Research

Oikos 118: 1687–1694, 2009
doi: 10.1111/j.1600-0706.2009.17650.x,

Subject Editor: Heikki Setälä. Accepted 25 May 2009

Biological activities as patchiness driving forces in wetlands of northern Belize

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Patchiness in wetlands is a common and well documented phenomenon. Oligotrophic wetlands of northern Belize display noticeable vegetation heterogeneity at both large and small scales. In this paper, we document the small scale patches in herbaceous wetlands, describe differences between patches and surrounding wetland habitats and explain patch formation and sustenance.

We conducted a survey of patches and confirmed their occurrence by spatial analysis. Patches were distinguished from a surrounding wetland by denser and taller vegetation, higher amount of empty snail shells and elevated soil phosphorus (P). Plants in patches had higher tissue nitrogen (N) and P content and there was also higher total N and P per m^2 incorporated in plant biomass. In terms of stable isotopes, plants in patches were enriched in ^{15}N; patch soils were depleted in ^{13}C.

Observations of focal individuals of *Aramus guarauna*, limpkin, a wading bird feeding almost exclusively on snails, revealed the origin of the snail shell piles frequently found in patches. An adult limpkin captured on average 18 snails daily, of these 80% were handled in patches and birds often repeatedly used the same patch.

Experimental patch creation by adding chicken manure or P to 1 m^2 plots resulted in higher and denser vegetation with values increasing in order: control, P, manure plots. The effect was significant at both experimental locations six months after the treatment and at one location even 40 months after the treatment.

We present a simple mechanistic explanation for nutrient redistribution in wetlands and their eventual accumulation in patches. Both nutrient and isotopic differences result from animal input into patches, e.g. bird droppings or prey remnants. Foraging activity of *Aramus guarauna* is most likely responsible for patch formation. A positive feedback (repeated use of a suitable patch) is apparently the mechanism sustaining patches in these marsh environments.

Vegetation heterogeneity called patchiness is displayed in many wetland systems worldwide. In tropical and subtropical regions, among the most prominent examples of wetland patchiness are the Florida Everglades, Pantanal in Brazil, and Okavango Delta in Botswana (Loveless 1959, Prance and Schaller 1982, Diniz de Araujo Neto et al. 1986, Ellery et al. 1990, Wetzel et al. 2005). Both abiotic and biotic mechanisms causing patchiness have been documented, and in many cases the two mechanisms interact. The abiotic causes include raised topography in otherwise flat wetland, groundwater discharge or uneven soil conditions (Ellery et al. 1990, Sklar and van der Valk 2002). The biotic mechanisms include positive plant interactions or facilitation (Callaway 1995) or animal activities (DeOliveira 1992).

Oligotrophic wetlands of northern Belize, Central America are a part of the limestone-based complex of marshes that cover extensive areas of the Yucatan Peninsula. Large-scale patchiness is represented by small tree islands in otherwise macrophyte dominated marshes. In addition, prominent small scale patchiness is also apparent in many marshes. No information is known about causes and processes leading to the formation and sustenance of small scale patchiness in these wetlands. Belizean marshes are dominated by emergent macrophytes of genus *Eleocharis*, with other species including genera *Cladium*, *Typha* and *Rhynchospora*. Among these, *Eleocharis* forms large homogeneous almost monodominant stands with a noticeable patchiness in form of denser and higher plant clumps conspicuous for their abundance of empty snail shells.

A large operculate apple snail, *Pomacea flagellata* (mean $\pm$ SD aperture size $= 27 \pm 3$ mm, mean $\pm$ SD shell length $= 37 \pm 7$ mm), is an abundant inhabitant of Belizean wetlands. It feeds on plant tissue (Lege 2001) and behaves similarly to *Pomacea paludosa*, described from the Everglades (Sharfstein and Steinman 2001, Darby et al. 2002). *Pomacea* is the prey of numerous snail-eating animals, including diverse avifauna. Among them, two bird predators are almost exclusive food

specialists: *Rostrhamus sociabilis*, snail-kite and *Aramus guarauna*, limpkin (Reed and Janzen 1999). While snail-kite piles the shells under its preferred perch, limpkin creates piles throughout a wetland. The majority of shells in these piles are perforated because, contrary to snail-kite, limpkin extracts snail tissue by a couple of hard blows to the shell (Tanaka et al. 2006), thus making these shells easily distinguishable.

A simple way to reveal different degree of processes happening within a nutrient limited ecosystem is a measure of nutrient concentrations in different system components. A use of ecosystem markers, e.g. stable isotopes, represents another elegant method to elucidate different processes in the ecosystem (Dawson et al. 2002). Although the most important nutrient in our case (P) lacks its stable isotopes, the use of other elements constituting living tissue (carbon, C and N) is feasible to trace the nutrient circulation in the system (Fry 2006). Measures of both ^{13}C and ^{15}N represent a method commonly used in nutrient circulation descriptions in tropical and subtropical wetlands (Fellerhoff 2002, Williams and Trexler 2006).

In this study, we will investigate the degree and scale of patchiness in selected marshes of northern Belize. We will then characterize differences between patch and surrounding wetland habitats and explain patch formation and sustenance. Through both the observations and manipulative experiments, we gathered data to support our working hypothesis: in the dry season, *Pomacea* snails cluster in shrinking water areas and are foraged upon by limpkins. The piles of shells are formed throughout the wetland. Bird droppings and prey remnants increase the nutrient status of these places. The nutrients are eventually utilized by plants that then form denser and taller stands, which result in patches. We further expect that these bird activities are reflected into nutrient status and isotopic composition of both macrophytes and soils in patches in terms of $\delta^{15}N$ and $\delta^{13}C$ values respectively.

Material and methods

Study sites

We selected three locations in a large wetland system in northern Belize. We conducted a patchiness survey in large Quiet marsh (58 ha; 18°10′N, 88°31′W). We established manipulative experiments in Quiet marsh and Buena Vista marsh (75 ha, 18°14′N, 88°31′W). None of these two large marshes was suitable for bird observations (for their large surface) and thus we observed the avian predator behaviour in a small Calabash marsh (4.9 ha, 18°27′N, 88°28′W).

The selected marshes are characterized by a dominance of *Eleocharis cellulosa* and *Eleocharis interstincta*, water conductivity in the range of 1000–1500 μS, and similar water level fluctuations ranging from completely flooded (up to 1.5 m) to almost completely dry. Sediments are composed of peaty marls with total N and P content of 3.3 mg cm^{-3} and 0.08 mg cm^{-3} respectively, indicating a strong P limitation (Rejmánková 2001). For a more detailed description of soil, hydrology, climate and vegetation of marshes of northern Belize see Rejmánková et al. (2008).

Patchiness survey

In 2002, we measured 60 patches and 12 control plots (2.25 m^2) in about 200×50 m area of Quiet marsh. We arbitrary defined a patch as a clump of dense vegetation with minimal size of 1 m^2, while control plots were randomly selected in between patches. We recorded vegetation height, live and dead stem density (averaged from three 20×20 cm counts) and collected and counted empty snail shells. Plant material for nutrient analyses originated from 12 randomly selected paired plots.

In 2006, we selected a 50×50 m area to quantify the patchiness on a precise scale (unit size: 1 m^2). In each unit, we recorded the average water level and vegetation height, live and dead stem density per inner 20×20 cm and we searched and counted living snails and empty snail shells. We measured patch elevation as a distance between soil and water surface when all patches were flooded.

Limpkin observations

We observed focal individuals of limpkin from a tree observatory at the wetland edge in March–April 2004 and 2006. Total observation time was 63 h of bird activities (episodic observations shorter than 20 min we excluded from the analyses). We could not avoid repeated observations of same individual; however, we observed a minimum of 14 different bird individuals (sighted simultaneously in the marsh area). We distinguished five main activities such as (1) resting (i.e. passive standing with no moves), (2) moving (i.e. walking through vegetation but without searching for prey), (3) foraging (i.e. active searching for snails in various vegetation types and returning with prey; foraging differs from moving by low speed of the steps and probing moves), (4) eating (including prey handling) and (5) grooming (e.g. preening, feather ruffling, bill cleaning). We recorded limpkin activities, their duration and location in a wetland (i.e. open water, sparse vegetation, dense vegetation, patch and *Cladium* thicket). Sparse vegetation is characterized by scattered *Eleocharis* shoots (<150 shoots m^{-2}) with large portion of open water. Dense vegetation consists of small portion of open water and regular cover of *Eleocharis* shoots. A patch is a clump of dense vegetation (>500 shoots m^{-2}) with no open water and *Eleocharis* shoots elevated over surrounding vegetation. *Cladium* thicket represents tall dense vegetation consisting of different species dominated by *Cladium jamaicense*.

Experimental patch creation

We selected two 30×10 m areas with homogeneous *Eleocharis* for experimental chicken manure and P addition in two different wetlands in August 2003. The areas consisted of 60 (1 m^2) permanent plots with 1 m buffer at each side. We randomly assigned them one of each treatments, manure, P and control, and each treatment was replicated 20 times. We installed plastic walls around each plot before treatment application and we left them in place for 48 h by which time the applied nutrients were already incorporated in various ecosystem components (Rejmánková 2001). We added chicken manure (250 g

fresh weight) simulating bird droppings with the total P content of 1.6 g and 3 g of P (as KH_2PO_4) into plots in a single addition. The amount of chicken manure we chose as an equivalent of 75 g fresh weight of droppings from a rooster nourished by snail meat (Macek unpubl.). We recorded water depth and vegetation height as well as the number of live and dead shoots per 20×20 cm in each plot prior the treatment, 6 and 40 months (in 2004 and 2006) after treatment application. We carried out the last measurement at Buena Vista location only, because fire damaged permanent plots at Quiet marsh.

Nutrient analyses and isotopic composition

Shoot tissue and chicken manure we dried at 70°C, ground and assayed for total N with an elemental analyser. Total P we measured spectrophotometrically using ascorbic acid reduction of phosphomolybdate complex after combustion and consequent acid digestion (McNamara and Hill 2000). For comparisons of PO_4-P content in soil of 12 patches and 12 control plots we used anion exchange membranes (Cooperband and Logan 1994). We exposed the membranes (25×25 mm, three replicates) vertically in sediments (10 cm deep) for 11 days. After the exposure, we rinsed the membranes in H_2O and kept moist and refrigerated until processing. We extracted PO_4-P from anion exchange membranes using 1 M NaCl, then we analysed it spectrophotometrically by ascorbic acid reduction of phosphomolybdate complex (American Public Health Association 1985).

For isotopic composition we analysed the oven dried samples of four important marsh constituents: emergent macrophytes (*Eleocharis cellulosa*), soils originating from below sparsely vegetated marsh and below patches (upper soil layers without plant remnants, 1–5 cm deep), apple-snail tissue and snail-eating bird droppings. We analysed carbon and nitrogen isotope ratio ($\delta^{13}C$ and $\delta^{15}N$) using an elementar analyser linked to isotope ratio mass spectrometer. The obtained $^{13}C/^{12}C$ ratios of all samples, Rp, we referenced to $^{13}C/^{12}C$ of standard VPDB (Vienna-Pee-Dee Belemnite), Rs, and expressed as $\delta^{13}C = (Rp/Rs–1) \times 1000$ in ‰. We expressed $\delta^{15}N$ for $^{15}N/^{14}N$ ratios (referenced to atmospheric N_2) in a similar way. The standard deviation of $\delta^{13}C$ and $\delta^{15}N$ determination in standard samples was lower than 0.1‰ and 0.2‰ respectively.

Data analyses

For patchiness quantification we used spatial analysis by distance indices method (Perry 1995). In this method, we counted the clustering index v_i for each unit as a measure of the degree to which the unit contributes to clustering, as a member of a group of donor units that constitute a patch (positive clustering). Similarly, we counted the clustering index v_j to measure the negative clustering, presence of a gap (Perry et al. 1999). We based our tests on 45 random permutations. We considered the absolute indices values greater then 1.5 as contributing to cluster formation and the values close to unity indicating random placement of the unit in relation to others nearby. The other patchiness survey data we analysed using regression and student's t-test. For manipulative experiment evaluation we used ANOVA with post-hoc comparisons among treatments (Tukey HSD test). Finally, we used PCA (principal component analysis) in the CANOCO package (ter Braak and Šmilauer 2002) to visualize limpkin activities together with their timing in the day and location in the wetland vegetation. Each focal sample of continuous activity constituted a row in input matrix (when one activity took place in two distinct locations, it was considered as two rows), resulting in total of 382 rows.

Results

Patchiness survey

The number of live *Eleocharis* shoots in the 50×50 m plot showed highly significant patch and gap arrangement ($p < 0.001$). Mean clustering indices v_i and v_j were 3.13 and −3.32 respectively. Gaps were present on 48% of the area, patches covered 16.5% of the area, the rest, 35.5%, was randomly covered by live shoots (Fig. 1). Surveyed patches were characterized by denser *Eleocharis* shoots, both live ($t = 7.05$, $p < 0.001$) and dead ($t = 4.87$, $p < 0.001$, Fig. 2). The shoots were also taller than those in control plots ($t = 10.93$, $p < 0.001$). Shoot height and shoot density were positively correlated ($R^2 = 0.53$, $p < 0.001$). The amount of empty snail shells in patches was an order of magnitude higher than in control plots, (means: 21 and 2 shells m^{-2}, respectively; $t = 4.56$, $p < 0.001$). No trends were found in numbers of living snails (data not shown). Average patch size was 2.5 m^2. Patches were slightly elevated (2.9 cm) over

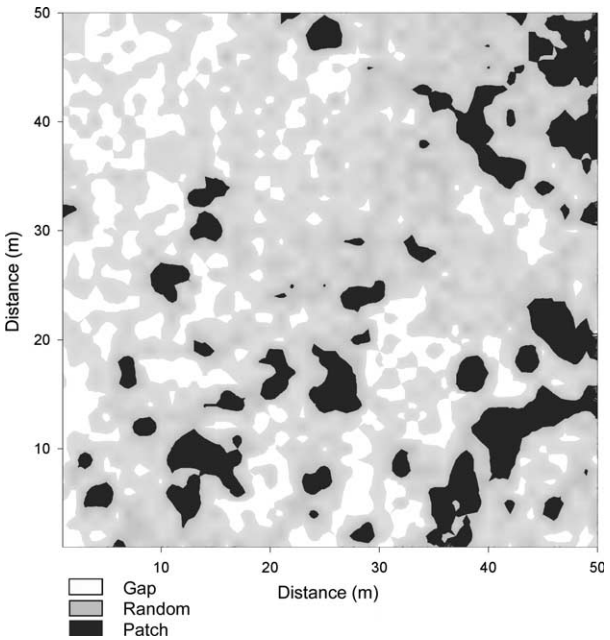

Figure 1. Distribution of gaps and patches on a 50×50 m area based on live *Eleocharis* shoot numbers. Patches (black) are places with clumped shoots (more than 20 shoots per 0.04 m^2), gaps (white) are places with very sparse shoots (less than 5 shoots per 0.04 m^2), and places in between, called random (grey), are represented by average shoot numbers.

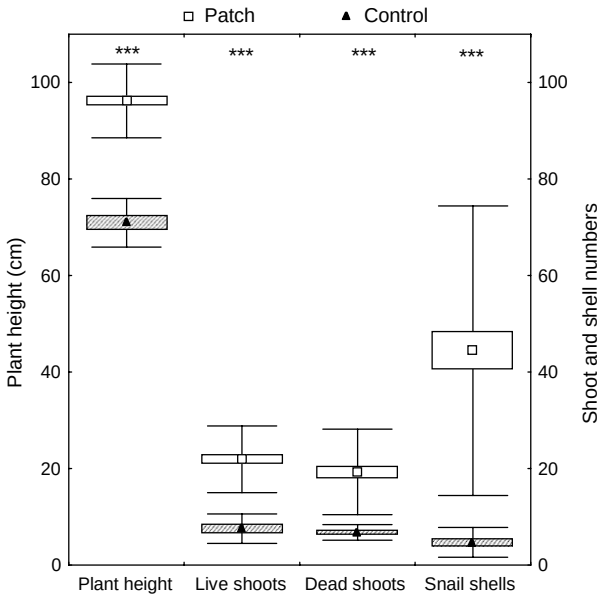

Figure 2. Differences between patch and control plots in terms of vegetation characteristics (plant height, *Eleocharis* live and dead shoot densities) and amount of empty *Pomacea* shells. Symbol: mean; box: mean ± SE; error bar: mean ± SD ***p < 0.001.

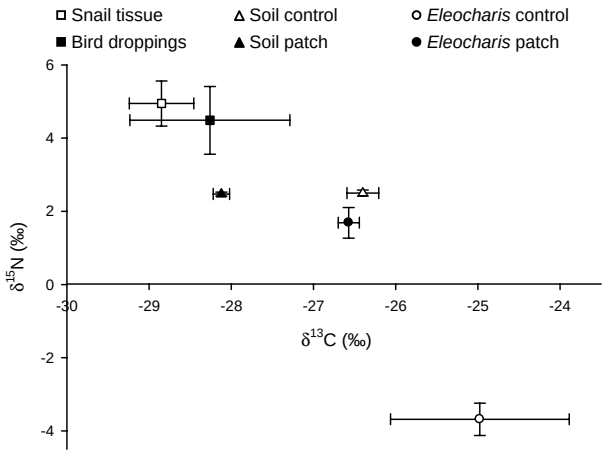

Figure 3. $\delta^{13}C$ and $\delta^{15}N$ composition of emergent macrophytes (*Eleocharis cellulosa*; n = 16), soil originating from below marsh and patch sites (n = 16), snail tissue (n = 10) and snail eating birds droppings (n = 4). Error bars represent mean ± SE.

control plots ($t = 3.37$, $p = 0.006$). Soil PO_4-P was significantly higher in patches than in control plots (means: 0.231 and 0.024 μg membrane^{-1}, respectively; $t = 4.45$, $p < 0.001$). The plants in patches had higher tissue N and P contents than control plots. In combination with higher shoot density, this resulted in a higher amount of both nutrients per m^2 in patches (Table 1). Our mean values of $\delta^{15}N$ and $\delta^{13}C$ in snail and control plant tissue were $\delta^{15}N = 4.9$, $\delta^{13}C = -28.8$ and $\delta^{15}N = -3.7$, $\delta^{13}C = -25.0$ respectively, which are very close to the values from sparsely vegetated sites in Everglades (Williams and Trexler 2006). We documented differences in $\delta^{15}N$ values in plants (*Eleocharis cellulosa*) from patches and controls (Tukey HSD, $p < 0.001$), but not in values of $\delta^{13}C$ (Tukey HSD, $p = 0.286$). In other words, plants in patches were enriched in ^{15}N compared to control marsh plants. The patch and marsh soil did not differ in either ^{13}C signatures (Tukey HSD, $p = 0.210$), and ^{15}N (Tukey HSD, $p = 0.999$). Snail tissue and snail-eating bird droppings were close together both in $\delta^{13}C$ and $\delta^{15}N$ values (Fig. 3).

Limpkin observations

PCA resulted in three main correlated groups of limpkin activities, time of the day and preferred microhabitats: (1) In the early morning (7–9 a.m.), birds were usually resting in dense vegetation or *Cladium* thicket and they started to move toward wetland center and prepare for foraging. (2) Foraging time came in late morning (10–11 a.m.) and it took place predominantly in open water and sparsely vegetated wetland. (3) After snail capture, eating was tightly correlated to patch habitat. The birds waded toward a neighboring patch (wading distance longer than 15 m was not observed) and there they handled and ate the snail tissue leaving the shell. Only a small portion of captured snails was handled at the place of capture. This resulted in significantly higher piling of shells in areas suitable for prey handling, i.e. patches ($t = 7.0$, $p < 0.001$), compared to sparse vegetated marsh. At the same places, the birds had midday (12–2 p.m.) and afternoon (3–6 p.m.) siestas spent by grooming and occasional foraging. The visualization of limpkin activities is in Fig. 4. The correlation coefficients between the limpkin activities and their location in the marsh are shown in Table 2.

Estimation of limpkin impact on vegetation

Limpkin foraging efficiency was 4.6 snails per an hour of foraging. Average daily time devoted to foraging was 4 h, resulting in 18 snails captured per day. Of these, 80% (14.5 snails) were handled in patches. Average snail shell number found in a patch was 44 and it could potentially be produced by a single bird in three days. Patchiness survey revealed the approximate number of patches to be 60 ha^{-1}. The marsh area, where focal observation was conduced

Table 1. The mean ± SE of total aboveground biomass (g m^{-2}), plant nutrient content (μg g^{-1}) and total nutrients in plant biomass (g m^{-2}) in patches and control plots. The results of student's t-test are shown.

	Patch	Control	t	p
Total biomass	2248 ± 219	450 ± 52	7.76	<0.001
Plant tissue N	9630 ± 150	8650 ± 250	3.31	0.003
Plant tissue P	369 ± 12	309 ± 17	2.92	0.006
Total aboveground biomass N	21.66 ± 0.34	3.89 ± 0.11	49.68	<0.001
Total aboveground biomass P	0.82 ± 0.03	0.15 ± 0.01	21.19	<0.001

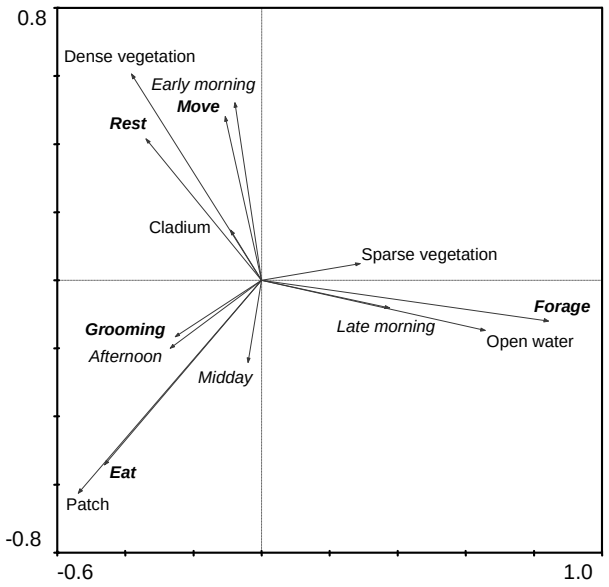

Figure 4. Results of PCA (principal component analysis) of limpkin activities (bold, italics) and their spatial location (normal font) and time of the day (italics; early morning = 7–9 a.m., late morning = 10–11 a.m., midday = 12–2 p.m., afternoon = 3–6 p.m.). Smaller angles between response and explanatory variables mean stronger positive correlation, variables with perpendicular arrows are not correlated, opposite arrows are negatively correlated. For correlation coefficients between limpkin activities and their locations see Table 2.

(extent of 2.5 ha), had ~150 patches and usually hosted from 5 to 10 birds. Hence, potentially, these birds can produce piles of shells in this marsh over a ~60 day's period. However, this reasoning assumes that the birds use the patches evenly. Over time, nutrients from bird droppings and left snail tissue cumulate in the sediment and consequently in the vegetation.

Experimental patch creation

None of the locations, chosen for experimental patches creation, had significantly different vegetation characteristics prior to the treatment. At both locations addition of P or chicken manure resulted in significant increase of *Eleocharis* shoot density and height, and consequently higher aboveground biomass. The effects were visible six months after treatment and stayed significant 40 months after treatment at Buena Vista location (Table 3). Further, after 40 months, plant height was significantly different between all treatments (Tukey, $p < 0.036$, Fig. 5) and it increased in order: control, P, manure plots. *Eleocharis* live shoot number responded in a similar manner (Tukey, $p < 0.016$, Fig. 5). Dead shoot number increased in manure plots only (Tukey, $p < 0.001$, Fig. 5).

Discussion

We documented a small-scale patchiness in wetlands of northern Belize in terms of plant physiognomy, patch elevation and nutrient content. Both positive and negative indices of clustering in spatial analyses were quite high (Perry et al. 1999) documenting significant patchiness in plant height and *Eleocharis* shoot numbers, as well as the presence of the gaps in the vegetation. Patches in our study area cover much smaller area than gaps and regularly spaced vegetation and can thus be considered as a specific vegetation type. Furthermore, a comparison of patches and controls, revealed small, but significant differences in water depth, probably as a result of increased sedimentation in patches (Tomassen et al. 2005). In our case, sedimentation rate will probably increase even more, once other less water tolerant woody species (e.g. *Mimosa* spp.) get established in a patch.

We proved that limpkins prefer patches with dense vegetation for prey handling and eating. After eating, limpkin usually excretes in a patch. Nutrients are increased not only by bird droppings, but also by the remnants from a messy act of meat extraction from the shells (Snyder and Snyder 1971). The amount of snail shells in patches was substantial (mean 44 shells per patch) and the activities connected with consumption of these snails probably resulted in elevated P contents in patch soil. In concordance, the increased nutrient input was reflected in higher N and P contents in terms of plant tissue nutrients.

Most of the available nutrients were rapidly incorporated in plant tissue; hence, macrophytes in patches were enriched in ^{15}N compared to surrounding marsh vegetation. This is concordant to elevated ^{15}N values of emergent macrophyte leaves from nutrient enriched sites of Florida Everglades (Inglett and Reddy 2006). Since wetland macrophytes respond to P addition by a decrease of discrimination during N uptake (Inglet et al. 2007), recorded difference in ^{15}N between patch and marsh plants is a strong support for selective P enrichment of patches. Such enrichment could be an indirect evidence of the animal origin of patches. Similar conclusions were applied in several other studies of bird–plant system (Erskine et al. 1998). As expected, there were no differences in plant $\delta^{13}C$ values as plant carbon uptake was always from the same source regardless of plant location (and water availability did not limit plant growth there). Nevertheless, the animal impact in patches was reflected in patch soils, which were depleted in ^{13}C and

Table 2. The correlation coefficients (R) between limpkin activities and their locations within the marsh based on the PCA analysis (Fig. 4). The values in bold represent significant correlation ($p < 0.05$).

	Move	Forage	Eat	Grooming	Rest
Patch	**−0.166**	**−0.322**	**0.419**	**0.206**	−0.014
Dense vegetation	**0.193**	**−0.273**	**−0.126**	0.072	**0.274**
Cladium thicket	**0.132**	**−0.150**	0.065	−0.065	0.037
Sparse vegetation	0.005	**0.243**	**−0.151**	−0.089	**−0.103**
Open water	**−0.115**	**0.417**	**−0.152**	**−0.144**	**−0.179**

Table 3. The vegetation response to experimental patch creation by adding P or chicken manure (results of one-way ANOVA). Two locations were measured six months after treatment (Quiet 2004, Buena Vista 2004), the later one only was measured 40 months after treatment (Buena Vista 2006). The F-values and response significance (p) are presented.

	Quiet 2004		Buena Vista 2004		Buena Vista 2006	
	F	p	F	p	F	p
Live shoots	22.3	<0.001	41.8	<0.001	30.9	<0.001
Dead shoots	12.3	0.001	29.5	<0.001	27.7	<0.001
Plant height	57.3	<0.001	41.4	<0.001	36.6	<0.001
Water depth	0.3	0.586	–	–	0.66	0.519

their values of $\delta^{13}C$ were much closer to the animal than plant tissue. However, we are aware that the ^{13}C values in soils can be influenced by other factors, e.g. microbial processes (Šantrůčková et al. 2000).

Changes in plant cover in response to bird droppings are relatively common (Anderson and Polis 1999, Dean et al. 1999), some studies reported changes in species composition as well (Tomassen et al. 2005). Similarly to our results, other authors reported an increase in soil nutrient content as a response to bird dropping (Anderson and Polis 1999, Ligeza and Smal 2003, Hobara et al. 2005). However, to our best knowledge, all these studies focused on perching birds, and the impact of a wading bird, *Aramus guarauna,* limpkin, is therefore quite unique.

According to nutrient status in patches, bird activities clearly have an impact on nutrient cycling there. The limpkin is a solitary bird with little difficulties in prey capturing (Bennetts and Dreitz 1997). In our sites, its average daily intake was 18 snails [comparable to *Rostrhamus sociabilis* snail tissue daily intake; (Beissinger 1983)] of which 14.5 were handled in patches. An average amount of shells in a patch can be potentially gathered in three days of limpkin activity. It can even be sooner, as we did not observe night foraging, which is reported as not uncommon to limpkins (Bryan 1996). Our observation confirmed that limpkins usually forage throughout a smaller area very rigorously (Snyder and Snyder 1971). In several cases, individual limpkins were rather conservative and returned toward the same patch repeatedly. These observations are also supported by numerous findings of piled fresh shells found in P enriched plots that were part of another experiment (Rejmánková and Macek unpubl.). When birds are present under prolonged stable conditions of water level, their nutrient input increases plant height and density in patches. These in turn represent better conditions for snail handling and therefore are more suitable for further bird eating visit. Such positive feedback can guarantee the patch sustenance for a long period. Both limpkin observations and results from the manipulative experiment confirmed that this avian predator plays a major role in patch formation. However, other animals, e.g. shelter seeking turtles, cichlids or eels (*Ophisternon aenigmaticum*, whose holes were found in many patches) can further impact patch nutrient status. Yet, we believe, the presence and impact of other animals is rather small compared to the effect of limpkin activities (Dean et al. 1999). Similarly to Anderson and Polis (1999), we can conclude, that allochthonous nutrient input via bird dropping might be an acceptable explanation of system dynamics.

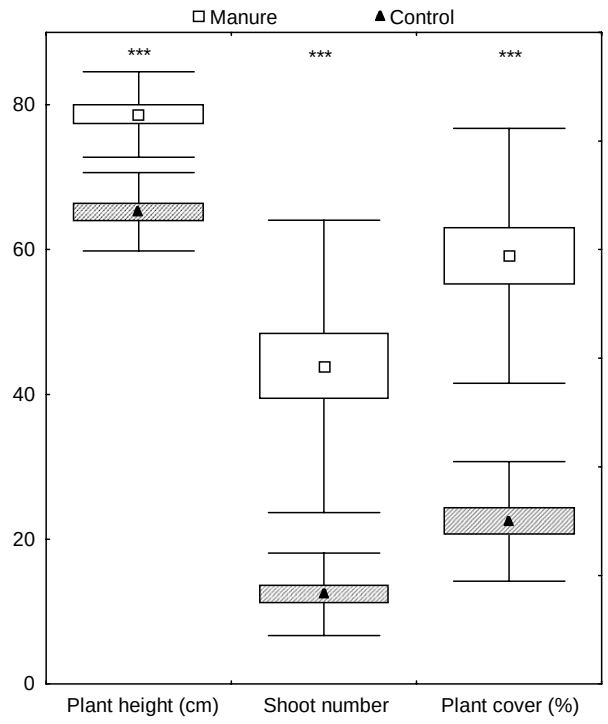

Figure 5. Vegetation characteristics comparison of treated (manure) and control plots 40 months after chicken manure addition at the location Buena Vista. Symbol: mean; box: mean ± SE; error bar: mean ± SD. ***$p < 0.001$.

However, only a small number of such 'fortunate' patches can be sustained. Patch retrogression can have several reasons ranging from nutrient output by environmental factors (i.e. fires and extreme flooding) to decrease of predator activity. Patches that are not repeatedly used slowly degrade and the nutrients are redistributed by clonal growth of macrophytes to the surrounding wetland. In our patchiness survey, we documented that observed wetland patterns consist of the whole scale of patches ranging from growing to disintegrating ones.

Limpkin occurrence and feeding in a larger geographical scale are rather scattered, site and time unpredictable and irregular depending mainly on water level and prey availability (Macek and Rejmánková unpubl.). During dry season, snails are concentrated to shrinking water bodies with limpkins foraging on them there. On the other hand, during high water, both snails and limpkins are more scattered, as the extent of marshes is much larger. Unpredictable movements between wetlands were also documented for *Rostrhamus sociabilis* (Bennetts and Kitchens 2000), and both might result from snail density

and water level fluctuations. Variable water level forces limpkins to change their eating places from time to time. We hypothesize this necessity sometimes results in creating a pile directly on sparsely vegetated ground in the vicinity of open water. Such piles might occasionally serve as patch starting points, although various other processes (e.g. topographic irregularities) can certainly be behind formation of patches. We did not document high density of living snails in our patchiness survey, probably due to low water level and snail ability to aestivate (Kushlan 1975). However, the snail abundance can be temporarily quite high (3–4 m^{-2}; Lege 2001) in suitable locations (Bennetts et al. 2006). Snail densities are reported to be higher in sparsely vegetated marsh (Karunaratne et al. 2006), where bird visual orientation is better, which also explains why foraging activities are performed there.

As for the further destiny of well utilized patches with continuous nutrient supply we predict that the litter decomposition rates will increase (Tomassen et al. 2005, Rejmánková and Houdková 2006), higher nutrient content will lead to higher microbial activity, and, generally, to increased biogeochemical activity of these patches (Van Miegroet et al. 2000). Similarly, in Florida Everglades, patches represented by tree islands were described as hotspots of biogeochemical cycling in the landscape (Troxler Gann et al. 2005, Wetzel et al. 2005). The nutrients will slowly accumulate compared to surrounding wetland and can be stable even over longer periods without any further supply (Facelli and Brock 2000). This may result in creation of a hospitable (e.g. elevated) environment for other species such as *Mimosa* spp., which can extend to previously not accessible habitat (Hacker and Bertness 1995, Zanini and Ganade 2005, Scheffer et al. 2006), although this process is probably quite slow. This might also lead to the succession towards tree islands as described from the Everglades (Wetzel 2002). In this way, patches may play an important role in increasing ecosystem complexity, providing habitat for other plant and animal species. Although tree islands are also present in our system, links between patches and tree islands are not supported by any strong evidence yet.

Acknowledgements – We are grateful to Jan Lepš and Jana Karbulková for their helpful comments to the manuscript. We thank laboratory of Jiří Šantrůček for isotopic analyses. Jenise M. Snyder kindly helped with linguistic revision. The project was supported by SGA 2006-18, MŠMT 6007665801 and AV0Z60050516.

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