Instability in newly-established wetlands? Trajectories of floristic change in the re-flooded Hula peatland, northern Israel

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SUMMARY

Drainage of the 6,000 ha Hula Lake and peatland in northern Israel in the late 1950s caused the loss of a very diverse and rare ecosystem and an important phytogeographic meeting zone for Holarctic and Palaeotropical species. Draining the Hula peatland was only partially successful in creating a large fertile area for cultivation, and in 1994 this led the authorities to re-flood 100 ha of the valley—the Agamon (Agmon)—with the aim of rehabilitating the diverse wetland landscape, promoting ecotourism and creating a clear-water body that would contribute to the purification of Lake Kinneret. The vegetation of the restored wetland was monitored for ten years (1997–2006), recording the establishment and abundance of vascular plant species. More than 20 emergent, submerged and riparian species became established. Like a number of other shallow-water wetlands, the Agmon is characterised by considerable ecological fluctuations. This has been expressed in prominent floristic changes in the Agamon since it was created. An increased abundance of *Ceratophyllum demersum* and *Najas minor* and a decline in *Potamogeton* spp., *Najas delilei* and filamentous algae have been observed. A long-term decline in water level and sediment accumulation has brought about a significant rise in the incidence of *Phragmites australis*, *Typha domingensis* and *Ludwigia stolonifera* in the south-eastern area. A GIS analysis of changes in species dominance shows fluctuations over the years, with only a partial trend of succession towards a *P. australis*, *T. domingensis* and *L. stolonifera* community.

KEY WORDS: *Ludwigia stolonifera*; macrophyte; peatland restoration; *Phragmites australis; Typha domingensis*; wetland stability

INTRODUCTION

The drainage of the 6,000 ha Hula Lake and peatlands in northern Israel in the late 1950s resulted in the loss of a very diverse and rare ecosystem and an important phytogeographic meeting zone for holoartic and palaeotropical species. The wetland complex was an important feeding station for migrating birds, a wintering area for many species and a breeding ground for others. The flora was described as diverse, with thickets of *Cyperus papyrus* and clear waters with *Nymphaea alba* and *Nuphar lutea* (Washbourn & Jones 1936, Zohary & Orshansky 1947).

The establishment of the 320 ha Hula Reserve in 1958 promoted partial rehabilitation of an area of the original habitats, but not of the ecosystem as a whole; nor did it prevent the extinction of species (Livneh 1999). The aim of draining the Hula peatland to reclaim a large fertile area for cultivation was only partially successful. Oxidation, wind erosion and underground fires resulted in soil subsidence (Shaham 1994). Moreover, the fields tended to produce vegetative growth due to nitrate surplus, restricting farmers to hay production (Shaham 1994). Given predictions that the subsidence would continue, in 1994 the authorities reflooded 100 ha of the drained peatland and established approximately 300 ha of shallow lake, wetland and grasslands—the Agamon (Agmon). The aim was to rehabilitate the wetland ecosystem and create an area that would attract ecotourism, provide a compensatory income for local farmers, and create a clear-water body contributing to the purification of the water flow to Lake Kinneret, Israel’s largest freshwater reservoir.

The restoration and the flora in the new Agamon lake and its environs have been described by Henkin *et al*. (1997), Kaplan & Oron (1997), Kaplan *et al.* (1998) and Kaplan & Niv (1999, 2000, 2001, 2002, 2003, 2004). A comparison with botanical descriptions from the first half of the twentieth century, before drainage took place (Washbourn & Jones 1936, Zohary & Orshansky 1947), indicates that 44 wetland and riparian species were established after restoration, 33 of which were recorded in the wetland prior to drainage (Kaplan & Oron 1997).

Monitoring of the Agamon vegetation began in 1996 (Kaplan & Oron 1997), with two objectives: to describe the flora and related dynamics of the Agamon; and to estimate the contribution of the flora to the nutrient content of the lake and the water flowing out of it, which is used for agriculture. At the same time, other researchers monitored additional ecological variables in Lake Agamon. Markel *et al.* (1997) studied the biogeochemistry of the lake and Kadmon *et al.* (2010) monitored and analysed sediment accumulation in the years 1994–2009, reporting data for the whole lake but most prominently for its southern and eastern parts.

Like several other shallow-water wetlands, the Agamon is characterised by considerable ecological fluctuations (Hambright & Zohary 1998) including variability in macrophyte communities (Kaplan *et al.* 1998, Kaplan & Niv 1999, 2000, 2001, 2002, 2003, 2004). These fluctuations can be ascribed to temporal changes in the geochemistry of the Agamon's sediment (Markel 1998, Ashkenazi *et al.* 1999). Ashkenazi *et al.* (1999) reported that nutrient availability in Lake Agamon varied significantly from year to year and exhibited strong seasonality. For example, total P concentrations were low in winter (0.2–2.0 μM) and high in summer (1.5–8.0 μM), whereas nitrate concentrations were extremely high in early 1995 (2,000–3,000 μM) but quite low towards the end of 1996 (2–30 μM). Ashkenazi *et al.* (1999) reported *Typha* dieback in the Agamon, which they attributed mainly to sulphide toxicity in the transition zone between the anaerobic lower sediment layers and the aerobic upper layer of the rhizosphere. They developed a conceptual model that explained sulphide formation as a result of physicochemical processes. The *Typha* dieback began with the transport of a large quantity of floating filamentous algae debris into the south-eastern corner of the lake. This resulted in an increase in the volume of organic matter, causing a high level of dissolved organic carbon (DOC) and supporting intensive microbial activity which, in turn, released sulphide and ferrous (FeII) ions. The increase in sulphide concentration was greater than the rate of FeS precipitation, which brought about sulphide toxicity in the rhizosphere. Concurrently, the strong reducing conditions facilitated intensive denitrification, which created another stress in the form of N deficiency. Gophen (2000a) showed a high correlation between the location of *Typha* habitat and P availability and on this basis proposed a different model, linking the *Typha* dieback to acute P deficiency.

Van der Valk (1981) argued that any change in the relative abundance of species is a successional change in freshwater wetlands, even when there is instability in the successional pathway due to water-level changes (Galatowitsch & van der Valk 1996). Middleton (1999) found a cyclic succession of up to 25 years in restored wetlands and showed that a succession pathway can be interrupted by anthropogenic or natural changes in factors such as climate, water level and nutrient flux, resulting in unstable plant communities. In most habitats—terrestrial ecosystems as well as wetlands—a directional succession towards a climax or prevailing climax is believed to take place (Shimwell 1971, Miller 2005).

Prominent changes in the flora of the Agamon have been recorded since its establishment. Kaplan & Niv (2004) noted an increased abundance of *Ceratophyllum demersum* and a decline in *Potamogeton nodosus*. Kaplan & Oron (1997) examined the collapse of certain annual species such as *Najas delilei*, *Potamogeton* spp., filamentous algae and *Typha domingensis*. As mentioned earlier, the collapse of the last of these may be related to geochemical factors (Markel *et al.* 1997), but may also be due partly to the consumption of the leaves by *Myocastor coypus* (coypu) (Ashkenazi *et al.* 1999, Gophen 2000b).

Some plant species have been re-introduced. Of these, *Potamogeton pectinatus*, *Utricularia australis* and *Marsilea minuta* were unsuccessful; two species (*Nuphar lutea, Butomus umbellatus*) partially survived, and the others (*Nymphaea alba, Ludwigia palustris, Iris pseudacorus, Cyperus papyrus*) flourished. Spontaneous establishment was documented for submerged and emergent species (six *Potamogeton* and two *Najas* species), and for other aquatic species that had not been observed in Israel since the drainage, but several of them disappeared rapidly (Kaplan *et al.* 1998).

The objectives of this study were to investigate the flora and dynamics of the Agamon in conjunction with other studies of sedimentology and geochemistry, in order to contribute to a better understanding of long-term processes in the ecosystem. In particular, it was hoped that this would further our ability to achieve the goals set for re-flooding and to test the hypothesis that the Agamon, like several other shallow-water wetlands, is characterised by considerable ecological fluctuations which are expressed in its macrophyte dynamics.

METHODS

Plant units of the 100 ha Agamon lake, defined by the three most abundant species in a polygon, were mapped on the basis of rectified low-altitude aerial photography (ground resolution 25 cm) produced in July or August of each year, according to the following procedure:

1. Stratigraphical analysis of the photo-map was performed using a GIS program (ArcView 9.2) and polygons were drawn of uniform plant groupings that could be visually detected.
2. Two plant surveys were conducted in the Agamon area in July and August of each year from 1997 through 2006. The plant groupings identified by GIS analysis were characterised, verified and marked on the map. In 1998, only one plant inventory was carried out.
3. Plant units were sampled in 50 permanent 1×1 m plots in the lake and an additional 6–12 transects across the lake (300–800 m long), selected each year to cover all the recognisable units in the photomap. In each sample and transect, the relative cover of plants in the plot or the transect–polygon intersection, respectively, was recorded and the three dominant plants were selected to characterise the unit. Superposition of the annual polygon maps resulted in 7652 polygons. Therefore, the annual maps were transformed to a raster grid of 10×10 m, and a GIS analysis was conducted by comparing the number of changes of the dominant species in each 10×10 m pixel across the 10 years of vegetation mapping. The 'count' of changes referred to changes from one year to the next (compared with the previous year's pixel content) and to episodic pixel change, i.e. the number of years in which the same species/vegetation unit appeared in a given pixel, regardless of its temporal order.

RESULTS

Table 1 presents the list of species found in the water of the Agamon in the years 1997–2006. The flora of the lake was characterised by yearly fluctuations of species dominance, with *C. demersum* and *P. nodosus* the dominant species in the water body in most years. Patches of *L. stolonifera* had also established themselves, especially on bars created by the accumulation of silt and the low water level. The *L. stolonifera* re-established itself on land in the spring of each year, and crept into the water during spring and early summer, especially in June. The dominant phenomenon was the establishment of clumps, mainly of *P. australis* (60–80 % of the clump) on the mud bars or close to the banks. *T. domingensis* was also found (20–40 %) in these clumps, as was *L. stolonifera* (30–40 %), particularly closer to the water. A long-term decline in the water level evidently brought about a significant rise in the incidence of *Phragmites australis*, *Typha domingensis* and *Ludwigia stolonifera* in the southern part of the lake. *Potamogeton nodosus*, *C. demersum* and *N. minor* were also found in localised spots with higher coverage.

The episodic appearance of some species, such as *Potamogeton trichoides* and *Zannichellia palustris*, was prominent; while some riparian species, such as *Polygonum lapathifolium* and the very rare *Polygonum lanigerum,* became established, as did the tropical *Cyperus odoratus,* reported as a new invader plant in Israel (Dufour-Dror 2010).

The GIS analysis of changes in species dominance indicated directional succession over the season, but also fluctuations between years, with only a slightly directional trend of the *Phragmites australis*, *Typha domingensis* and *Ludwigia stolonifera* community.

The cover of each of the main plant species found in the water in the years 1999–2006 is shown in Figure 1. The instability and fluctuation over the years is prominent for *Ceratophyllum demersum, Najas minor, Potamogeton nodosus* and most of the other species, with the *Phragmites australis-Typha domingensis* plant unit being an exception.

Figure 2 presents the cover of the *Phragmites australis*, *Typha domingensis* and *Ludwigia stolonifera* community in the Agamon in the years 2000 and 2005. During these five years, cover increased constantly within individual polygons. In contrast, other species were unstable over time, with individual species occurring in new locations each year, as shown in Figures 3 and 4 for *Ceratophyllum demersum* and *Najas minor,* respectively, with somewhat greater abundance of *Najas minor* in the north-eastern parts of the Agamon.

Figures 5–8 show the stability gradient represented by the number of changes in dominant species (Figures 5–6) or vegetation units (Figures 7–8) over the years. These data demonstrate the same trend of only slight alternation in the south-eastern part of the peatland—where a clear succession took place—and in the north-western part, where *Najas minor* showed some stability; and a high number of alternations in most other parts. The alternation of the vegetation unit (assembly of three dominant species) over the years was higher than that of the dominant species. The alternation based on temporal appearance of the species in consecutive years was greater than the change based on their appearance in the same pixel, regardless of their temporal order.

Table 1. Plant species found in the water of the Agamon in the years 1997–2006.

	Sampling Year									
	1997	**1998**	**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Submerged & emergent species										
Filamentous algae	+	+	+	+	+	+	+	+	+	+
Potamogeton berchtoldii	+	+	+	+	+	+	+	+		
Potamogeton crispus	+	+	+	+	+	+	+		+	
Potamogeton pectinatus	+		+		+		+			
Potamogeton trichoides					+	+				
Potamogeton nodosus	+	+	+	+	+	+	+	+	+	+
Najas delilei	+	+	+	+						
Najas minor	+	+	+	+	+	+	+	+	+	+
Typha domingensis	+	+	+	+	+	+	+	+	+	+
Phragmites australis	+	+			+	+	+	+	+	+
Ceratophyllum demersum	+	+	+	+	+	+	+	+	+	+
Riparian species										
Polygonum lapathifolium							+		+	+
Polygonum lanigerum									+	+
Eclipta alba									+	+
Cyperus fuscus					+	+	+	+		+
Cyperus papyrus	+	+	+	+	+	+	+	+	+	+
Lycopus europaeus					+	+			+	+
Paspalum paspalodes					+	+		+	+	+
Cyperus odoratus					+		+	+	+	+
Zannichellia palustris	+		+							
Ludwigia stolonifera								+	+	+

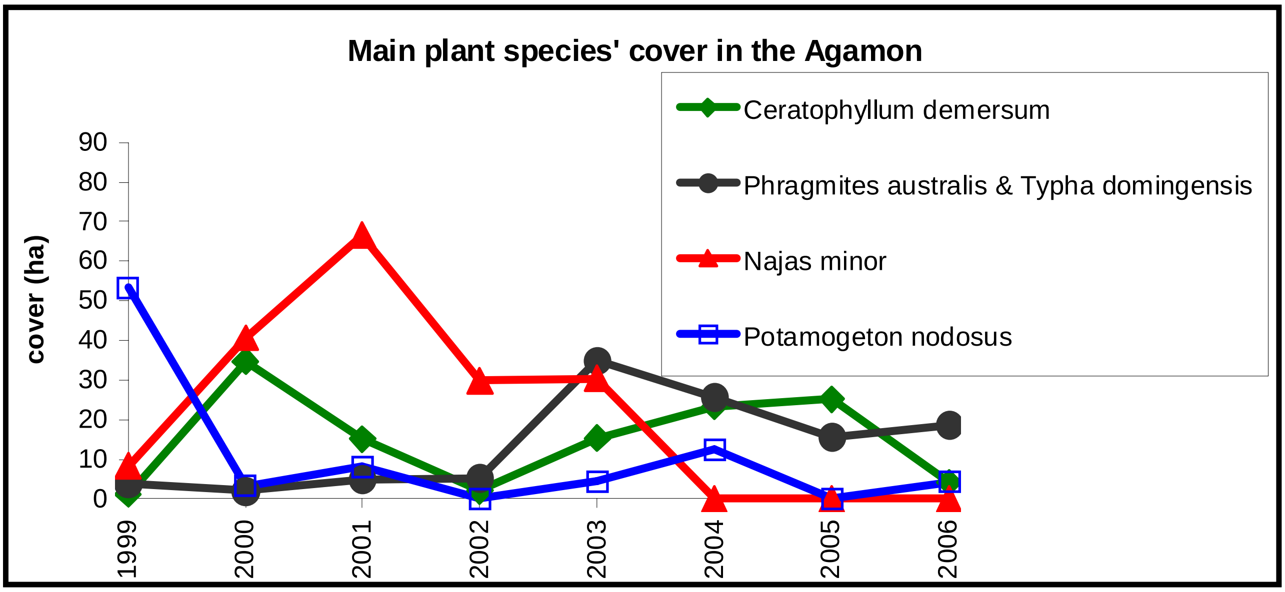

Figure 1. Cover of main plant species found in the water of the Agamon, 1999–2006.

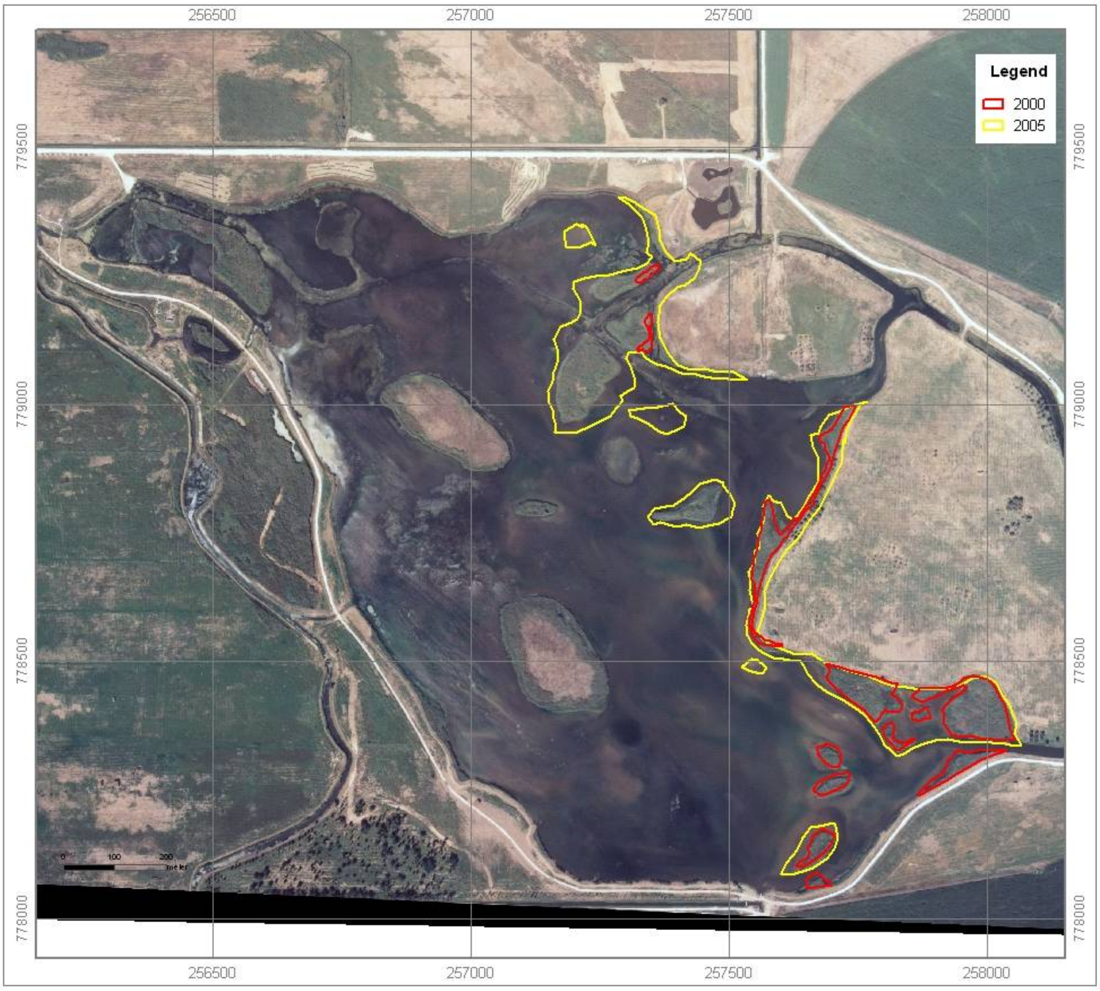

Figure 2. Cover of the *Phragmites australis*, *Typha domingensis* and *Ludwigia stolonifera* community in the Agamon in the years 2000 and 2005, overlaid on a 2005 photomap.

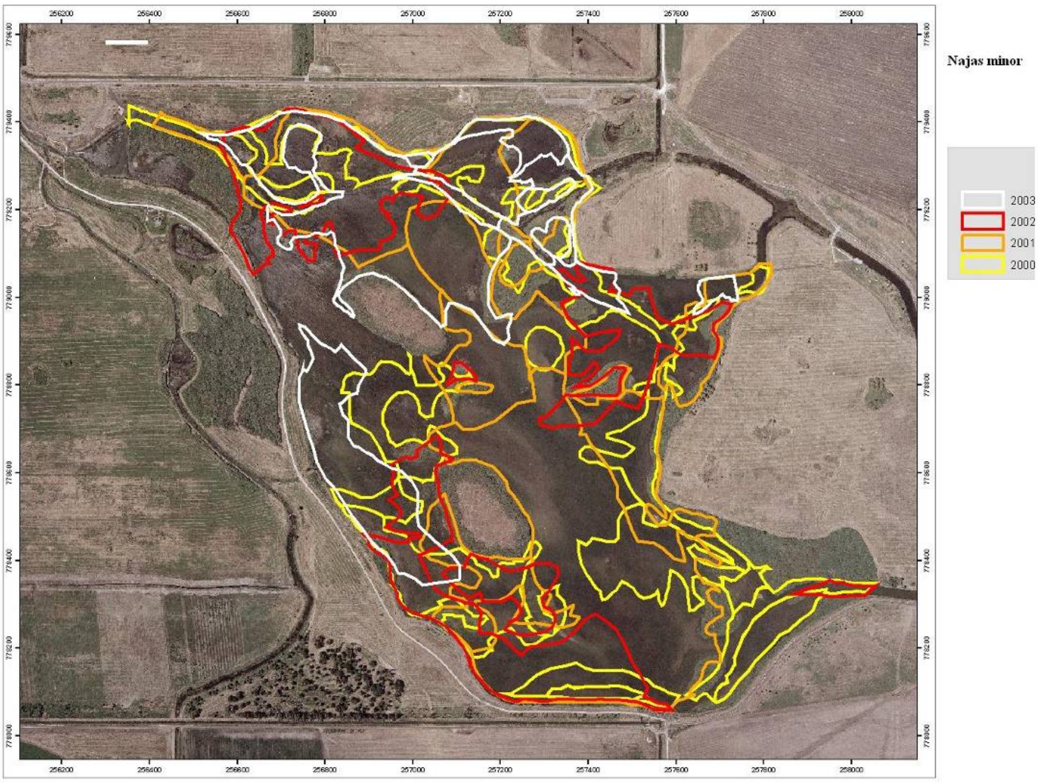

Figure 3. *Najas minor* cover in the Agamon in the years 2000–2003, overlaid on a 2005 photomap. The scale bar at the top left represents a distance of 100 m.

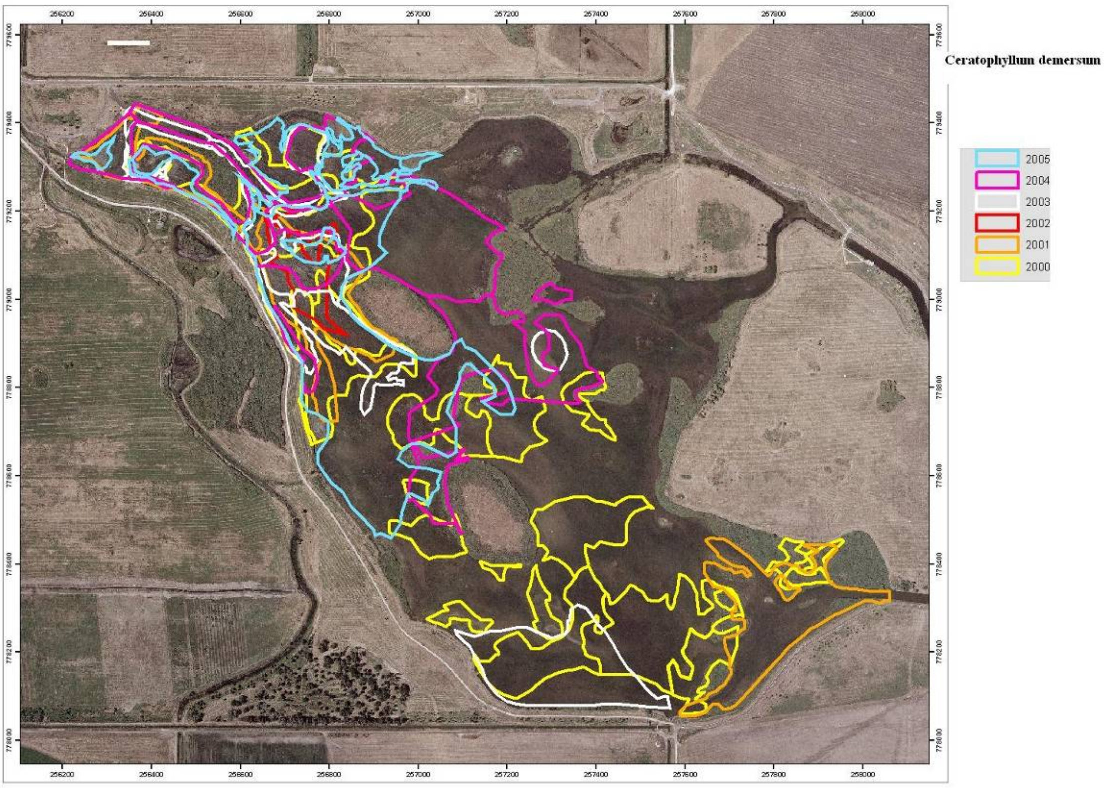

Figure 4. Cover of *Ceratophyllum demersum* in the Agamon in the years 2000–2005, overlaid on a 2005 photomap. The scale bar at the top left represents a distance of 100 m.

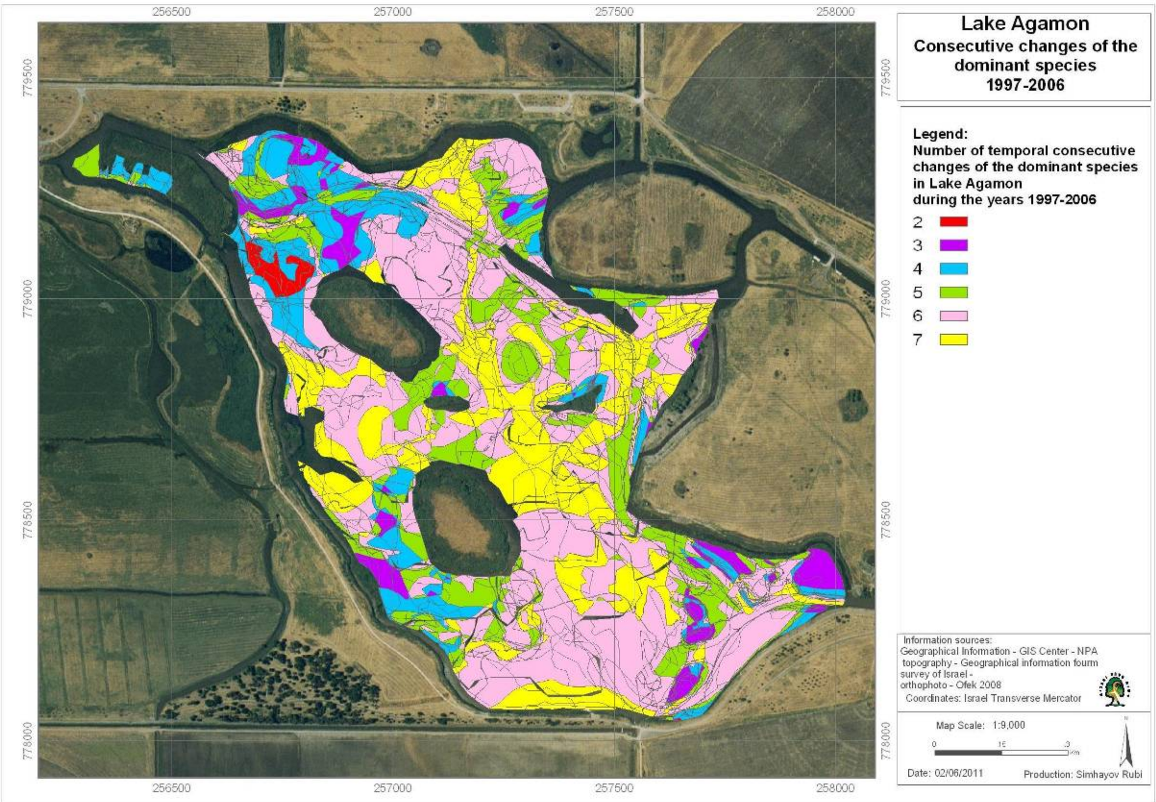

Figure 5. Number of consecutive temporal changes of the dominant species in the Agamon, in 10×10 m pixels during the years 1997–2006.

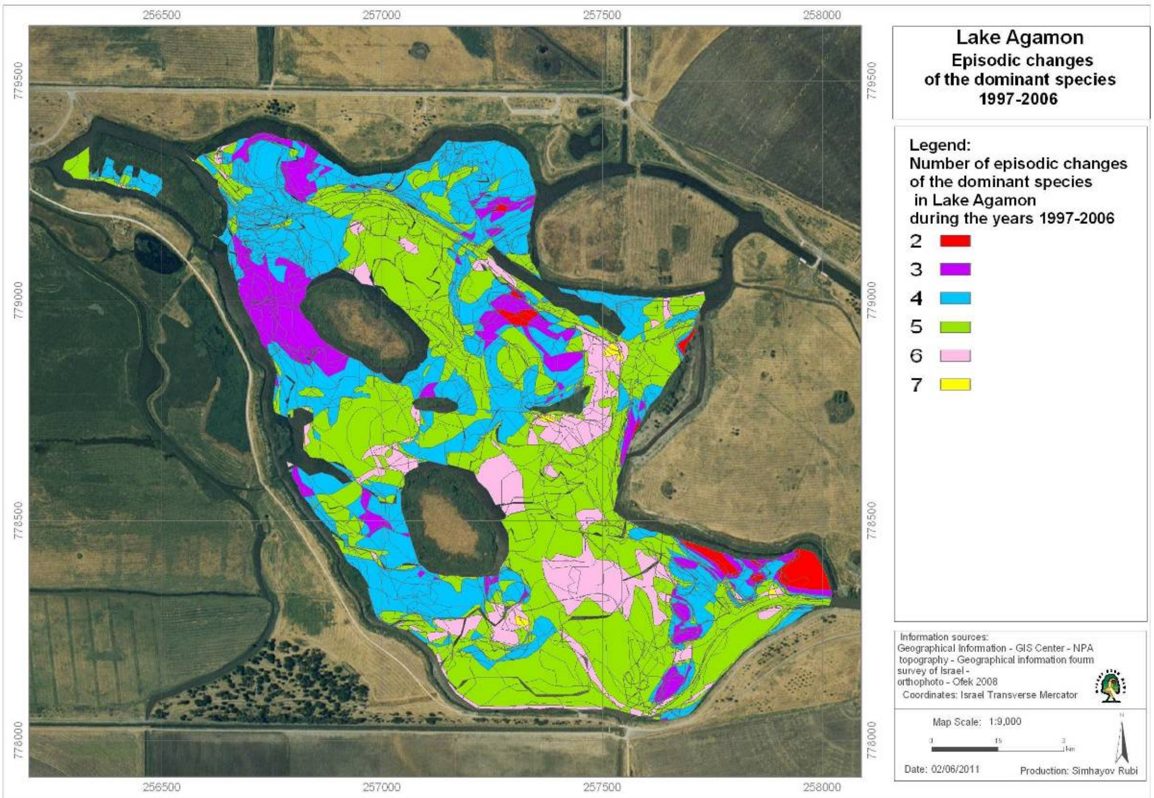

Figure 6. Number of episodic changes of the dominant species in the Agamon, in 10×10 m pixels during the years 1997–2006.

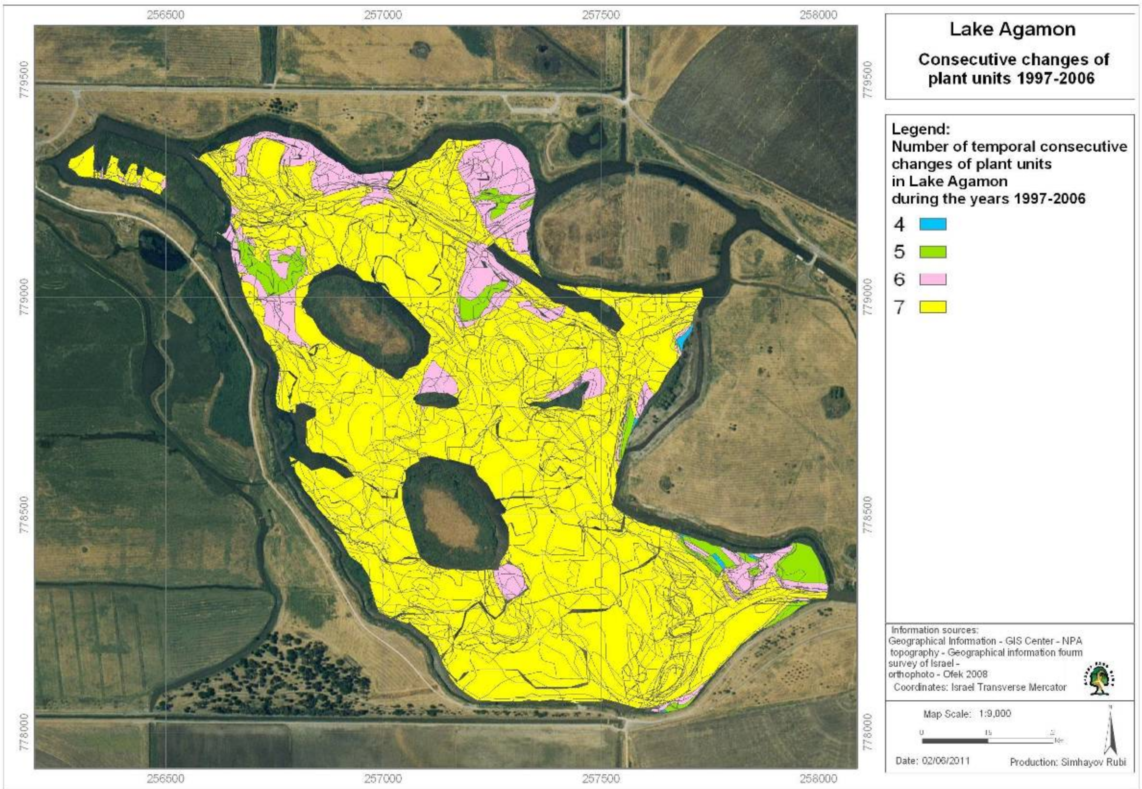

Figure 7. Number of consecutive temporal changes of plant units in the Agamon, in 10×10 m pixels during the years 1997–2006.

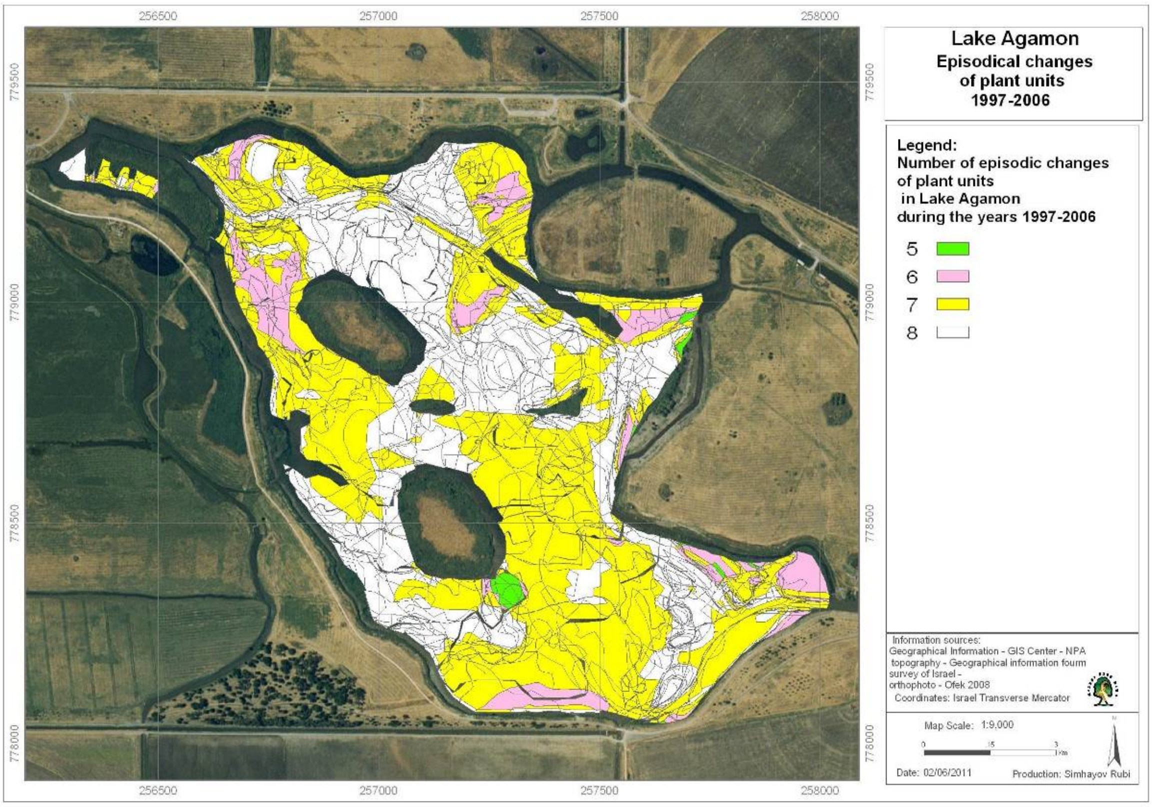

Figure 8. Number of episodic changes of plant units in the Agamon, in 10×10 m pixels during the years 1997–2006.

DISCUSSION

In created wetlands in Wisconsin, *Typha* spp. accounted for 15 % of the cover of native wetland species in one-year-old wetlands; and this increased to 55 % in three-year-old wetlands. It was predicted that near monocultures of *Typha* spp. would develop at the margins of naturally colonised wetlands (Reinartz & Warne 1993). On the basis of 40 years of experience in wetland restoration in Central Europe, it was concluded that the restoration process very often simply proceeds along successional pathways; however, it has also been shown that a certain degree of unpredictability must be assumed. Unexpected changes may also arise from intrinsic species fluctuations or the arrival of invasive species (Klötzli & Grootjans 2001).

The instability of a small lake like the Agamon is expressed through the incidence of macrophytes**.** The only directional succession trend towards a stable composition observed in the Agamon peatland is in the *Typha domingensis–Phragmites australis–Ludwigia stolonifera* thickets, where sediment accumulation has also been demonstrated (Kadmon *et al.* 2010). It seems that the accumulation of a muddy shallow-water substrate and bars has contributed to the stability of this niche. Most of the instability may be unexpected in a newly restored wetland, where ecological changes and unpredicted species fluctuations may occur, as reported by Klötzli & Grootjans (2001) and Hambright & Zohary (1998).

Different species periodically assume dominance in the lake, especially in the cases of *T. domingensis, P. nodosus* and two species of *Najas*. In later years, *N. delilei* disappeared altogether, and *N. minor* has become the dominant submerged plant, together with *C. demersum*. The succession of the species over the season contributes an additional aspect to the dynamics of the system. It would be very interesting to follow up this study in order to ascertain whether stabilisation of the system becomes a part of the dynamic balance, or alternation between species prevails as the dominant phenomenon.

Water level, sediment accumulation and water and sediment geochemistry are being monitored, providing a prime opportunity to investigate the correlations of these variables with the dynamics of the vegetation. The better understanding of the system thus gained would enable more appropriate management of the lake towards meeting the goals of restoring the diverse wetland ecosystem and improving the quality of water delivered to Lake Kinneret.

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