Pak. J. Bot., 44(3): 927-932, 2012.

NORTH-SOUTH FACING VEGETATION GRADIENTS IN THE VILLÁNY MOUNTAINS: A CASE STUDY ON THE POPULATION AND THE COMMUNITY LEVEL

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Abstract

The study of gradients can provide basic information about the ecology of plant populations as well as about community organization. In this study, north-south facing vegetation gradients were investigated in a submediterranean region of South Hungary. Vegetation was examined along five contiguous belt transects, each 200 m long, crossing the mountain ridge or plateau. Plant community sequences were identified visually during field studies. Moreover, community boundaries were delineated objectively, using the moving-split window analysis. In addition, number and size of the population patches were analyzed. This study revealed that mesic forest communities of the northern slopes are replaced by shrubforests and closed rock swards near the ridge, whereas mosaics of shrubforests and open rock swards occur on the southern slopes. Number of significant community boundaries was higher on the southern slopes than on the northern ones. Southern slopes support much more plant species. They have more population patches, which are significantly smaller than patches of the northern slopes. Community sequences along north-south gradients in the Villány Mts are similar to those of the nearby mountainous areas, with one fundamental difference of the xeric grasslands near the ridge. The conclusion of the present paper is that this sequence represents a transitional type between the submediterranean-subcontinental and the continental types. In addition, southern slopes support higher biodiversity and are more patchy than northern ones.

Introduction

Population performances and community patterns along gradients belong to the most basic issues in vegetation ecology (Crawley, 1986; Austin, 2005; Erdős *et al.*, 2011a), which may be important both from a theoretical and a practical point of view. The study of gradients can provide insight into the organization of plant populations and communities (Ricklefs, 1983; Begon *et al.*, 1990). Vegetation gradients have been intensively studied, both elevation gradients (Werger *et al.*, 1983; Wierenga *et al.*, 1987; Carter *et al.*, 1994; Muňos-Reinoso & García Novo, 2005; Hegazy *et al.*, 2011; Khan *et al.*, 2011) and gradients across edges (Oosterhorn & Kappelle, 2000; Stanisci *et al.*, 2000; Hennenberg *et al.*, 2005; Erdős *et al.*, 2011b), the scales ranging from a few meters (van der Maarel & Leertouver, 1967; Körmöczi & Balogh, 1990; Zalatnai & Körmöczi, 2004) to several kilometers (Muňos-Reinoso & García Novo, 2005). However, more case studies are needed, particularly through mountain ridges, which could also support a better understanding of landscape patterns.

In the temperate zones, microclimates of north-exposed slopes differ considerably from those of south exposed ones (Pócs, 2000). Correspondingly, vegetation of north-facing and south-facing mountain sides is also distinct (Hicks & Frank, 1984; Kevey & Borhidi, 1998; Nazarian *et al.*, 2004; Khan *et al.*, 2011). However, the results of Hegazy *et al.* (2011) emphasize that variance between sites or disturbance may conceal the differences between differently oriented slopes. Therefore, analyses examining differences between differently oriented slopes should be carried out in relatively undisturbed areas with minor variances between sites.

In this paper, north-south spatial gradients are described from the northern slopes through the ridge to the southern slopes in the Villány Mountains (Hungary). First, the communities and their spatial sequences along the gradient are identified, and the boundaries between them are characterized. Second, the population distributions along the gradients are scrutinized. Following questions are addressed: (1) What is the sequence of the communities along the gradient? (2) How sharp are boundaries between the communities? (3) What are the main differences between north-exposed and south-exposed slopes on the community level and on the population level?

Materials and Methods

Study area: Research was carried out in the Villány Mountains (Hungary). The bedrock consists of limestone and dolomite (Lovász, 1977; Marosi & Szilárd, 1981), which is partly covered by loess (Ádám *et al.*, 1990). Mean annual temperature is 10-10.5°C. The coldest month is January, the hottest July (Fodor, 1977). Mean annual precipitation is 670-690mm (Ambrózy & Kozma, 1990). Because of the east-west direction of the Villány Mountains, microclimates of the southern and of the northern slopes are quite different, the southern slopes being considerably hotter and dryer (Horvát & Papp, 1964). The Villány Mountains belong to the phytogeographic province Pannonicum, region Praeillyricum, district Sopianicum (Borhidi & Sánta, 1999; Borhidi, 2003). In spite of its very small area, the vegetation of the Villány Mts is quite diverse, supporting more than 1000 vascular plant species (including a large number of rare, endangered, protected, endemic and relict species) and several plant associations (submediterranean mesic forests, xeric scrubs and grasslands) (Dénes, 2000).

Vegetation sampling: Five contiguous belt transects were established on the most natural parts of the Villány Mountains: Mt Szársomlyó, Mt Tenkes and Mt Fekete. All transects were north-south facing, and consisted of 1m² plots. Transect lengths were 200m. Transects were established perpendicular to the ridges. During field works, presence of all vascular plant species of the field layer was recorded in April and in July. Identification of the plants was done using the key of Simon (2000).

The GPS-coordinates of the endpoints of all transects were identified, and relief profiles were drawn using topographical maps and the program ArcView GIS (ESRI).

Vegetation stands and boundary locations were identified on the field visually, considering all vegetation layers. All vegetation stands were classified into one plant association within the system of Borhidi & Sánta (1999) and Borhidi (2003).

Data analysis: According to Whittaker (1967), it is possible to study spatial gradients on three levels: environmental background factors, populations and communities. In this paper, characterization of the gradients is made at two hierarchical levels: at the community level and at the population level, but guesses on the possible background factors are also suggested.

At the community level, moving-split window (MSW) analysis (Webster, 1978) was used to detect boundaries between vegetation stands. It seemed to be an appropriate choice because this method proved to be useful in vegetation boundary detection (Ludwig & Cornelius, 1987; Choesin & Boerner, 2002; Körmöczi, 2005), and in fact, it has been widely used in vegetation science recently (Muňos-Reinoso & García Novo, 2000; Stanisci *et al.*, 2000; Hennenberg *et al.*, 2005; Kröger *et al.*, 2009; Erdős *et al.*, 2011b). MSW identifies boundary location objectively, by comparing the neighbouring areas of the transect at several spatial scales. As comparative function, Squared Euclidean Distance was used. The significance of the boundaries was tested with the z-score transformation according to equation (1).

$$z = (d_{i,k} - d_{exp,k}) / SD_{exp,k} \qquad \text{(Eq. 1)}$$

where z is the z-score, $d_{i,k}$ is the Squared Euclidean Distance at position i if half-window size is k, $d_{exp,k}$ is the overall mean of Squared Euclidean Distance from randomized data for half-window size k (expected mean), and $SD_{exp,k}$ is the standard deviation of the Squared Euclidean Distance values from the randomized data for half-window size k (overall mean and standard deviation are computed from 99 randomizations and for the whole transect). Random reference was made with random shift of species. The distribution of each species is shifted a random number of units along the transect. Occurrences which are shifted beyond the end of the transect are wrapped back on to the opposite end (Palmer & van der Maarel, 1995; Horváth, 1998). Z-scores averaged over 1-10 half-window sizes were plotted against window midpoint position, resulting in a z-score profile. In the profile, vegetation boundaries appear as peaks. Z-scores above 1.85 were regarded as indicating significant ($p<0.05$) boundaries. For the MSW-computations, the statistical language R 2.10.1 was used (Anon., 2009).

Population level investigations were carried out to examine possible spatial pattern differences among the southern and northern sides of the transects. Patch sizes of the particular populations were examined. Population patches were defined according to the criteria system used by Méri and Körmöczi (2010), specially built for this purpose. The database handling was implemented with the software Enthought Python Distribution 6.3 (Anon., 2011). Species with occurrence in less than 10 quadrats were ignored. To investigate the significant effect of the exposure on the patch sizes in the individual transects, 3 generalized linear models with negative binomial error were built, using the library MASS (Crawley, 2007). The statistical analysis was performed with R 2.10.1 statistical software (Anon., 2009). Finally, the average numbers of patches per population of the northern sides were compared to those of the southern sides.

Results

In the 1000 plots, a total of 284 species were found. 167 of these, occurring in at least 10 plots, were included in the population level analyses. Southern slopes proved to be more species rich than northern ones (Table 1).

The identified communities along the gradients are shown in relation to the topographical circumstances with the examples of 2 transects (Fig. 1, Fig. 2).

Table 1. Differences between north-facing and south-facing slopes in the Villány Mts. Exp.=exposition, N=north, S=south.

Location	Exp.	Number of significant boundaries	Mean patch size (m) ±SE	Median patch size (m)	Number of patches	Number of species	Patch number/ species
Mt Fekete	N	1	7,173±0,075	3	104	13	8,000
	S	6	7,537±0,016	3	456	52	8,769
Mt Szársomlyó #1	N	3	10,364±0,004	5	143	18	7,944
	S	4	5,747±0,064	2	584	49	11,918
Mt Szársomlyó #2	N	2	10,942±0,050	3,5	138	17	8,118
	S	6	5,898±0,021	3	588	48	12,250
Mt Szársomlyó #3	N	2	8,453±0,040	4	161	19	8,474
	S	4	6,923±0,003	3	652	55	11,855
Mt Tenkes	N	2	7,144±0,013	5	146	15	9,733
	S	3	6,264±0,008	4	508	50	10,160

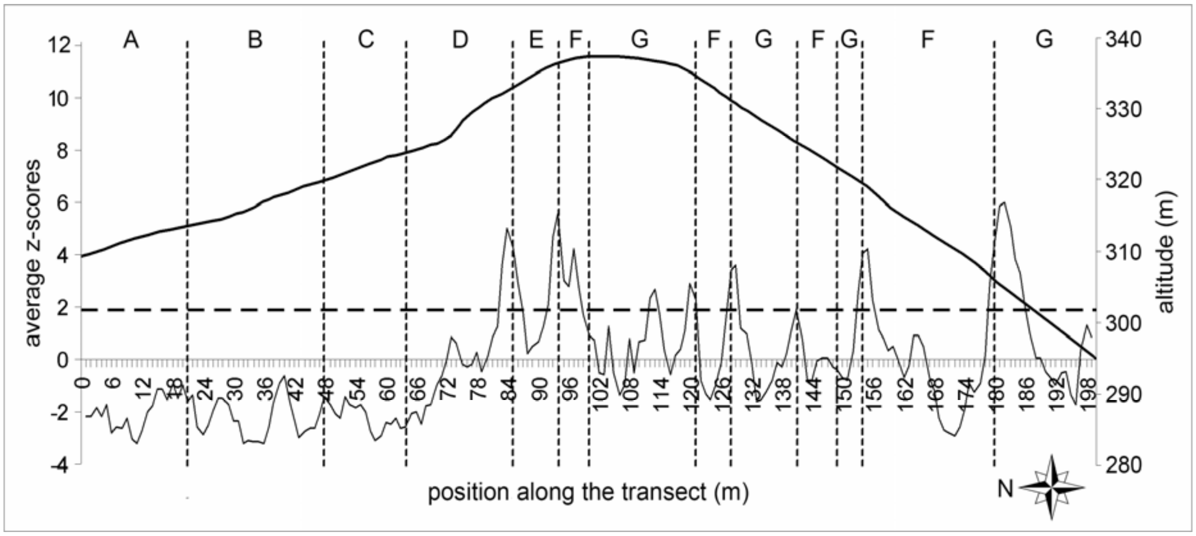

Fig. 1. Community sequence, morphological profile and z-score profile of transect #2 on Mt Szársomlyó. Vertical dashed lines indicate visually identified boundaries between communities. Bold solid line is the morphological profile, thin line is the z-score profile. Horizontal dashed line is the critical value, above which z-scores indicate significant ($p<0.05$) boundaries. A: *Asperulo taurinae-Carpinetum*, B: *Tilio tomentosae-Fraxinetum orni*, C: *Anthrisco cerefolii-Robinietum*, D: *Aconito anthorae-Fraxinetum orni*, E: *Festuco rupicolae-Arrhenatheretum*, F: *Inulo spiraeifoliae-Quercetum pubescentis*, G: *Sedo sopianae-Festucetum dalmaticae*.

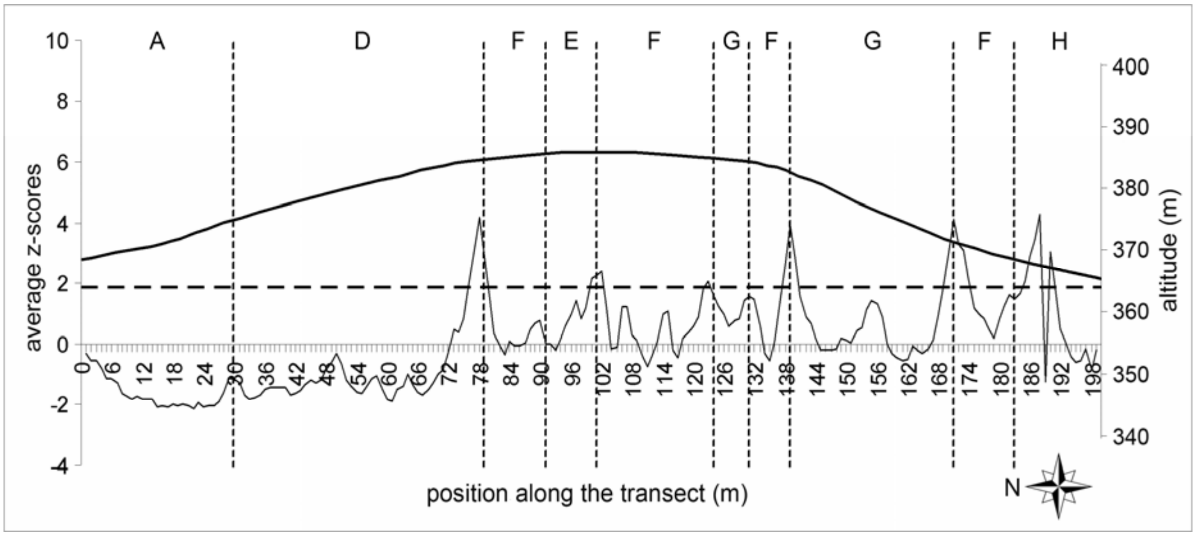

Fig. 2. Community sequence, morphological profile and z-score profile of the transect on Mt Tenkes. Vertical dashed lines indicate visually identified boundaries between communities. Bold solid line is the morphological profile, thin line is the z-score profile. Horizontal dashed line is the critical value, above which z-scores indicate significant ($p<0.05$) boundaries. A: *Asperulo taurinae-Carpinetum*, D: *Aconito anthorae-Fraxinetum orni*, E: *Festuco rupicolae-Arrhenatheretum*, F: *Inulo spiraeifoliae-Quercetum pubescentis*, G: *Sedo sopianae-Festucetum dalmaticae*, H: *Tamo-Quercetum virgilianae*.

The northern slopes are covered mainly by mesic forests. The lowest parts of the transects reach the illyrian oak-hornbeam forests (*Asperulo taurinae-Carpinetum*). In most cases, these forests extend far behind the northern endpoints of the transects. In two cases, non-typical fragments of the scree-forest *Tilio tomentosae-Fraxinetum orni* could also be identified. Nearer to the ridge, the top-forest *Aconito anthorae-Fraxinetum orni* is typical, occurring in 4 of the 5 transects. In some cases, stands of the shrubforest *Inulo spiraeifoliae-Quercetum pubescentis* also occur on the northern slope, although this community is typical on the southern slopes. In northern exposures, a closed rock sward community (*Festuco rupicolae-Arrhenatheretum*) can be found near the ridge or plateau along all transects.

The southern slopes are covered mainly by a mosaic of karst shrubforests and open rock swards (*Sedo sopianae-Festucetum dalmaticae*). Near the hillfoots, where soil is deeper, the slope steppe *Cleistogeni-Festucetum rupicolae* or even the hairy oak-chestnut oak forest *Tamo-Quercetum virgilianae* can be found. (Near to the foot of Mt Szársomlyó, there is a stripe of the slope steppe *Cleistogeni-Festucetum rupicolae*, but transects did not reach this community because of the great distance.)

Number of significant ($p<0.05$) boundaries was generally lower on the northern slopes than on the southern slopes (Table 1).

On the northern slopes, no significant peaks can be found between the various mesic forest communities (in fact, z-scores are very far from the significance level), while there are prominent boundaries near the edges of the closed rock sward stands (Fig. 1., Fig. 2.). On Mt Tenkes, an additional significant boundary is located between the top-forest and the neighbouring shrubforest. Situation is quite different on the southern slopes, where sharp boundaries exist between the rock sward and shrubforest patches. In general, boundaries identified by the MSW correspond well to the visually observed boundaries. However, in some cases, MSW identified additional boundaries where no discontinuities were detected during field works. These boundaries may refer to internal heterogeneities within communities. Most z-score peaks are pronounced, indicating rather abrupt boundaries (i.e. sudden changes in the vegetation) (Fig. 1., Fig. 2).

The most frequent species along the northern sides of the transects were mostly mesic plants: *Anemone ranunculoides* L., *Corydalis cava* (L.) Schw. et Koerte, *Helleborus odorus* W. et K., *Ranunculus ficaria* L., *Ruscus aculeatus* L. and *Veronica hederifolia* L. In addition, *Anthriscus cerefolium* (L.) Hoffm., *Galeobdolon montanum* Pers. ex Rchb. and *Mercurialis perennis* L. also had considerable frequences in some of the transects. In contrast, the most frequent species of the southern slopes were xeric plants: *Botriochloa ischaemum* (L.) Keng, *Chrysopogon gryllus* (Torn.) Trin., *Elymus hispidus* (Opiz) Melderis, *Festuca dalmatica* (Hack.) K. Richt. and *Orlaya grandiflora* (L.) Hoffm. Occasionally, *Artemisia alba* Turra, *Cleistogenes serotina* (L.) Keng, *Melica ciliata* L. and *Potentilla arenaria* Borkh. were also very frequent.

To justify the assumption that patch sizes differ between the northern and southern sides of the transects, 3 generalized linear models were built with negative binomial error correction. The best model was chosen with model selection by Akaike's information criterion (AIC) value ($p<0.001$, $z=-6.793$, $df=3410$). It included only exposure, which means that it has significant effect on the patch sizes of the plant populations, patches of the northern slopes being greater (Table 1).

Patch number on the southern sides was about four times greater than on the northern sides along each transect (Table 1). Although the southern sides were much more species-rich, this can only partly explain the differences in patch numbers, since average patch number per species is consequently greater on the southern slopes. Thus southern slopes possess more population patches which are smaller on average, whilst northern sides have fewer patches which are more extensive.

Discussion

In this paper north-south gradients of the Villány Mts (South Hungary) were examined at the community and at the population level. Several studies on gradients have been carried out, but most of them focused either on edge-to-interior gradients (Oosterhorn & Kappelle, 2000; Stanisci *et al.*, 2000; Hennenberg *et al.*, 2005; Erdős *et al.*, 2011b) or on elevation gradients (Werger *et al.*, 1983; Wierenga *et al.*, 1987; Khan *et al.*, 2011). Generally, gradients through a mountain ridge form a neglected area.

Marked differences between the vegetation of north-facing and south-facing slopes have been found in several environments (Hutchins *et al.*, 1976; Armesto & Martínez, 1978; Hicks & Frank, 1984; Kutiel & Lavee, 1999; Nazarian *et al.*, 2004; Bátori *et al.*, 2011; Khan *et al.*, 2011). Results of the present research showed that along the gradients of the Villány Mts, oak-hornbeam forests of the northern slope change into scree-forests and top-forest. Nearer to the ridge, shrubforests and closed rock swards occur. On the southern slope, there is a mosaic of shrubforest and rock sward patches (Fig. 1, Fig. 2). Similar community sequences have been reported from the nearby Mecsek Mts (Morschhauser, 1995; Kevey & Borhidi, 1998), although objective methods have rarely been used so far (Erdős *et al.*, 2008b). In South Hungary, mountainous areas often have similar ecological conditions: soils on the northern slopes are deeper than on the southern slopes, and northern slopes receiving less solar radiation are cooler and moister than southern ones. Similar ecological conditions result in similar community sequences along the north-south gradients. However, a fundamental difference between the Mecsek Mts and Villány Mts is that no xeric grasslands can be found near the ridges in the Mecsek Mts.

It has been revealed in some studies that, under mediterranean and continental climates, slopes facing the equator are likely to have shrubby vegetation, while slopes facing the opposite direction often support forests (Armesto & Martínez, 1978; Khan *et al.*, 2011). The same is the case in the Villány Mts, which may be attributed to the different microclimates of the different slopes.

Although Hegazy *et al.*, (2011) pointed out that variation between sites or disturbance may hide the differences between south-facing and north-facing mountain slopes, this was clearly not the case in the Villány Mts. The explanation of this is that study sites are relatively intact, and there is little between-site variance in the Villány Mts.

Jakucs (1972) published 6 hypothetical north-south vegetation profiles across mountain ridges according to the main European climate types. Based on the results of this study, a seventh type may be added: the gradients of the Villány Mts form a transition between the submediterranean-subcontinental and the continental types. Mosaic of xeric shrubforests and rock swards on the southern slope is typical of the submediterranean-subcontinental climate, whereas xeric grasslands near the ridge form a characteristic of the continental type.

Several forest communities were identified on the northern slopes visually, concerning all vegetation layers. However, no significant boundaries were detected using the MSW in the field layer of the mesic forest communities. The possible cause for this incongruity may be the different mechanisms controlling the canopy and the field layer. It is supposed that the most important factor controlling the canopy layer is thickness of the soil: as soil gradually becomes shallower, forests get lower (this can be seen along the sequence oak-hornbeam forest-scree-forest-top-forest) and finally they are replaced by a closed rock sward. In contrast, light could be the most important environmental factor for the field layer.

Therefore, from the point of view of the field layer, the most important parameter is whether or not there is a dense canopy above. This is an explanation of the fact that sharp boundaries have been found where mesic forests adjoin a closed rock sward or a shrubforest with an open canopy, but boundaries could not be revealed between the forest communities using the MSW-method.

On the southern slopes, visually observed boundaries of all vegetation layers coincide with MSW-detected boundaries of the field layer, because changes in soil depth coincide with changes in canopy cover.

The results of Werger *et al.*, (1983), Wierenga *et al.*, (1987) and Brunet *et al.*, (2000) suggest that soil conditons may primarily be responsible for the vegetation gradients. However, if there is a marked change in canopy cover values through an edge, this could have a considerable effect on the field layer (Brunet *et al.*, 2000). The studies of Tyler (1989) and Holeksa (2003) also point to the importance of canopy cover in controlling the distribution of field-layer species. These results are in good agreement with our guesses.

In a heterogeneous landscape, boundaries are important structures from an ecological point of view (Cadenasso *et al.*, 2003). Since sharpness belongs to the most important structural characteristics of boundaries (Strayer *et al.*, 2003), this study focused on the sharpness of the boundaries between the communities of the field layer. Most peaks of the z-score profile are relatively high and narrow, indicating sharp boundaries. Results of the present study point out that one must be careful when evaluating MSW profiles. First, along the transects under scrutiny, MSW revealed some boundaries within communities. Although these may refer to internal heterogeneities, it is important to note that MSW tends to detect heterogeneities which are statistically significant, but ecologically meaningless (Choesin & Boerner, 2002). Second, some non-significant boundaries coincide with visually observed boundaries. Since significance of the peaks greatly depends on transect length and the number of boundaries (Körmöczi, 2005), this study emphasizes that nearly-significant z-score peaks have to be considered potential boundaries.

The results of this study show that southern slopes tend to have more significant boundaries between communities than do northern slopes (Table 1). Moreover, population patches of the southern slopes are smaller in diameter and greater in number than patches of the northern slopes (Table 1). Conclusion is that in the Villány Mts southern slopes are much more patchy than the northern slopes both on the population and the community level. Similarly, southern slopes have been found more patchy in earlier studies (Jakucs, 1972; Erdős *et al.*, 2008a, 2008b).

The present investigation also revealed that south-facing slopes are much more species-rich than north-facing ones (Table 1). There is no consensus between different studies concerning the species richness of differently exposed slopes: species richness may be greater on the north-facing slopes (Hutchins *et al.*, 1976), or on the south-facing slopes (Kutiel & Lavee, 1999), or it may not differ significantly on the different slopes (Armesto & Martínez, 1978). It seems that generalizations can only be made concerning particular regions. In the submediterranean mountains of South Hungary, it seems that southern slopes are more species rich than northern ones, although more case studies are needed in this field.

Acknowledgement

The authors are thankful to the Inspectorate for Environment, Nature and Water for allowing us to carry out these studies in the strictly protected nature reserves of the Villány Mountains. We would like to thank Tamás Morschhauser and the University of Pécs, Department of Plant Taxonomy and Geobotany for supporting this study.

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(Received for publication 15 March 2011)