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RESEARCH ARTICLE

# Turbary Restoration Meets Variable Success: Does Landscape Structure Force Colonization Success of Wetland Plants?

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## Abstract

Peat ponds have been restored widely in the Netherlands to enhance the available habitat for species-rich plant communities that characterize the early succession stages toward land. Colonization success of 33 target aquatic species has been quantified in eight complexes of new ponds. It has been related to the lay-out of these ponds, the structure of the surrounding landscape, (historic) prevalence of source populations within the complex and within a perimeter of 10 km, and pond water quality. Colonization success was variable: between 6 and 26 target species had reached the complexes in 1998. This success was coupled to the first principal component (PC) in a principal component analysis (PCA) explaining 44% of the variation in 27 variables. This first PC correlated with historical perimeter and local within-complex species richness, the number

of ponds in the complex, the SW orientation of ditches in these complexes and pH, and transparency of the water. Age of the ponds (1–9 years), area of open water (8–42%), and shoreline density (13–43 km/km<sup>2</sup> in the complex) did not contribute significantly to colonization success. Separation of the effect of a species-rich surrounding landscape, the possibility to disperse through that landscape, the spatial lay-out of the complex and transparency of the water were precluded by the strong covariance along the first PC. Probably all three are independently important. It is speculated that diel migration by waterfowl may be responsible for the dispersal of plant propagules to the pond complex, whereas within-complex dispersal to establishment sites is enhanced by wind and water movement.

**Key words:** area water, colonization, historical abundance data, landscape configuration, shoreline density.

## Introduction

Lowland peat has been excavated at a large scale for the fuel needs of expanding cities in the Netherlands since the middle ages (Gotschalk 1956; Pons 1992). Excavation left a regularly patterned landscape of long and narrow ponds, called turbaries (30–50 m wide and up to several hundreds of meters long) separated by narrow strips of land. These turbaries were recolonized by vegetation and peat accumulated again, which eventually would be excavated anew. This practice ended around 1950 with the wide availability of fossil fuel. Turbary complexes rapidly terrestrialized and former turbaries turned into alder carr, marsh vegetation dominated by *Alnus glutinosa* (L.) Gaertn. and *Betula pubescens* Ehrh., with some *Salix aurita* L. and *S. cinerea* L., within circa 50 years (Bakker et al. 1994). This led to a widespread decline of the early successional vegetation stages. These are species-rich communities of submerged and floating plants, water soldier

(*Stratiotes aloides* L.) rafts, floating fens, and species-rich mesotrophic fens (Schaminée et al. 1995; Verhoeven & Bobbink 2001), together communities with a high biodiversity and considerable conservation value (Van Leerdam & Vermeer 1992). This decline led to a recognition of urgency in national biodiversity conservation policy (e.g. Bal et al. 1995) and the launching of several restoration programs involving reexcavation of old turbaries or dredging of new ponds (e.g. Staatsbosbeheer 1994), with the aim to restore the historical cyclic pattern of pond creation and succession.

Different complexes of such newly restored ponds, however, met with different success in terms of colonization rates by target species, characteristically representing these early succession stages (Beltman et al. 1996, 2005). This variation may have a number of possibly interacting causes. Firstly, target species may have gone extinct in the local seed banks, or from existing stands in the surrounding landscape (Bakker et al. 1994; Beltman & Allegrini 1997). Secondly, present dispersal from remaining stands may be hampered by present-day land use (Boedeltje et al. 2004; Soons & Ozinga 2005; Van den Broek et al. 2005; Wichmann et al. 2008). Thirdly, the newly created habitat could be a too small target or it could have become unsuitable for colonization, possibly due to water quality change (Sand-Jensen et al. 2000; Geertsema 2002).

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Beltman et al. (2005) found a relation between colonization success and the number of ponds in a complex, suggesting a quantitative role of the number of ponds as a target, but they did not quantify the role of the other factors.

In the present study, we attempt to unravel these possibly interacting causes by simultaneously quantifying them for eight newly created turbary complexes across the Netherlands (Fig. 1). Our case can be considered an application of classical island theory (MacArthur & Wilson 1967; Møller & Rørdam 1985), with swarms of ponds in complexes as archipelagoes in a largely agricultural landscape matrix (Brose 2001) where pastures mix with stands of alder carr.

Our aim was to assess the relative importance of each of the following four aspects for macrophyte colonization success into these pond complexes: the availability of and distance from source populations, the degree to which a landscape enables dispersal of propagules (here shortly transmissivity), or the spatial lay-out, and habitat quality of the receiving pond complexes.

## Methods

We selected a total of 43 turbaries in eight complexes spread over the peat district in the Netherlands (Fig. 1a). Shoreline and aquatic vegetation were assessed in 1998 and abundance of all macrophyte species was recorded (Kardol & Zorn 1999). These complexes differed in age (1–9 years in 1998), total area (0.1–49 km<sup>2</sup>), number of new ponds (2–8), and also somewhat in pond design due to differences in interpretation of historical local conventions. Median pond depth was 45 cm (mean 47, standard error 3, range 35–175 cm). All 33 selected target macrophyte taxa (Appendix) are listed as characteristic for the early succession vegetation types of the Charicion, the Potamion, and the Phragmition classes of Schaminée et al. (1995). In all ponds, six sediment samples of 10 cm depth were collected randomly with a corer of 8 cm diameter. Sediment samples were sieved and seeds were identified according to Beijerinck (1976) and Cappers et al. (2006). Water quality data have been collected on three visits during the growing season in 1998 (Kardol & Zorn 1999) and analyzed according to standard methods. We used Secchi depth (cm), pH, conductivity ( $\mu\text{S}/\text{cm}$ ) chloride, sulfate, bicarbonate, nitrate, ammonium, and phosphate (mg/L).

Historical presence of the 33 target species in the surrounding landscape was derived from the national database with vegetation relevés TURBOVEG (Hennekens & Schaminée 2001). Relevé data were extracted from TURBOVEG when at least one of these species was found present since the oldest record of 1933. The locations of the relevés in this dataset are stored as a 1 × 1 km grid covering the Netherlands. We distinguished two zones: the grid cells containing the complex and the grid cells within a 10-km perimeter. For the relevés in the 10 km zone, we calculated the orientation and distance to the complex (cf Fig. 1b). Using geo-referenced historical data on 33 target aquatic and littoral shoreline plant species (Hennekens & Schaminée 2001), we quantify the potential abundance and

distance of sources of diaspores in the surrounding landscape, we estimate the transmissivity of the surrounding landscape from the spatial pattern of surface waters, and we estimate the habitat quality of the receiving complex of ponds from its spatial pattern and water quality.

Landscape characteristics of each complex and its surrounding perimeter were derived from a detailed digital topographic map (Kadaster 2007) and analyzed using a Geographic Information System (GIS; cf Vermaat et al. 2007, 2008). For every complex and 10 km perimeter (Fig. 1c & 1d), we quantified the total length of open water shores in ditches and larger open water bodies (in the complex often mainly the turbaries, but also lake complexes), as well as the surface area of both ditches and larger water bodies. In addition, we estimated the compass bearing of the ditches in the complex and perimeter. From these we derived the proportion of ditches with a SW–NE orientation, which is the prevailing wind direction in the Netherlands (58%; www.KNMI.nl). All in all, a total of 11 vegetation, 18 landscape pattern and 9 water quality variables were quantified (Table 1). Their patterns of covariance were analyzed with principal component analysis (PCA) (based on correlations, no varimax rotation) and stepwise regression using SPSS 16.0, as in fx. Vermaat et al. (2007).

## Results

The number of target species that had established in a peat complex ranged from 6 to 26, or 19–77% of the total of 33 target species. In the PCA (Fig. 2; Table 2), this number of target species as well as the total number of species in a complex covaried distinctly with the first principal component (PC), and so did the other variables quantifying species richness (number of species that had been present historically in the complex and perimeter, the number of species that had emerged from the sediment seed bank), the number of new ponds in a complex, transparency and pH of the water, as well as the proportion of SW-oriented ditches in a complex (Fig. 2; see also pairwise correlations in Fig. 3). This first PC explained a substantial proportion of the total variance (Fig. 2; Table 2). So, overall, historically species-rich landscapes surround historically rich complexes with richer seed banks and a higher successful recruitment of target species and a higher overall macrophyte species richness. These landscapes also have a higher transparency and pH of the water (Fig. 3e & 3f). The negative correlation with the minimum distance between a complex and a positive TURBOVEG grid cell can be interpreted as reflecting the effect of a more species-rich landscape as well; such grid cells are more densely spaced around the complex. Remarkably, the proportion of open water in the complex and ditch density in the landscape corresponded to a second, separate, PC, and did not correlate with aquatic plant species richness at all (Fig. 2). The opposite position of these two variables along this axis is understandable: the more open water, the less room for agricultural land with ditches (cf Fig. 1). The only other significant water quality variable was NH<sub>4</sub>, which correlated negatively with PC1, this may correspond with a

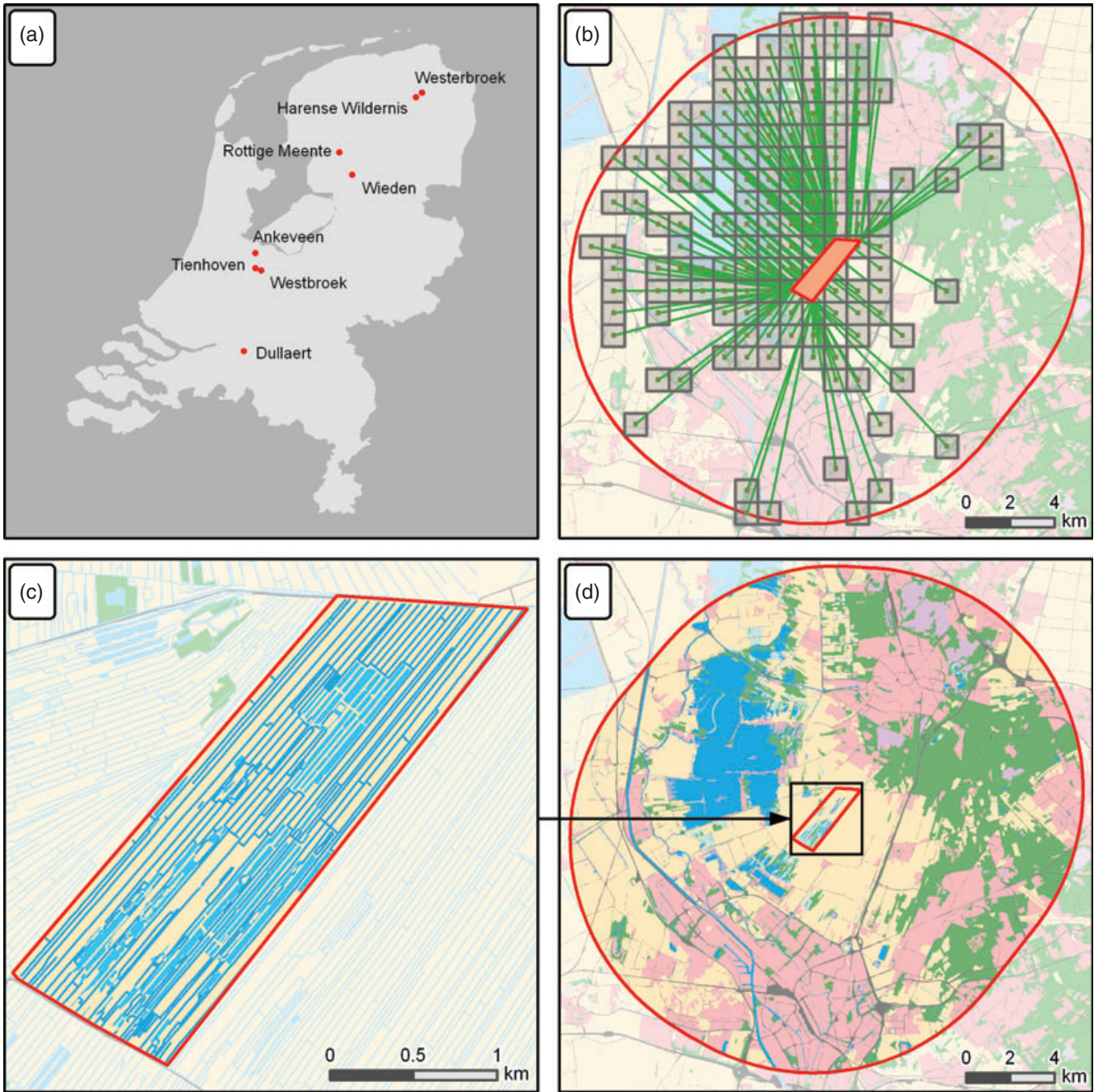


Figure 1. Location of the eight turbary complexes in the Netherlands (a); distribution of TURBOVEG grid cells (1 km<sup>2</sup>) in the perimeter where at least one target species has been recorded (b); the drawn lines indicate how distance and orientation toward the complex have been estimated (c); configuration of a specific wetland complex (Westbroek) with a number of new and old turbaries (c); topographic setting of this specific example in its 10-km perimeter (d).

lower pH influencing the distribution of dissolved inorganic nitrogen species and an overall, higher nutrient availability. A PCA with only water quality variables (not shown), suggests that both take place: NH<sub>4</sub> covaried positively with NO<sub>3</sub> and PO<sub>4</sub>, and negatively with pH and transparency.

The overall pattern of the PCA was largely confirmed by a stepwise regression with the number of target species

in the complex as dependent variable. From 16 landscape and species richness variables in the complex and perimeter as well as pH, transparency and NH<sub>4</sub>, it selected pH ( $r^2$  at first step 0.86), the number of new ponds, the proportion of water in a complex, and the proportion of ditches with a southwesterly orientation (final  $r^2 = 0.99$ ). However, the considerable collinearity between pH and the number

**Table 1.** Description of landscape characteristics and plant presence records quantified for the aquatic and shoreline vegetation of each turbary complex, its 10 km perimeter, or both (see text).

<i>Variable</i>	<i>Abbreviation</i>	<i>Source, Resolution, Analysis</i>
<b>Vegetation</b>		
Total number of plant species in a complex	NspecC	Own field data, turbary
Mean number of species per turbary	MnspecT	Own field data, turbary
Number of species emerged from sediment seedbank	NspecseedC	Own field data, turbary
Number of target species in complex in 1998	NtargetspecC	Own field data, turbary
Number of target species historically present in complex, and in perimeter (maximum 33); also expressed as percentage of 33	NtargethisC, -P	TURBOVEG, complex
Number of positive TURBOVEG grid cells with at least one target species in the perimeter, and density of the same (per square kilometer)	Nturbopos, Dturbopos	TURBOVEG, GIS
Distance between TURBOVEG grid cells and complex (km, mean, minimum)	DisTURBO	TURBOVEG, GIS
Proportion of the TURBOVEG grid cells oriented SW toward the complex	SWTURBO	TURBOVEG, GIS
<b>Landscape structure</b>		
Area of the complex	AreaC	GIS, × m <sup>2</sup>
Number of new ponds/turbaries in the complex	NpondC	Complex
Age of new turbaries in the complex	AgeturbC	Complex
Area of the perimeter	AreaP	GIS, × m <sup>2</sup>
Ditch length and ditch area in complex and perimeter	DitchlenC, -P, ditchareaC, -P	GIS, × m; ditch widths derived from medians of three classes, that is 1.5, 4.5 and 6 m
Proportion of ditches with a SW–NE orientation (0–90° and 180–270°), the prevailing wind direction; in complex and perimeter	SwditchC, -P	GIS
Circumference and area of nonlinear surface waters in complex and perimeter	CircumwaterC, -P, areawaterC, -P	GIS, × m
Proportion of surface water in complex and perimeter (km <sup>2</sup> /km <sup>2</sup> )	PropwaterC, -P	
Ditch and water line (ditch + pond shores) density in complex and perimeter (km/km <sup>2</sup> )	DitchdensC, -P; ShoredensC, -P	Derived from the above

of new ponds (Figs. 2 & 3e) necessitates caution in the interpretation of the relative importance of these explanatory variables.

### Discussion

Our analysis suggests that the successful colonization by macrophytes of restored ponds in complexes was determined by the species richness of the landscape in the perimeter around the ponds, by the number of these ponds, and by the orientation of ditches within the complex. At the same time, water quality in these richer complexes was also more favorable to macrophyte establishment, because of a higher water clarity (Secchi depth around 50 vs. 20 cm) and possibly better buffering capacity indicated by a higher pH (8.4 vs. 5.6). Our aim was to separate the effect of a species-rich surrounding landscape, the transmissivity of that landscape, the spatial lay-out of the complex and water quality. However,

many indicators were found to covary strongly. Probably all three are independently important: a species-rich surrounding landscape as a source of colonizing propagules, a large number of ponds forming the newly available habitat and habitat quality, which is here specifically clear, well-buffered water.

The delineation of a complex of new ponds included the immediate surroundings of existing, not yet terrestrialized ponds, ditches, meadows, and alder carr. The historic species richness of this complex is reflected in the abundance of viable diaspores of target species in approximately 50-year-old seed banks that emerged after the removal of the alder carr on recent peat, and it corresponds with the overall historic richness in target species of the surrounding landscape. Viability of such Chara seed banks has been reported for one of our study areas (Beltman & Allegrini 1997). Brose (2001) suggests that many wetland species have long-lived seed banks, but Thompson et al. (1997) point at the variability of the data and lack of

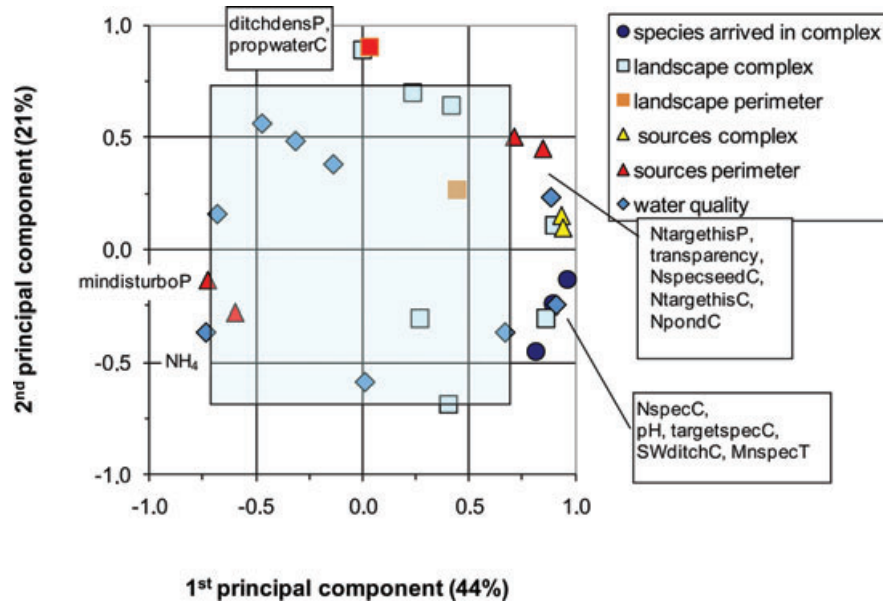


Figure 2. Correlation among variables of target species presence, vegetation composition, landscape characteristics, and water quality from eight wetland complexes and their 10 km perimeter with the first two PCs in a PCA (Table 2). The grouping of variables in categories did not affect the PCA. It is used as a graphical aid only. The blue frame indicates  $r = 0.71$ , within this frame linear correlations have a significance of  $p > 0.05$ .

information on viability for most of the submerged species. Our local species richness in the complex was closely related to the larger scale regional richness (perimeter; Fig. 3a), a common pattern in spatial biodiversity scaling (Koleff & Gaston 2002; Dahlgren & Ehrlén 2005). Our total number of macrophyte species was comparable to the range observed for small Danish ponds by Møller and Rørdam (1985): we observed 40–107, they had 10–70.

Remarkably, our indicators reflecting transmissivity of the perimeter were not found to relate to colonization success. Only within the complex, dispersal was apparently enhanced by the orientation of the ditches, where correspondence with the prevailing wind direction probably facilitated dispersal by wind and water. Similarly, Soons (2003) found that 95% of wind-dispersed seeds is deposited within 100 m from the source, often wind-dispersed seeds have a short period of positive buoyancy. Boedeltje et al. (2004) and Bornette et al. (2001) found that high connectivity enhanced species richness at the small scale of cut-off channels in floodplains, all in support of our finding that the nearby vicinity of a site is important as potential source of successful colonization.

Next to water quality, the major factor explaining colonization success was rather the number of new ponds than any other feature of the landscape. This is paralleled by the position of the variables in the PCA-plot. Rather than the length of shoreline or area of water (Møller & Rørdam 1985; Brose 2001), this crude, simple indicator explained most of the variation among complexes. We suggest that our findings imply that the chance to successfully arrive in a pond is critical for colonization success of these mainly water-dispersed aquatic

and littoral macrophyte species. Water quality then is secondary and determines the subsequent establishment. These ponds can be regarded as traps and a design with many traps apparently was more conducive than one single large trap-area (cf the SLOSS-debate, e.g. Kingsland 2002). This may well be related to the spatial lay-out of turbaries as small pockets of enhanced shelter in an otherwise adverse landscape. As most target species are dispersed by water movement or waterfowl (31 of 33, Appendix; Charalambidou & Santamaria 2002; Green et al. 2002; Soons et al. 2008), the underlying mechanism might be found in the movement pattern of seed-eating, herbivorous, or omnivorous waterfowl but also in the function of ponds, a direct trap for wind dispersal. The birds forage in the wider landscape but often visit the ponds, either as night-time resting sites where they are safe from predation, or during molting. In Scandinavia (Nummi et al. 1994; Elmberg et al. 1993), guilds of dabbling ducks were found to aggregate and be most abundant in productive lakes with high habitat heterogeneity. Our colonization success was also correlated to the presence of SW-oriented ditches. Possibly, once arrived within a complex, propagules are redistributed by wind and waves to arrive at sites available for settling. Hence, at a more detailed scale nested within a single complex or pond, the distribution of shoreline species is determined by SW-wind direction (Sarneck et al. 2010), whereas at the cruder landscape scale this is rather the number of ponds and the prevalence of diaspore sources.

Three issues of concern need to be discussed. Firstly, the presently studied turbaries were highly similar in shape, and this may have reduced a quantitative effect of shoreline length and pond area. However, contrary to Møller & Rørdam (1985)

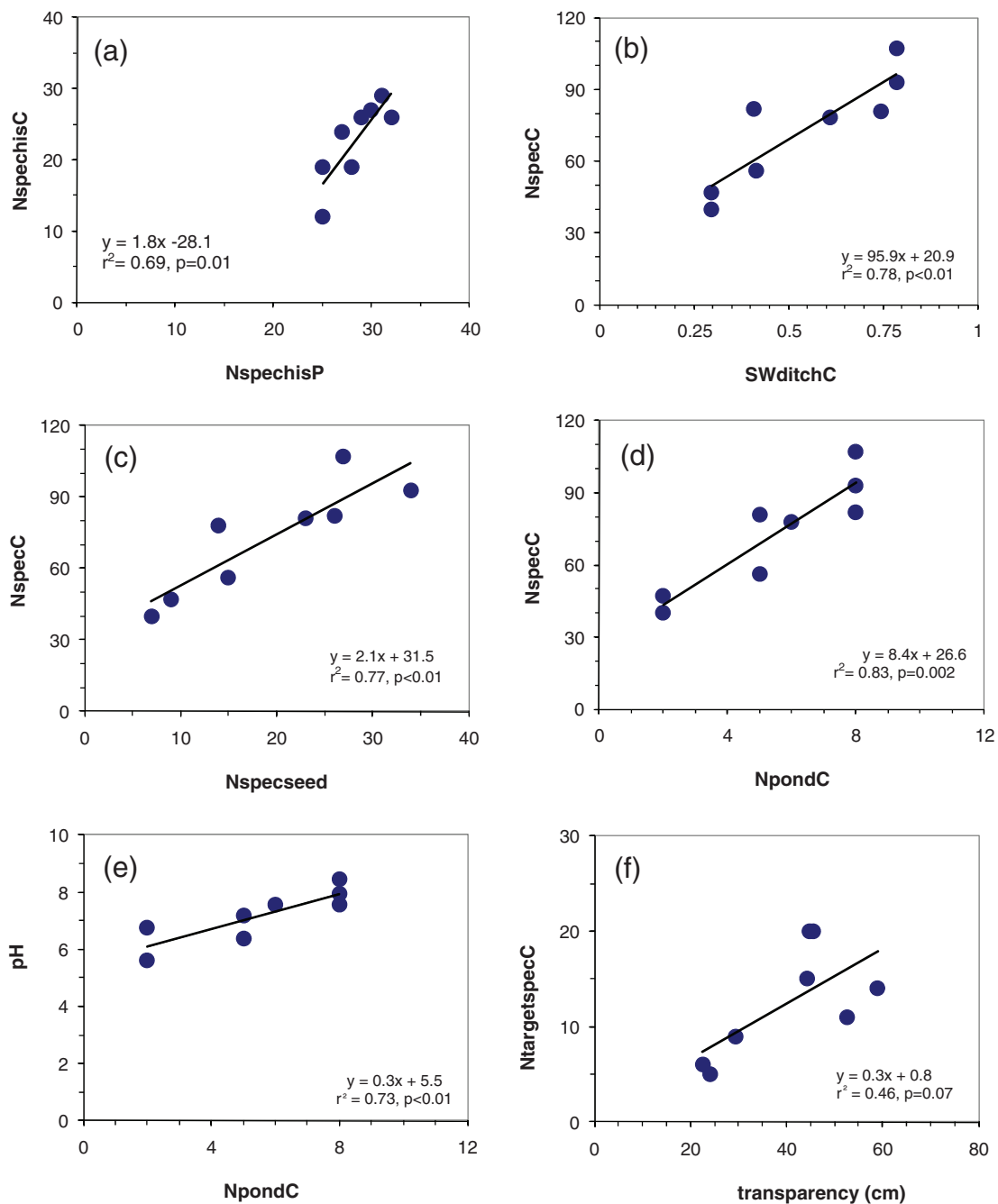


Figure 3. Pairwise linear relations between (a) the number of species historically present in the complexes and the perimeter; (b) total species richness in a complex and the proportion of ditches with a SW–NE orientation; (c) total species richness in a turbary complex and the number of species emerged from the seed bank; (d) total species richness in a complex and the number of new turbaries in that complex; (e) mean growing season pond water pH and number of ponds in the complex; and (f) number of target species arrived in a complex and mean growing season Secchi disk transparency.

and Brose (2001), we studied complexes of several ponds rather than individual ones. Secondly, our floristic database is extensive but not complete (Hennekens & Schaminee 2001). We pooled all data on presence in a  $1 \times 1$  km grid cell for 1933–1998 to reflect the most extensive spatial coverage of historical presence without separating old from recent records.

Absence from the database, however, may not imply absence in the field as some regions are better covered than others. Thirdly, the resolution of our digital topographic map has its limitations. Ditch area, in particular, was derived from known lengths and rule-of-thumb estimates of width for different size classes. This may have affected our estimation of aquatic area

**Table 2.** Correlation of 27 plant presence records, water quality variables, and landscape characteristics within the new turbary complexes and around them in the 10-km perimeter with the first three components of a PCA (81% explained variance).

Variable	PC1	PC2	PC3
Species arrived in complex			
Total number of plant species in a complex	<b>0.96</b>	-0.13	0.08
Mean number of species per turbary	<b>0.81</b>	-0.31	-0.31
Number of target species arrived in the complex	<b>0.85</b>	0.29	0.29
Sources complex			
Number of species emerged from sediment seedbank	<b>0.93</b>	0.07	0.07
Number of target species historically present in the complex (TURBOVEG)	<b>0.94</b>	0.11	0.19
Sources perimeter			
Number of target species historically present in the perimeter (TURBOVEG)	<b>0.85</b>	0.45	-0.19
Density of TURBOVEG grid cells with target species in the perimeter	<b>0.71</b>	0.50	-0.39
Proportion of TURBOVEG grid cells SW, upwind of complex	-0.60	-0.28	0.70
Minimum distance between grid cells with target species and the complex	<b>-0.73</b>	-0.13	-0.45
Landscape characteristics complex			
Area of the complex	0.24	0.70	-0.24
Proportion of surface water in the complex	0.00	<b>0.89</b>	-0.39
Ditch density in complex	0.40	-0.69	0.58
Proportion of ditches with a SW-NE orientation in the complex	<b>0.86</b>	-0.31	-0.09
Number of new turbaries in the complex	<b>0.90</b>	-0.11	-0.35
Age of the turbaries in the complex	0.42	0.64	-0.23
Landscape characteristics perimeter			
Proportion of surface water in the perimeter	0.44	0.27	0.64
Ditch density in perimeter	0.03	<b>0.90</b>	-0.30
Water quality complex			
Transparency	<b>0.88</b>	0.23	-0.10
pH	<b>0.91</b>	-0.25	0.24
Conductivity	-0.14	0.38	<b>0.87</b>
HCO <sub>3</sub>	0.67	-0.37	0.43
Cl	-0.31	0.48	<b>0.71</b>
NH <sub>4</sub>	<b>-0.73</b>	-0.37	0.37

The three components explained 44, 21, and 17%, respectively, of the total variability. Correlations over 0.71 are significant at  $p = 0.05$  (printed bold). Only variables are displayed that had  $r > 0.60$  with at least one of the PCs. A fourth PC explained an additional 9%. It correlated significantly with the waterline density in the complex ( $r = 0.88$ ).

(Nol et al. 2008), but will probably not have greatly altered the major covariance patterns.

Thus, we conclude that the landscape structure indeed forces colonization of target species, but mainly within the complex and at a small spatial scale in the order of 1–5 km. Our

findings support the plea for a shift in focus in restoration projects from site to landscape scale (Fahrig 2003; Verberk et al. 2009). In addition, our findings seem to suggest that the links between water plants and waterfowl may well be profitable to exploit in habitat restoration.

### Implications for Practice

This evaluation of restoration success of 43 newly excavated turbaries produced a number of guidelines for managers, who worked up till now by trial and error. Failures can be avoided by saving money and restoring more successfully biodiverse habitats for nature conservation. These guidelines are:

- For the restoration of peat pond complexes aiming at the reestablishment of species-rich early succession stages, it appears that a complex of several small ponds is preferable over a single larger one.
- Within such a complex alignment to the prevailing wind direction (here SW-NE) the southwest-northeast orientation of connecting ditches seems to be an important additional factor for success.
- Colonization was favored by a high transparency and a high pH of the pond water.
- Regions that have historically been rich in target species have the highest probability of a successful recolonization by target species.
- Diel movements of waterfowl may well be used profitably to enhance dispersal of target aquatic plants.

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### LITERATURE CITED

Bakker, S. A., N. J. Van den Berg, and B. P. Speleers. 1994. Vegetation transitions of floating wetlands in a complex of turbaries between 1937 and 1989 as determined from aerial photographs with GIS. *Vegetatio* **114**:161–167.

Bal, D., H. M. Beije, Y. R. Hoogeveen, S. R. J. Jansen, and P. J. Van der Reest. 1995. Handbook of nature target types (in Dutch, English summary). IKC Natuurbeheer, Wageningen.

Beijerinck, W. 1976. *Zadenatlas der Nederlandsche Flora*. Backhuys & Meesters, Amsterdam.

Beltman, B., T. Van den Broek, K. Van Maanen, and K. Vaneveld. 1996. Measures to develop a rich-fen wetland landscape with a full range of successional stages. *Ecological Engineering* **7**:299–313.

Beltman, B., and C. Allegrini. 1997. Restoration of lost aquatic plant communities: new habitats for Chara. *Netherlands Journal of Aquatic Ecology* **30**:331–337.



- Beltman, B., T. Van den Broek, and P. Vergeer. 2005. The limited success of peat pond restoration (in Dutch, English summary). *Landschap* **22**:173–179.
- Boedeltje, G., J. P. Bakker, A. ten Brinke, J. M. Van Groenendael, and M. Soesbergen. 2004. Dispersal phenology of hydrochorous plants in relation to discharge, seed release time and buoyancy of seeds: the flood pulse concept supported. *Journal of Ecology* **92**:786–796.
- Bornette, G., H. Piegay, A. Citterio, C. Amoros, and V. Godreau. 2001. Aquatic plant diversity in four river floodplains: a comparison at two hierarchical levels. *Biodiversity and Conservation* **10**:1683–1701.
- Brose, U. 2001. Relative importance of isolation, area and habitat heterogeneity for vascular plant species richness of temporary wetlands in east-German farmland. *Ecography* **24**:722–730.
- Cappers, R. T. J., R. M. Bekker, and J. E. A. Jans. 2006. Digital seed atlas of the Netherlands. Barkhuis Publishing & Groningen University Library, Groningen.
- Charalambidou, I. and L. Santamaria. 2002. Waterbirds as endozoochorous dispersers of aquatic organisms: a review of experimental evidence. *Acta Oecologia* **23**:165–176.
- Dahlgren, J. P., and J. Ehrlén. 2005. Distribution patterns of vascular plants in lakes—the role of metapopulation dynamics. *Ecography* **28**:49–58.
- Elmberg, J., P. Nummi, H. Poysa, K. Sjöberg. 1993. Factors affecting species number and density of dabbling duck guilds in North Europe. *Ecography* **16**:251–260.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology Evolution and Systematics* **34**:487–515.
- Geertsema, W. 2002. Plant survival in dynamic habitat networks in agricultural landscape. Ph.D. thesis. Alterra Scientific Contributions 9, Wageningen.
- Gotschalk, M. K. E. 1956. De ontginning der Stichtse venen ten oosten van de Vecht. *Geografisch Tijdschrift* **6**:92–101.
- Green, A. J., J. Figuerola, and M. I. Sanchez. 2002. Implications of water-bird ecology for the dispersal of aquatic organisms. *Acta Oecologia* **23**:177–189.
- Hennekens, S. M., and J. H. J. Schaminée. 2001. TURBOVEG, a comprehensive data base management system for vegetation data. *Journal of Vegetation Science* **12**:589–591.
- Kadaster. 2000. Bestand bodemgebruik Netherlands digital land use map. Netherlands Statistics Service, Voorburg.
- Kadaster. 2007. Productspecificaties basisregistratie topografie. Apeldoorn, The Netherlands, 64 pp.
- Kardol, P., and M. Zorn. 1999. Mesotrofe verlanding in nieuw gegraven petgaten. Mesotrophic terrestrialization in new excavated turbaries (in Dutch). M.Sc. thesis. Landscape Ecology, Utrecht University.
- Kingsland, S. E. 2002. Creating a science of nature reserve design: perspectives from history. *Environmental Modeling and Assessment* **7**:61–69.
- Koleff, P., and K. J. Gaston. 2002. The relationships between local and regional species richness and spatial turnover. *Global Ecology and Biogeography* **11**:363–375.
- MacArthur, R., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey.
- Mander, U., M. Kulvik, and R. Jongman. 2003. Scaling in territorial ecological networks. *Landschap* **20**:113–128.
- Møller, T. R., and C. P. Rørdam. 1985. Species numbers of vascular plants in relation to area, isolation and age of ponds in Denmark. *Oikos* **45**:8–16.
- Nol, L., P. H. Verburg, G. B. M. Heuvelink, and K. Molenaar. 2008. Effect of land cover on nitrous oxide inventory in fen meadows. *Journal of Environmental Quality* **37**:1209–1219.
- Nummi, P., H. Poysa, J. Elmberg, and K. Sjöberg. 1994. Habitat distribution of the mallard in relation to vegetation structure, food, and population density. *Hydrobiologia* **279/280**:247–252.
- Pons, L. J. 1992. Holocene peat formation in the lower parts of the Netherlands. Pages 7–81 in J. T. A. Verhoeven, editor. Fens and bogs in the Netherlands: vegetation, history, nutrient dynamics and conservation. *Geobotany* **18**.
- Riitters, K. H., R. V. O'Neill, C. T. Hunsaker, J. D. Wickham, D. H. Yankee, S. P. Timmins, K. B. Jones, and B. L. Jackson. 1995. Landscape Ecology **10**:23–39.
- Sand-Jensen, K., T. Riis, O. Vestergaard, and S. E. Larsen. 2000. Macrophyte decline in Danish lakes and streams over the past 100 years. *Journal of Ecology* **88**:1030–1040.
- Sarneel, J. M., B. Beltman, A. Buijze, R. Groen, and M. B. Soons. 2010. Role of wind in the dispersal of floating seeds in ponds. *Freshwater Biology* (in revision)
- Schaminée, J. H. J., E. J. Weeda, and V. Westhoff. 1995. De Vegetatie van Nederland. Deel 2: Wateren, moerassen, natte heiden. Opulus Press, Uppsala, Sweden.
- Soons, M. B. 2003. Habitat fragmentation and connectivity. Spatial and temporal characteristics of the colonization process in plants. Ph.D. thesis, Utrecht University, Utrecht.
- Soons, M. B., and W. A. Ozinga. 2005. How important is long-distance seed dispersal for the regional survival of plant species? *Diversity and Distributions* **11**:165–172.
- Soons, M. B., C. Van der Vlugt, B. Van Lith, G. W. Heil, and M. Klaassen. 2008. Small seed size increases the potential for dispersal of wetland plants by ducks. *Journal of Ecology* **96**:619–627.
- Staatsbosbeheer. 1994. Ruimte voor moeras. SBB-regio Holland/Utrecht. Beheerseenheid, Vechtstreek.
- Thompson, K., J. P. Bakker, and R. M. Bekker. 1997. Soil seed banks of NW Europe: methodology, density and longevity. Cambridge University Press, Cambridge.
- Van den Broek, T., R. Van Diggelen, and R. Bobbink. 2005. Variation in seed buoyancy of species of wetland ecosystems with different floating dynamics. *Journal of Vegetation Science* **16**:579–586.
- Van Leerdam, A., and J. G. Vermeer. 1992. Natuur uit moeras, naar een duurzame ecologische ontwikkeling. Ministry of Agriculture, Nature and Fisheries, Den Haag.
- Verberk, W., A. P. Grootjans, and A. J. M. Jansen. 2009. Scaling local nature restoration efforts up to landscapes (in Dutch, with English summary). *De Levende Natuur* **110**:105–111.
- Verhoeven, J. T. A., and R. Bobbink. 2001. Plant diversity of fen landscapes in the Netherlands. Pages 65–87 in B. Gopal, W. J. Junk, and J. A. Davis, editors. Biodiversity in wetlands: assessment, function and conservation. Volume 2. Backhuys Publ, Leiden, The Netherlands.
- Vermaat, J. E., H. Goosen, and N. Omtzigt. 2007. Do biodiversity patterns in Dutch wetland complexes relate to variation in urbanisation, intensity of agricultural landuse or fragmentation? *Biodiversity Conservation* **16**:3585–3595.
- Vermaat, J. E., N. Vigneau, and N. Omtzigt. 2008. Viability of meta-populations of wetland birds in a fragmented landscape: testing the key-patch approach. *Biodiversity Conservation* **17**:2263–2273.
- Wichmann, M. C., M. J. Alexander, M. B. Soons, S. Galsworthy, L. Dunne, R. Gould, C. Fairfax, M. Niggemann, R. S. Hails, and J. M. Bullock. 2008. Human-mediated dispersal of seeds over long distances. *Proceedings of the Royal Society B* **276**:523–532.

**Appendix.** List of target species used including their modes of dispersal.

<i>Species</i>	<i>Growth Form</i>	<i>Long-Distance Dispersal</i>	<i>Wind, Water, Animals</i>
<i>Calla palustris</i>	Littoral emergent, clonally branching	Seeds, turions	Water
<i>Caltha palustris</i>	Littoral emergent, clonally branching	Seeds, turions	Water
<i>Carex pseudocyperus</i>	Littoral emergent, clonally branching	Seeds	Water, ducks
<i>Chara aspera</i> <sup>a</sup>	Submerged, benthic	Spores, fragments	Water
<i>Chara contraria</i>	Submerged, benthic	Spores, fragments	Water
<i>Chara contraria</i> var. <i>hispidula</i>	Submerged, benthic	Spores, fragments	Water
<i>Chara major</i>	Submerged, benthic	Spores, fragments	Water
<i>Chara vulgaris</i>	Submerged, benthic	Spores, fragments	Water
<i>Chara vulgaris</i> var. <i>longibracteata</i>	Submerged, benthic	Spores, fragments	Water
<i>Cicuta virosa</i>	Littoral emergent, semelparous	Seeds	Water
<i>Elodea nuttallii</i>	Submerged, benthic	Seeds, turions, fragments	Water
<i>Fontinalis antipyretica</i>	Submerged, benthic	Spores, fragments	Water
<i>Hottonia palustris</i>	Submerged, aerial flowering	Seeds, turions	Water
<i>Hydrocharis morsus-ranae</i>	Floating	Seeds, turions	Water
<i>Lysimachia thyriflora</i>	Littoral emergent, clonally branching	Seeds	Unknown
<i>Myriophyllum verticillatum</i>	Submerged, benthic	Seeds, turions	Water
<i>Nitellopsis obtusa</i>	Submerged, benthic	Spores, fragments	Water
<i>Nuphar lutea</i>	Nymphaeid, floating-leaved and rooted in the sediment	Seeds	Water, no ducks
<i>Nymphaea alba</i>	Nymphaeid, floating-leaved and rooted in the sediment	Seeds	Water, no ducks
<i>Phragmites australis</i>	Littoral emergent, clonally Branching	Seeds, fragments	Wind, then briefly water
<i>Potamogeton acutifolius</i> <sup>b</sup>	Submerged, benthic	Seeds, turions	Water
<i>Potamogeton compressus</i>	Submerged, benthic	Seeds, turions	Water
<i>Potamogeton lucens</i>	Submerged, benthic	Seeds, turions	Water
<i>Potamogeton mucronatus</i>	Submerged, benthic	Seeds, turions	Water
<i>Potamogeton pectinatus</i>	Submerged, benthic	Seeds, turions	Water, ducks
<i>Potamogeton praelongus</i>	Submerged, benthic	Seeds, turions	Water
<i>Potamogeton pusillus</i>	Submerged, benthic	Seeds, turions	Water
<i>Potamogeton trichoides</i>	Submerged, benthic	Seeds, turions	Water
<i>Ranunculus circinatus</i>	Submerged, benthic	Seeds, turions	Water
<i>Ranunculus lingua</i>	Littoral emergent, clonally branching	Seeds	Water
<i>Stratiotes aloides</i>	Floating	Seeds, turions	Water
<i>Typha angustifolia</i>	Littoral emergent, clonally branching	Seeds	Wind, then briefly water
<i>Utricularia vulgaris</i>	Submerged, not-rooted	Seeds, turions	Water

Animal dispersal can occur internally, after ingestion, as well as externally on feathers or feet (based on Charalambidou & Santamaria 2002; Green et al. 2002; Boedeltje et al. 2004; Soons et al. 2008; and Vermaat & Beltman, personal observations).

<sup>a</sup> Unspecified charophytes are reportedly eaten by Red-crested Pochard, Teal, Shoveller, and Mallard.

<sup>b</sup> Probably seeds of all *Potamogeton* species are eaten by ducks.