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Author(s): Eddy van der Maarel
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Pattern and process in the plant community:
Fifty years after A.S. Watt

van der Maarel, Eddy

Department of Ecological Botany and Ecological Research Station Öland, Uppsala University, Villavägen 14,
S-752 36 Uppsala, Sweden; Fax +46 18 553419; E-mail Eddy.van_der_Maarel@Vaxtbio.UU.SE

Abstract. This paper is a tribute to A.S. Watt who published his 'Pattern and process in the plant community' almost 50 years ago. Watt's interpretation of the plant community "as a working mechanism, which maintains and regenerates itself" is still highly relevant, although the keywords have changed. 'Process' in Watt's view involves both upgrade and down-grade aspects, whereas 'Pattern' was not specified, neither quantified. Nowadays, process is mainly approached as 'disturbance', that is natural disturbance and 'pattern' as patch structure. Together they make up the 'patch dynamics' of the community. Some implications of patch dynamics for phyto-sociology are discussed. A 'Wattian' concept of the plant community combines the Gleasonian idea of individualistic behaviour of species with the Clementsian (or rather Braun-Blanquetian) notion of community dynamics. Later work by Harper (demography), Grubb (regeneration niche) and earlier work of Sernander (forest gap dynamics) is significant for the understanding of the patch-dynamic nature of the community.

Recent interest in plant species mobility can easily be linked to the concept of patch dynamics. Examples of mobility in a limestone grassland are given and a system of mobility types is proposed.

Some perspectives for the study of patch dynamics are mentioned. Numerical pattern analysis should have a more prominent place in this type of study; the significance of the study of small permanent plots in a stand is emphasized, and unprejudiced demographic studies, as well as experimental studies of small-scale species replacement are recommended.

Keywords: Disturbance; Forest gap; Limestone grassland; Patch dynamics; Small-scale dynamics; Species mobility.

Introduction

Almost 50 years ago, Alexander Stuart Watt (1892-1985) published his '*Pattern and process in the plant community*' (Watt 1947), a synthesis of facts and ideas on community dynamics and a milestone in the history of plant ecology. Watt was a remarkable personality. He developed his ideas on the plant community as an ecologist, after having studied forestry as part of an agricultural degree in Aberdeen and worked for his Ph.D. degree in Cambridge under A.G. Tansley. His life and work were summarized by Gimingham (1986) and Greig-Smith (1990), the latter paper containing a bibliography.

Watt (1947) then stated that the dynamic concept in ecology was half a century old. He must have thought of the major works of Cowles (1899) and Clements (i.a. 1916), which he mentioned specifically in another semi-nal paper (Watt 1964) on 'The community and the individual'. He also referred to his own pioneer work on the dynamics of beechwood. The main message of the 1947 synthesis is about what we may call the internal dynamics of the community, or, in Watt's words, "*the plant community as a working mechanism, which main-tains and regenerates itself*". 'Process' in the commu-nity refers in part to what we now would call (natural) disturbance and in part to the development cycle of the dominant species in the community. Watt also con-cluded that individuals and species often form local patches, which together make up a community. It is their 'pattern', which is related to the 'process'. He advocated the study of patches rather than that of individuals and species – although he presented many interesting details on individual species, particularly *Pteridium aquilinum*. In other words, Watt introduced the concept that was later called patch dynamics (Pickett & White 1985; van der Maarel 1993), and which is similar to the concept of cyclic succession as first described for heathland (Watt 1947; Stoutjesdijk 1959) and to the concept of mosaic cycle (Remmert 1989), concepts which are usually linked to mature communities.

Disturbance is defined here as an event causing the disruption of ecosystems or parts thereof and changing resource availability (simplified after Pickett & White 1985); the disruption should always be specified ac-cording to spatial extent, time involved and magnitude (Glenn-Lewin & van der Maarel 1992). In the case of internal dynamics of the plant community, disturbance is of low intensity and small spatial extent, and patch dynamics is the predominant process while the commu-nity as a whole is stable (van der Maarel 1993). Much work has been published on 'Mechanisms and processes in vegetation dynamics' (e.g. Agnew et al. 1993). In this work Watt's ideas were not, or only occasionally, men-tioned and the idea of patch dynamics is largely missing.

In this paper I will mention some developments of Watt's ideas as well as some spatial aspects of species mobility within the plant community which I consider as a further extension of Watt's concept of patch dynamics. Although much literature has been studied, this paper cannot provide a complete review of the topic.

Evidence and significance of patch dynamics

Watt (1947) presented evidence for the occurrence of patch-dynamics from seven communities, the first three examples dealing with cyclic succession.

1. A bog regeneration complex, i.e. a hollow-hummock system.
2. A mosaic of building, mature and degeneration phases that occur in *Calluna* heath.
3. A dynamic mosaic of eroded *Racomitrium lanuginosum* heath with patches of dwarf shrubs.
4. A population of *Pteridium aquilinum* invading a grass-heath; Watt showed that the same phases occur in this system (see Watt 1971).
5. A species-rich grassland on basic soil dominated by *Festuca ovina* showing heterogeneity based on variation in microtopography. Four phases were distinguished here: building, mature, degenerate and hollow.
6. A grass-heath on acid soil where *Agrostis tenuis* (now *capillaris*) and *A. canina* (probably *canina* s.s.) were expanding in rings, leaving space for *Cladonia* in zones where the grass had degenerated.
7. Beechwoods Watt had studied since the 1920s (e.g. Watt 1923). In managed forest *Fagus sylvatica* occurred in different age classes, and gaps arose through cutting and death of individual trees. Some age phases may occupy relatively large areas for some periods of time, for instance *Betula* stands, which might be recognized as a separate community, but which, according to Watt, are just parts of the woodland regeneration complex.

In summary, the 1947 paper on *Pattern and Process* is a unique combination of (1) a synthesis of 50 years of patch dynamics and (2) the initiation of a new type of study of the plant community.

Some lines of research linked to Watt's ideas on pattern and process

Although we today think of it as a crucial contribution, Watt's paper on Pattern and Process was not immediately, nor generally appreciated. The reception of his ideas has been 'varied' (Watt 1964). 24 years later John L. Harper (1988), one of the few ecologists who was aware of Watt's significance and who initiated follow-up research, wrote: "Perhaps the most important devel-

opment in plant population biology and vegetation science in the past 20 years have stemmed from the belated appreciation of the work of Watt". Although Watt (1947) has been cited often, only a few ecologists, mainly British and Dutch, have followed and extended the patch-dynamics approach.

Patch dynamics in heathlands

At first, Watt's ideas were further developed in heathland ecology. Stoutjesdijk (1959; see also Stoutjesdijk & Barkman 1992) described a cyclic succession in Dutch heathlands - also in terms of microclimatic changes - while paying attention to disturbance through fire and outbreaks of the heather beetle (*Lochmaea suturalis*). This work was continued by de Smidt (e.g. 1977), Berdowski & Zeilinga (1983) and others; it included further research on the impact of the heather beetle and on the application of simulation models to predict the internal (as well as successional) dynamics of heathland (Lippe et al. 1985: Markov models; van Tongeren & Prentice 1986: gap replacement model).

Heathland dynamics were also studied by Charles H. Gimingham (a pupil of A.S. Watt; cf. Gimingham 1986) and his associates. The cyclic dynamics were confirmed for Scottish heathland and detailed information was obtained on the longevity of the various species involved and the conditions for degeneration and re-establishment; also the nutrient cycling involved in patch dynamics was analysed, and species associations in the various stages described (Gimingham 1978). Barclay-Estrup & Gimingham (1994) have shown the role of seed production in maintaining cyclic dynamics. A further parallel to the Dutch work is found in the application of Markov models to describe post-fire succession (Hobbs 1983). Later work was directed towards the impact of community-level disturbance, notably with fire and insect attacks (see Gimingham 1978, 1988).

Patch dynamics in grasslands

An important development in grassland dynamics according to Watt concerns the demography of species as initiated by John L. Harper and his associates at Bangor (e.g. Sarukhán & Harper 1973) on three related *Ranunculus* species in a species-rich permanent pasture in North Wales. They showed small-scale changes in the extension of local populations and phenological differentiation between species. Studies by Turkington (Turkington & Harper 1979; Turkington et al. 1985) revealed short-term changes in the local distribution patterns of species and found many interspecific associations on a small scale, albeit mainly negative ones. The role of *Trifolium repens* as a dominant species, with

building and degenerating phases in the grassland appeared similar to the function of Watt's dominants. Thórhallsdóttir (1990) studied spatio-temporal patterns in the same grassland in North Wales. On the scale of 1 cm^2 she found patterns of spatial arrangement and short-term (seasonal) species replacement. Gaps were continuously created and filled by several stoloniferous species, notably *Agrostis capillaris* and *Trifolium repens*. There were large differences between species as to their reappearance on the same cm^2 as the year before, i.e. some species were moving around while others were more stable.

Harper (1982, 1988) summarized part of the work at Bangor in two general contributions on population ecology and presented a summary which may serve as an introduction to recent studies in which I myself am involved: "the apparently stable mixtures of species in a community are really space-time mosaics of replacements, local extinctions and colonizations". Note that Harper's 1982 paper appeared in a symposium volume entitled "The plant community as a working mechanism" (Newman 1982), a tribute to Watt on the occasion of his 90th birthday.

Watt's approach to grassland ecology was also continued by Peter J. Grubb, a student of Watt in Cambridge. In his review of the importance of the regeneration niche, Grubb (1977) elaborated Watt's idea of continuous regeneration. He emphasized the continuous creation and filling of gaps, especially in relation to the short-term replacement of plant units (individuals or ramets) of one species by units of the same or another species. Further work in Cambridge includes the control of the relative abundance of species in species-rich grasslands as well as their demography, particularly their longevity (e.g. Grubb et al. 1982; Mitchley & Grubb 1986). For several species half-life values for genets were estimated (Grubb 1990); less is known about the turnover of ramets.

Grubb (1990) also contributed to the understanding of the internal dynamics of grasslands by proposing a comprehensive system of growth forms, in which the capacity for horizontal extension of ramets is a decisive criterion. Species with wide-spreading rhizomes, e.g. the grass *Brachypodium pinnatum*, or above-ground runners, e.g. *Hieracium pilosella*, are considered to be able to "wander through the turf over the years". Grubb's system deserves more attention than it has received so far. People are apparently more attracted by behavioural 'strategies', particularly those known under belligerent but hardly appropriate terms like 'phalanx' and 'guerilla' (Lovett Doust 1981; Herben et al 1993b).

Grime and co-workers added a new dimension to grassland dynamics by systematically collecting information on the ecophysiological behaviour of grassland species as well as gap dynamics (Grime 1990; Hillier 1990; Hendry & Grime 1993). Although this work has no explicit bearing on 'pattern and process', it provides useful insights in competitive relations between species, on the significance of the nutrient status, including the presence of mycorrhizal networks, and on germination conditions for many species.

As Grubb pointed out, an important aspect of pattern dynamics in grasslands is the continuous creation of gaps by animal excretion, trampling, locally heavy grazing, ant activities and the death of short-lived individuals, ramets and modules. In grassland, these gaps may vary in size from 1000 to only a few cm^2. Such gaps can be colonized by invading stoloniferous species or through germination of seeds from the local seedbank.

Information on the seedbank and the germination of limestone grassland species was presented by Rusch (1988; Rusch & van der Maarel 1992) and on seedbank germination conditions in similar grassland types by Ryser (1990, 1993), Willems (1995) and Hendry et al. (1995). From these studies we know that gaps arise continuously in limestone grassland and their regeneration by seedlings is important. Not only all annuals, making up 15-20% of the local species assemblage in the limestone grassland studied by Rusch, but also many perennials, up to 25% of this assemblage, regenerate frequently by seed.

Patch dynamics in forests

The study of patch-dynamics in Sweden had already been initiated by Rutger Sernander (1866-1944), who noticed that natural forests are continuously regenerating through the formation of gaps. Sernander (e.g. 1918, 1936) published almost entirely in Swedish and did not get the international attention he deserved. His major object of study was the natural forest 'Fiby urskog' near Uppsala, the major part of which blew down during a gale in 1795. This forest has been characterized by regeneration dynamics and the creation of smaller 'storm-gaps' ever since. Sernander (1936) paid special attention to the storm-gaps and recognized the significance of suppressed (spruce) trees in the regeneration.

In the 1980s a new dimension was added to Sernander's classical studies by re-analysing large permanent plots established by him in the 1930s; these plots included gaps which were present at the time the plots were established or developed later on. By comparing the new analyses with the original ones, gap dynamics could be quantified and their spatial aspects better understood (Hytteborn & Packham 1987; Liu & Hytteborn 1991; Glenn-Lewin & van der Maarel 1992) and modelled, with a regeneration simulation model in the sense of Watt (e.g. Prentice & Leemans 1990). This model

predicts the outcome of the regeneration process following gap formation. In instances where a gap formed by the fall of a single canopy individual is large (and light) enough to allow pioneer phases to establish, a Watt-type patch-dynamic regeneration will occur. Such a regeneration pattern is found in many broad-leaved forests as well as in *Calluna* heath. However, gaps will be filled very slowly by the same species if the gaps are not large enough relative to the height of the tree, i.e. do not receive enough light. This is the case in boreal coniferous forest with usually slender trees, notably *Picea abies*.

Patch dynamics and conservation ecology

Another field heavily influenced by Watt's ideas is plant conservation ecology. Watt himself was fully aware of the bearing of his work on conservation and management (Gimingham 1986). As to conservation ecology in the Netherlands, the idea of pattern and process fitted the Relation Theory developed in the 1960s by Christiaan G. van Leeuwen (1966). Two of van Leeuwen's keyword pairs are 'Structure and dynamics' and 'Convergent and divergent boundary zones', the latter also being called ecotones and ecoclines, respectively (van der Maarel 1990). One of van Leeuwen's main postulates was the dominance of dynamics over structure, which in Watt's terms means that process governs pattern. In cases of high levels of environmental dynamics (high disturbance intensity) a relatively homogeneous spatial situation (ecotone) with species-poor communities develops. In cases of low disturbance intensity or/and a spatial gradient of disturbance intensity superimposed on a spatial gradient, a heterogeneous spatial situation (ecocline) is formed with a series of species-rich communities (Westhoff 1971).

Spatial dynamics of species

An important aspect of 'pattern and process' is the spatial dynamics of species. This can be investigated through repeated analysis of permanent small plots in a plant community. Such analyses are still scarce. Watt (1962) had collected exactly this type of data, but only for a grassland that was rapidly changing after heavy grazing by rabbits had been stopped. Glenn & Collins (1990, 1993) studied the mobility of species in tall-grass prairie in terms of immigration to and extinction from patches (patches defined as local assemblages of species) and found that this mobility is unpredictable at small spatial scales.

Stampfli (1991, 1995) found considerable small-scale changes in a species-rich meadow. Herben et al. (1993a)

concluded that small-scale variability in mountain grassland is a mechanism for larger-scale stability and diversity, while Herben et al. (1993b) started to link species mobility to the capacity for long-distance spreading. Hobbs & Mooney (1995) used small permanent plots of 10 cm × 10 cm, 25 cm × 25 cm and 50 cm × 50 cm in annual grassland in California to interpret small-scale plant species composition in terms of responses to fluctuations in precipitation and disturbance by gophers, but they did not include patch dynamics in their analysis. Maubon et al. (1995) described patch dynamics of *Vaccinium myrtillus* patches in mountain spruce forest on 50 cm × 50 cm plots, but they presented data for two years only. Zhang & Skarpe (1995) concluded on the basis of repeated recordings of 0.25-m^2 plots in a very open semi-arid steppe vegetation in Inner Mongolia, that small-scale species dynamics were relatively low.

Species mobility can be measured as species turnover on small plots in the community analyzed yearly, or as species accumulation on such plots, i.e. the sum of species which appeared newly in the plots after the starting year of observation. Van der Maarel & Sykes (1993) calculated mobility data for species occurring in subsequent years on 40 subplots of 10 cm × 10 cm situated in two rows of 20 subplots alongside the long sides of 2.5 m × 1 m plots in a species-rich alvar limestone grassland on the Swedish island of Öland, assigned to the *Veronica spicata-Avenula pratensis* association. The conclusion of this study was presented in the form of a phenomenological 'Carousel model' suggesting that most species would move freely around in the community, with different turn-around times.

Work in progress (M.T. Sykes & E. van der Maarel) will quantify both individual and community-average species mobility in terms of the observed species accumulation in subplots relative to theoretical mobility levels. These levels are: (1) random mobility; (2) minimal mobility, where species are expected to occupy plots already inhabited; and (3) maximum mobility, where species are expected to not occupy plots they had already visited. The results show that species such as *Helianthemum oelandicum* and *Cerastium semidecandrum*, mentioned by van der Maarel & Sykes (1993: Fig. 2) as examples of species with a stable pattern and a high degree of mobility, respectively, have accumulation values near to the minimum and random model, respectively.

Comments on the Carousel model include the supposition that the alvar grassland might be a particular type of community. This is true: it has a long history of human influence (Rosén 1982), it has been continuously grazed for probably more than 2000 yr, is low in stature, subject to local disturbances by grazers and, most importantly, subject to recurrent drought in the growing

season (Rosén 1982, 1995; Huber 1994). These droughts (see Table 1) tend to be the driving force for species changes in this community, because they create gaps which new species can occupy. Amongst these species are relatively many short-lived species.

However, a comparative study of apparently less extreme grasslands (Sykes et al. 1994) showed similar high small-scale turnover and accumulation of species in 0.01-m² and 0.25-m² plots; the examples were (1) a no longer grazed alvar grassland, (2) Dutch chalk grassland (Willems et al. 1993) with few annuals, and North American moist, tall grass-sedge savanna grassland (Walker & Peet 1983), with no annuals at all.

An essential characteristic of the communities studied is the short life span of most participating plant units; most of the plant parts of the perennials are short-lived as well. For instance, rosette leaves may appear and disappear; perennial plants with bulbs may, for various reasons, not appear above-ground in certain years. Apparently, the turnover of individuals and plant parts is high at all sites compared. Probably, it does not matter for newly arriving species whether the gaps created result from the death of an individual or the definitive or temporal disappearance of an organ. The speed of the carousel is a function of both the average life span of the plant units and the speed with which species colonize or re-colonize subplots.

Sykes et al. (1994) estimated the average annual accumulation for the grasslands mentioned above and found a decreasing accumulation over the years which could be described with a logarithmic function:

$$\log AC = 0.516 - 0.621 \log YR.$$

The average accumulation on 0.01-m² plots drops from 3.3 after 1 yr to less than 0.5 after 10 - 12 yr. The total accumulation would increase to 13 - 14 after 15 yr. If we add the latter figure to the average species number in the first year of analysis, we would obtain an impressive total of 28 - 30 species in 0.01-m² subplots after 15 yr. This would mean that ca. 65 % of the species pool found on the plots, measuring 2.5 m², would have reached all subplots. Watt (1981) may have been the first to use a cumulative species number to characterize a permanent plot; this was in a rabbit enclosure where the change in vegetation was followed from 1942 to 1970.
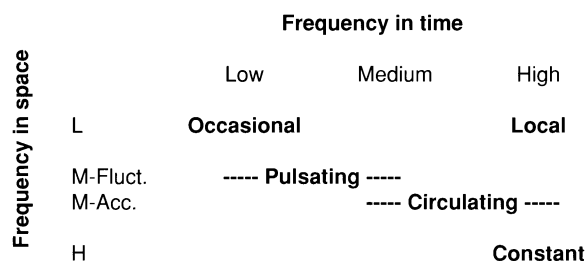

Frequency in time

		Low	Medium	High
	L	Occasional		Local
	M-Fluct.	----- Pulsating -----		
	M-Acc.		----- Circulating -----	
	H			Constant

(left axis: Frequency in space)

Fig. 1. Types of within-community species mobility as a function of small-plot frequency in space and in time. Typology based on observations from 1986-1994 on 40 100-cm² subplots in an alvar limestone grassland plot on Öland, Sweden. Spatial frequency categories are based on mean values over the years and divided into: high, H: > 75 %; medium, M: 25 - 75 %; and low, L: < 25 %. Species in the medium frequency category are divided into fluctuating (M-Fluct.), with large between-year differences, and accumulating (M-Acc.), with small such differences and appearances in new subplots. Temporal frequency categories include H: occurring in > 66 % of the years; M: 33 - 66 % and L: < 33 %.

Species mobility types

As suggested by van der Maarel & Sykes (1993; Sykes et al. 1994), species can be typified as to their mobility on the basis of the spatio-temporal pattern of occurrence in subplots. For the purpose of this paper, I present a simple preliminary typology, based on the observations on the 0.01-m² plots in the alvar limestone grassland mentioned above (Fig. 1). The five types correspond to combinations of spatial and temporal frequency, each in three degrees: low, medium and high. They become clear from the text to Fig. 1 and the examples given in Fig. 2. Occasional species have a low frequency in space and time, meaning that they usually are present somewhere but change position. The annual *Arenaria serpyllifolia* is an example. Local species are also low-frequent but largely occur in the same plots throughout the years, e.g. *Veronica spicata*, one of the character species of the association. Pulsating species have a low or medium spatial frequency but vary much from year to year. The example, the annual *Trifolium striatum*, was absent in several years but it had also years of high frequency. This species is frequent in the

Table 1. Precipitation data (mm) from Ölands Södra Udde, 20 km south of Gettlinge. Note the two extremely low values in 1992. Bold: two highest values; italics: two lowest values. Mean = mean value over 30 years.

	'85	'86	'87	'88	'89	'90	'91	'92	'93	'94	'95	Mean
Annual	**579**	410	548	553	*367*	489	378	*359*	484	**637**		457
April - August	203	*153*	209	**216**	*144*	166	168	164	157	**244**		190
May -June	*41*	52	**116**	51	53	75	**121**	37	42	52	78	59
July - August previous year	**149**	110	80	**70**	148	99	74	**37**	103	105	124	103

Arenaria serpyllifolia   'occasional' $F_{mean} = 1.4$

	F	F$_{cum}$
1986	0	0
1987	4	4
1988	0	4
1989	0	4
1990	5	9
1991	2	11
1992	0	11
1993	1	12
1994	1	13

Veronica spicata   'local' $F_{mean} = 6.8$

	F	F$_{cum}$
1986	3	3
1987	7	7
1988	7	7
1989	7	7
1990	5	7
1991	9	9
1992	5	10
1993	10	13
1994	8	14

Trifolium striatum   'pulsating' $F_{mean} = 6.1$

	F	F$_{cum}$
1986	9	9
1987	1	10
1988	2	11
1989	0	11
1990	21	25
1991	0	24
1992	0	24
1993	22	29
1994	0	29

Anthyllis vulneraria   'circulating' $F_{mean} = 20.0$

	F	F$_{cum}$
1986	21	21
1987	23	29
1988	29	32
1989	25	33
1990	22	35
1991	33	38
1992	8	38
1993	6	38
1994	24	38

Fig. 2. Examples of occasional, local, pulsating, circulating and constant species occurring in plot G1, Gettlinge alvar, Öland. + = appearance; . = (above-ground) absence; ± = new appearance.

seedbank and is dependent on favourable conditions in the summer and autumn of the previous year in order to occur abundantly. Circulating species, such as the usually biennial *Anthyllis vulneraria*, have a medium to high frequency with little variation, but move around and attain a high cumulative frequency. Constant species occur almost everywhere and in every year. *Filipendula vulgaris*, another character species, is a good example. Although this species has a high spatial frequency, it is still missing in 17 plots at least once. The examples of these categories may vary with the grassland type and maybe also with time, but no data are available yet.

Table 2 suggests a relation between mobility type

according to Fig. 1 and life form according to van der Maarel (1988). Out of the 40 species occurring in the alvar grassland plot Gettline A-1, no less than 20, or 50 %, are either circulating or pulsating, and together with the occasional species as many as 80% of the species are mobile (Table 2). The constant and local species are represented by only one life-form type, the constant species by longer-lived hemicryptophytes and the local species by chamaephytes. The short-lived hemicryptophytes and the therophytes are all mobile; this may be expected, but 15 mobile species are longer-lived. The occasional species are fairly equally distributed over the categories.

Fluctuation in species richness

On the community level, species mobility can be expressed as year-to-year turnover, but also as variation in species number. Table 3 shows two drops in species richness, one in 1990 and one in 1992. Both can be related to precipitation, particularly the parameters 'May-June' and 'previous July-August' (Table 1). The lower richness in 1990 can be related to the combination of the dry midsummer of 1989 and the dry early summer of 1990. In fact, most of the vegetation died late July 1989 and, even if the following month of August was extremely moist, several species did not appear in 1990. (Note that the species recordings are always in the middle of June.) After a return to about normal in 1991 the drop in species number in 1992 was even much larger, which can be explained by the combination of the very dry summer of 1991 and the very dry early summer of 1992. The return to a normal situation lasted several years, in fact until 1995. In this year, richness figures were about average again, apparently in connection with the very high precipitation in 1994 and quite normal conditions in May-June 1995. Of course, these trends are based on a small number of observations.

Because of the high variance of the temporal series of values (the columns in Table 3) and of most of the spatial series (the rows) the only significant difference is that between years, notably 1988-1989 vs 1992-1994

Table 2. Relation between the five mobility types and four life-form types (see van der Maarel 1988). C = Chamaephyte; Hl = Longer-lived hemicryptophyte; Hb = Short-lived hemicryptophyte; T = Therophyte.

	C	Hl	Hb	T	Tot
Occasional species	5	4	4	2	15
Pulsating species		1	2	4	7
Circulating species	2	3	5	3	13
Local species	3				3
Constant species		5			5
Total	10	11	13	9	40

Table 3. Numbers of species in the first half of the 40 100-cm^2 subplots in plot Gettlinge A-1 from 1986-1995. In addition to the mean values, the highest and lowest values are presented, with the subplot(s) added in brackets. Also, mean values for subplots and mean cumulative species number are given, with the highest and lowest values added.

	Mean	Highest	Lowest
1986	15	23 (5)	12 (7, 19)
1987	14	19 (11)	10 (19)
1988	16	20 (1, 10)	11 (15, 20)
1989	16	19 (2)	11 (9)
1990	12	18 (2)	8 (16)
1991	15	20 (10)	9 (16)
1992	9	14 (7)	6 (6)
1993	10	15 (7)	7 (10)
1994	11	15 (8)	6 (16)
1995	13	17 (6, 10)	8 (16)
Mean	13	16 (2)	11 (16)
Cum. no.	26	31 (3)	21 (20)

and 1992-1994 vs 1995. Still, when combined with the floristic fluctuations (under preparation), the species richness fluctuation is certainly real. This conclusion concurs entirely with the findings of Rosén (e.g. 1995) on the effects of drought on the long-term dynamics of alvar grassland. Also Stampfli (1995) mentioned such relations between small-scale species fluctuation and changes in weather conditions.

Table 3 shows also how fast the species accumulation can proceed. The average cumulative species number after 9 yr is almost double the average in the starting year 1986, and in one subplot the cumulative species number has increased to 30. These figures compare well with the prediction based on Fig. 2.

Perspectives

The role of pattern analysis.

So far, this contribution has hardly dealt with the measurement and interpretation of spatial pattern as such. This must be seen against the following background. Ever since the first numerical analysis of pattern was developed (see Kershaw & Looney 1985 for a survey), methods of pattern analysis have been refined, corrected and replaced by new methods, both for individual species and for species groups (examples and references in Ver Hoef et al. 1993; Dale & Zbigniewicz 1995). Also, spatial aspects of species associations and spatial autocorrelation have been emphasized (e.g. Bartha et al. 1995; Herben et al. 1995; Palmer & van der Maarel 1995). Apparently, there is still much uncertainty about the appropriate method(s) and hence about their interpretation. Few studies have tried to relate results of

pattern analysis to ecological factors, in order to better understand whether patterns are determined by the growth form of the species involved, by environmental patchiness, by species interactions, or by a combination of those. In addition to the studies of the spatial dynamics of species and species groups which make clear that small-scale distribution patterns are changing from year to year, more exact measurements of pattern should be further developed in order to interpret patch dynamics.

Small-scale dynamics

John L. Harper once said: "Plants are sitting there, waiting to be counted". Yes, plants should be counted, but they are not just sitting there. They are moving around, as individuals, ramets or modules. Analysis of the (few) series of year-to-year records in permanent small plots in plant communities yet available has thrown new light on patch dynamics and it suggests a much higher spatial mobility of plant species – or at least their above-ground parts – than most vegetation ecologists seem to suppose. We need more comparative studies of species mobility and I am grateful for information on any data set which, even if not collected for this purpose, could be used. Studies by Pärtel & Zobel (1995), Klötzli (in press) and R. Huber and own work in progress reveals that small-scale dynamics and community dynamics can be largely independent.

Patch dynamics as discussed here is supposed to refer to a stable community, i.e. a community which maintains its structure and floristic composition over a long period of time, i.e. much longer than the cycle(s) of patch-dynamics. In the case of the alvar grassland on Öland this condition seems to be fulfilled. However, there may be long-term trends, for instance the entrance of species in geologically young regions, or the evolutionary development of new species in isolated communities, or slow changes related to past climatic changes, or regeneration from an earlier large-scale and intensive disturbance or change in management. As an example, the Fiby natural forest discussed above was generally considered as a primaeval, and thus stable forest with largely small-scale dynamics. However, combined contemporary and paleoecological studies (Bradshaw & Hannon 1992) made clear that this forest has been used for grazing for at least 2000 yr and that major changes have occurred in the forest as a result of changes in its use.

The combination of small-scale turnover (Pärtel & Zobel 1995; Huber 1994) and accumulation figures should be further explored for a better understanding of the species dynamics. Also the possibility of 'species group' mobility and of fixed sequences of disappearances and appearances of species should be studied.

Demography

Long-term recording of the occurrence of individuals of herbaceous species as initiated by Tamm (e.g. 1948, 1972) and summarized by Harper (1977) is of direct importance for a better understanding of the processes underlying species mobility. Without reviewing the rapidly growing literature on this topic it is fair to conclude that many individuals reach an old age. This seems contradictory to the main conclusion of the above analysis of patch dynamics. Two remarks may elucidate this contradiction. First, mobility on a very small scale may be on the module, rather than the individual level. Thus, modules of long-lived individuals may appear and disappear and exchange position with modules of other plants or small short-lived individuals. Second, forest meadows may indeed have slower turnover rates than the grasslands discussed above. Long series of observations on small permanent plots in such environments are needed. Anyway, it is highly recommended to extend the demographic studies of individual species, particularly of the type Grubb (1990) emphasized.

Community theory

Patch dynamics in the wider sense developed from the original ideas of A.S. Watt, must be assumed to be a characteristic of each plant community. In terms of the debate on the nature of the plant community, still being referred to as the controversy between Gleason and Clements, the idea of the 'individualistic behaviour' of plant species seems to be confirmed by their small-scale dynamics and as such it is a reinforcement of the Gleasonian idea. This aspect of the plant community maybe primarily a response to the stochastic external fluctuations acting upon the community. Klötzli (in press) presented a similar conclusion for long-term community dynamics. At the same time, growing knowledge of competition and exclusion on the one hand and about mycorrhiza and dependence relations on the other hand, and last but not least the dynamics of coherent patches, point to a community concept à la Watt and Braun-Blanquet - who was supported by Watt (e.g. 1964).

In this connection, a conceptual problem in phytosociology must be mentioned. In grassland and heathland communities, the various patches and phases are usually considered as intrinsic parts of an association; in the case of bog regeneration complexes, phases are distinguished as associations, while in more complex forests early and late gap-colonizing phases are recognized as units from different classes, e.g. gap pioneer communities (*Epilobietea*), gap-shrubland (*Rhamno-Prunetea*), and mature forest (*Querco-Fagetea*). It may be more

logical to apply the syntaxonomical system to all patches with their own species combinations.

Plant communities can be considered real entities even if their boundaries in space and time cannot always be detected. It may then be less urgent to search for 'assembly rules' which Wilson (e.g. 1994) suggested as the necessary evidence for the existence of plant communities, which view relates to those expressed by Palmer & White (1994) and Mirkin (1994) in the debate about this matter in the *Journal of Vegetation Science*.

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