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REGULAR PAPER

Past and present distribution of the rare aquatic plant *Luronium natans* (Alismataceae) in Belgium shows marked decline and bad conservation status

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Background and aims – *Luronium natans* is a rare endemic plant of West- and Central-Europe and protected by the Habitats Directive. The present study gives a comprehensive and up-to-date overview of its past and present distribution in Belgium, which lies within the core area of *Luronium natans*.
Methods – We assessed the distribution by consulting herbaria, literature and databases, and by additional field visits, recording the number of ramets, flowering, general site characteristics and accompanying plant species for extant populations.
Key results – The core area of *Luronium natans* is located in the Campine phytogeographical district, a region with sandy soils in northern Belgium. Overall, it was recorded at c. 250 sites in 155 16 km^2-squares, with 93 populations occurring since 1980. Field observations show thirty extant populations, all but one in the northern part of the country. Less than half of them are large flowering populations with a good conservation status as far as the species population characteristics are concerned; 30% are located in nature reserves and 70% in Special Areas of Conservation. The number of records decreased since 1985, especially outside the core area. This decline related well to eutrophication, but not to anthropogenic acidification. In general, populations are short-lived and population size fluctuates strongly. Population size correlates with flowering incidence. For one isolated population it appears that the species was introduced with fish.
Conclusions – The number of *Luronium natans* records shows that the Belgian territory accounts for a significant part of its global distribution. There was however a marked decline of records since 1985, especially outside its core area. Moreover, most of the remaining populations are small and have a bad conservation status. They show little or no flowering, which is worrying, considering the alleged importance of sexual reproduction for the survival of the species.

Key words – *Luronium natans*, Belgium, distribution, trend, Natura 2000, Habitats Directive.

INTRODUCTION

The floating water-plantain, *Luronium natans* (L.) Raf., is a rare amphibious or fully aquatic plant endemic to West- and Central-Europe. Relying strictly on confirmed records, Lansdown & Wade (2003) described its range as extending from southern Norway and Sweden in the north, through the British Isles up to northern Spain and eastward to Poland; it appears to be extinct in the Czech Republic (see also http://bd.eionet.europa.eu/article17, accessed on 3 Jan. 2013). It is most frequent in the western part of its range, which includes Britain, France, the Netherlands, Belgium and northern Germany. According to Arts et al. (1990) and Nielsen et al. (2006), soft-water lakes and ponds appear to be its natural habitat; on the other hand, it also occurs in rivers and canals with more calcareous water (e.g. Willby & Eaton 1993, Bornette et al. 1996).

L. natans is included in Annex I of the Bern Convention (1979) on the Conservation of European Wildlife and Natural Habitats. Moreover, it is listed in Annexes II and IV of the European Union Directive on the Conservation of Natural Habitats and of Wild Fauna and Flora (92/43/EEC), the so-called Habitats Directive. It is also included in the IUCN red list of threatened species, listed as least concern (Lansdown 2011). The species occurs on many national Red Lists, e.g. as critically endangered in the Czech Republic (Grulich 2012) and as endangered in Spain (Moreno 2008) and Germany (Hauke 2003). Consequently, the distribution and ecology of *L. natans* received considerable attention throughout Europe lately (e.g. Greulich et al. 2000, Szańkowski & Kłosowski 2001, Lansdown & Wade 2003, Nielsen et al. 2006), not in the least because of its importance for delimiting Special Areas of Conservation (SAC) and for Article 17 reporting of the Habitats Directive which requires detailed survey, data compilation and surveillance of current populations and metapopulations.

Belgium lies well within the main distribution area of *L. natans*. As in other EU member states, the species is considered here to be characteristic of the Natura 2000 habitat type 3130, "oligotrophic to mesotrophic standing waters with vegetation of the *Littorelletea uniflorae* and/or the *Isoëto-Nanojuncetea*". In northern Belgium, Flanders, it is also indicative of habitat type 3260, "water courses of plain to montane levels with the *Ranunculion fluitantis* and *Callitricho-Batrachion* vegetation". Furthermore, it also extends into habitat type 3110, "oligotrophic waters containing very few minerals of sandy plains (*Littorelletalia uniflorae*)" (Ronse & Van Landuyt 2007, Denys et al. 2008). In Flanders, the species is listed as rare (Ronse 2006), whereas only one recent population is known from Wallonia, the southern part of Belgium (Saintenoy-Simon & Goffart 2012).

In view of the importance of the species for the delimitation of SACs and in view of its rarity, a research programme was started in 2003 for the conservation biology of *L. natans* in Belgium. The first aim of this project was to make a comprehensive and up-to-date overview of the past and present distribution of *L. natans* in the country. We therefore made a compilation of distribution data from all available sources, and checked the status of as many as possible populations in the field, examining their persistence, their size, and flowering. Furthermore, we aimed to investigate the genetic structure of the Belgian populations as well as the environmental requirements of the species, two subjects that are reported separately (Cox et al. 2014, Leyssen et al. in prep.). This paper thoroughly reviews the current and historical status of the species in Belgium. It also investigates which factors, mainly general abiotic site characteristics, may influence the range of the species, both the geographical range and its trend in time. These factors are related to the condition of the species and the conservation status of its current populations; these results are also viewed in the light of the hypotheses of acidification and of eutrophication, and compared to literature data from outside Belgium.

MATERIAL AND METHODS

Record sources

Records of *L. natans* in Flanders were primarily retrieved from the database Florabank 1, that contains distributional data on the wild flora of Flanders and the Brussels Capital Region (Florabank; http://flora.inbo.be, accessed on 8 Mar. 2012). For Wallonia, the website "La biodiversité en Wallonie, flore, plantes protégées et menacées" was consulted (http://biodiversite.wallonie.be/fr/liste-des-taxons.html?IDD=1755&IDC=3076, accessed on 17 Mar. 2014). These databases include all the records used for published plant atlases of the territory as well as more recent observations. These atlases are the Belgian plant atlas with data from 1939 to 1971 (Van Rompaey & Delvosalle 1979; abbreviation BPA), and the Flemish plant atlas containing data from the northern part of the country of 1972 to 2004 (Van Landuyt et al. 2006; abbreviation FPA).

Historical observations were complemented with data from Durand (1899). For the period 1940–1971, the original recording sheets of the Institut Floristique Belgo-Luxembourgeois (IFBL) were scrutinized to obtain specific information on the time of observation and precise location within the surveyed 1 km^2-squares. Moreover, specimens of *L. natans* were sought in all publicly accessible Belgian herbaria (herbarium acronyms follow Index Herbariorum): Botanic Garden Meise (BR), also including the herbaria of Van Heurck (formerly AWH), Katholieke Universiteit Leuven (formerly LV), Centre Grégoire Fournier, Abbaye de Maredsous (formerly MAR) and De Langhe; Université Libre de Bruxelles, Brussels (BRLU); Vrije Universiteit Brussel, Brussels (BRVU); Universiteit Gent, Ghent (GENT); Institut de Botanique, Sart Tilman, Université de Liège, Liège (LG); Université Catholique de Louvain, Louvain-la-Neuve (MUCL); Facultés Universitaires Notre-Dame de la Paix, Namur (NAM).

Furthermore, we identified additional occurrences from on-going habitat mapping by INBO staff, as well as from volunteer-based biodiversity recording programs (http://www.waarnemingen.be, accessed on 3 Jan. 2013).

In order to establish the recent distribution of *L. natans*, the large majority of all sites with observations since 1971 was visited (about 100 sites). Fourteen additional sites were checked by the original recorder and a further eighteen could not be checked because their location was known too imprecisely. All field work was carried out between 2005 and 2012.

Where possible, the exact year of observation was noted. In other cases, the indicated time range, e.g. the atlas interval, was used. All records were attributed to 16 km^2-squares (4 × 4 km) of the IFBL grid that is the basis for floristic records and plant atlases in Belgium, and to a 1 km^2-square or more precise location where possible. We defined a population as consisting of plants situated either in one and the same water body, or in distinct water bodies connected by surface water during at least part of the year. Typically, populations covered only a small part of a single kilometre square but some extended over several such squares. Where possible, lentic and lotic conditions were distinguished.

We separated reliable records (corroborated by herbarium specimens, photographs of flowering plants or confirmation by trained observers) from non-confirmed records, the latter mostly originating from historical botanical literature. Recent observations were verified by field visits. The reliability of older records of *L. natans* deviating markedly from the general distribution pattern ('outliers') was assessed based on the co-occurrence in the square of the eighteen most frequently associated but uncommon plant species. These eighteen species were selected by identifying the ten species that were observed most frequently together with *L. natans* in the present survey, excluding those that are very common according to FPA; furthermore other species were added, that have been reported by Murphy (2002) as commonly associated in northern Europe. The names of these species are shown in fig. 1, that will be explained further in the text. Their presence in the squares was checked using the BPA for the period until 1972 and the FPA for the period after 1972.

Overall distribution pattern

Databases of the records were made in Access. Maps of the records per square were made in ESRI ArcMap 9.1. An overlay of the distribution pattern was made with the Belgian phytogeographical districts (Lambinon et al. 2004), distinguishing between confirmed and non-confirmed records as a control on old records for which no herbarium specimens were present. The distribution pattern was also compared with the major soil regions (Verbruggen et al. 1996) and the Flemish ecodistricts (Sevenant et al. 2002).

The number of populations per square and the time span of occurrence per square were also examined as a proxy for the persistence of individual populations, which cannot be determined precisely for the older records. The number of populations per square should be viewed as a minimum, since the old records often lacked the accuracy required to distinguish separate populations. The time span or persistence of records in a square is defined as the number of years from the first to the last observation.

Overall distribution trend

The trend or evolution of the overall distribution was analysed by grouping the number of records per 25 year periods, starting from 2012. This length of periods results into sufficient periods to detect a trend, while some of the most important dates for the floristic recording intensity (1862 and 1939: see under Discussion) fall at the end or in the beginning of the periods, making it possible to detect their influence. The total number of squares in each period was calculated, accounting for the possible duration of occupancy. Records spanning two or three periods were weighed for each period as 0.5 or 0.33, respectively. The sum of all frequencies was rounded to unity, yielding the total number of squares per period.

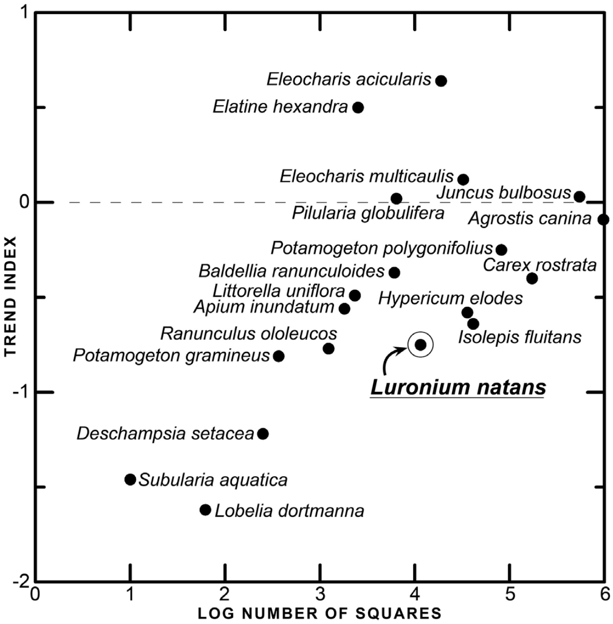

Figure 1 – Number of squares (log) and trend index of *Luronium natans* and most frequently associated species.

The trend was also related to the floristic recording intensity. The latter was quantified as the annual number of recording lists with more than 90 species, extracted from the Belgian IFBL-database for the years 1939–1971, and from the Flemish Florabank for 1972–2012. The distribution trend was expressed as the annual number of records of *L. natans* since 1939. The Pearson correlation coefficient between both metrics was calculated.

Recent distribution

For the recent distribution, populations recorded at least once between 2009 and 2012 were considered extant. The condition of the populations was assessed by estimating the population size (as the number of ramets on an ordinal scale with classes of 1–10, 11–20, 21–50, 51–100, 101–1000, and > 1000), the cover in m^2, and by recording if flowering occurred. It should be noted that the population size is prone to large fluctuations from year to year, and that plants may be entirely absent for several years before reappearing. Sometimes, this is even the case for large populations. Therefore, population size was defined as the largest of the values observed between 2009 and 2012.

The protection status of the populations was determined by checking the occurrence within an official nature reserve (officially recognized by Flemish or Walloon governments) and/or SAC (https://metadata.agiv.be/zoekdienst/apps/tabsearch/index.html?uuid=7B9424F7-BBB6-4248-9728-AE207F541780&hl=dut&hl=dut; https://metadata.agiv.be/zoekdienst/apps/tabsearch/index.html?uuid=a8cfffb8-7579-4a5e-af81-73ee624adcc6&hl=dut&hl=dut). Some additional variables were recorded that may be important for the presence and condition of the species, viz. whether the populations occurred in flowing or in standing water, the water depth at which the plants were growing (± 5 cm), as well as the accompanying plant species and the cover of species groups indicating eutrophication or acidification. Their relation to population size was investigated. Species population characteristics used to assess the conservation status of the populations were determined, a good conservation status requiring, amongst others, a flowering population of more than 100 ramets covering more than 5 m^2 (Denys et al. 2008). The conservation status of the populations was also looked at per province, and related to the average population density per province (http://www4.vlaanderen.be/dar/svr/cijfers/Exceltabellen/demografie/1_Bevolking/2_Provincies/1_Bevolking_prov.xls).

The persistence of individual populations recorded after 1972 (the first recording year for the FPA) was used as a proxy for the longevity of the populations. The persistence after 1999, respectively after 2005, was computed for populations known in the 1970's, and for populations discovered in the 1980's and in the 1990's. The trend index – a measure of the relative change in occurrence between the first (1939–1971) and second period (1972–2004), presented in the FPA – was related to the number of squares with records of the species during the second period. This was done for *L. natans* as well as for the eighteen most frequently associated species (see above).

Nomenclature

The names of taxa follow Lambinon et al. (2004).

RESULTS

Overall distribution pattern

The distribution of *L. natans* in Belgium since 1800 is shown in fig. 2A as the presence or absence per 16 km^2-square. Overall, the species was recorded in 154 16 km^2-squares (7% of the total number of squares in Belgium); documented evidence was only available for 93 squares (60%). Non-confirmed observations of *L. natans* must be addressed cautiously, as non-flowering plants are easily mistaken for several co-occurring species, such as *Alisma plantago-aquatica*, *Baldellia ranunculoides*, *Ranunculus flammula* and *Sparganium* species (Lockton 2009, author's pers. obs.). Nevertheless, records in non-confirmed squares fit well with the ascertained distribution, suggesting that many of them may be trustworthy. The core distribution area of *L. natans* lies within the Campine district in northern Belgium and contains 77% of all squares with the species. The second largest area with 17% of all squares lies more to the west, in the Flemish phytogeographical district. The Ardennes, Brabant, Lorraine and Meuse districts have two squares each, and there was only one coastal location (Maritime district).

In Flanders, there appears to be only one outlier square. Situated in the western coastal dunes, it has five of the eighteen commonly associated species (see fig. 1 for their identity). The situation is slightly different in Wallonia where the records are more dispersed. Only ten of the associated species are fairly widespread in this region (*Agrostis canina*, *Apium inundatum*, *Baldellia ranunculoides*, *Carex rostrata*, *Elatine hexandra*, *Eleocharis acicularis*, *Juncus bulbosus*, *Litorella uniflora*, *Pilularia globulifera* and *Potamogeton polygonifolius*). Five to nine of them were recorded within or close to all outlying squares, except for those in the Meuse district, where only two such species were noted. This suggests that *L. natans* was likely to occur at most sites but flags the reports from the Meuse region as peculiar. Nevertheless, examination of the specimens collected from these ponds (*A. Charlet* s.n., 18 Jul. 1891, "Huy, mare" and *A. Maréchal* s.n., Aug. 1908, "mares à Tamines", both at LG) convinced us of a correct identification.

More than 90% of all squares with the species in Flanders are located on more or less sandy soils (fig. 2B). The few records of *L. natans* in Wallonia are from gravelly loam and loamy clay soils with slates and sandstones.

Figure 2C shows the overlay of the distribution pattern in the Campine phytogeographical district with the Flemish ecodistricts. It appears that the species is largely missing from the central part of the 'Noord-Kempisch kleisubstraatdistrict' as well as from a large part of the 'Oost-Kempisch puinwaaierdistrict' and some adjacent parts of the 'Roerdalslenkdistrict'.

The number of *L. natans* populations per square (fig. 3A) clearly shows that squares with more than one population are restricted to the Campine area. Figure 3B shows the time

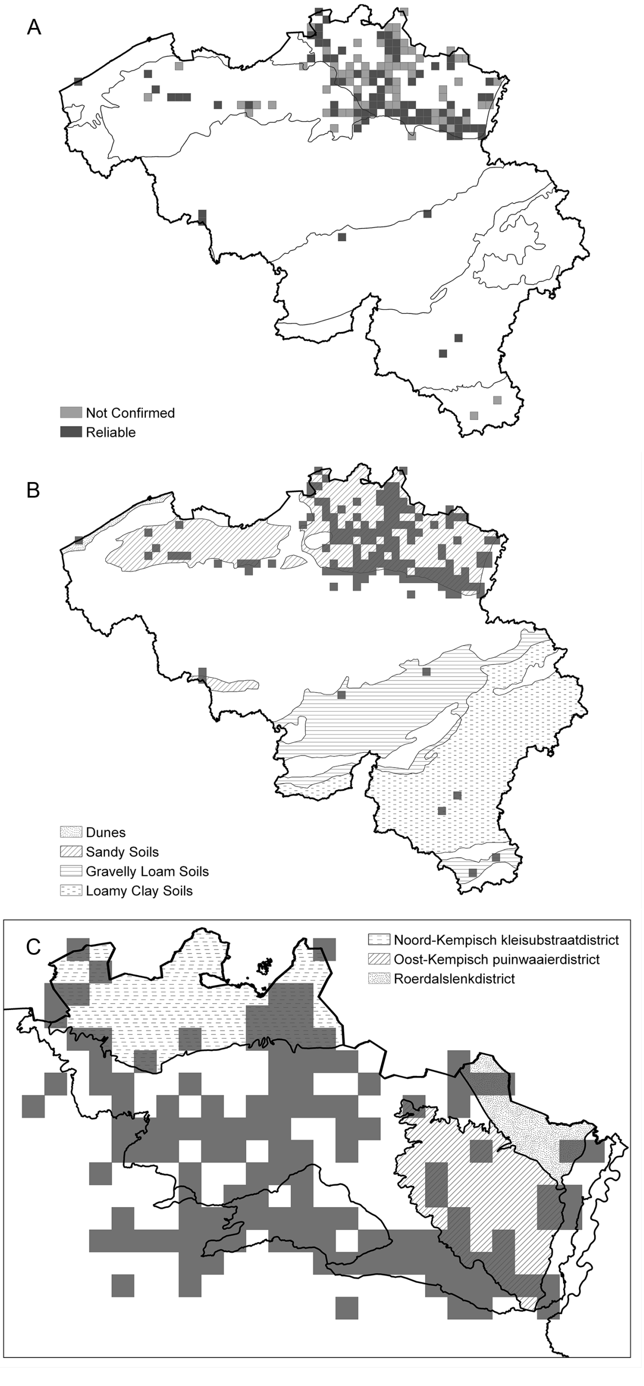

Figure 2 – Overall distribution of *Luronium natans* in Belgium since 1800: A, overlay with phytogeographical districts; B, overlay with major soil regions; C, overlay with ecodistricts of the Campine ecoregion.

span of all records for each square. This ranges from one to 160 years, with a mean of 34 years. All squares with a more than average persistence are also situated in the Campine district, except for one in the Flemish district, where the species is known to have occurred for at least 134 years. Persistence at square level correlates positively with the number of populations per square (Spearman's rho correlation coefficient, two-tailed, r = 0.72, p < 0.01).

Overall distribution trend

The number of records per 25 year period is shown in fig. 4A. The earliest records go back to 1803. The number of records increased up to a maximum of 63 in 1963–1987, only interrupted by a decrease between 1888 and 1937. The generally increasing trend halted in the last 25 year period (1988–2012).

Figure 4B displays the evolution of the annual number of floristic lists as well as of the annual number of *L. natans* records after 1939. This shows that floristic recording increased until 2000, after which it decreased. The number of records of *L. natans* increased until around 1985 and correlated positively with the overall floristic effort (r = 0.46; p < 0.001). After 1985 the number of records decreased somewhat but picked up again after 2005; it no longer correlated with general recording intensity (r = -0.31; p = 0.120). The breakdown of this relation after 1985 suggests interference of external causes, more so as targeted mapping of sites with *L. natans* for the Habitats Directive started in 2004.

The geographical shift of locations with *L. natans* per 25 year time period was analysed (results not shown), which shows that the decrease of *L. natans* in the last period mainly occurred outside the main Campine core area. Moreover, there appears to be a recent separation of distinct smaller strongholds in this area, especially since 2000 with sites mainly disappearing in the northwest. In the Ardennes district, on the other hand, a few new sites were noted in the two last periods.

Table 1 shows the number of populations recorded for the first time in each decade between 1972 and 1999, as well as after 2000; for each decade the persistence of the populations is expressed as the percentage of surviving populations after 1999 and after 2005. Since 1972, 118 individual populations

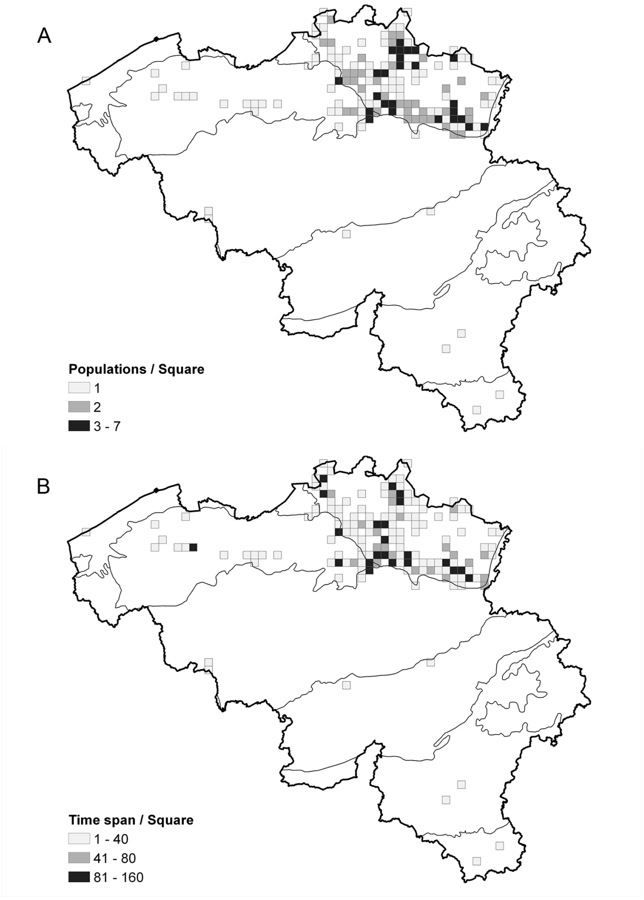

Figure 3 – A, number of populations per 16 km^2-square; B, persistence (range between first and last observation) per 16 km^2-square.

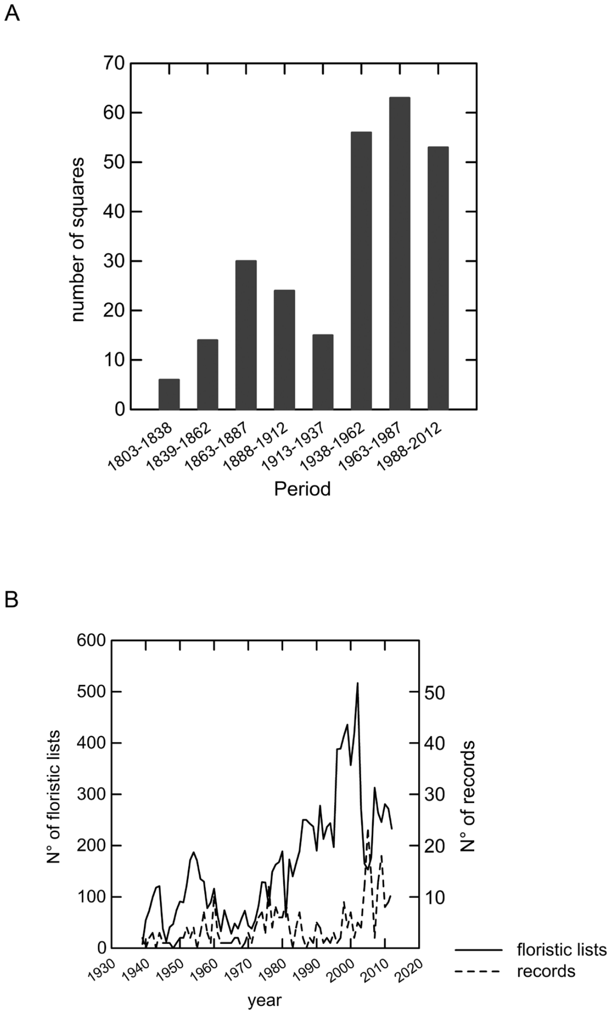

Figure 4 – A, number of 16 km^2-squares with *Luronium natans* in Belgium per 25 year time period; B, annual number of floristic lists and squares with *L. natans* from 1939 to 2012.

Table 1 – Number of populations of *Luronium natans* recorded for the first time between 1972 and 2012 and their persistence. Persistence expressed as the percentage of populations remaining.

Earliest record	N° of populations	Persistence (%)	
		after 1999	after 2005
1972–1979	46	22	11
1980–1989	25	44	8
1990–1999	13	69	46
1972–1999 (subtotal)	84	36	15
2000–2012	34	100	56
1972–2012 (total)	118	42	27

were recorded in total, of which 84 had a first record before 1999. It appears that of all populations observed in the seventies, only 22% persisted after 1999, while this increased to 44% for those recorded in the eighties and further to 69% for the nineties. Overall, only about one third (36%) of the populations recorded between 1972 and 1999 was still present after 1999. This shows that the lifespan of most populations was rather short within this period. Some populations lasted at least from the seventies up to or beyond 2009 (province Antwerpen: Zwart Water and Mellevijver, Turnhout; Langdonken, Herselt; province Limburg: Laambeekvijvers, Houthalen; De Maten, Genk; Heuvelsven, Lanklaar). Some extant populations were only discovered in the 1990's (Grote Dorst, Lummen; Kolberg, Zonhoven; Het Wik, Genk), all in the province of Limburg. After 1999, 34 new populations were discovered, and nineteen populations occurred after 2005. Of all populations recorded since 1972, only 27% has persisted after 2005.

The relationship between the trend index and the number of squares of *L. natans* and its associated species is shown in fig. 1. It displays a positive global correlation between these parameters, meaning that the rarest species have known the strongest decline. Moreover, *L. natans* is located on the lower edge of this distribution, showing the most negative trend index compared with species of comparable rarity. Its decline has even been stronger than that of several rarer species, such as *Apium inundatum*, *Baldellia ranunculoides* and *Littorella uniflora*.

Recent distribution

Of the 64 populations of *L. natans* recorded after 1999 (located in 46 16 km^2-squares), 34 (53%) were unknown prior to 2000, suggesting a low persistence. Moreover, only thirty of them are still extant (recorded at least once from 2009 to 2012). Table 2 shows some characteristics of these populations in relation to their size.

Population sizes range from less than ten to more than 1000 ramets. Almost half of the populations (43%) have more than 100 ramets, but one quarter (24%) has less than twenty. The age of the populations varies between one and 49 years. Although the oldest population is also one of the largest, age and population size appear unrelated. On the other hand, the occurrence of flowering is positively related with the population size (Spearman rho = 0.63; p = 0.01); no flowering was observed in populations with less than twenty ramets, whereas this was the case for nearly 90% of the larger populations. The proportion of flowering ramets is often quite low, amounting to less than 5% in 80% of the flowering populations. Only in two populations did more than half of the ramets produce flowers.

L. natans plants were growing up to about one meter deep. The smallest populations with less than twenty ramets tend to grow more shallowly and in conditions where inundation is limited to the wettest season.

The large majority of the Belgian populations occur in standing water (83%). A clear relation was not found be-

Table 2 – Characters of extant *Luronium natans* populations per population size (number of ramets).
Number of populations, age (in years; mean, minimum and maximum between brackets), flowering (number of flowering populations, percentage between brackets), water depth (in m; median, minimum and maximum between brackets), occurrence in standing water (number; percentage between brackets), occurrence in nature reserves and in Special Area of Conservation (number; percentage between brackets).

Population size	n° of populations	age	flowering	water depth	standing water	nature reserve	SAC
> 1000	4	30 (4–49)	4 (100%)	0.21 (0.00–0.40)	3 (75%)	2 (50%)	3 (75%)
100–1000	10	6 (1–11)	8 (80%)	0.44 (0.02–1.00)	10 (100%)	2 (22%)	7 (70%)
50–99	5	14 (1–37)	5 (100%)	0.29 (0.00–0.70)	3 (60%)	1 (20%)	3 (60%)
20–49	4	20 (4–43)	3 (75%)	0.29 (0.10–0.50)	4 (100%)	2 (50%)	4 (100%)
10–19	2	6 (1–10)	0	0.18 (0.05–0.30)	1 (50%)	1 (100%)	1 (50%)
< 10	5	12 (1–35)	0	0.14 (0.00–0.60)	4 (80%)	1 (20%)	3 (60%)
total	30	10 (1–49)	20 (67%)	0.30 (0.00–1.00)	25 (83%)	9 (30%)	21 (70%)

tween the population size and the occurrence in standing versus flowing water, but it is remarkable that the average age of populations in flowing water is only half (six years) of that in standing waters (fifteen years; results not shown).

Only 30% of all populations occur within the limits of an official nature reserve, but 70% are situated in designated SACs. Population size is independent of protection status.

DISCUSSION

Importance of Belgian populations at European level

Overall, *L. natans* was recorded at c. 250 sites in 155 16 km^2-squares since 1800. After 2000, 63 populations were found in Belgium and there were 36 populations after 2005, of which at least thirty are extant (reported from 2009 to 2012). These numbers show that Belgian territory is more important for the global distribution and conservation of the species than generally assumed. Lansdown & Wade (2003) considered *L. natans* to be "most frequent in the western part of its range, in Britain, the Netherlands, France and northern Germany". They report 127 sites in Great Britain, whereas their only reference to Belgium suggests that only three populations remained after 1980. This was based on a paper reporting new locations in 1976 but without details on the Belgian situation. Bardin et al. (2011) mention 578 municipalities with an unspecified number of sites in France and 455 sites in Germany, but report less than five locations for Belgium. In comparison, the former total of 250 sites in Belgium is relatively high, especially when taking their density into account. Relative to the 204 km^2-squares in Belgium, the Netherlands – an area only 1.36 times larger – has a considerably higher number of 859 km^2-squares (Lucassen et al. 2007). In fact, as the main Belgian distribution area, the Campine district, and the area of Noord-Brabant (The Netherlands) with the majority of the Dutch records, are ecogeographically contiguous and separated only by national borders.

Belgium is not only important for the historical distribution of *L. natans*, it still presented a substantial number of populations in more recent times. Since 1980, 93 populations were recorded, compared to 179 sites in Germany, 123 in the Netherlands and 58 in the UK (Lansdown & Wade 2003). After 2000, the species was observed in 306 French municipalities (Bardin et al. 2011), compared to 63 populations occurring in Belgium.

Distribution in Belgium

Historically, the Belgian distribution of *L. natans* mainly includes the northern part of the country, in particular the Campine phytogeographical district. This is clearly the core area, as it presents the largest number of squares (77%), the highest number of populations per square (up to seven), as well as the longest time span between first and last observation per square. The second most important region is the Flemish district, although the species no longer occurs there at the moment. With top soils derived mainly from Pleistocene sands, both phytogeographical districts are closely related. They concur with the palaeoecological regions of Kempenland and Sandy Flanders, respectively, where postglacial vegetation evolution was similar except for more pronounced heathland expansion in the former due to poorer, more acid soils (Verbruggen et al. 1996). The floristic correspondence of some parts of the Flemish district with the Campine phytogeographical district is still apparent (Vanhecke et al. 2009) and also reflected by the former distribution of *L. natans*.

Within the Campine district, *L. natans* is not evenly distributed and records are scarce in the central part of two of its ecodistricts, the 'Noord-Kempisch kleisubstraatdistrict' in the north, and the 'Oost-Kempisch puinwaaierdistrict' in the central east. In the adjacent Dutch region of Noord-Brabant, the local presence of iron-rich seepage, resulting in low phosphorus availability, was suggested as an explanation for the distribution of the species; moreover a high iron content of its tissue pointed to tolerance of potentially toxic iron concentrations for this species (Lucassen et al. 2007). Seepage of iron-rich water is also common in the Belgian Campine area, especially where the glauconiferous or pyrite-rich fluvial deposits of the Diest Formation (Upper Miocene) are close to the surface. The latter is the main aquifer and lies close to the surface, except in the 'Noord-Kempisch kleisubstraatdistrict', where this formation is covered by sand and clay of the Kattendijk and Kasterlee Formation (Pliocene), and in the 'Oost-Kempisch puinwaaierdistrict', which corresponds mainly to the Campine High Plateau overlain with ancient Meuse deposits (Laga 1996). Thus, the distribution of *L. natans* in its core area might concur with the presence of outcrops of the Diest Formation resulting in high levels of iron and thus low levels of phosphorus. Analyses show that *L. natans* mostly grows where phosphorus is low but also where there is little iron (Leyssen et al. in preparation). Although coprecipitation of metals with phosphorus may be locally important, it seems that other factors, such as lower alkalinity and density of surface waters in seepage-poor areas contribute to the overall distribution of the species.

L. natans was also recorded in the Ardennes, Brabant, Lorraine, Meuse and Maritime districts, but in all cases with only very few, mostly old, records. Van Rompaey & Delvosalle (1978) already listed it as a species restricted to the Campine district, with a few locations elsewhere, similar to inter alia *Hypericum elodes*, *Apium inundatum* and *Eleocharis multicaulis*. *E. multicaulis* often occurs in the company of *L. natans* and we found them in or close to these isolated locations as well. This would imply that the same favourable ecological conditions are locally present or occurred in the past. From a phytogeographical point of view, it is well known that the Ardennes district shares many similarities with the Campine district, and to a lesser degree with the Flemish district. For one thing, they all have the so-called strictly acidophilous species. *L. natans* is not one of these species, but here also the acidity or buffering capacity of soils and water and low phosphorus availability are pointed out as important. Similarly, this appears to be the case in the Brabant district, where the old records (Peruwelz) concern canals in a small area with sandy soils (fig. 2B), not far from 'Mer de Sable' in Stambruges, where glauconite rich sands of the Landen formation lie close to the surface (Depasse et al. 1970). Records are also known from the more calcareous but nutrient-poor fens of the Lorraine (Wijten 1996) as well as from the western part of the Maritime district, in a dune area where iron-rich seepage is also present at places and several species from acidic or oligotrophic environments used to occur. The sites in the Meuse district (ponds in Tamines and Huy) are less easily characterized.

Trends in distribution and current status

From 1800 to 1985, distribution data of *L. natans* in Belgium reflect the general effort devoted to floristic surveying. Indeed, there was a steady increase in floristic activity from 1800, with a marked boost around 1862, when the Royal Botanical Society of Belgium was founded, followed by a decrease between 1888 and 1937. From 1939 on, a second revival occurred, caused by the onset of systematic floristic inventories for the Belgium atlas project. However, records of *L. natans* decreased after 1985 in spite of generally increased floristic attention and even intensive search in the last decade. A decreasing trend of the species in Flanders was already evident from the plant atlas data for 1939–1971 and 1972–2004, respectively, which yielded a trend index of -0.75 when corrected for recording intensity (Van Landuyt et al. 2006). Ronse (2006) suggested that the decline even might have been stronger, because the species disappeared from many sites in the course of the second atlas period. This can now be confirmed: less than one third of all populations observed between 1972 and 1999 still remained after 2005.

L. natans mainly decreased outside its core area, resulting in a smaller distribution range. All but one of the extant populations are situated in the Campine area. Population numbers and size declined also markedly along the southwestern edge of the Campine district (Ronse et al. 2008) in the province of Vlaams-Brabant, which now has only 10% of all populations, all of them small and in a bad state of conservation (Louette et al. 2013). The records outside the Campine district are quite old, except for the Ardennes, where two post-date 1975, including a large extant population occupying more than 280 m^2 and with many flowering plants (L.-M. Delescaille, DEMNA, Gembloux, pers. comm. 2013). A similar strong decrease was reported in more marginal areas elsewhere, e.g. in France, where the species mainly persists in the central and western parts of the country (Bardin et al. 2011). In Germany, it receded to three Bundesländer, becoming extinct in some other regions (Hacker et al. 2008). In Britain, the species holds ground in most of Wales, but declined rather dramatically elsewhere (Lansdown & Wade 2003). In the Netherlands, the species disappeared from several areas as well (Arts et al. 1989, Lucassen et al. 2007), decreasing further since 2007, especially from its outskirts (Anonymous 2012).

Of the thirty extant populations (observed at least once between 2009 and 2012), less than half (43%) has a good local conservation status as far as the species characteristics are concerned. If we look at the numbers per province, we see that local conservation status is good for none of the populations in the province Vlaams-Brabant (n = 3), for 27% of the populations in Antwerpen (n = 11) and 53% in Limburg (n = 15), as well as for the single population in Luxembourg. Moreover, the relative decline of the number of sites per province (number of extant squares with the species divided by the total number of squares) is somewhat lower in Limburg (71%) than in Antwerpen (86%) and Vlaams-Brabant (85%). This shows that the situation is best in Limburg, that has the lowest population density (351 inh/km^2), intermediate in Antwerpen (621 inhabitants/km^2) and worst in Vlaams-Brabant (520 inh/km^2). The only site in the province of Luxembourg, that has the lowest human population density, is in a good condition. Thus it appears that there is some negative correlation between the conservation status and the human population density, an all-in proxy for anthropogenic pressure; however, it is not very strong, and in Vlaams-Brabant the decrease is larger than would be expected based on these numbers.

The two most frequently cited reasons for decline of *L. natans* are anthropogenic eutrophication and acidification, especially for oligotrophic lakes (Bazydlo & Szmeja 2004). In Britain, nutrient enrichment is considered to be one of the main causes in canals and rivers (Willby & Eaton 1993). Both are very much an issue in Belgium as well (e.g. Dumortier et al. 2003a, 2003b, Schneiders et al. 2007). Our result that a number of other species from the same habitat as *L. natans* did not show an equally strong decrease, also indicates that environmental quality rather than habitat availability was key to its decline. In some parts of northern Belgium with carbonate-depleted soils and where deposition of acidifying substances still exceeds critical levels, acidification is likely to have been instrumental. However, soils are more loamy and base-rich and thus less prone to anthropogenic acidification at the southern margin of the Campine district (Menschaert et al. 2002), so this is not a likely explanation here. In addition, the majority of surveyed sites showed little vegetation evidence for acidification (Leyssen et al. in prep.), and thirdly *L. natans* survived at certain sites which underwent periods of severe acidification. We therefore consider acidification not to be the prime reason for its decline. This concurs with Arts (2002) who considers *L. natans* to be one of the more acidification resistant isoetids in the Netherlands, and with Willby & Eaton (1993) who concluded that acidification was not implicated in loss of the species in Britain. Conversely, the large majority of current sites in Belgium show a considerable abundance of eutrophication indicating plant taxa (Leyssen et al. in prep.).

As noted above, the decline of *L. natans* was most notable in its marginal distribution area. This is associated with shorter population persistence, as all but one of the records there lasted less than five years. This could indicate conditions were unfavourable to maintain *L. natans* for longer periods, e.g. with rapid succession, and/or lack of a habitat configuration able to support a lasting metapopulation structure. In the core area, the time span between the first and last observation within a square extended to well over a century, but this may also have involved multiple (sub-)populations. The age of recent populations could be estimated more accurately and ranged from one to 49 years with an average age of ten years. This matches the observation of Lansdown & Wade (2003) that a large proportion of site records represent short-term or failed colonisation events, even though some populations can persist for centuries. They hypothesize that the few sites with large, stable populations act as diaspore sources for dispersal into new suitable habitat. Overall, this would keep occurrence of *L. natans* within a region at any moment restricted to a small number of rivers and lakes.

Differences in population longevity are partly explained by the ecological requirements of the species. Where succession proceeds slowly and disturbance contributes to an open-structured vegetation, such as in oligotrophic wind-stressed lakes, *L. natans* may persist permanently. Although it can be abundant as an early colonizer after physical disturbance in more productive waters, it is out-competed there in later stages by more vigorous species (Willby & Eaton 1993). Long-term persistence in such habitats depends on processes limiting community plant biomass (Greulich et al. 2000). Our data indeed indicate that the average age of populations in flowing water is only half that in standing water. We also assume that reduced traditional maintenance of ponds and ditches exacerbated the effects of eutrophication on *L. natans* occurrence in Belgium.

In spite of the general decline of the species, time and again, new populations are being discovered. In Belgium, more than half of the populations recorded after 2000 are new. In the UK, 17% of all known sites are younger than 1980, and in the Parisian Basin (France) this number amounts to 22% (Lansdown & Wade 2003). In Noord-Brabant (the Netherlands), 55% of all sites with records since 1990 are new, which Lucassen et al. (2007) ascribe to a more intensive floristic recording. However, we found a marked decrease in records since 1985, even with an increased floristic recording intensity. New observations are viewed better in the light of opportunistic colonization attempts and markedly fluctuating population size. Even large and persistent populations may ‘disappear’ completely one year, only to ‘return’ again the next one. Such rapid recovery implies maintenance of a soil seed bank, hence the importance of sexual reproduction (Nielsen et al. 2006). On the other hand, the species can colonize new habitats by means of floating shoots and detached inflorescences, whilst numbers are re-established rapidly by formation of runners or pseudostolons (Barrat-Segretain & Amoros 1996). Dispersal to new sites mainly depends on transport by water, as vegetative shoots are vulnerable to desiccation and only root in very shallow water of less than 4 cm (Nielsen et al. 2006). More occasionally, birds may carry seeds over ground (Fritz 1989, Halvorsen & Grøstad 2002).

In some cases, unintentional introduction by man may explain establishment of *L. natans*. This is very likely the case for its fairly recent appearance in the Belgian Ardennes, in a period when it appeared to be lacking entirely in the South of Belgium. The first record was made here in 1976 in fish-farming ponds. It disappeared in the following years, to be found again in other fish ponds some 20 km away in 2012. In the meantime, fish had been transferred between these ponds (L.-M. Delescaille, DEMNA, Gembloux, Belgium, pers. comm.) and shoots or seeds of *L. natans* were probably inadvertently introduced with them. There is growing evidence of seed dispersal by fish (ichtyochory) for a number of plant species (Pollux 2011) and this may also have been involved in the initial introduction of *L. natans* in 1976, as the site was nearly 150 km apart from the nearest known populations.

In agreement with Nielsen et al (2006) who found that flowering ceased in small populations with the lowest overall genetic diversity, no flowering was observed in Belgian populations with less than twenty ramets. In view of the importance of seed formation for intermittent perennation, this adds to their narrow genetic basis to increase the vulnerability of small populations if they come into a phase where the soil seed bank is depleted.

CONCLUSIONS

The Belgian locations of *L. natans* make up an important part of the total distribution area of the species in Europe, both from a historical perspective and presently. Within the country, the species mainly occurs in the phytogeographical Campine region. Formerly, the species occurred sparingly in six other ± sandy districts, mainly in a small part of the Flemish district along with several other species typical of the Campine district. The longevity of the populations was much higher in the Campine district than elsewhere. Even within this region, the distribution of the species was not uniform, however, but linked to the geology and its influence on (ground) water quality.

Up to 1985, the number of records reflected floristic recording intensity. Hereafter, the species undeniably declined in spite of increased survey effort. The decrease was especially strong outside the core of the Campine area and at present the species is almost completely receded to this stronghold. A marked exception is the recent colonization of a fish-farming pond in the Ardennes, possibly due to inadvertent introduction with fish.

More than half of all remaining populations have a bad conservation status, and there is some negative correlation with the human population density. Our observations suggest that eutrophication, not acidification, might be the main reason for decline of *L. natans* and deterioration of its populations. The persistence of populations is much higher in ponds and lakes than in more nutrient rich streams, where it depends more on physical disturbance, whilst small-scale maintenance of ditches and waterways was reduced. Flowering is reduced in small populations, which may be a problem for their survival, considering the alleged importance of sexual reproduction for this species. As many of the remaining populations are already quite small, conservation of the species requires special attention.

SUPPLEMENTARY DATA

Supplementary data are available as Excel files at *Plant Ecology and Evolution*, Supplementary Data Site (http://www.ingentaconnect.com/content/botbel/plecevo/supp-data), and consist of: (1) all known records of *Luronium natans* in Belgium until 2013 per 16 km^2-square, including the first and last year of observation and its presence in different time periods; and (2) all known records (also negative observations) per population or 1km^2-square from 1972 to 31 Dec. 2012. Both files display a data sheet and a legend sheet that explains the variables of the data sheet.

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