Swan consumption maintains variance but not pattern in the abundance of pondweed tubers

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submitted

Sampling the 10 x 10 m grid to assess spatial pattern in the distribution of pondweed tuber densities was always a social event.
Spatial heterogeneity in resource abundance (i.e. patchiness) provides a forager with an opportunity to bias foraging effort towards areas that are on average, richer in resources (Valone and Brown, 1989). Taking advantage of small-scale patchiness allows a forager that strategically regulates time in patches as well as movement between patches to achieve a higher energy gain rate (Klaassen et al., in press). Patchiness at the landscape scale allows mobile foragers to compensate for local and temporal variability in resource abundance, facilitating long-term population persistence (Fryxell et al., 2005). Accordingly, for conservation of animal populations it is vital to understand the origin and persistence of spatial heterogeneity in their resources, especially where this does not simply reflect heterogeneity in habitat characteristics (i.e. a heterogeneous template) (Bascompte & Sole, 1998). We investigated within-year spatio-temporal patterns in a monoculture of a submerged plant experiencing heavy exploitation by migratory swans, with the novelty that we distinguished between different forms of heterogeneity: spatial variance i.e. the frequency distribution of densities, and spatial pattern, i.e. the spatial distribution of densities (Li & Reynolds, 1995; Wiens, 2000). We conclude that variance and pattern each have their own temporal dynamics, and are maintained by different biological processes. This contrasts to the traditional view that heterogeneity is maintained by a single process (Hutchins, 1997). Our results stress the need to distinguish between these different forms of heterogeneity when trying to understand the functioning of an ecosystem.
**Introduction**

Heterogeneity in the abundance of resources (i.e. spatial variance and spatial pattern) is the rule rather than the exception in natural ecosystems (Stewart *et al.*, 2000; Wiens, 2000). The general notion is that foragers benefit under heterogeneous conditions (Sparrow, 1999; Fryxell *et al.*, 2006; Klaassen *et al.*, in press). It is thus important to understand how heterogeneity is maintained in the ecosystem, especially since foraging itself can have an enormous impact on the degree of heterogeneity (Adler *et al.*, 2001). Variance and pattern are linked by the fact that pattern cannot exist without variance, but on the contrary there can be variance without pattern (i.e. a random configuration) (Tenhumberg *et al.*, 2001). Obviously, variance and pattern can only develop and persist if supporting effects are stronger than counteracting effects (Adler *et al.*, 2001; Hutchings, 1997).

Fennel pondweed *Potamogeton pectinatus* is a pseudo-annual macrophyte that survives the winter via belowground tubers (Santamaria & Rodríguez-Gironés, 2002; Van Wijk, 1988). In autumn (September) the distribution of tubers is strongly heterogeneous, despite the fact that pondweed occurs in a near-monoculture and on a template that is relatively homogeneous regarding abiotic conditions (own unpublished data). This marked spatial variance and spatial pattern in tuber abundance allows the migratory Bewick’s swan *Cygnus columbianus bewickii*, that feeds on tubers in October, the season covered by our observations in the Netherlands, to achieve a higher energy gain rate (Klaassen *et al.*, in press), and consequently a higher speed of migration (Hedenström & Alerstam, 1998). *Potamogeton* tubers are exploited by swans in other areas during spring migration (Nolet & Drent, 1998) and both systems are characterized by repeatability: the swans return to the same tuber beds every year.

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**Figure 1** Scheme of the life cycle of Fennel Pondweed, emphasizing processes that affect spatial heterogeneity in the distribution of pondweed tubers. 1. Plant growth (April-August), 2. Swan grazing (October), 3. Winter mortality (December-February).
Here we are interested in how variance and pattern in the abundance of tubers develop throughout the year, and whether three important biological processes in the pondweed's life cycle act in the same direction on variance as on pattern. These processes are (i) “plant growth”: the production of tubers in summer, (ii) “swan foraging”: the feeding on tubers by swans in autumn, and (iii) “winter loss”: the decomposition and displacement of tubers in winter (Fig. 1) (Jonzén et al., 2002; Nolet, 2004).

Methods

Study site Data were collected in the Lauwersmeer, The Netherlands (53°22'N, 06°13'E), a shallow freshwater lake. In parts less than 0.7 m deep (750 ha) Fennel Pondweed grows from April to August. Tubers are mainly formed in August (Santamaría & Rodríguez-Gironés, 2002). In October the lake is visited by 500-6500 Bewick’s swans (Beekman et al., 1991; Nolet et al., 2002).

Sampling Tubers were sampled by taking 40-cm deep cores (diameter 10 cm) and sieving the sediment through a 3-mm sieve. Tubers were dried at 70 °C for 72 h and weighed individually to the nearest 0.001 g. Biomass densities are given in dry weight (g·m⁻²).

Small-scale spatial variance Tubers were sampled in 33 squares (1x1 m, 12 cores·m⁻²), arranged in a regular 3 x 11 array (20 m between squares) in September (2001-2004), November (2001, 2003-2004) and March (2002-2004). 20 m between squares ensures that tuber biomass densities are independent (Nolet & Mooij 2002). Data were ln-transformed to normalize frequency distributions. For every period we calculated the average and the coefficient of variation (CV) of tuber biomass density.

Small-scale spatial pattern We sampled biomass densities per 1x1 m squares (12 cores·m⁻²) within a 10 x 10 m plot in September (2001, 2003), November (2001, 2003) and March (2002, 2004). Spatial relationships between tuber densities were investigated for different periods by calculating omni-directional standardized variograms (see Appendix A) (Rossi et al., 1992). The sum of the absolute Moran’s I index (Moran, 1950) for lag distances 1-6 m was used to describe the degree of local spatial autocorrelation, i.e. the strength of spatial relationships.

Large-scale spatial variance We enhanced large-scale variation in tuber biomass density by removing all aboveground biomass at different moments during the growing season (June, July and August 2003) in 24 plots (10 x 10 m). These plots were intermingled with 8 control plots according to a random-block design spread over 40 x 80 m. We measured the average tuber density by taking 24 cores·plot⁻¹ in September (2003, 2004), November (2003) and March (2004).
**Results and discussion**

Plant growth increases whereas winter loss and particularly swan foraging decreases tuber biomass densities (Fig. 2a). Tuber biomass production is constant for different initial (March) densities, indicating that growth rate is depressed at higher densities (Fig. 3a). In contrast, swan exploitation rate is a function of density (Fig. 3b). From the exploitation pattern we can infer that swans exploit patches to a threshold density of 8.5-13.0 g/m$^2$ (regression intercept) and that 88-96% (regression slope) of tuber biomass is available to the swans (Nolet et al., 2006a). Winter losses (Fig. 3c) are similarly a function of density in which a higher proportion is lost of an initial high biomass than of an initial low biomass.

Within-year temporal fluctuations in variance and pattern were studied at two spatial scales because effects of processes might be scale dependent (Levin, 1992; Wiens, 1989). At a small spatial scale, equal to the foraging scale or grain (Wiens, 1989) of swans, we monitored the natural development of variance and pattern (sub-plots measured 1 m$^2$, Fig. 2). Plant growth decreased the degree of variance, whereas it increased the degree of pattern. In contrast, swan foraging increased the degree of spatial variance, whereas it decreased the degree of spatial pattern. Winter mortality enhanced both variance and pattern, which demonstrates that effects on variance and pattern are not always inversely related. Variance is maintained in the ecosystem by swan foraging, whereas pattern is maintained by winter mortality.

At a large spatial scale, equal to the natural size of a pondweed clump (10 m in diameter, see Nolet & Mooij, 2002), we monitored how natural variance developed over time (sub-plots measured 100 m$^2$, Fig. 4). A lower degree of spatial variance was observed at this larger scale (variance in September is 0.13 and 0.06 for small and large plots, respectively), corroborating a negative scaling relationship between the scale of variance and pattern.
Figure 3 Changes in the amount of tuber biomass for different processes in the life cycle of Fennel Pondweed as a function of initial tuber biomass density. **A.** biomass produced in summer (biomass in September – biomass in March). **B.** biomass removed by swans in autumn (biomass October – biomass November). **C.** biomass died off in winter (biomass November – biomass March). Lines represent linear regressions. Slopes \((a)\), intercepts \((b)\), and \(r^2\)-values are presented. In these graphs x- and y-axis are not independent. Tuber biomass densities are measured with an error of 20\% (as determined in the field)(Nolet & Mooij, 2002), causing spurious correlations. For swan grazing and winter mortality, but not for plant growth, this is smaller than the 95\% confidence interval for the observed slope (see Appendix B). At right a seasonal clock (1=January, 6=June, 12=December) clarifies the intervals concerned between successive sampling moments.
measurement and the observed level of spatial variance (Levin, 1992; Wiens, 1989). In accordance with our observations at a smaller spatial scale, plant growth increased and swan foraging decreased the degree of variance. Interestingly, winter mortality reduced the degree of variance, which is opposed to the effect observed at a smaller spatial scale (Fig. 4). Apparently, the direction of an effect can be scale dependent. At this large spatial scale we also experimentally increased the degree of large-scale spatial variance in September by removing aboveground biomass in subplots at different times in summer. Within one year experimentally enhanced variance had returned to the natural level of variance, which indicates that equilibrium levels of variance might be rather stable.

The direction of an effect of a biological process on the degree of variance and pattern is not straightforward but depends on specific circumstances. We might for example expect that small-scale variance decreases if a forager depletes patches down to a fixed threshold level (as swans apparently do)(Nolet et al., 2006a; Klaassen et al., in press). In contrast, we observed that swan foraging strongly increased the level of variance, which is explained by the swans giving-up foraging (and leaving the pondweed bed) before all patches are exploited, as demonstrated by Nolet et al. (2006b). A general rule for the effects of a process on variance and pattern remains to be established (Adler et al., 2001).

Spatial heterogeneity in the abundance of food not only affects the behaviour and survival of foragers (Valone & Brown, 1989; Fryxell et al., 2005; Klaassen et al., in press), but also is key to understanding interactions between species and the coexistence of species (Maron & Harrison, 1997; Stoll & Prati, 2001; Tilman, 1994). In this study we showed that spatial variance and spatial pattern are different and independent aspects of a heterogeneous environment that have their own temporal dynamics. We advocate that it is in any case important to make a distinction between variance and pattern to be able to ultimately understand biodiversity and the functioning of ecosystems (Levin, 1992; Sparrow,
1999; Stewart et al., 2000). For our study system, the most urgent question is to investigate the long-term interaction between swan exploitation and the renewal of the pondweed resource at the same site year after year. The integrity of the long-distance migratory system of the swans depends on site-specific and reliable tuber stocks at critical fuelling episodes during spring as well as autumn.
Appendix A. Small-scale spatial pattern in the abundance of pondweed tuber densities.

**Figure A1** Spatial pattern in the distribution of tuber biomass densities, as depicted in omni-directional variograms, for different moments during the life cycle of Fennel Pondweed: A. March, B. September, and C. November. $\gamma(h)/s^2$ is the relative variation in food abundance between pairs of points, as a function of the separation distance $h$ of these points (after Rossi et al., 1992). A relative variance of 1 (horizontal grey line) equals the degree of variation in tuber biomass independent of separation distance.
Appendix B. Estimating the slope for spurious correlations between biomass changes and initial biomass density

In Fig. 3 we depict changes in tuber biomass density for different processes in the Fennel pondweed’s life cycle as a function of initial tuber biomass density. In these graphs x- and y-axis are not independent because the change in biomass on the y-axis was calculated from the initial biomass on the x-axis. For example, the amount of biomass consumed by swans (Fig. 3b) was calculated by subtracting the density in November from the density in September. When biomasses are measured with an error, this could result in spurious correlations. We estimated the slope for these spurious correlations as a function of the degree of sampling error by simulation.

One thousand patches were considered in these simulations. For each patch we drew an initial density $D_i$ from the observed normal distribution of initial densities, a final density $D_f$ from the observed normal distribution of final densities, and a density change $\delta D$ from the observed normal distribution of density changes. The linear regression between $D_i$ and $\delta D$ has a slope of 0 since $D_i$ and $\delta D$ are not related. Subsequently we simulated that densities were measured with a relative error $e$. For every patch we generated a random sampling error ($E$) for $D_i$ and $D_f$. The frequency distribution of all relative errors equals a normal distribution with an average of 0 and a standard deviation of $e$. The adjusted initial density $D_i'$ is calculated by adding the sampling error $E_{D_i}$ to the initial density $D_i$. The adjusted density change $\delta D'$ is calculated by adding the sampling errors $E_{D_i}$ and $E_{D_f}$ to the density change $\delta D$. For $e>0$, spurious correlations between $D_i'$ and $\delta D'$ exist (see Fig. B1b-d).

The slope of this spurious correlation is a function of the sampling error $e$ (see Fig. B1a). Tuber biomass densities are measured with an error of 20% (as determined in the field, see Nolet & Mooij, 2002). This corresponds to spurious correlations between initial densities and biomass changes with slopes of -0.20, 0.19 (see Fig. B1c), and 0.17 for plant growth, swan grazing, and winter mortality, respectively. The observed correlation between initial densities and biomass changes is significantly different from the spurious correlation resulting from a 20% sample error, when the slope of the spurious correlation falls outside the 95% confidence interval for the slope of the observed correlation. For swan grazing (see Fig. B1a) and winter loss, but not for plant growth the slope of the spurious correlation is smaller than the 95% confidence interval for the observed slope. In other words, the change in biomass is a function of initial density for both swan grazing and winter loss, but for plant growth there is no statistical evidence for an effect of density.
Figure B1 Here we consider the example of the correlation between the tuber biomass in September and the amount of biomass subsequently consumed by swans (see Fig. 3b). (a) Slope of the spurious correlation between initial densities and biomass changes as a function of sampling error e (black dots). The grey bar depicts the 95% confidence interval for the slope of the observed correlation (see Fig. 3b). The slope of the spurious correlation is much smaller than this interval for an error of 20%, indicating that the observed relationship between biomass change and initial biomass is significant. Panels b–d provide the relationship between simulated initial densities $D_i'$ and biomass changes $\delta D'$ for sampling errors e of 0% (panel b), 20% (panel c), and 40% (panel d).