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Ecological and Socioeconomic Correlates of Plant Invasions in Denmark: The Utility of Environmental Assessment Data

Control of plant invasions requires regional knowledge of invasive species' distribution and the factors that promote their spread. We studied the distribution of invasive alien plants in Denmark at 2 spatial scales ("site" and "municipality") based on habitat descriptions and species lists from 2343 sites recorded within environmental assessments for planned infrastructure projects and conservation management. We created a Geographic Information System database of the sites and supplemented the field data with information on traffic routes, water courses, and socioeconomic indicators from the respective municipalities. The percentage of invaded sites within a municipality decreased with increasing tax percentage and it increased with (sub-)urbanity. The number of invasive species at the sites was positively correlated with resident plant diversity, disturbance, and proximity to traffic routes. We conclude that current plant invasions in Denmark are mainly an anthropogenic (sub-)urban phenomenon. The results are discussed with respect to the utility of environmental assessment data for studying plant invasions and improving control of invasive species.

INTRODUCTION

Studying factors that control the invasibility of habitats has become an important issue of ecological research with the aim of developing general theories and improving the efficiency of management. Experimental and correlational studies have led to a number of hypotheses about the relationship between local environment and invasibility, and recent years have seen some efforts to combine these into unifying theories in which habitat disturbance and native species richness play a key role (1–3). Furthermore, it has been recognized that invasions are also influenced by landscape structures, such as river systems and road corridors, that can facilitate the spread of invasive species (4–7). In human-dominated landscapes, biological invasions may also be correlated with socioeconomic factors, such as population density, land use, trade, and urbanity (8–11).

Management plans for alien invasive species require knowledge of the factors that promote their spread (9). However, the relative significance of the various factors for habitat invasibility is likely to vary among different sets of non-native species (12) and different geographical regions and scales. To improve the management of biological invasions, we need empirical studies that are regionally specific and consider subsets of non-native species that are currently invasive, that is, show exponential population growth and spread.

Some studies have used grid-based data of plant species' distribution from national floristic monitoring programs (12–14). However, a substantial limitation of such data sets is that they are not habitat specific but lump species and environmental data within spatial grid cells. Thus, they do not allow direct investigation of invader–environment relationships, and, particularly, they preclude spatially explicit analyses of potential effects of dispersal corridors. These limitations can be solved by using site-specific datasets that cover large spatial ranges (e.g., counties, countries). Unfortunately, such datasets are rare in the fields of ecological science and invasive species management. A promising source of suitable data are environmental impact assessments, which are produced in association with building projects and conservation management. Such data are massively collected in many countries without being used for integrated ecological analyses, because the value has not yet been recognized by ecologists or the data were not easily accessible.

The aim of this study was to explore the potential value of environmental assessment data for testing theoretical predictions of habitat invasibility and for providing an improved knowledge basis for regional management programs of invasive species. The concrete objectives were *i)* to assess invasion frequencies of the most invasive plant species in Denmark in different habitat types and *ii)* to identify environmental and socioeconomic factors that correlate with habitat invasibility at 2 spatial scales ("site" and "municipality").

MATERIALS AND METHODS

Database

We used a data set from environmental assessments of the consultancy COWI A/S comprising 2343 sites across Denmark that were surveyed in the period 1997–2006 (Fig. 1). We focused on terrestrial inland invasions and, therefore, excluded sites located within 3 km of the coastline. The areas of the study sites ranged from 0.1 to 10 ha with occasional larger areas. The field surveys produced comprehensive lists of vascular plant species and descriptions of the habitats that were used to assign the sites to 8 broad habitat types (Table 1). Sites that made up more than 1 habitat type were excluded. Further, we used the habitat descriptions for classifying the sites into "undisturbed" and "disturbed" habitats. The undisturbed habitats were those that had not been considerably altered by human or natural disturbance for several decades, indicating continuity of the respective vegetation type. These included forests and forest swamps, old plantations, natural bogs, and lakeshores. In contrast, those sites that had undergone recent changes in land use or otherwise experienced vegetation change were classified as "disturbed," such as ruderal sites and abandoned grasslands. We had to leave 35% of the sites as unclassified because of missing details in their habitat descriptions.

We constructed a Geographic Information System database of all sites and supplemented the field data with geodata at the site scale (geographical coordinates, site area, proximity to roads and water courses [<300 m], recreational value), at the municipality scale (deposition of nitrogen and sulphur, human population and farm density, average income tax percentage, land area tax), and by contrasting major Danish regions (the western mainland Jutland and the eastern islands Sealand and Funen). Some sites had to be excluded because of missing or incomplete species lists so that the effective data set comprised 1639 sites.
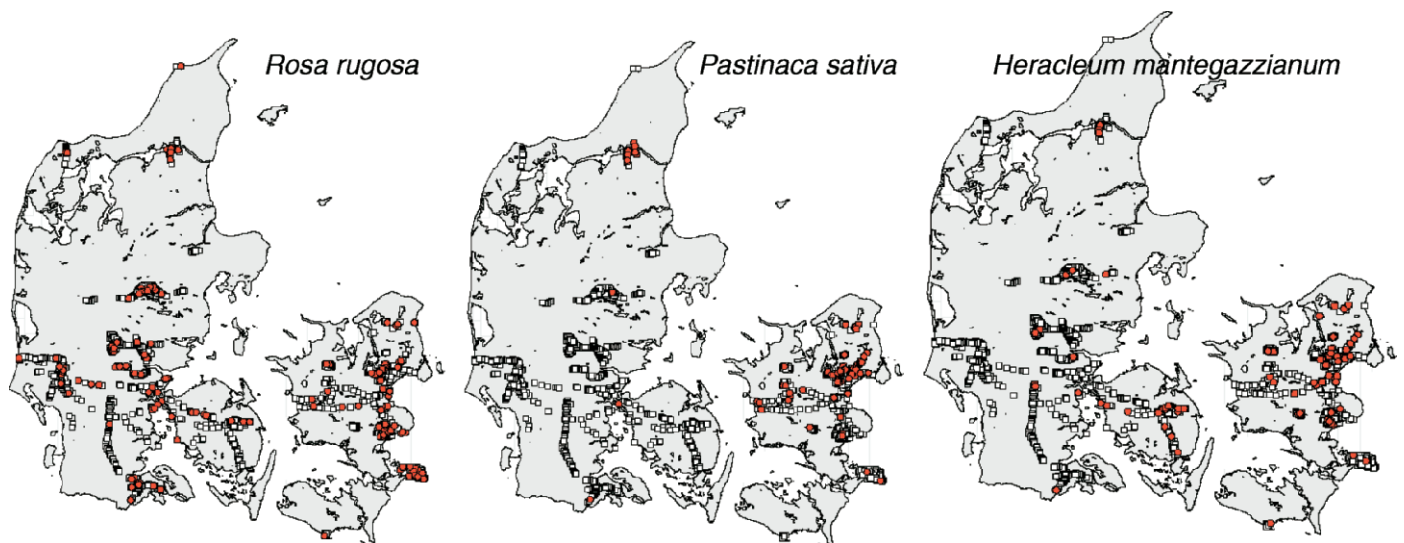
Figure 1. Distribution of study sites in Denmark, including records of the 3 most frequent invasive alien species: *Rosa rugosa*, *Pastinaca sativa,* and *Heracleum mantegazzianum*.

Our study focused on 11 terrestrial plant species that currently show exponential population growth and invasive spread in Denmark based on expert knowledge, albeit without quantitative information (15). These species represent a broad diversity of life forms (Table 2). We considered all other plant species as "residents," including non-native species that have more or less completed their invasion (e.g., *Acer pseudoplatanus*). We also made supplementary analyses with all non-native species introduced after 1500 ("neophytes," 73 species). Nomenclature follows Flora Europaea (16), except for *Fallopia japonica* (syn. *Reynoutria japonica* Houtt.) and *Fallopia sachalinensis* (syn. *Reynoutria sachalinensis* [F. Schmidt] Nakai).

Data Analyses

We set up 2 variables to measure habitat invasibility. At the municipality scale, we calculated the percentage of sites that were invaded by at least 1 of the invasive plant species (hereafter "invasion percentage"), whereas we used the number of invasive species at the site scale. To test the significance of predictor variables, we used R-2.4.1 (17) to calculate Poisson regressions, because both dependent variables were approximately Poisson distributed. We selected best subsets out of the 2 sets of potential predictor variables described above based on Akaike's information criterion (18) and, in case of close Akaike's information criterion values, decided for the simpler model to follow the principle of parsimony (19). We tested for collinearity among the predictor variables by regressing each of them on all the other predictors. The R^2 values of these regressions never exceeded 0.27 and, thus, indicated that there was no considerable collinearity. For graphical analyses, we used the lattice package in R (20) and SigmaPlot 10.0.

RESULTS

Habitats and Species

The 3 most invaded habitat types of the present survey were ruderal sites, heathlands, and man-made habitats, including urban parks, yards, and sports grounds, with invasion percentages of up to 70% (Fig. 2). In contrast, the least invaded habitat types were riparian habitats and swamps that showed invasion percentages of approximately 20%.

Regarding all habitat types, *Rosa rugosa* (10.6% of 1639 sites) had the highest frequency of the 11 study species, followed by *Pastinaca sativa*, *Heracleum mantegazzianum*, *Petasites hybridus*, *Pinus mugo*, *Prunus serotina*, *Solidago canadensis,* and *Fallopia japonica* in decreasing order (Table 2). *Impatiens glandulifera* (0.2%), *Fallopia sachalinensis* (0.1%), and *Solidago gigantea* (0.1%) were relatively rare.

The proportions of the invasive species within habitat types showed some degree of variation (Fig. 3). Heathland invasions were, for the most part, attributable to *Pinus mugo*, and in forest plantations, woody species (*P. mugo*, *P. serotina*, *R. rugosa*) accounted for 80–90% of all observations. In contrast, grasslands were prevalently invaded by tall herbs (*H. mantegazzianum*, *P. sativa*, *P. hybridus*), and in man-made and ruderal sites, *P. sativa* was the most frequent invader.

Invasibility of Municipalities and Sites

The percentage of invaded sites within municipalities was negatively correlated with average tax percentage, and there was also a regional difference, with lower invasion percentages on the mainland Jutland compared with the islands of Sealand and

Table 1. Categories of habitat types used in the assessment of invasion frequencies in this study.

Habitat type	Description	Sample size
Ruderal sites	Abandoned industrial land, disturbed railway and road embankments, uncovered parking sites	17
Man-made habitats	Artificial sites, e.g., parks, sports grounds, residential areas	14
Heathlands	Dwarf-shrub heath, usually dominated by *Calluna vulgaris*, with varying cover of grasses or shrubs and trees	16
Forest plantations	Afforestations with coniferous or deciduous trees	53
Deciduous woodlands	Natural beech forests and mixed deciduous forests without larger occurrence of conifers	184
Grasslands	Agricultural meadows and pastures, low-intensity pastures, and abandoned grasslands that were formerly used as meadows or pastures	222
Riparian habitats	Pond and lake shores; banks of rivers, brooks, and larger ditches	496
Swamps	Swamps, marshes, (partly)drained bogs	243

Funen (Table 3, Fig. 4). Within regions, the negative correlation of tax and invasion percentage was significant on Sealand and Funen but not in Jutland. Including an interaction of region and tax percentage did not, however, improve the model significantly. The regional affiliation was highly correlated with the deposition of nitrogen and sulphur (multiple $R^2 = 0.83$), so that the lesser-invaded Jutland showed higher nitrogen but lower sulfur deposition levels.

The number of invasive species per site was positively correlated with the number of resident species, that is, natives and fully naturalized neophytes, over all habitat types (Table 4). Also within habitat types, the association of invasive species and residents was positive or neutral (Fig. 5). Proximity to traffic corridors (<300 m to the state road network) and disturbance were positively associated with the number of invasive species, and, further, there was a trend of increasing numbers of invasive species toward the east and the north of Denmark (Table 4). When we performed this analysis with the number of all neophytes instead of only the invasive species, we found the same results, apart from a somewhat lesser significance of disturbance.

DISCUSSION

Invasive Species Frequencies

The present study is one of the first showing quantitative differences in frequency of invasive species based on environ-mental assessment data. *R. rugosa*, which typically spreads along coastlines of northern Europe and northeastern America (22), is the most frequent invasive plant in Denmark, and it has apparently become invasive throughout the whole country. This result would probably be even clearer if coastline sites had been included. On the other hand, *I. glandulifera, S. gigantea,* and *F. sachalinensis* showed only rare incidences, although they are common and widespread invaders in central Europe (23, 24). They have apparently not yet reached phases of exponential increase in Denmark, although this could be expected in the near future.

In contrast to the majority of the study species that are invasive in several countries of Europe and on other continents, *P. mugo* is invasive only in Denmark and Norway (and considered potentially invasive in Latvia and Lithuania) (25) and outside Europe in New Zealand (26). Its wide distribution in Denmark is promoted by planting, especially on sandy soils. Its spread has negative implications for nature conservation because it often invades seminatural heathlands.

Regarding the ranking of the study species according to frequencies, our study sites roughly compared to the 25 km^2
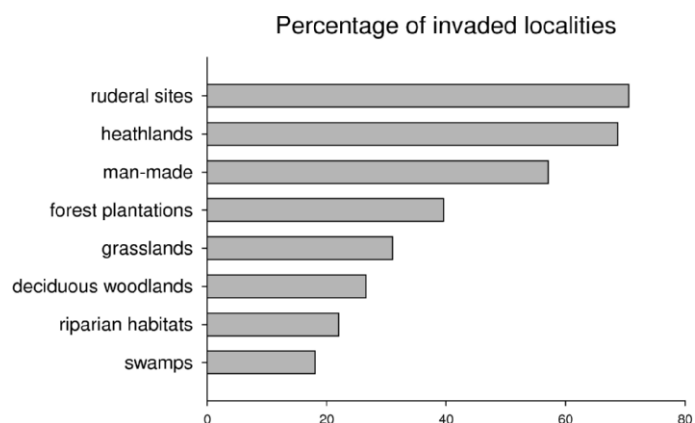

Figure 2. Percentage of invaded sites for 8 habitat types in Denmark. All sites that contained at least 1 invasive plant species were considered to be invaded. Sample sizes: ruderal sites, 17; heath-lands, 16; man-made habitats, 14; forest plantations, 53; grasslands, 222; deciduous woodlands, 184; riparian habitats, 496; swamps, 243.
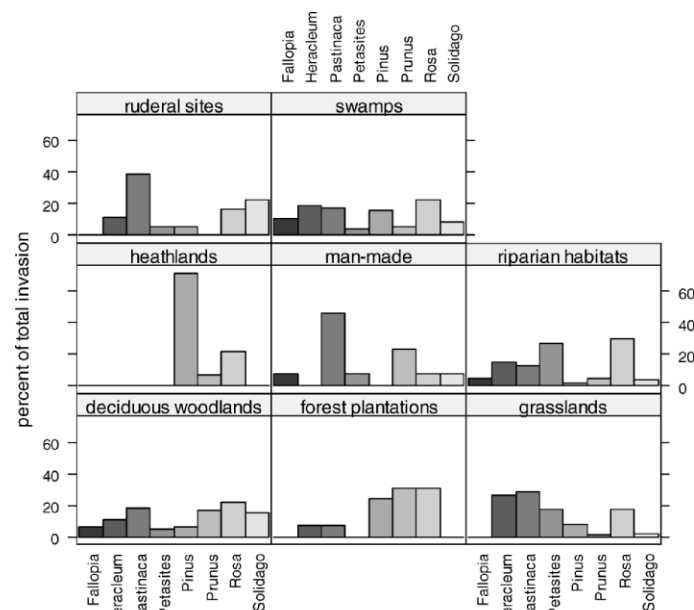

Figure 3. Relative frequency of invasive species in invaded sites of 8 Danish habitat types. For full plant species names, see Table 2. *Fallopia* and *Solidago* spp. were merged; *Impatiens glandulifera* was omitted because of too few occurrences.

grid cells of the Atlas Flora Danica, as indicated by a significant Spearman rank correlation (Table 2). However, *F. japonica* ranked considerably lower, and, in contrast, *P. mugo* ranked higher than in Atlas Flora Danica. Higher ranking at the smaller scale (study sites) indicates substantial spread among sites in some parts of Denmark, whereas higher ranking on the larger spatial scale (Atlas grid cells) indicates a wide and even distribution but little invasive spread among sites.

Invaded Habitat Types

The ranking of habitat types in order of invasion percentage was, by and large, similar to those found in other central and northern European countries. However, the high invasion percentage of heathlands and, on the other hand, the low figures for riparian habitats were surprising. Although many studies found man-made habitats to be more vulnerable to invasion than natural ones (27, 28), it appears that heathlands in Denmark are open to invasion by woody species, particularly *P. mugo*, but also *R. rugosa* and *P. serotina*. Invasions of seminatural inland heath in Denmark are probably facilitated by decreasing management and increasing nutrient loads, which trigger secondary successions leading to scrub and woodland encroachment (29). Early stages of succession offer good opportunities for invasive plant species (30, 31).

Riparian habitats have frequently been recognized as particularly vulnerable to invasion (32, 33). However, we found a low invasion percentage of Danish riparian habitats. This might be because Danish rivers and ditches have relatively little natural dynamics, with short and infrequent inundation. Further, most water courses are adjacent to agricultural land, and, therefore, riparian habitats are often intensively managed (34). In a related grid-based study, water courses were a marginally significant predictor of the distribution of *H. mantegazzianum* in Denmark (14).
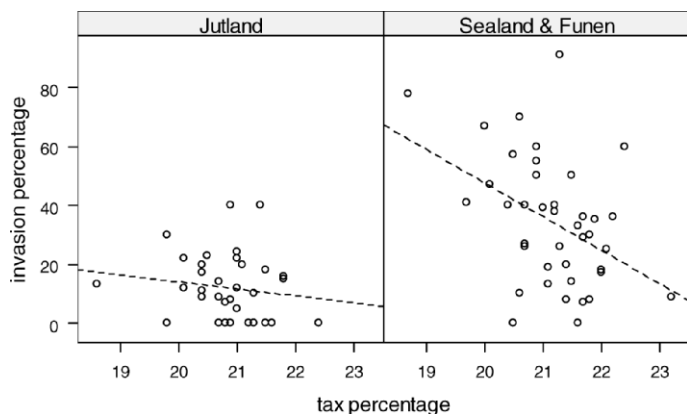
Municipal Invasion Percentage

Contrasting our expectations, we did not find any significant relationship between the percentage of invaded sites within municipalities and human population density or number of farms per area. However, our results revealed regional differences between Jutland, and Sealand and Funen, and a correlation with tax percentage that together explained a fairly large amount of the variation in the municipal invasion percentages (R^2 = 0.36). The regional differences were highly correlated with the deposition of nitrogen and sulphur that can be interpreted as correlates of agriculture and urbanity, respectively. High nitrogen deposition seems to point toward a high intensity of agriculture (35, 36), which, in this study, is associated with comparatively low invasion percentages. In contrast, high sulphur deposition indicates a high degree of urbanity (37), associated with high invasion percentages. Thus, it appears that current invasions of non-native plant species in Denmark tend to be mostly a (sub-)urban phenomenon, while intensive agriculture seems to reduce invasion at the municipality scale.

The municipal tax percentage, which was negatively correlated with invasion, represents the average income tax percentage paid by the municipality's inhabitants and, thus, reflects prosperity of the population. We can only speculate about the mechanisms behind this negative correlation between

Figure 4. Correlation between the municipal invasion percentage and average tax percentage for the 2 main regions of Denmark. The correlation was significant within the Sealand and Funen region (r = −0.42, p = 0.006, n = 40) but not within Jutland (r = −0.15, p = 0.399, n = 35).
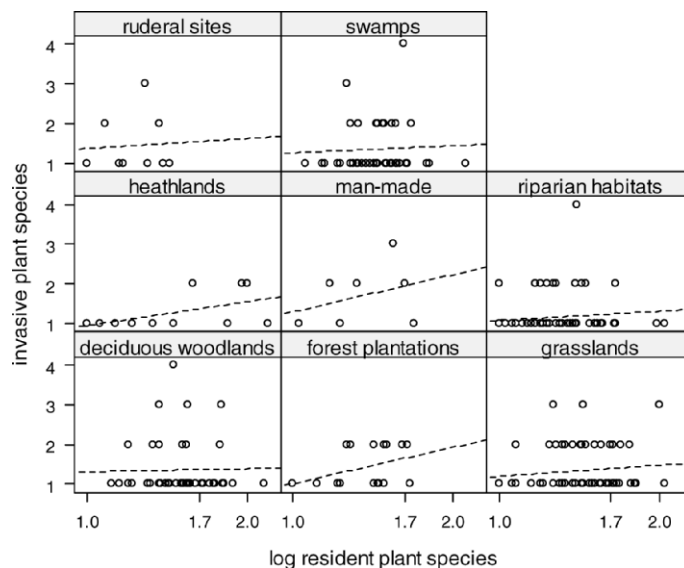
Figure 5. Correlation between the number of invasive and the number of resident plant species per site. Only sites invaded by at least 1 species are plotted. The slope of the regression line within habitat type was significant for forest plantations only (Poisson regression, p = 0.047). Sample sizes: deciduous woodlands, 49; forest plantations, 21; grasslands, 70; heathlands, 11; man-made habitats, 8; riparian habitats, 115; ruderal sites, 12; swamps, 45.

prosperity and invasion. It would be conceivable that prosperous municipalities and citizens spend more money on conservation, landscape management, and garden and park maintenance, which should result in lower amounts of ruderal and neglected land area and, consequently, fewer plant invasions. Moreover, prosperous municipalities might also spend more on the maintenance of roadsides, which could reduce their corridor function for the spread of invasive species. Another explanation may be that well-off citizens choose to live in rather undisturbed areas with high proportions of natural forests and low levels of disturbance by large infrastructure projects. Altogether, the results of the municipal invasion model indicate that plant invasions are, to a large extent, a socioeconomic issue, as pointed out by Hobbs and Humphries (8).

Site Invasibility

The site-scale invasion model showed that disturbed sites have higher numbers of invasive species, which is in agreement with other correlational studies (38) and with experimental studies that found facilitative effects of small-scale disturbance for establishment of *R. rugosa* (39), *H. mantegazzianum* (J. Thiele, unpubl. data), and other species (40).

We found that the number of invasive species per site increased in proximity (<300 m) to traffic routes, indicating that the major roads function as dispersal or migration corridors for the invasive species in Denmark. However, we did not find any significant corridor effect of water courses, which dissents from other studies that found enhanced spread along river corridors of invasive species (32, 41). Reasons for this may be that the riparian habitats of this study showed comparatively low invasibility and that only some of the study species show affinity to flowing waters, such as *H. mantegazzianum* (14, 42), *Fallopia* spp. (43), *I. glandulifera* (13), and *P. hybridus* (44), whereas the others are less associated with rivers.

The positive correlation of resident and invasive species numbers within and across habitat types appears to contradict the classical theory of biotic resistance (45). However, it has been shown that correlations of species numbers largely depend on spatial scales and that correlations tend to be positive across habitat types and negative at very fine spatial scales (few square meters) as a consequence of a sampling effect (46). At intermediate scales, previous studies showed variable patterns (47). Although we cannot preclude biotic resistance effects at smaller scales within the sites, our study suggests that resident and invasive diversity are controlled by similar factors at the site scale within and across habitat types, which was also found by several other studies (28, 48).

Potential of Environmental Assessment Data

Our study shows that large environmental assessment data sets can be useful for scientific studies of plant invasions. Even though the data set used here has some disadvantages, because it is not a random sample and the sampled sites are not evenly distributed over the study region, we could identify some environmental and socioeconomic factors associated with occurrences of invasive plant species and habitat invasibility. Strong points of the data set are the large number of sites, the wide geographical range, and the comparatively short time span between the earliest and most recent records (1997–2006). Based on our experience made during this study, we encourage other scientists to use similar data from environmental assessment programs to test invasion theory and to identify the generality or regional specificity of environmental and socioeconomic factors across geographic regions.

Perspectives for Management

Because monetary resources are a limiting factor, it is mandatory to set management priorities of species and areas to be treated (49). Here, environmental assessment data or similar data sets could give useful information on the habitat-specific frequencies of invasive species and for assessing invasion risks, such as at the municipality scale, as a basis for planning management programs. An additional perspective could be to integrate environmental assessment data into monitoring systems of invasive species, such as by passing on the species records to floristic mapping projects or specialized invasive plant databases. Finally, we believe that the environmental impact assessments or conservation management projects could be combined with management measures of the invasive species found in the records. The usefulness of environmental assessment data could still be enhanced by recording abundance estimates together with the species lists, which would allow a more detailed assessment of the local invasion intensity of the species.

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50. First submitted 22 November 2007. Accepted for publication 18 February 2008.

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