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ORIGINAL PAPER

# Do biodiversity patterns in Dutch wetland complexes relate to variation in urbanisation, intensity of agricultural land use or fragmentation?

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**Abstract** Red list species densities of birds (maximally 22 km$^{-2}$), and angiosperms (maximally 39 km$^{-2}$) were used as biodiversity indicators in 21 larger complexes of wetlands across the Netherlands. Their covariability with a range of indicators of human land use was assessed, including population, road and visitor density, area covered by agriculture, open water, forest and residential housing. Data were collected on the wetland complexes as well as for a perimeter with 10 km radius. In a principal components analysis (PCA) with all land use variables, it was found that the population-density-related complex of urbanisation, fragmentation (by roads), and intensity of fertilizer use together explained most of the variability present (i.e. the first PCA axis explained 50%), whilst land use within these complexes was second with an additional 19% and waterside recreation third with 12%. Red list bird species density did not correlate with that of angiosperms, nor with any of the indicators used. For the 13 complexes on organic peatland, we observed an increase in maximum red list angiosperm species density with the proportion of open marshland ($P < 0.01$, $r^2 > 0.55$), which, in turn, was negatively and closely correlated with the first PCA axis reflecting an urbanisation gradient across the Netherlands.

**Keywords** Species richness · Indicators · Land use intensity gradient · Spatial pattern · Mires · Multivariate analysis

## Introduction

Biodiversity of wetlands is considered to have substantial conservation (Cornwell and Grubb 2003) and economic value (Brander et al. 2006). It has been observed to decline due to a range of reasons generally linked to human activities (Wheeler 1988; Gibbs 2000; Balmford et al. 2002).

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Due to its particular geomorphology, the Netherlands abounds with wetlands (Verhoeven 1992). These wetlands have been subject to human exploitation for centuries, resulting in a highly anthropogenic landscape with spatial pattern governed by ditches and narrow elongate parcels of land since medieval reclamation in the 12th to 14th century. With the rise of adjacent towns such as Amsterdam in the 16th and 17th century, peat excavation has been carried out at large scales to satisfy the urban needs for fuel. This practice has often led to the formation of artificial lakes, where excessive excavation enabled erosion by winter storms.

In the 20th century these complexes of lakes, fens and carr were recognized as important areas for nature conservation (Barendregt et al. 1995). Most of these wetland complexes now harbour nature reserves as well as areas of intensive aquatic recreation (for example, several hundreds of boats pass the locks of the Loosdrechtse Plassen in a day; Vermaat and De Bruyne 1993), water quality is often poor (Van der Molen and Portielje 1999, Lamers et al. 2002), and roads, intensified agriculture and built-up area have fragmented these wetland habitats (Vos and Chardon 1998). The concerted impact of these pressures is thought to have led to a substantial decline in wetland biodiversity (Graveland 1998; Vereniging Natuurmonumenten 1998; Lamers et al. 2002). The relative importance, however, of these different pressures has not been addressed simultaneously so far, although negative effects of fragmentation and eutrophication on species richness are covered well in the literature (Phillips et al. 1978; Hough et al. 1989; Vos and Chardon 1989; Brose 2001; Verboom et al. 2001; Bailey et al. 2002; Blomqvist et al. 2003; Pellet et al. 2004). Our aim was to assess the relative importance of these different interacting factors. Our research questions were (1) does variability exist in biodiversity among these wetland complexes, and (2) does this present variation co-vary with contemporary patterns in human population density, intensity of agricultural land use, recreation or fragmentation. The database consists of contemporary data (~2000–2005), hence historically important determinants and past change cannot be inferred directly from observed patterns.

## Materials and methods

We carried out a comparative multivariate analysis for 21 wetland complexes of substantial size (mean 20, range 0.4–62 km$^2$). All these wetland areas had parts with a conservation status and parts with free access and a range of economic activities. We focused on identifiable landscape complexes of sufficient size, to overcome the well-established and potentially strong effect of small habitat size on species richness (e.g. Møller and Rørdam 1985; Brose 2001; Verboom et al. 2001). In addition to 13 peatland complexes, which were mires, fens or partly drowned bogs on organic peat soil (Table 1) two other types of common wetland landscapes were included: (a) coastal wetlands, generally with substantial areas of salt marsh ($n$ = 4 complexes), (b) riverine, containing reed beds, backwaters and softwood forest ($n$ = 4).

In our analysis biodiversity indicators would serve as dependent variables, and indicators of agricultural land use intensity, human population density with associated built-up land, recreation intensity and landscape fragmentation as independent explanatory variables. Past changes in either of these or other factors may well have affected biodiversity strongly, but have not been incorporated here. Principal

**Table 1** Names, codes and areas of 21 studied wetland complexes as delimited in this study grouped into the types "coastal", "riverine" and "fens or bogs". Each entry has name of wetland, then in brackets code in Fig. 1 and area of the complex (km$^2$)

| Type | Wetland complex |
|---|---|
| Coastal | 'T Zwin (19–0.4), Verdronken land van Saeftinghe (20–29.5), Boschplaat (1–15.8), Zwanenwater (4–4.5) |
| Riverine | Biesbosch (18–46.9), Ooijpolder (17–3.0), Blauwe Kamer (16–1.3), Oostvaardersplassen (8–52.2) |
| Fen or bog | Vinkeveense Plassen (12–13.8), Reeuwijkse Plassen (15–10.9), Nieuwkoopse Plassen (14–15.9), Loosdrechtse Plassen (13–34.4), Kortenhoefse Plassen (11–3.1), Ankeveense Plassen (10–4.4), Naardermeer (9–6.3), Wieden (7–49.2), Weerribben (6–42.1), Rottige Meenthe (5–13.2), Fochteloer Veen (3–23.0), Alde Feanen (2–18.0), Worm, Jisp and Neck (21–27.1) |

component analysis (PCA), analysis of variance, bivariate and stepwise multiple linear regression were used as analytical tools.

Data were collected from the Netherlands Statistics Service (CBS 2005) and the freely accessible data depository of joint Dutch organisations for nature protection and natural history (Natuurloket 2004), and published literature (Table 2). The Natuurloket depository allows queries for numbers of individual red list species and related aggregate statistics for separate cells of the Dutch national km$^2$-grid. Spatial extent and reliability of the data varies depending on availability, administrative units applied and effort made during the original collection (compiled in Table 2). Using arcGIS software, we delineated the individual complexes as separate spatial units on the digital land use map of The Netherlands (CBS 2000) primarily as

**Table 2** Data sources and spatial resolution of variables used

| Variables used | Resolution | Data source |
|---|---|---|
| *Biodiversity indicator* | | |
| Number of red list bird and angiosperm species (mean, median, maximum, standard deviation) | Wetland complex, aggregated from km$^2$ | Natuurloket (2004) |
| *Within wetland complexes* | | |
| Visitor density, scaled to a per km$^2$ and per year basis | Wetland complex | Hein et al.(2005), Vereniging Natuurmonumenten (1998) |
| Percentage of marshland, agricultural land, forested land, open water, residential and recreative built-up land, road cover, also perimeter exact area of the wetland complex | Wetland complex, aggregated from km$^2$ | CBS (2000) |
| *Land use in perimeter of 20 km diameter* | | |
| Density of main and secondary roads (m km$^{-2}$), percentage of area residential and recreative | Perimeter | CBS (2000) |
| Nitrogen fertilizer use in 2002; population density | Municipality | CBS (2005) |

hydrologically homogeneous polder units and apparent geographically distinct entities in the surrounding landscape. This latter part has a subjective component and was therefore carried out by two people at the same time. In addition, a perimeter with radius of 10 km was delineated and a range of land use statistics were quantified (Table 1 and Fig. 1). The digital land use map distinguishes 38 types of

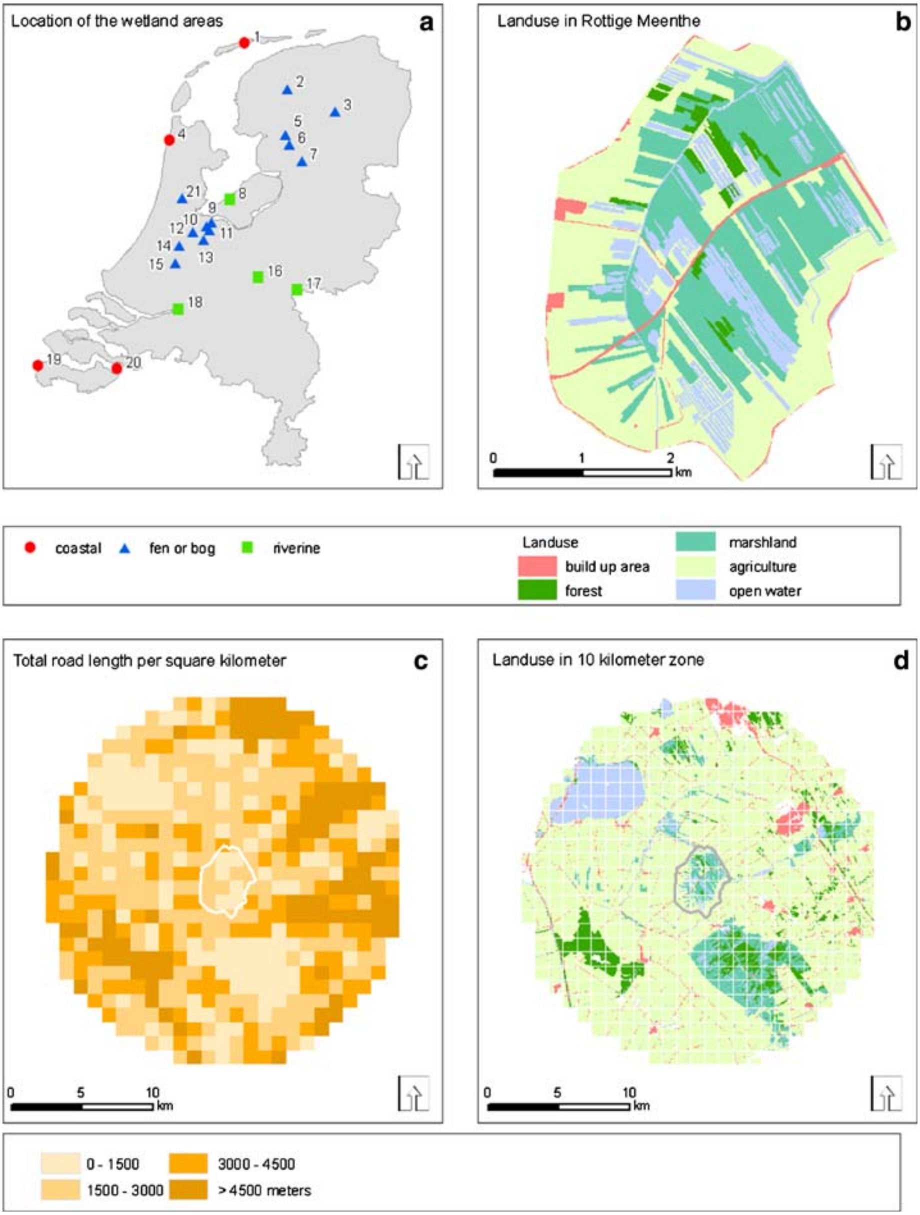


**Fig. 1** (**a**) Location of the 21 wetland complexes across The Netherlands, (**b**) different types of land use in a sample wetland complex (Rottige Meenthe—area 5 in (**a**)), (**c**) delineation of the wetland complex in the surrounding perimeter, with road density indicated in a $km^2$-grid, (**d**) land use in the surrounding perimeter

land cover including forest, marshland (wetland without trees, such as fens and reed beds), and open water.

Part of the data has been collected at a $km^2$-resolution, but we use wetland complex as our basic replicate unit, since these can be considered as spatially sufficiently separate to reduce the degree of spatial dependence and pseudoreplication (Hurlbert 1984). This approach led to a variable grain (area of the complex) and an extent of about 50,000 $km^2$ (i.e. the whole of The Netherlands).

We limited ourselves to the occurrence of red list birds and angiosperm plants, since only these two biodiversity indicators had a satisfactory coverage of the $km^2$ grid across the country. Initially we included the species on both the red list as well as the alternative 'Flora and Fauna'-list. We found however, that these two were correlated well ($r^2 = 0.65$, $P < 0.001$, $n = 308$ $km^2$ units pooled over wetland complexes).

## Results

The spatial gradient in population density across The Netherlands (Fig. 2a and Table 3) could be grasped well by the simple metric of travelling distance to Amsterdam, the capital, which was also correlated closely to estimated travelling time by car ($r^2 = 0.74$, $P = 0.001$). Distance from Amsterdam varied from 22 to 250 km for the wetland complexes studied (Table 3). A range of factors co-varied significantly with distance from Amsterdam, such as area of built-up land for residential or recreative purposes, road density in the wetland complex, visitor density, intensity of fertilizer use and proportion of open water in the complex (Fig. 2). The proportion covered by marshland increased with distance from Amsterdam (Fig. 2).

A principal component analysis (Table 3) revealed that half the variance in this multivariate dataset could be explained by a first component that reflects a complex of factors related to population density and urbanisation. Notably, the percentage of marshland correlated negatively to this component and agricultural fertilizer use did so positively. The second component related to agricultural land use within the wetland complex and explained 19% of the variance. The last component was correlated negatively to open water and visitor density, hence, may be interpreted as associated with recreation on water. It explained an additional 12%. When the same PCA was carried out for the peatland wetlands only, most patterns of significance remained identical to Table 3 and the overall explained variance of 86% was also comparable. Two exceptions were fertilizer application (no correlation with PC1 but with PC3, –0.66, $P < 0.05$) and percentage agriculture in the wetland complex (now also with PC3, +0.64, $P < 0.05$).

Biodiversity, expressed as the number of red list angiosperms or birds, varied substantially among wetland complexes (Table 4), but these numbers did not differ significantly among the three types of wetland distinguished (Table 4). The maximum number of red list plant species observed in a $km^2$-grid square was 39, whereas for birds this was 22 (Table 4). Means, medians, maxima and standard deviations of these indicators across wetland complexes all co-varied significantly ($r^2$ over 0.54, $P$ allways $< 0.05$), i.e. when the mean number was high in a particular complex, also the maximum and the variability expressed as standard deviation were high. Thus, within these wetland complexes, only limited areas had high numbers of rare and protected species. Plant nor bird biodiversity indicators were correlated significantly

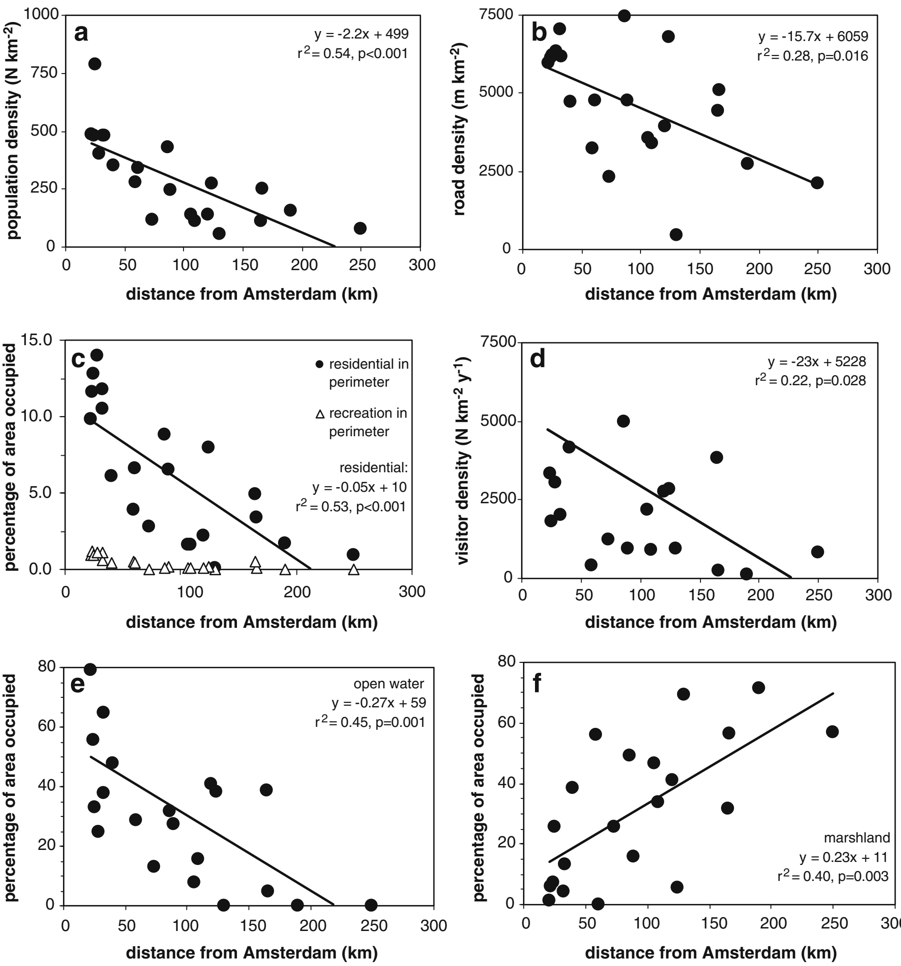


**Fig. 2** (**a**) Human population density, (**b**) road density, (**c**) percentage of perimeter occupied by residential and recreative housing, (**d**) visitor density, (**e**) percentage open water, and (**f**) percentage marshland for 20 wetland complexes in The Netherlands plotted against distance to Amsterdam, the capital

with distance to Amsterdam (Fig. 3a), or to any other variable reflecting population density or land use intensity in a simple, linear fashion. Also, the number of red list bird species and plants did not co-vary significantly (Fig. 3b). When only the wetland complexes on peat were considered, we found a significant positive correlation of maximum red list plant species with the proportion of marshland in a stepwise multiple regression ($r^2 = 0.50$, $P < 0.01$). Thus, presence of endangered plants increased with the available area of marshland habitat, but this was not apparent for birds.

## Discussion

Our primary aim was to establish the degree of variability in two simple indicators of biodiversity and in a range of potentially causal factors among wetland complexes in

**Table 3** Correlation of land use variables within and around the 21 wetland complexes with the first three components of a principal component analysis (81% explained variance)

| Variable | PC1 | PC2 | PC3 |
|---|---|---|---|
| *Outside wetland complex* | | | |
| Distance to Amsterdam | *–0.82* | +0.12 | –0.05 |
| Population density | *+0.84* | +0.34 | +0.17 |
| Visitor density | *+0.65* | +0.11 | *–0.71* |
| Road density in perimeter | *+0.89* | +0.25 | +0.05 |
| Percentage area residential in perimeter | *+0.94* | –0.05 | +0.23 |
| Percentage area recreation in perimeter | *+0.85* | –0.08 | +0.25 |
| Fertilizer Nitrogen application | *+0.57* | +0.23 | –0.40 |
| *Inside wetland complex* | | | |
| Percentage marshland in wetland | *–0.84* | –0.14 | +0.07 |
| Percentage agriculture in wetland | +0.27 | *+0.77* | +0.44 |
| Percentage forest in wetland | +0.33 | *–0.64* | +0.48 |
| Percentage residential and recreative in wetland | +0.40 | *+0.72* | +0.30 |
| Percentage water in wetland | *+0.78* | –0.01 | *–0.57* |
| Percentage covered by roads in wetland | –0.03 | *+0.92* | –0.01 |

The three components explained 50, 19 and 12%, respectively of the total variability. The first component is interpreted as a complex of factors interrelated to urbanisation and population density, the second to agricultural land use within the wetland complexes and the third to recreation on water. Correlations over 0.43 are significant at P = 0.05 and those over 0.55 at P = 0.01 (italicized here)

Note, a varimax rotation converged in 6 iterations, but did not alter the pattern and explained variance compared to that after initial extraction. The latter is therefore shown here

The Netherlands. Indeed, present-day patterns in the distribution of rare species across these wetland complexes displayed substantial variation, and for red list plants in peatlands, one particular type of wetland, this was correlated to the availability of open marshland. This variable correlated negatively with the first urbanisation-related principal component. For riverine or coastal wetland complexes, however, we could not detect any co-variability among our biodiversity indicators and those of land use, recreation or fragmentation. Furthermore, bird diversity was not affected markedly by any of the factors quantified here. We conclude that wetland red list birds are probably less sensitive to either form of human interference, as quantified here, than angiosperm plants.

The co-variablity among our different indicators of land use suggests that a separation of agriculture and urbanisation as different causal agents is not straightforward. Intensity of fertilizer use by agriculture covaried with the first urbanisation/population density-related PCA-axis, but area occupied by agriculture and road density within the wetland complex did so with the second PCA-axis. Also visitor density illustrates this multicausal variability: it correlated both with the first PCA axis and with the third, which was linked to the area of open water in a wetland. Together, these patterns reveal the existence of a distinct gradient in population density and urbanisation across some 250 km in the Netherlands, with two separate, but less important gradients superimposed.

Our results may prompt several questions, related to the spatial resolution, the appropriateness of the indicators of biodiversity (taxonomic resolution and completeness or congruence), and of those of human impact. We argue here that the applied spatial resolution ($km^2$ and wetland complex) serves well when aggregate questions of overall, regional variability in species richness is the target, as in

**Table 4** Means and ranges of indicators of biodiversity, wetland complex land use and fragmentation and recreation pressure as well as of the surrounding perimeter with a 10 km radius. Means are broken down over the three types (Table 2) and presented with standard error

| Variable | Coastal | Riverine | Fen or bog | Total range |
|---|---|---|---|---|
| *Biodiversity* | | | | |
| Mean number of red list angiosperm plant species over all km$^2$-squares in the wetland complex | 14 ± 5 | 7 ± 4 | 8 ± 1 | 1–24 |
| Maximum number of red list angiosperm species | 24 ± 6 | 11 ± 4 | 17 ± 2 | 3–39 |
| Standard deviation of the number of red list angiosperm species | 5 ± 1 | 3 ± 1 | 4 ± 1 | 1–9 |
| Mean number of red list bird species | 8 ± 3 | 11 ± 3 | 7 ± 1 | 2–18 |
| Maximum number of red list bird species | 12 ± 5 | 16 ± 2 | 11 ± 1 | 4–22 |
| Standard deviation of red list bird species | 2 ± 1 | 4 ± 1 | 3 ± 1 | 1–6 |
| *Wetland complex* | | | | |
| Percentage of the area covered by marshland (all % km$^{-2}$) | a 56 ± 11 | ab 32 ± 12 | b 24 ± 5 | 0.2–72 |
| Percentage agriculture | a 1 ± 1 | b 17 ± 4 | ab 16 ± 5 | 0–66 |
| Percentage forested | 3 ± 3 | 9 ± 4 | 15 ± 4 | 0–38 |
| Percentage built-up (residential and recreative) | 0 | 0 | 1.1 ± 0.7 | 0–9 |
| Percentage open water | a 3 ± 3 | ab 32 ± 3 | b 41 ± 7 | 0–88 |
| Percentage covered by roads | 0.7 ± 0.3 | 0.8 ± 0.2 | 0.8 ± 0.2 | 0–2 |
| Visitor density (number km$^{-2}$ y$^{-1}$) | 789 ± 240 | 2307 ± 1040 | 4087 ± 936 | 119–11111 |
| *Surrounding perimeter* | | | | |
| Distance to Amsterdam (km) | 161 ± 38 | 90 ± 13 | 72 ± 15 | 22 – 250 |
| Population density (number km$^{-2}$) | 103 ± 23 | 309 ± 42 | 350 ± 55 | 54–786 |
| Percentage of area covered by residential housing | 1 ± 1 | 7 ± 1 | 7.5 ± 1 | 0.1–14 |
| Percentage covered by recreative facilities | 0 | 0.3 ± 0.1 | 0.6 ± 0.1 | 0–1 |
| Density primary roads (m km$^{-2}$) | a 111 ± 40 | b 323 ± 35 | b 388 ± 32 | 0–539 |
| Density secondary roads (m km$^{-2}$) | a 1796 ± 463 | b 5231 ± 958 | b 4824 ± 298 | 450–7030 |
| Nitrogen use as fertilizer by agriculture in 2002 (kg ha$^{-1}$) | a 96 ± 18 | a 133 ± 27 | b 245 ± 12 | 62–327 |

When these three differ significantly (Tukey test, EER = 0.05, CER = 0.017) this is denoted with lower-case lettering, where means sharing the same letter do not differ. The last column gives the total range observed across the 21 wetland complexes studied

nationwide assessments (Andelman and Fagan 2000; Cornwell and Grubb 2003). The appropriateness of our indicators could have been questioned due to the constraint of data availability. We argue that our indicators are sufficiently appropriate for local conservation practice, since we used red-list taxa. The usefulness of vegetation as a biodiversity indicator has been stressed before (Dobson et al. 1997; Kati et al. 2004).

We have stressed before that our observations reflect present day patterns, which may have causes that are still operational or have been so in the past only. The percentage of open water in a complex, for example, is closely related to the distance to Amsterdam, as a surrogate for the densily populated part of the country. This probably has its roots in the large-scale 16th and 17th century peat excavation

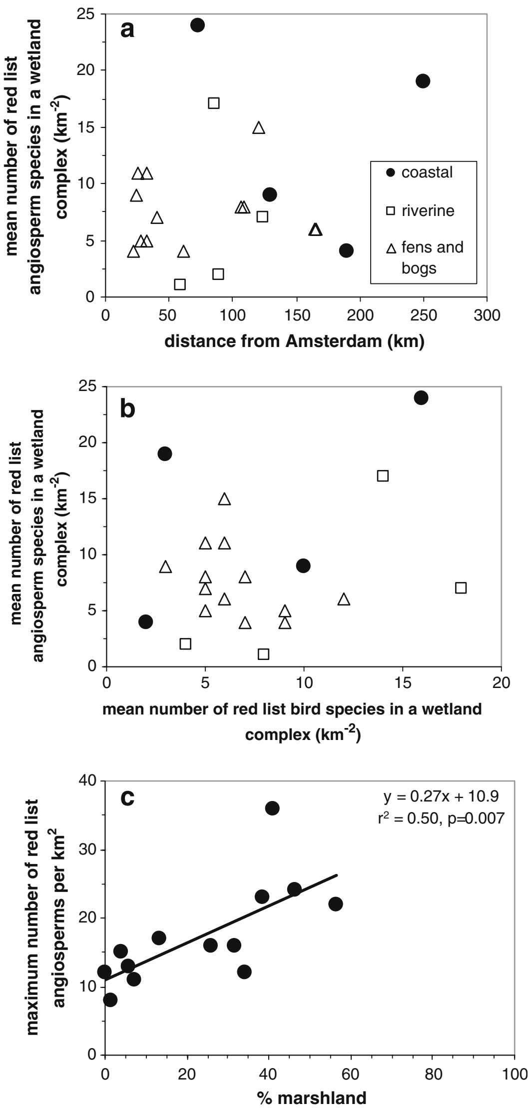


**Fig. 3** (**a**) mean number of red list angiosperm plant species per square kilometer in three different types of wetland complexes plotted against distance to Amsterdam; (**b**) scatter plot of red list plants against red list birds for the same three types of wetlands; (**c**) maximum angiosperm red list species density in thirteen fen- and bog wetlands as a function of the proportion of marshland. When absolute area was used instead of percentage in the wetland complex, the $r^2$ increased to 0.75

activities, and the adjacency of urban markets. However, this major landscape pattern has become fixed in the 20th century when open water came to serve recreation as a new economical strength and succession into reed beds and fenland came to a standstill, whereas existing fens turned into alder or willow carr (Bakker et al. 1994; Van Diggelen et al. 1996). Thus, the temporal dynamics of these wetland landscape complexes were probably greatly reduced (Verhoeven 1992; Graveland 1998). It is difficult to argue decisively how much this has affected biodiversity patterns when many angiosperm taxa are long-lived and dispersal capacity is insufficiently known (Ozinga et al. 2005), but habitat availability must have been reduced greatly, particularly for herbaceous fens and marshes of low nutrient availability (Soons et al. 2005), and this will have reduced the extent of surviving populations of a number of habitat specialists that feature on red lists. Restoration efforts targeted at these habitats appear justified (Beltman et al. 1996). We conclude that wetland plant biodiversity reduction presently is primarily due to habitat loss coupled to this major complex of regional-scale urbanisation-related factors.

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## References

Andelman SJ, Fagan WF (2000) Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? Proc Natl Acad Sci 97:5954–5959
Balmford A, Bruner A, Cooper P et al (2002) Economic reasons for conserving wild nature. Science 297:950–953
Barendregt A, Wassen MJ, Schot PP (1995) Hydrological systems beyond a nature reserve, the major problem in wetland conservation of Naardermeer (The Netherlands). Biol Conserv 72:393–405
Bailey SA, Haines-Young RH, Watkins RC (2002) Species presence in fragmented landscapes: modelling of species requirements at the national level. Biol Conserv 108:307–316
Bakker SA, Van den Berg NJ, Speleers BP (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
Beltman B, Van den Broek T, Bloemen S, Witsel C (1996) Effects of restoration measures on nutrient availability in a formerly nutrient poor floating fen after acidification and eutropication. Biol Conserv 62:59–65
Blomqvist MM, Vos P, Klinkhamer PGL, Ter Keurs WJ (2003) Declining plant species richness of grassland ditch banks – a problem of colonisation or extinction? Biol Conserv 109:391–406
Brander L, Vermaat JE, Florax RJGM (2006). The empirics of wetland valuation, a meta-analysis. Envn Resour Econ 33:223–250
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
CBS (2000) Bestand bodemgebruik/Netherlands digital land use map. Netherlands Statistics Service, Voorburg
CBS (2005) Statline, online data depository. Netherlands Statistics Service. www.cbs.nl. Accessed in August 2005
Cornwell WK, Grubb PJ (2003) Regional and local patterns in plant species richness with respect to resource availability. Oikos 100:417–428
Dobson AJP, Rodrigue JP, Roberts WM, Wilcove DS (1997) Geographic distribution of endangered species in the United States. Science 275:550–553
Gibbs JP (2000) Wetland loss and biodiversity conservation. Conserv Biol 14:314–317
Graveland J (1998) Reed die-back, water level management and the decline of the Great Reed Warbler *Acrocephalus arundinaceus* in The Netherlands. Ardea 86:187–201
Hein L, De Groot R, Van Ierland E (2005) Spatial scales, stakeholders and the valuation of ecosystem services. In: Hein L, Optimizing the management of complex dynamic ecosystems, an ecological-economic modelling approach, Thesis Wageningen University, pp 73–92
Hough RE, Fornwall HD, Negele BJ et al (1989) Plant community dynamics in a chain of lakes, principal factors in the decline of rooted macrophytes with eutrophication. Hydrobiologia 173:199–217
Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. Ecol Monogr 54:187–211
Kati V, Devillers P, Dufrene M et al (2004) Testing the value of six taxonomic groups as biodiversity indicators at a local scale. Conserv Biol 18:667–675
Lamers LPM, Smolders AJP, Roelofs JGM (2002) The restoration of fens in the Netherlands. Hydrobiologia 478:107–130

Møller TR, Rørdam CP (1985) Species number of vascular plants in relation to area, isolation and age of ponds in Denmark. Oikos 45:8–16

Natuurloket (2004) Natuurloket, online biomonitoring data depository, www.natuurloket.nl, accessed in November 2004

Ozinga WA, Schaminée JHJ, Bekker RM et al (2005) Predictability of plant species composition from environmental conditions is constrained by dispersal limitation. Oikos 108:555–561

Pellet J, Guisan A, Perrin N (2004) A concentric analysis of the impact of urbanisation on the threatened European tree frog in an agricultural landscape. Conserv Biol 18:1599–1606

Phillips GL, Eminson DF, Moss B (1978) A mechanism to account for macrophyte decline in progressively eutrophicated waters. Aquat Bot 4:103–125

Soons MB, Messelink JH, Jongejans E, Heil GW (2005) Habitat fragmentation reduces grassland connectivity for both short-distance and long-distance wind-dispersed forbs. J Ecol 93:1214–1225

Van der Molen DT, Portielje R (1999). Multi-lake studies in The Netherlands, trends in eutrophication. Hydrobiologia 408/409:359–365

Van Diggelen R, Molenaar WJ, Kooijman AM (1996) Vegetation succession in a floating mire in relation to management. J Veg Sci 7:809–820

Verboom J, Foppen R, Chardon P et al (2001) Introducing the key patch approach for habitat networks with persistent populations: an example for marshland birds. Biol Conserv 100:89–101

Vereniging Natuurmonumenten (1998) Omkijken naar laagveen. Resultaten van beheer en wensen voor de toekomst van de laagvenen van Natuurmonumenten. ‘s-Graveland, 84 pp (in Dutch, policy document on the management of Dutch fenlands)

Verhoeven JTA (ed) (1992) Fens and bogs in The Netherlands, vegetation, history, nutrient dynamics and conservation. Kluwer, Dordrecht. Geobotany 18

Vermaat JE, De Bruyne RJ (1993) Factors limiting the distribution of submerged waterplants in the lowland river Vecht (The Netherlands). Freshw Biol 30:147–157

Vos CC, Chardon JP (1998) Effects of habitat fragmentation and road density on the distribution pattern of the moor frog *Rana arvalis*. J Appl Ecol 35:44–56

Wheeler BD (1988) Species richness, species rarity and conservation evaluation of rich-fen vegetation in lowland England and Wales. J Appl Ecol 25:331–352