Modelling the distribution of Ilex aquifolium at the north-eastern edge of its geographical range

María José Bañuelos, Johannes Kollmann, Per Hartvig and Mario Quevedo


Plant distribution borders are key features to characterise the ecological niche of a species and to monitor effects of climate change. Here we focus on an evergreen small tree, Ilex aquifolium, which reaches its north-eastern range edge in Denmark. Our main objectives are to describe and to model the current distribution of the species, to identify the most important climatic and land use factors which shape this distribution pattern, and to analyse the species’ habitat requirements. For this purpose we used data from a national mapping project, complemented by information from forest owners. The distribution and abundance of I. aquifolium in Denmark have markedly changed during the past 40 years. It is now found in almost all districts, although the centres of abundance still coincide with the historical records. Our model shows lower habitat suitability for the species in northern and eastern districts, where winters are more severe and spring precipitation is lower. To a lesser extent, land use influences I. aquifolium occurrence, but it is more common in areas with a high proportion of forests and/or urban sites. The analysis of habitat requirements supports these results, since I. aquifolium occurs mainly as a forest species in deciduous stands, on relatively nutrient-rich moist soils, and under moderately high light conditions. However, some records may be the product of seed dispersal from planted individuals nearby. The results suggest that the range edge of the species has moved at least 100 km east within half a century. Since I. aquifolium is sensitive to winter frost, this change in distribution may be due to increasingly mild winter temperatures.

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Introduction

The dynamics of plant distributions are a focal area of current biogeographical research, especially in relation to recent trends in climate and land use (Hoffmann & Blows 1994, Walther et al. 2002, Travis 2003; for an overview see Gaston 2003). These dynamics are expected to be especially visible at distribution borders, where populations usually grow under ecologically marginal conditions, and therefore should react strongly to changes of the environmental factors (Loik & Nobel 1993, Bruehlheide & Heinemeyer 2002, Jump & Woodward 2003). The development of predictive distribution models has

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become an effective tool in ecology (Guisan & Zimmerman 2000), and their application at dynamic distribution edges has both fundamental and applied interest. Basic research uses information about populations at the edge of the range to understand the habitat niche of the species and to model plant dispersal and distribution. Applied studies are concerned with both the regression of rare native species and the spread of invasive alien plants, processes that should be closely monitored, especially at their distribution borders.

It is widely accepted that the distribution of most plant species is controlled by climatic factors, often through detrimental effects on reproduction (Woodward 1987, Pigott 1992, Despland & Houle 1997, García et al. 2000, Gaston 2003). Temperature is considered the main variable controlling the range of many plant species but precipitation is also important (e.g. Beerling 1993, Thuiller et al. 2003). However, the correlation between climatic variables and species distribution might only be meaningful when applied to near-natural environments for a restricted time period. Anthropogenic influences determine the distribution of many species through for example plantations, accidental dispersal and habitat alteration. Moreover, climatic shifts may lead to changes in plant distribution (Walther 2004), although there might be a time-lag between these shifts in environmental conditions and apparent effects on species distribution (Chapin & Starfield 1997).

Here we report on a modelling study to describe recent trends in distribution and abundance of a regionally rare evergreen tree, *Ilex aquifolium*, at the edge of its range. The species range is characterised by mild winter temperatures and relatively high summer precipitation (Peterken & Lloyd 1967). Its north-eastern distribution border is crossing Denmark, and in the first half of the 20th century the absolute border was believed to run between the islands of Funen and Zealand (Fig. 1). Therefore, Iversen (1944) suggested a close correlation of this border with the January isotherm of −0.5 °C. However, recent field

![Fig. 1. Historical distribution of *Ilex aquifolium* in Denmark, including the eastern border line of its natural distribution as suggested by Iversen (1944). The map is based on field observations mostly from 1964-1966 and herbarium records summarised in Odum (1968). Included are the names of those parts of the country which are mentioned in the main text.](image-url)
observations during a national mapping project (‘Atlas Flora Danica’; cf. Hartvig 2004) revealed that the species is now present in many eastern parts of the country, and this shift in distribution might be related to changes in climate and/or land use.

The aim of the study is (1) to describe the current distribution of the species and to compare this pattern with historical records, (2) to identify the most important climatic and land use factors which might determine the current distribution, (3) to model the current potential distribution including areas from which no records are available, and (4) to describe the habitat association of the species as an indicator for future trends in dispersal and distribution of *I. aquifolium*.

**Material and methods**

**Study species**

*Ilex aquifolium* L. (Aquifoliaceae) is a small tree (<10–17 m, <300 yrs) occurring in Europe and North Africa (Peterken & Lloyd 1967, Odum 1968). The species has spiny evergreen leaves; it is dioecious and flowers in May–June. Fruits ripen in late autumn and usually last throughout the winter, when frugivorous passerine birds are the major dispersers (Snow & Snow 1988). In addition, vegetative regeneration can be prominent especially after damage of adult trees. It is found as a sparse but usually gregarious understorey plant in deciduous forests of western and southern Europe (Peterken & Lloyd 1967, Odum 1968, Pott 1990, Sebald et al. 1992, Obeso 1997).

**Study area**

Denmark was chosen as a study area (43 093 km²) because old records describe that the north-eastern distribution border of *I. aquifolium* is crossing this country (Odum 1968). The relief of Denmark is relatively simple with a maximal elevation of 173 m a.s.l., and most soil types have developed from glacial deposits (Jacobsen 1989). Western Denmark is characterised by podzol soils on sandy outwash areas, while in the eastern parts young till and clayey luvisol soils predominate. Rocky outcrops of chalk and granite are found in northern and eastern parts albeit sparsely. The climate is mild-temperate, with mean annual temperatures about 8 °C; August and February are the warmest and coldest months with mean temperatures around 16 °C and 0 °C, respectively. Coastal areas are milder, showing an annual temperature about 0.5 °C higher than the slightly more continental inner Jutland. Average annual precipitation is approx. 700 mm and distributed fairly even throughout the year, but with maximum values usually in autumn. Highest differences in precipitation occur between areas inside Jutland (approx. 900 mm) and some small islands and the western parts of Zealand (approx. 500 mm; Scharling 2000). For a phytogeographical description and the major forest types of Denmark see Lawesson (2000) and Lawesson & Skov (2002).

**Collection of data**

Four types of data were collected for selected cells in a national grid system: (1) presence-absence of *I. aquifolium*, (2) habitat information, (3) land use and soil characteristics, and (4) climate data.

We extracted all available data about *I. aquifolium* from the data base ‘Atlas Flora Danica’ (Hartvig 2004). This mapping project aims at a registration of all vascular plant species within selected grid cells of 5 × 5 km², including some information on plant communities, habitat traits and management. The project produces an inventory of 1100 grid cells, which eventually will cover approximately 50% of Denmark. Presently, 75% of all grid cells have been sampled. They are distributed more or less randomly over the country but with slightly higher density close to the major cities (cf. Fig. 2). The project started in 1991 and will continue until 2006. We used the information on *I. aquifolium* presence-absence in 698 grid cells, supported by 220 records from three Danish herbaria (Copenhagen University, Århus University, Royal Veterinary and Agricultural University) and from a questionnaire sent to selected Danish forest districts in southern and eastern Jutland (63 questionnaires returned of 163 sent).

We characterised the habitat association of *I. aquifolium* by choosing randomly one population per 5 × 5 km² grid cell (n = 358) and recording the type of habitat (deciduous forest, coniferous forest, scrubland, grassland or open areas, secondary habitat), soil nutrient status (poor, rich), soil moisture (low, high), light availability (low, high), habitat history (near-natural, plantation, other), origin and size of the *I. aquifolium* population (natural, planted; 0–10, 11–100, >100 plants), and for forest populations location (inner area, edge, gap) and forest age (old, young). Although the habitat traits and the community type information have been compiled by different observers and in different years, the trait classes are robust and should be sufficiently reliable for the purpose of the study. Nevertheless, we discarded all
records with unclear or doubtful information.

We obtained digital climatic data from the Danish Meteorological Institute. Specifically, we used two grids with data on average annual and monthly temperature, and precipitation from 1961–1990 (cf. Figs 3a, b; Scharling 2000). The grid cell-size for temperature, originating from 35 stations, was $20 \times 20$ km$^2$, whereas for precipitation it was $10 \times 10$ km$^2$ (data from 290 stations).

Information on forest cover and urban area was obtained from vectorial digital maps developed by The Danish Institute of Agricultural Sciences (Danmark Jordbrugsforsknings) with a resolution of 25–250 m (cf. Figs 3c, d). The main geological substrate types of all populations were used to describe the habitat association based on the digital map ‘Danmarks jordarter 1:200.000’ developed by GEUS (Geological Survey of Denmark and Greenland).

Fig. 2. Current distribution of *Ilex aquifolium* in Denmark based on records from 1991–2003 in the ‘Atlas Flora Danica’ data base (grid cell size $5 \times 5$ km$^2$, n = 698, blank areas = no data available).

Logistic regression analysis

We used a logistic regression model (logit link, binomial error distribution) to characterise the key variables explaining the distribution of *I. aquifolium* in Denmark. The basic units for our analysis were the $5 \times 5$ km$^2$ grid cells (n = 698) with information on *I. aquifolium* presence or absence.

The potential explanatory variables were seasonal precipitation in spring (April–June), summer (July–August), autumn (September–November) and winter (December–March), mean temperature of the coldest and warmest months, proportion of forest cover and of urban area. We checked the correlation matrix of the explanatory variables to correct for excess correlation among them ($r > 0.75$). In case two explanatory variables were strongly correlated, we kept the one that better predicted the dependent variable in univariate trials. The resulting variables were then combined with the $5 \times 5$ km$^2$ grid cells of presence/absence of *I. aquifolium*, so that each grid cell had a value for each specific variable, and we quantified the relationship among the presence of the study species and the explanatory variables with a logistic
multiple regression (Legendre & Legendre 1998).

We randomly halved the cells of the grid into a training and an evaluation dataset (n = 349 for each one). To build the minimal adequate model that best explained *I. aquifolium* presence we fit univariate models to the training dataset. A significance level of P < 0.1 was fixed for entrance of the explanatory variables, i.e. less restrictive than in parametric statistic (cf. Crawley 2002, Quinn & Keough 2002). From these initial models, we chose the one with the lowest Akaike information criterion (AIC). Subsequently we proceeded with bivariate models and so forth. We compared models by means of Chi-square tests, and the process ended when addition of new variables not further improved the model according to AIC. Potential non-linearity and interactions were checked by fitting the model with quadratic terms and interactions between the explanatory variables, and then comparing differences between models (Chi-square).

We bootstrapped the model 1000 times to check for stability and to obtain a robust estimation of the parameters. We chose a ‘P cut-off’ level for the probability of *I. aquifolium* presence that optimized the proportion of correctly predicted presence on the basis of higher reliability of presence data compared to absences. Still, the cut-off level kept the balance between the probability of correctly predicting pres-
ence and the probability of correctly detecting absence. We used the evaluation dataset to validate the predictive power of the model, and evaluated its performance by means of Cohen’s kappa statistic (Siegel & Castellan 1988). Finally, we applied the model to the whole area of Denmark, to provide an idea of the current potential distribution of I. aquifolium. The probability of I. aquifolium presence for any specific 5 × 5 km² grid cell can be calculated as

\[
P = \frac{1}{1 + e^{-\text{logit}(P)}}
\]

where logit (P) is the linear combination of the variables in the model (Legendre & Legendre 1998).

**Ordination analysis**

In order to summarize the descriptive information on I. aquifolium localities, we performed a non-metric multidimensional scaling analysis (NMDS; Legendre & Legendre 1998). This analysis reduced the dimensionality of the data set to the two main axes. The first step in the analysis was a dissimilarity matrix representing the distance between each pair of locations, based on shared characteristics. Every location was therefore represented by a k-1 dimensional data vector of distances, where k was the total number of locations. Then, the NMDS optimized the spatial representation in a lower-dimensional space (in general two- or three-dimensional), so that the distances between locations in the two-dimensional space were as close to the original k-dimensional distances as possible. In other words, NMDS minimized the difference between the distance measures (obtained from the dissimilarity matrix) and the distance in the ordination space. We used Sammon’s mapping (Sammon 1969), one of the non-linear projection methods that normalize the errors in distance preservation with the distance in the original space, making the stress scale-free and emphasizing the preservation of small distances. This is especially useful when the items (locations in our case) show very similar characteristics. The stress values in the NMDS, representing the lack of fit between the dissimilarity matrix and the two-dimensional ordination, were relatively low (final stress after 100 iterations = 0.10), indicating that the ordination was acceptable.

All statistical analyses were done with the statistical environment R and its specific libraries boot, cluster, concord, pcurve and vegan (R Development Core Team 2003).

**Results**

**Current distribution**

The records of Ilex aquifolium from 1991–2003 showed that natural populations were found in almost all parts of Denmark albeit with pronounced differences in density (Fig. 2). The observations were clumped in southern and central-eastern Jutland, on the islands of Funen and Bornholm, and in northern Zealand. Rather few records were from northern and western Jutland and southern Zealand. Compared to the map from Ødum (1968) the number of records has greatly increased, especially in western Jutland and on the eastern Danish islands, whereas there is no evidence for extinction of the historical populations.

<table>
<thead>
<tr>
<th>Name</th>
<th>Z</th>
<th>P</th>
<th>Effect</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring rainfall</td>
<td>3.18</td>
<td>0.001</td>
<td>+</td>
</tr>
<tr>
<td>Mean February temperature</td>
<td>2.10</td>
<td>0.03</td>
<td>+</td>
</tr>
<tr>
<td>Forest cover</td>
<td>1.95</td>
<td>0.05</td>
<td>+</td>
</tr>
<tr>
<td>Urban area</td>
<td>1.84</td>
<td>0.06</td>
<td>+</td>
</tr>
</tbody>
</table>

Table 1. Univariate relationships between presence of Ilex aquifolium in Denmark and the four most tightly related explanatory variables. Presence/absence of the species and the climatic and land use variables were sampled in 5 × 5 km² grid cells (n = 698, logistic regression).
Table 2. Parameters of the logistic regression model to describe the potential distribution of *Ilex aquifolium* in Denmark (***, P < 0.001; **, P < 0.01; *, P < 0.05).

<table>
<thead>
<tr>
<th>Parameters (±1SE)</th>
<th>Z</th>
<th>Bootstrap parameters (±1SE)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>-3.94 ± 1.18</td>
<td></td>
</tr>
<tr>
<td>Mean February temperature</td>
<td>1.49 ± 0.43</td>
<td></td>
</tr>
<tr>
<td>Spring rainfall</td>
<td>0.028 ± 0.008</td>
<td></td>
</tr>
<tr>
<td>Urban area</td>
<td>3.29 ± 1.23</td>
<td></td>
</tr>
<tr>
<td>Forest cover</td>
<td>2.59 ± 1.08</td>
<td></td>
</tr>
</tbody>
</table>

Modelling the current observed distribution

The explanatory variables ‘spring rainfall’, ‘mean February temperature’, ‘forest cover’ and ‘urban area’ were positively correlated with the presence of *I. aquifolium* when analysed individually (Fig. 3, Table 1). All of them optimized the explanatory power of the logistic model (Table 2) yielding the following function:

\[
\text{logit (P)} = -4.00 + 1.54 \text{ mean February temperature} + 0.027 \text{ spring rainfall} + 3.57 \text{ urban area} + 2.68 \text{ forest cover}
\]

The cut-off P value that best described actual presence probability was P = 0.45, correctly classifying 77% of the grid cells with *I. aquifolium* presence and 37% of the absence ones. The kappa statistic was significant (k = 0.12; Z = 2.16; P = 0.015), indicating that the discrimination ability of the model was not achieved by chance alone.

Predicting the current potential distribution

According to the model, 31.1% of Denmark is highly suitable for *I. aquifolium* today (P ≥ 0.6), with a centre of potential distribution in south-western Jutland but also in southern Funen and north-eastern Zealand (Fig. 4). Almost half of the country (47.5%) shows intermediate suitability values (0.4 ≤ P < 0.6), and 21.2% is of low quality (P < 0.4), corresponding mainly to north-eastern Jutland and north-western Zealand.

Habitat preferences

Most of the 358 records of *I. aquifolium* considered for this study were located in forest (90%), mainly deciduous stands with *Fagus sylvatica* as the dominant tree species (Table 3). The species was also present in other community types, both deciduous stands (*Quercus* forests, moist forests with *Betula pubescens*, *Alnus glutinosa* and/or *Fraxinus excelsior*) and coniferous plantations (mainly of *Abies* sp., *Picea* sp. or *Pinus* sp., but also some *Larix* sp. and *Thuja* sp.), as well as in scrubland (with *Corylus avellana*, *Crataegus* sp., *Prunus spinosa* and *Salth* sp.). However, the species was also found in heathland, grassland and in ruderal habitats such as embankments, abandoned fields or gardens. Most habitats had a near-natural appearance (70%), but a considerable number were more recent forest plantations.

The geological substrate of most sites with *I. aquifolium* was clayey moraine (42%) or glacial sands (40%); the moist sites were on organic freshwater deposits (11%). The species was more common on relatively nutrient-rich and moist soils. Most records came from sites with fairly high light availability, and though the species was found more often in interior sites (74% of the forest locations) than in edges (24%) or clearings (1.4%), it showed a prevalence for old deciduous forests (74%), where the amount of light in the understory was relatively high.

Most records corresponded to non-planted populations of *I. aquifolium* (92%). And although there was only information for 70 of the 358 populations regarding population size, these data
Table 3. Characteristics of *Ilex aquifolium* habitats and populations surveyed in Denmark (n = 358).

<table>
<thead>
<tr>
<th>Habitat characteristics</th>
<th>Records (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Habitat type</strong></td>
<td></td>
</tr>
<tr>
<td>Forest</td>
<td>90.3</td>
</tr>
<tr>
<td>Deciduous forest</td>
<td>78.9</td>
</tr>
<tr>
<td>Coniferous forest</td>
<td>21.1</td>
</tr>
<tr>
<td>Non-forest habitat</td>
<td>9.7</td>
</tr>
<tr>
<td>Scrubland</td>
<td>59.7</td>
</tr>
<tr>
<td>Grassland or open areas</td>
<td>13.4</td>
</tr>
<tr>
<td>Ruderal habitats</td>
<td>26.9</td>
</tr>
<tr>
<td><strong>Habitat origin</strong></td>
<td></td>
</tr>
<tr>
<td>Natural</td>
<td>69.5</td>
</tr>
<tr>
<td>Plantation</td>
<td>16.3</td>
</tr>
<tr>
<td>Others</td>
<td>14.2</td>
</tr>
<tr>
<td><strong>Light availability</strong></td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>86.0</td>
</tr>
<tr>
<td>Low</td>
<td>14.0</td>
</tr>
<tr>
<td><strong>Geological substrate</strong></td>
<td></td>
</tr>
<tr>
<td>Clayey moraine</td>
<td>41.9</td>
</tr>
<tr>
<td>Glacial sands, sandy moraine, dunes</td>
<td>40.5</td>
</tr>
<tr>
<td>Organic freshwater deposits</td>
<td>10.6</td>
</tr>
<tr>
<td>Other substrates</td>
<td>7.0</td>
</tr>
<tr>
<td><strong>Soil nutrient status</strong></td>
<td></td>
</tr>
<tr>
<td>Rich</td>
<td>68.9</td>
</tr>
<tr>
<td>Poor</td>
<td>31.1</td>
</tr>
<tr>
<td><strong>Soil moisture level</strong></td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>71.8</td>
</tr>
<tr>
<td>Medium</td>
<td>28.2</td>
</tr>
<tr>
<td><strong>Origin of <em>I. aquifolium</em> population</strong></td>
<td></td>
</tr>
<tr>
<td>Natural</td>
<td>92.1</td>
</tr>
<tr>
<td>Planted</td>
<td>7.9</td>
</tr>
</tbody>
</table>

showed that 64% were quite small (0–10 plants), 31% corresponded to medium-sized populations (10–100 plants), and only 4.3% were big populations with more than 100 plants.

The non-metric multidimensional scaling of the *I. aquifolium* sites revealed some additional relationships between traits of the associated plant communities, although no sharply distinct groups emerged (Fig. 5). Axis 1 described mostly a light to shade gradient (Fig. 5c), corresponding to edge vs forest interior microhabitats (Fig. 5d); some of the younger forest (plantations) were particularly dark (Fig. 5c). Axis 2 separated near-natural deciduous forests from coniferous plantations (Figs 5a, b); most plantations were established on sandy substrates (Fig. 5f). The variation in soil nutrient-richness and moisture showed a similar pattern but did not contribute strongly to the structuring of the plant communities with *I. aquifolium* (Figs 5g, h).
Discussion

Changes in distribution and abundance

The comparison of historical and recent records suggests that the abundance of *Ilex aquifolium* has markedly increased in Denmark over the past 40 years, and that its range edge has moved at least 100 km east. Unfortunately, no direct quantitative comparison of the recent records and the map of Ødum (1968) is possible due to methodological differences and incomplete sampling during the old survey in western and northern Jutland and in urban areas (S. Ødum, pers. comm.). However, the interpretation of climatic factors causing the eastward shift in distribution is supported by recent observations of the species in southern Sweden and on the islands of Öland and Gotland in the Baltic Sea (Berger & Walther 2003). These authors attribute the change in distribution of *I. aquifolium* to increasing winter temperatures. The observed response of the species to changed climatic conditions is promoted by more frequent planting as an ornamental tree together with effective seed dispersal (Hartvig 2002) as the fruits are attractive to frugivorous passerines (Snow & Snow 1988).

Limitations and perspectives of the distribution model

The environmental variables selected to model the distribution of *I. aquifolium* in Denmark introduce a new perspective on the factors controlling the species' range. The importance of winter temperatures
Fig. 5. Non-metric multidimensional scaling of the habitat types for the locations in which *Ilex aquifolium* was found in Den-
incides with the period of development of new leaves, which initially are soft and thus might be more sensitive to dry spells. The causal explanation for a higher frequency of *I. aquifolium* in urban areas might be higher abundance of planted (and fruiting) individuals supported by locally higher temperatures, as part of the ‘urban heat effect’ (Bottyan &

and the prevalence in areas with high forest cover are in line with the description by Peterken & Lloyd (1967). However, the influence of spring precipitation and the degree of urbanisation have not been considered before, and need to be included in large-scale investigations of changes in the species’ range. Spring rainfall may promote plant growth since it co-

Unger 2003).

This is the first published regional distribution model for *I. aquifolium*, which might be used for surveying and management of the species in Denmark, especially in small and locally endangered populations. The mean temperature of the coldest month (February) is −0.29 °C (±0.01 SE, n = 468 grid cells) in areas with low probability of presence of *I. aquifolium* (presence probability < 0.4), while in potentially suitable areas (presence probability > 0.6) it is +0.16 °C (±0.01, n = 757). A hypothetical scenario of +0.5 °C increase in mean February temperature would result in a high probability for the presence of the species in almost the whole country, provided
that the rest of the variables in the model remain constant. Global mean surface temperatures have increased by 0.6 °C over the past 100 years, with the largest increases in mid and high latitudes of the northern hemisphere (cf. Suárez et al. 2002). Therefore, the trend makes this hypothetical scenario likely within this century. The model could be extended to neighbouring countries where future shifts in the distribution border of the species will occur, as for example in south-western Norway, southern Sweden and eastern Germany (cf. Berger & Walther 2003).

However, the model might be improved by including other climatic variables, such as absolute minimum temperatures of the coldest months or the number of days with winter frost, but also biotic interactions corresponding to the most critical stages in the life cycle of the species. There is a paucity of data regarding the latter, and future research should focus on plant regeneration traits, including pollen quality, availability of pollinators, fruit set, seed dispersal and seedling establishment as done for other species by Pigott (1992), Bruehlheide & Heinemeyer (2002) and Jump & Woodward (2003). The model would also gain from including the effects of wind and salt spray at least in some parts of the Danish west coast where these may be detrimental. A general limitation of distribution models like ours is their static nature (Guisan & Zimmermann 2000), as it seems unlikely that the current distribution of *I. aquifolium* is in equilibrium with the climatic conditions. Both the analysis of post-glacial migration rates and that of invasive or regressive plants in modern landscapes indicate that environmental shifts are often faster than the response of the study species (Dyer 1995, Bakkenes et al. 2002). Certainly, the non-equilibrium nature of the distribution of a species limits the goodness-of-fit of any logistic model (Collingham et al. 2000). Moreover, future modelling may try a multi-scale approach to make more accurate predictions and to investigate the relevant variables explaining species distribution at different scales, as suggested by Wilbanks & Kates (1999) and Collingham et al. (2000). Previous studies show that climatic variables are important at regional and continental scales, while land use and human impact become more relevant at intermediate scales as the one used in the present study, whereas soil characteristics and biotic interactions are most meaningful at local scales (Thuiller et al. 2003, and references therein).

Habitat niche characteristics

Our data on the habitat niche of the species add significantly to existing descriptions from other European regions (Runge 1950, Peterken & Lloyd 1967, Pott 1990, Sebald et al. 1992, Oberdorfer 2001, Rackham 2003). These authors describe *I. aquifolium* as a common under-storey tree in most types of well-drained deciduous forests, being rare or absent from heavy clay soils, dry stony habitats and wet sites. In our survey the species was often found in relatively nutrient-rich habitats and it was most common in near-natural deciduous forests, although gardens might have been the seed source for the spread of the species at least in some areas. It seems questionable that *I. aquifolium* is a good indicator for ancient forests in Denmark as claimed by Lawesson et al. (1998), as it is quite frequent in young conifer plantations and seems to have followed climate shifts in a relatively short time period (Berger & Walther 2003).

Our data indicate that *I. aquifolium* can occur in rather different habitats and within different plant communities, suggesting that the species has a broader niche than previously described. In contrast, Lawesson & Oksanen (2002) in an analysis of a large set of Danish forests, found *I. aquifolium* among the woody species with the smallest niche, similar to *Ribes rubrum* but in marked contrast to *Corylus avellana* and *Sambucus nigra*. However, these authors admit that this result might partly be caused by the low number of vegetation records containing the species.

Future research should compare the community context and the dynamics of marginal populations of *I. aquifolium* with those from the core of the distribution range. Marginal populations might be better adapted to unfavourable conditions than populations in the core area, as has been shown, for example, for freezing tolerance in *Opuntia fragilis* (Loik & Nobel 1993). Special evolutionary processes occur in marginal populations determining the potential and setting limitations for changes of the distribution edge (Hoffmann & Blows 1994). Distribution borders are a natural laboratory to study both plant dispersal and certain dimensions of the habitat niche both from an ecological and an evolutionary perspective.

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