may also emerge from the locally established seed bank. Therefore, the model keeps track of seed bank age; based on the seed longevity the maximum seed bank age is estimated.

DIMO works with grids of cells, where each cell is considered to be homogeneous. The model can run with various grid-sizes, but in the presented studies 250*250m grids are used. Model runs are always done for one species; multiple species can be run in sequence. The model is initialized with three maps: 1) the distribution of a species for a chosen period, 2) a seed bank presence map and 3) a habitat suitability map. These data can be obtained from inventories, but can also be left blank or filled by an initial run. For the simulation of water dispersal a water speed map is needed. From a cell where the species is present DIMO calculates every year how far the seed can travel and which new cells can be reached, depending on dispersal distance, barriers and direction of water streams. If the dispersal distance is smaller than the grid cell size the model calculates how long it will take until the next cell can be reached. The seeds then arrive in the seed bank and will germinate and grow to reproductive plants if the habitat is favorable and the seeds are not or no longer dormant. When the reproductive stage is reached the cell becomes a seed source. Formulas and a flow diagram are given in Box 1.

Box 1. Formulas

DIMO is a GIS based model. For each individual grid cell the following update rules apply in each iteration (if applicable for the species).

Wind dispersal

$$Dwi_{x,st,r} = Dwi_x * (Wi_{st,r}/Wi_{max}) \quad \text{Eq. (1)}$$

$Dwi_{x,st,r}$: dispersal distance for species x by the wind for weather station st in direction r (m);
 Dwi_x : dispersal distance by the wind for species x (m);
 $Wi_{st,r}$: wind speed per station per direction r (m/s);
 Wi_{max} : maximum mean wind speed average from all weather stations (m/s).

Animal dispersal

$$Dan_{x,r} = \min (Danbar_{t,x} , Danmax_x) \quad \text{Eq. (2)}$$

$Dan_{x,r}$: dispersal distance for species x by animals in direction r (m); $Danbar_{t,x}$: dispersal distance for species x by animals till barrier in year t in direction r (m);
 $Danmax_x$: maximum dispersal distance by animals for species x (m).

Water dispersal

$$Dwa_{x,r} = Flx * Ws_r \quad \text{Eq. (3)}$$

$Dwa_{x,r}$: dispersal distance for species x in direction r by water (m), Flx : floating time of species x (s), Ws_r : water speed in direction r (m/s)

Resulting dispersal

$$D_{x,r} = \max (Dwi_{x,st,r} , Dan_{x,r} , Dwa_{x,r} , Dsi_x) \quad \text{Eq. (4)}$$

$D_{x,r}$: resulting dispersal distance for species x in direction r (m), Dsi_x : self inflicted dispersal distance for species x.

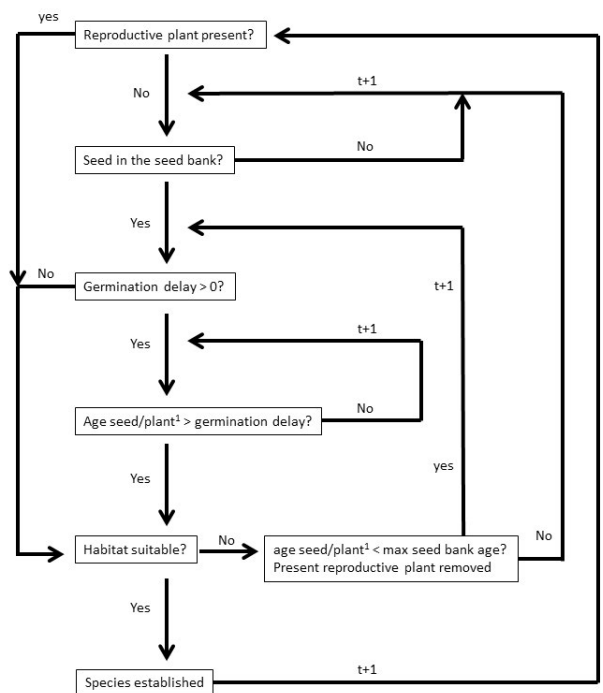
Germination delay, habitat suitability and species establishment

$$Ses_{t,x,r,i} = f(D_{x,r} , H_{t,x} , G_x) \quad \text{Eq. (5)}$$

$Ses_{t,x,r,i}$: Species establishment at year t for species x in direction r from grid i (-), $H_{t,x}$: habitat suitability for species x in year t (-), G_x : germination delay for species x (y)

After calculating all the above, the model progresses in each iteration with the following flow chart, again for each grid cell. The following four questions play an important role in DIMO:

1. Can a cell be reached from a neighbouring cell?
2. Is the arrived seed ready to reproduce?
3. Is the habitat suitable for the species?
4. Are there viable seeds present in the seed bank?



A description of the input maps is given in Annex 1. Many decision to build the model have been made, they are described in Annex 2. The parameter values are given in Annex 3 and Annex 4 ([See Document Annexes](#)).

Wind dispersal (anemochory)

A major form of dispersal in DIMO is wind dispersal. 1013 of the 1178 species currently present in DIMO have a form of wind dispersal. Data on wind dispersal are retrieved from LEDA (Knevel *et al.* 2003) database and based on an earlier project where we estimated the wind dispersal distance for plant species based on seed characteristics (expert knowledge, see Wamelink *et al.* 2011, <http://edepot.wur.nl/201667>). If data from LEDA (terminal velocity) were available we preferred these sources above our expert knowledge estimations. The dispersal distances for wind were thus partly based on terminal velocity experiments

and recalculated to distances, following the approach of Soons & Ozinga (2005). We took the 99 percentile of the resulting asymptotic dispersal curve as the dispersal distance for DIMO, representing long distance dispersal events. Wind speed influences the seed dispersal by wind. For the major weather stations in the Netherlands the wind speed data were collected and built in in the model as the average wind speed per year per direction. We assumed that the wind causes differences in the maximum dispersal distance. The realized dispersal is therefore corrected for the wind speed (Figure 1 and Annex 5). Not included in the model are the effects of wind turbulence and the effect of landscape structure. Wind dispersal also includes ballochory and ballistic dispersal. In this case, the dispersal is not based on a dispersal curve, but on expert knowledge and dispersal distance is limited to often less than one meter per year. These forms of dispersal for a species is only included

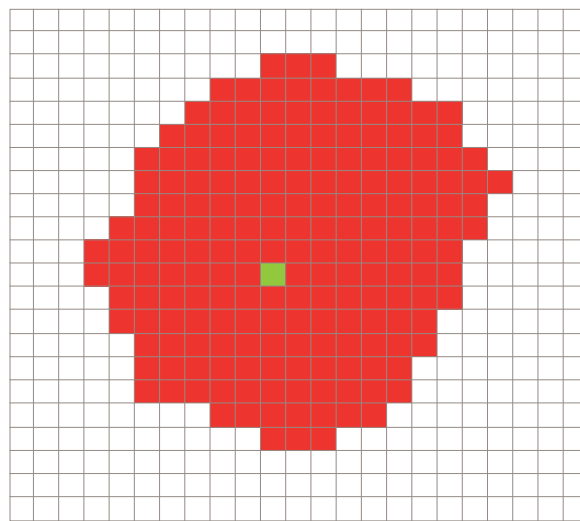
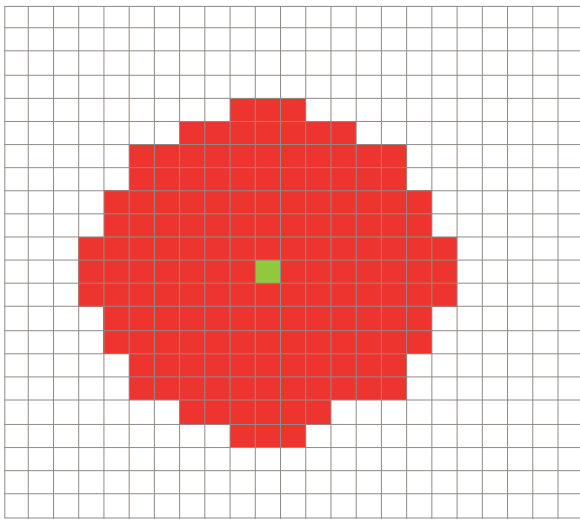


Figure 1. Example of the effect of wind on wind dispersal. Left the dispersal by wind from the green cell without the effect of difference in wind direction and force. The reached cells are given in red. On the right the effect of wind direction and force as implemented in DIMO. The reached cells (in red again), give no longer a circular dispersal front due to the wind (yearly average of averaged day wind speed and direction).

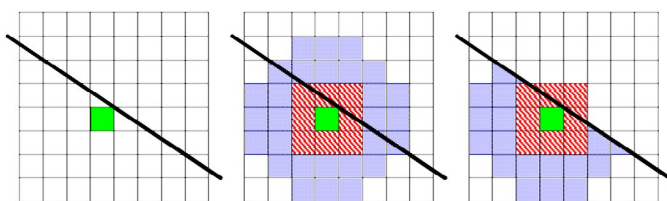


Figure 2. Example of plant dispersal by DIMO for a species dispersed by wind as well as by animals. The left figure represents the initial situation, the green grid cell indicates the seed source and is bordered by a for animals absolute barrier (black line). The figure in the middle gives the dispersal distance by wind (cells with red white striped color) and by animal (cells in blue color) without the effect of the barrier. The figure on the right gives the same situation as the figure in the middle but now with the effect of the absolute barrier. Some of the cells cannot be reached by the animals, but the barrier does not influence the wind dispersal, so the seeds can reach the other side of the barrier, but only due to wind dispersal. Cells that are partly colored are assumed to become occupied, but the animals cannot cross that cell and thus reach neighboring grid cells.

in the model if it is the only way of wind dispersal for a species. Wind dispersal may be combined with a barrier map, to calculate the influence of forest for instance.

Animal dispersal (zoochory)

Both external (epizoochory) and internal (endozoochory) dispersal by animals is simulated by DIMO. The dispersal distance is based on the estimated home range of the animals. We assume that the internal dispersed seeds leave the animal via excrements and that at least one seed per year survives. Survival of seeds varies largely between species; however this is not included in the model.

Dispersal may take place by all kinds of animals, we model just the distance of the animal with the largest effective dispersal distance. E.g. when a seed is dispersed by ants and by birds, the longest home range is used for the modeling. Like for wind dispersal, data are taken from LEDA (Knevel *et al.* 2003), and if no data were available dispersal distances were based on expert judgment. Animal dispersal can be limited by barriers such as roads or rivers. Dispersal then stops at the barrier, as animals and thus seeds do not travel beyond the barrier. If the seeds are also dispersed in other ways, eventually the seeds still may cross the barrier (Figure 2). If seeds are dispersed by birds barriers may be used as well, but as for all other animals, the model can also be run without barriers. Animal behavior is known to be influenced by the landscape, thus influencing the dispersal direction and distance. This influence on animal behavior is not included in the model, for this an individual based model is more suited.

Water dispersal (hydrochory)

The dispersal of seeds by water is based on floating capabilities. Data about floating time (maximum values) are taken from LEDA (Knevel *et al.* 2003). The floating time is combined with the direction and speed of water flow in rivers, streams and lakes. The floating direction is based on the altitude map, in our case of the Netherlands. This map is based on the national altitude map AHN (www.ahn.nl). The actual AHN map does not contain water levels. So in most cases the water level is an interpolation from the surrounding surface altitude. The average water speed is determined based on the water classification system as defined by Puijenbroek (2010). The subsequent dispersal distance in water is the product of the floating time and the water speed. We assume that at least one seed will reach the maximum dispersal distance (is the maximum floating time multiplied by the average water speed) and will germinate and thus produce new seeds in time. Barriers as dams can be included in the modeling and thus block dispersal. However, if the species also has other means of dispersal, e.g. wind dispersal, the dam still may be taken. Many seeds of many species may sink rapidly, but still be dispersed via underwater streaming and be deposited in still water and germinate. The dispersal distance may then even be greater than when floating (Wadsworth *et al.* 2000). This is not included in the model yet.

Table 1 Parameter settings for the sensitivity analyses of DIMO

Dispersal distance for wind (m)	Wind force (-)	Dispersal distance for animal (m)	Germination delay (y)	Barrier (-)
0.1	1.0	0	0	1
200	1.5	50	5	2
400	2.0	200	10	
800	2.5	1000	25	
1000		10000		
1600				

Self-dispersal (autochory)

The fourth dispersal method accounted for in DIMO is self-dispersal. This includes several kinds of explosive mechanisms (e.g. *Impatiens glandulifera*), rolling (e.g. *Quercus robur*) and raindrop-ballists (e.g. *Sedum acre*). Also included in this dispersal method is the vegetative growth. Barriers may have an effect on this form of dispersal, as long as a barrier map is presented to DIMO. Distances are again based on LEDA (Knevel *et al.* 2003) database and when no data were available based on expert judgment.

Germination delay

Not all seeds are able to germinate immediately after arrival in a new grid cell. For many species some kind of dormancy has to be broken in order to be able to germinate (Finch-Savage & Leubner-Metzger, 2006). This species specific delay is taken into account in DIMO. Seeds do not germinate before the dormancy period is over (which is a maximum value per species). Information on

dormancy is taken from literature, but is up till now often anecdotic and scattered over many sources. Also incorporated in the term germination delay is the number of years it takes for a species to become reproductive (Jensen & Nielsen, 1986). This can be up to twenty years for some tree species. In that period there will be no seed production and thus no dispersal. In the future this could be split into two separate parameters.

Sensitivity analysis

A sensitivity analysis was carried out for DIMO, both to test the model and to get insight for which parameters the model is sensitive. The parameter settings were varied for dispersal distance (separate for wind and animal), wind force, germination delay and the effect of barriers (Table 1). The values for the wind force have been multiplied by a factor, e.g. a value of two implies a wind force twice as strong as the standard average wind force. For barriers a value of one indicates no barrier and a value of two a non-permeable barrier for animals. Not all possible combinations of parameter values were examined; a full overview is given in Annex 6.

DIMO was run for the combination of parameter sets (from annex 6) for 10 simulation years, except for germination delay for which the model was run for 30 simulation years, from one single occupied cell. For each run the dispersal distance was calculated applying the Euclidean Distance technique (ArcGis, Hillier 2011), i.e. the dispersal was calculated as a 2-dimensional Euclidian distance. Results are discussed here below per parameter.

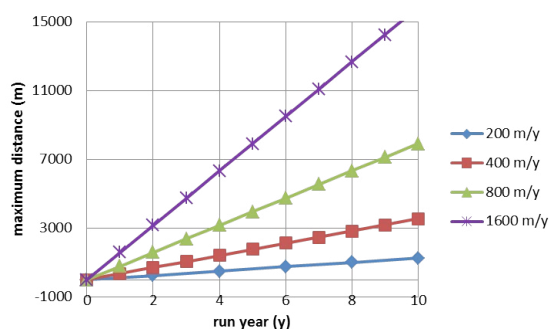
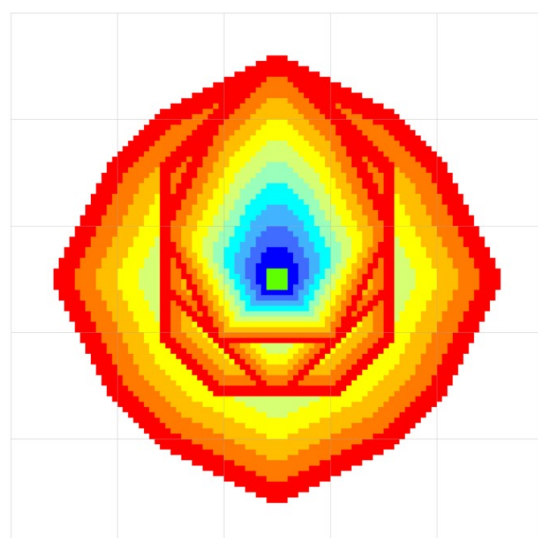


Figure 3a. Dispersal distance for an artificial species with different wind dispersal capacity.

Figure 3b. Effect of wind speed on the dispersal of an artificial species. The numbers indicate the number of years a species is present in a grid. Given are the dispersal distances for four situations with an increasing wind speed from the South, with the results of the strongest wind on top and equal wind strength from all directions as undermost. Results are given as if the maximum dispersal is the same, so the figure merely shows the limiting effect of wind from the south on the dispersal. The colors and numbers in the legend represent the number of years a species is present in the grid cell.



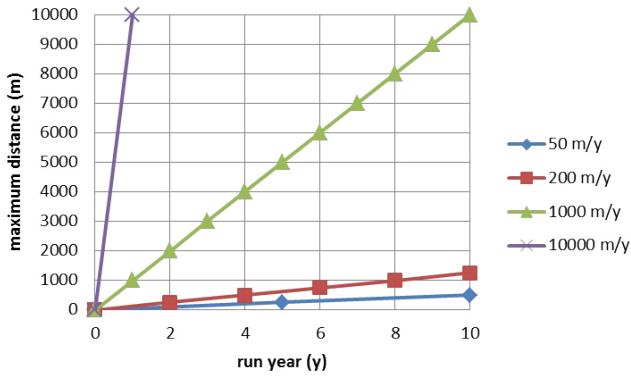


Figure 3c. Dispersal distance for an artificial species with different animal dispersal capacity. For dispersal capacity of 10.000m only the first two years are shown.

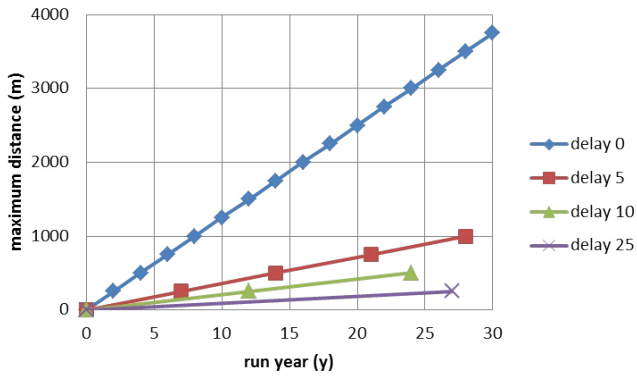


Figure 3d. Dispersal distance for an artificial species with germination delay time. Model runs are given for 30 years, since germination delay gives less output in a certain period not all runs have output in the same year.

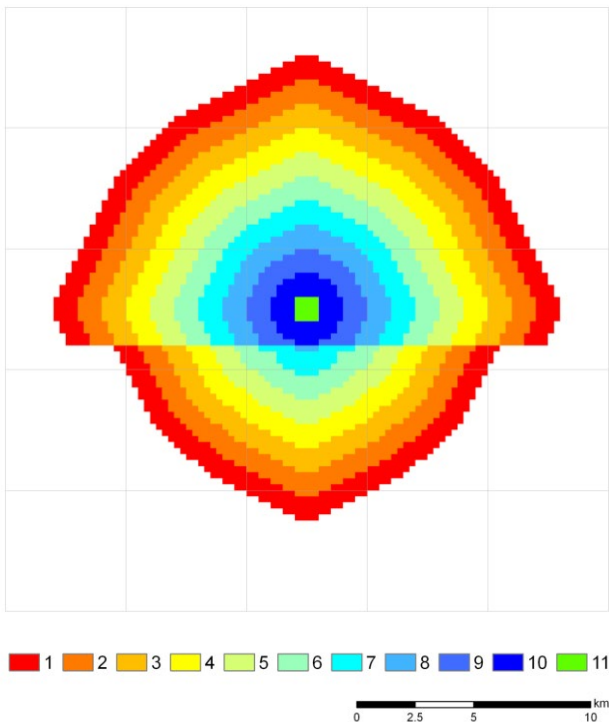


Figure 3e. Effect of a barrier for animals on the dispersal of an artificial species both dispersed by animals and wind. The numbers indicate the number of years a species is present in a grid.

As can be expected the dispersal distance in DIMO increases with the dispersal capacity (Figure 3a), which is a first qualitative test of the implementation of DIMO. Dispersal capacity is here defined as the maximum distance that a species can disperse. The dispersal distance of 0.1m is not included in the figure because the artificial species does not leave the original cell (250*250m) within the run time of 30 years. Differences in dispersal distances are large giving a relative large uncertainty. This implies that a correct estimation of the dispersal capacity is of high importance.

A variation in wind force gives a distinct dispersal pattern (Figure 3b). Here we assumed that the given dispersal distance for wind is the maximum, i.e. the calculated LDD based on the LEDA data represent the maximum. This implies that incorporating wind strength and direction in our case will not influence the maximum dispersal distance in the wind direction, but it does negatively influence the dispersal distance in other directions. Thus, southern winds have an impact on the dispersal in all dispersal directions (except in the northern direction), which increases the stronger the wind is. Effects are strongest in the southern direction, as can be expected. Overall effects, however, are less pronounced than the effect of the dispersal capacity.

As for wind dispersal, the effects of differences in animal dispersal capacity are large (Figure 3c), also because the interspecific variation in dispersal distance is for most species expected to be larger. Although the effects for animal dispersal are the same as for wind dispersal, the necessity of estimating the dispersal capacity for animal dispersal is therefore larger.

Germination delay, including effects of seed dormancy and generation time, influences the dispersal distance in a negative way, i.e. the longer the time to propagation the shorter the realized dispersal in a given time (Figure 3d). Germination delay has quite a large impact on the dispersal distance. Unfortunately, the number of years of germination delay is rather uncertain for a substantial group of species. Both seed dormancy and generation time are influenced by many factors, e.g. weather, that may vary from year to year. Therefore germination delay is probably the most uncertain model parameter for species that do have a germination delay factor larger than one year.

The effect of a barrier as has been tested here for a species that is also dispersed by wind is relative small (Figure 3e). After two simulation years the barrier is reached and the next year the wind takes over as the prime mean of dispersal, which gives a shorter dispersal distance for one year, but a continued dispersal nonetheless.

Validation

DIMO was validated for one species, *Juncus tenuis* (Willd.) known in English as Path Rush, Field Rush or Slender Yard Rush (we will use the name Path Rush, which reflects its occurrence). This species was chosen because we exactly know where and when it was introduced in The Netherlands. Path Rush was introduced, originating from North America, at three spots near Antwerp (Belgium), De Bilt and Breda (both in the Netherlands) between 1821 and 1824 (Weeda *et al.* 1987, see Figure 4). We assumed that the species gradually spread from these sites throughout the Netherlands, although nowadays the plant is sometimes sold in garden centres and thus spreads from miscellaneous sources. We did not include human-vectored dispersal in the model which may be of influence the results in the last decade of the validation. Unfortunately, there are no dispersal characteristics available for Path Rush. We assumed, however, that the dispersal characteristics are identical to *Juncus articulatus* (L.), that has similar seed characteristics. We furthermore assumed that the seeds are dispersed via manure of mammals or birds with a long distance dispersal of 1000 m/y and seed bank longevity of 50 years. The DIMO run starts with the three introduction sites in the year 1825 (Figure 4).

We assumed two types of landscapes, one where only the current natural areas are potential habitat and one where only the current built-up areas are not suitable habitat. This will reveal differences in landscape connectivity and the effect on dispersal. The model results were compared to field data present in the Dutch national vegetation database (Hennekens & Schaminee 2001), which is described in the Global Index of Vegetation-Plot Databases under number EU-NL-001 (<http://www.givd.info/559.html>; Schaminée *et al.* 2012). The database covers all existing plant communities in the Netherlands from 1868 up to now and is continuously updated with vegetation recordings (plots or relevés). Relevés were recorded following the Braun-Blanquet method (Braun-Blanquet 1964). In 2012 more than 600,000 relevés were incorporated in the database, which were used to select sites where Path Rush was present. Note that the used field data were not specially recorded for the dispersal of Path Rush, which gives an uncertainty in the field data and thus the obtained results; Path Rush may be present at more sites than recorded.

When assuming only current natural areas as suitable habitats the modelled species dispersal since 1825 cannot explain the current known distribution over the Netherlands of the species. There are barriers of unsuitable habitat present, preventing dispersal from the Antwerp spot almost totally and limiting the dispersal from the other spots to parts of the south of the Netherlands and the middle of the Netherlands. The coastal area and the North are not reached due to the barriers consisting of unsuitable habitats (Figure 5).

Table 2. Average distance between field observations outside the dispersal front of DIMO and the dispersal front per decade for *Juncus tenuis*. With avg: average, std: standard deviation, min: minimal distance and max: maximum distance.

Decade	n	Distance to front (km)			
		avg	std	min	max
1931-1940	5	7.4	7.7	0.8	15.8
1941-1950	2	10.7	0.6	10.2	11.2
1951-1960	1	2.6		2.6	2.6
1971-1980	31	7.0	4.0	0.4	21.7
1981-1990	4	22.1	6.9	12.6	28.4
1991-2000	6	18.7	4.4	10.4	22.7
Overall	49	9.8	7.0	0.4	28.3

Table 3. Number and percentage of the field findings outside and inside the simulated dispersal area for *Juncus tenuis* per decade.

Decade	n				
	total	out	in	% out	% in
1931-1940	23	5	18	22	78
1941-1950	6	2	4	33	67
1951-1960	9	1	8	11	89
1961-1970	27	0	27	0	100
1971-1980	244	31	213	13	87
1981-1990	216	4	212	2	98
1991-2000	486	6	480	1	99
Total	1011	49	962	5	95

When we assume that only present built-up areas are unsuitable habitat the dispersal pattern is different and matches the observed dispersal pattern since 1940 quite neatly (Table 2 and 3 and Figures 6-8). The overall average of the difference between the findings outside the dispersal front and the dispersal front is just below 10 km (Table 2). We calculated the error in the average distance of the findings outside the dispersal front till the dispersal front as a percentage of the simulated dispersal distance for the last decade. The distance dispersal front to De Bilt (the closest source) is app. 155 km. The average distance of the findings outside the dispersal front to the front is 18.7 km (Table 2). The error is then $18.7/155 * 100\% = 12\%$ of the dispersal distance.

The percentage of findings inside and outside the simulated dispersal area varies between the decades but is overall 95%. However, the results also depend on the number of recordings made within and outside the dispersal area and since the relevés are not made randomly this may influence the result. In our opinion both validation results show that the model simulations for Path Rush are adequate.

Case study: effect of a corridor on the occurrence of plant species

DIMO was applied to evaluate the effectiveness of an ecological corridor, part of the planned Dutch national ecological network, in the south of the Netherlands (Van

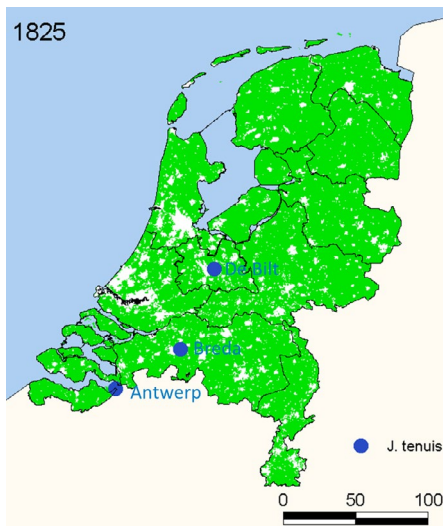


Figure 4. Occurrence of *Juncus tenuis* (Path Rush) around 1825. In green potential habitat (all land except built-up areas in 2000

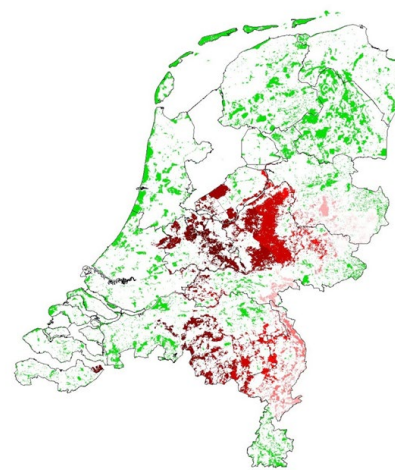


Figure 5. Dispersal of *Juncus tenuis* (Path Rush) from the three sources (Fig. 4) in the year 2000, as simulated by DIMO. In green potential habitat (in this case only current natural areas, built-up and agricultural areas are excluded). The red colour indicates the occupied area; the darker red the longer the species has been present.

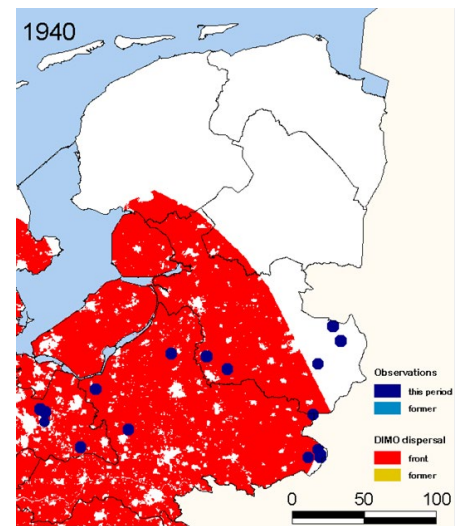


Figure 6. Dispersal of *Juncus tenuis* (Path Rush) from three source populations (Fig. 4) in 1940 assuming that all none built-up areas are suitable habitat. In red the potentially occupied area according to DIMO, blue dots indicate findings of *J. tenuis* till 1940.

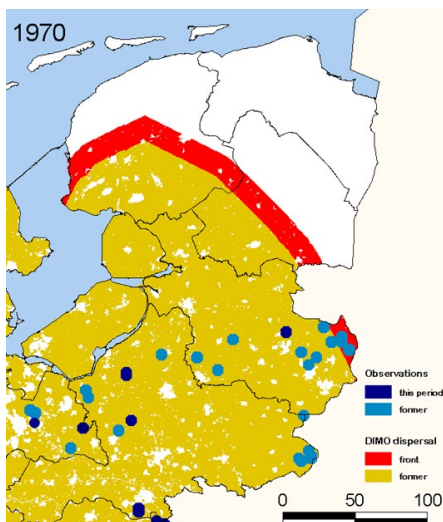


Figure 7. Dispersal of *Juncus tenuis* (Path Rush) from three source populations (Fig. 4) in 1970 assuming that all none built-up areas are suitable habitat. In red the potentially occupied area simulated by DIMO for the decade 1960-1970, in yellow the simulated occupied area before 1960, light blue dots indicate findings of *J. tenuis* till 1960, dark blue dots indicate findings in the period 1960-1970.

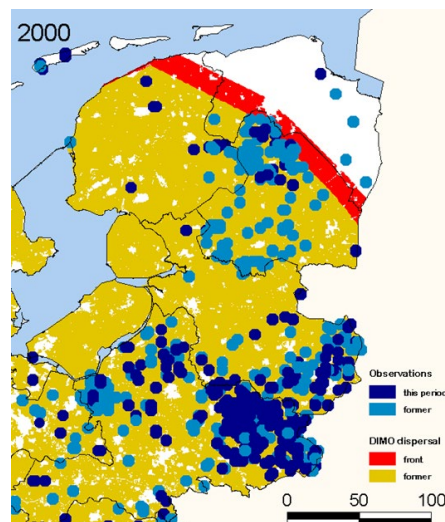


Figure 8. Dispersal of *Juncus tenuis* (Path Rush) from three source populations (Fig. 4) in 2000 assuming that all none built-up areas are suitable habitat. In red the potentially occupied area simulated by DIMO for the decade 1990-2000, in yellow the simulated occupied area before 1990, light blue dots indicate findings of *J. tenuis* till 1990, dark blue dots indicate findings in the period 1990-2000.

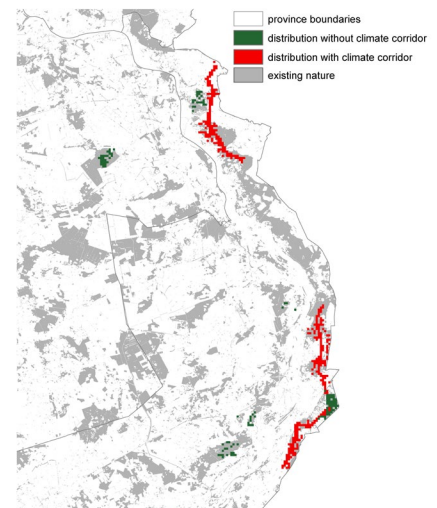


Figure 9. Expansion of *Nardus stricta* L. facilitated by a climate corridor in a fragmented landscape. Not only the corridor itself is colonized but also the neighbouring natural areas.

Table 4. Characteristics of the five species used for the evaluation of the climate corridor.

Name species	English	Ecosystem	Dispersal by	Dispersal capacity (m)	Germination delay (y)	Seed bank age (y)
<i>Dactylorhiza maculata</i> (L.) Soò	Heath spotted orchid	Wet grassland, heath	Wind	11000	3	4
<i>Eriophorum angustifolium</i> Honckeney	Common cottongrass	Wet heath, swamp	Wind	24	0	1
<i>Maianthemum bifolium</i> (L.) F.W. Schmidt	May lily	Forest	Birds	2000	0	1
<i>Nardus stricta</i> L.	Matgrass	Heath	Mammals	550	0	1
<i>Primula veris</i> L.	Cowslip	Forest	Ants Wind	55 0.12	0	1

der Zouwen & Van Tatenhove 2002). This region, the province of Limburg, is a partly densely populated area with in the south low hills. The landscape is highly fragmented with small patches of nature. Forests, heathland and species rich grasslands are the main vegetation types present. The corridor was designed to strengthen the spatial cohesion of natural areas by creating extra habitats of forest, heathland and grassland and it was designed to link nature areas on a larger, international scale. One of the aims was to enable dispersal from south to north and could therefore in principle also serve as a corridor to make migration possible from the south (Belgium) to the central Netherlands. Five plant species were chosen for the evaluation of the corridor. They represent different ecosystems and different dispersal characteristics (Table 4). For each species suitable habitat was identified based on a national map with nature target types (Bal *et al.* 2001), vegetation types similar to the habitat types, but more detailed and specifically designed for the Netherlands. Species occurrence is linked to these nature target types. We assumed that if the type is present, that all the habitat requirements of a species, including abiotic circumstances, are met and that the species in principle can occur. Potential habitat maps were produced for the five modelled species based on the location of suitable nature target types. The planned corridor consists of a mosaic of patches of forest, heathland and (wet) grassland. The exact distribution of those ecosystem types within the corridor was not known; therefore it was assumed that a continuous path would be available for the five species related to the ecosystem types in the corridor. The model was run for a 100 simulation years on a 250*250m grid scale for natural areas with and without the planned corridor. The simulation started with the actual distribution pattern of each species and we tested the colonization of the new potential suitable habitat with and without the corridor.

The results showed a clear relation between the effectiveness of the corridor and the plant characteristics (Annex 7). In the model scenario without the corridor the good dispersers (*D. maculate* and *M. bifolium*) were able to colonize all new suitable habitats. The poor and intermediate dispersers (*E. angustifolium*, *P. veris* and *N. stricta*) did not colonize any new suitable habitat. The results of the scenario with the corridor were similar to those of the scenario without the corridor: 100% colonization (habitat within corridor and new habitat) by good dispersers and 0% colonization by the poor dispersers. The intermediate disperser (*N. stricta*) however showed a clear difference: it did colonize the corridor and through the connection of the corridor it could also reach other new habitat. Colonization in all directions occurred and was not directional to the north or south (Figure 9), as all habitat lies within the same suitable climate zone (climate envelope). The results show

that DIMO can be used to evaluate corridors for plant species.

Discussion

The dispersal model presented in the paper (DIMO) is partly based on the principles described by Nathan and Muller-Landau (2000; especially the major relations given in their Figure 1) and answers some of the challenges for predicting global change impacts on plant species distributions as described by Thuiller *et al.* (2008). By linking the dispersal model to the model chain SMART2-SUMO2 which model soil processes and vegetation succession (Mol Dijkstra *et al.* 2009, Wamelink *et al.* 2009a, Wamelink *et al.* 2009b) and the plant species distribution model MOVE (Van Adrichem *et al.* 2010) we can simulate the effects of both land use change (SUMO2) and nitrogen deposition in combination with climate change on the dispersal and thus future distribution of over 900 plant species. This is particularly important since plant dispersal is just one of the limiting factors for species occurrence or re-establishment. Not only present natural areas may already suffer from excessive nitrogen deposition, desiccation or acidification (Wamelink *et al.* 2013). Newly acquired and re-developed areas may also suffer from these problems, limiting plant occurrence and thus dispersal. This asks for a combined model run not only looking at dispersal but also at other (abiotic) circumstances. Moreover, when the factor time is included also related to climate change, evaluations of corridors can most likely only be carried out by process models. Suitable habitat now may be no longer suitable within 25 to 100 years, whereas this is the time frame that dispersal events through corridors require.

DIMO has some similarities with the recent published BioMove model (Midgley *et al.* 2010), that is part of the LAMOS framework (Lavorel 2001). But where BioMove includes all kinds of management effects we choose to build a more simple dispersal model, relying on the disturbance effects and land use change effects and the abiotic effects on species occurrence to be modeled by the earlier mentioned models (SMART2-SUMO2-MOVE). These models are able to simulate habitat quality, e.g. conditions for soil pH and nutrient availability. Combined with our abiotic conditions database we can estimate which species in principle could occur at a certain site (Wamelink *et al.* 2005, Wamelink *et al.* 2012). The DIMO model can then simulate if a species can reach that suitable habitat. That habitat quality as simulated by these models is important was shown by e.g. Petit *et al.* (2004). They found that distribution of woodland species in the uplands was merely limited by habitat quality than by fragmentation, but for lowland woodland species fragmentation was the key factor. This shows that ideally dispersal models should be combined with habitat quality models.

DIMO is more species specific than e.g. the method used by Araujo *et al.* (2004) to evaluate the effect of climate change on the migration of plant species from nature reserves. The model can be applied more site specific than models based on the climate envelope method (Araujo *et al.* 2004, Vos *et al.* 2008) to estimate the effects of climate change. Within the climate envelope of species we can use site specific information on the dispersion and dispersal, which may lead to other conclusions on species survival under climate change, e.g. due to the lack of (internal) connectivity (see also Bertrand *et al.* 2012, Fordham *et al.* 2012).

The evaluation of the designed corridor in the South of the Netherlands illustrates the usefulness of DIMO as a planning tool for policy making and spatial planning to deal with nature, as was called for by Thuiller *et al.* (2008). DIMO may help to underpin presented adaptation approaches (Vos *et al.* 2010), to implement and translate adaptation strategies into plans such as designing a corridor. It answers questions like where to plan corridors, what the effect will be of different vegetation types in the corridor and can give a preliminary evaluation of the effectiveness of the corridor. From the case study presented in this paper it is clear that corridors probably will help only a limited number of plant species. This limitation is partly due to plant traits related to dispersal, but also due to the distribution of non-suitable habitats. The latter may play a major role when plant species have to migrate northwards due to climate change. Even when in theory species are able to keep up with the speed of climate change they have to find suitable habitat. Especially for the more chalk preferring species from France this may be a problem, since in the Netherlands more acid soils are dominant, specifically in Dutch natural areas.

As all models DIMO is a simplification of the real world. We have made assumptions on the dispersal distance for all means of dispersal by taking the long distance dispersal (LDD) as model input. This assumption is justified by many authors (e.g. Collingham *et al.* 1996, Corre *et al.* 1997, Cain *et al.* 2003, Pearson & Dawson 2004). Nathan *et al.* (2002) even state that 'LDD events will establish individuals that can critically affect plant dynamics on large scales'. LDD in itself however is extremely difficult to measure and quantify. A further important assumption is that at least one seed will germinate if abiotic circumstances and vegetation type are favorable. As LDD is limited to only a few or one seed this could lead to an overestimation of the establishment of species and thus the dispersal speed of species modeled by DIMO, though this contradicts with the good results for Path Rush. Not included in the model are effects of predation, and deterioration of seed viability due to fungi, which could lead to a lower dispersal rate than modeled by DIMO (Dalling *et al.* 2011). The dispersal of seeds by

humans is not included in the model, so modeling dispersal for species that e.g. are sold in garden centers and are able to escape from gardens is not possible. This limits the present day model applications to non-cultivated species. Including human-vectored modeling is almost impossible, because inventories of gardens are impossible. If data on what is for sale in garden centers would be available this could be taken as a source, but its results will still be very uncertain.

Since our aim was to build a relative simple, but adequate, model to review policy plans and corridors we included as many species as possible in the model. This gives per species a different uncertainty, which may sometimes be large due to lack of sufficient data. More data on species traits will make the model more robust. It will be one of the most important ongoing works to collect more data to improve the model.

DIMO was validated for just one species and though the results appear to be good, more validation is necessary, also because not all model features were validated, e.g. effects of wind dispersal, effect of barriers and dispersal via water. However, validation is difficult, because the necessary information is often lacking. A possibility is to use data about the spread of exotic species, but often it is not recorded when and where they were introduced first. Another possibility could be the use of genetic research on populations. This could reveal isolated populations, especially in a fragmented landscape as e.g. Western Europe.

DIMO was tested and validated for the Netherlands, but the model structure is set up in such a way that in principle the model can also be applied in other parts of the world, as long as the main dispersal vectors and dispersal distance of the species are known and in the case of water dispersal an altitude map and a water speed map. Data on present and past distribution and effects of barriers are helpful, but not obligatory, distribution of suitable habitat is. We conclude that DIMO could be a helpful tool for evaluating, but also for policy making and defining and implementation of adaptation measures to climate change on regional up to continental scale.

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