



Vegetation databases as a tool to analyse factors affecting the range expansion of the forest understory herb *Ceratocarpus claviculata*

Nicole Voss, Dietmar Simmering, Cord Pepler-Lisbach, Walter Durka & R. Lutz Eckstein

Keywords

Acidophytic oak-birch forest; Clearing; Climatic environmental zone; Disturbance; Ellenberg indicator value; Forest management; Global change; Habitat requirement; Invasibility; Therophyte

Abbreviations

ANOVA = Analysis of variance;
CCA = Canonical correspondence analysis; c, s, r = Strategy types (Grime 1977)
c = competitive, s = stress tolerant, r = ruderal;
DCA = Detrended correspondence analysis;
FA = Factor analysis; IV = Indicator value;
MANCOVA = Multivariate analysis of covariance; NE-G = Northeastern Germany; NW-G = Northwestern Germany; SD = Standard deviation; S-S = Southern Sweden

Nomenclature

vascular plants (Wisskirchen & Haeupler 1998; for species not included there: Tutin et al. 2001), bryophytes (Koperski et al. 2000),

Received 29 June 2010

Accepted 1 March 2011

Co-ordinating Editor: Jürgen Dengler

Voss, N. (corresponding author, nicole.voss@umwelt.uni-giessen.de); **Eckstein, R.L.** (lutz.eckstein@umwelt.uni-giessen.de) & **Simmering, D.** (dietmar.simmering@umwelt.uni-giessen.de): Institute of Landscape Ecology and Resource Management, Research Centre for BioSystems, Land Use and Nutrition (IFZ), Justus Liebig University Giessen, Heinrich-Buff-Ring 26-32, 35392 Giessen, Germany
Durka, W. (walter.durka@ufz.de): Department of Community Ecology, Helmholtz Centre for Environmental Research – UFZ, Theodor-Lieser-Straße 4, 06120 Halle (Saale), Germany
Pepler-Lisbach, C. (cord.pepler.lisbach@uni-oldenburg.de): IBE, Landscape Ecology Group, Carl von Ossietzky University Oldenburg, PO Box 2503, 26111 Oldenburg, Germany.

Abstract

Question: The eu-atlantic forest herb *Ceratocarpus claviculata* showed a recent increase in frequency within its native range and an eastward and northward range expansion in Central Europe. To gain deeper understanding of factors affecting the range expansion of the species, we analyzed vegetation relevés at three different scales and asked the following questions: As the species occurs in a wide range of vegetation types, is variation in community composition across the entire range related to climatic environmental zones and tree cover? Are there differences in species composition and habitat characteristics between the native range and the two invaded regions (S Sweden and NE Germany)? Did community composition and habitat characteristics within the native range (The Netherlands) change between ‘before 1970’ and ‘1990 to 2006’?

Location: W, C and N Europe.

Methods: We analysed vegetation-plot data with *C. claviculata* from various databases and own surveys using partial CCA, partial DCA, Indicator Species Analysis, MANCOVA and multiple regression.

Results: Using vegetation plots from the entire distribution range, climatic environmental zones explained 68.9% of the total canonical Eigenvalue. Differences in floristic composition and habitat characteristics between the two invaded regions were as large as between native and invaded range sites. However, relevés from the invaded range were generally characterized by anthropogenic disturbance. Accordingly, abundance of *C. claviculata* was positively linked to silvicultural intensity. New relevés from 1990 to 2006 were characterized by higher Ellenberg nutrient indicator values, lower species diversity, higher proportions of neophytic and hemerobic species and showed a lower cover of the study species than old relevés from before 1970.

Conclusions: Across the range of *C. claviculata*, climatic environmental zones determine vegetation composition. Accordingly, the species is characterized by a broad macroclimatic amplitude. Vegetation composition and structure differ significantly between the two regions of the new range. Thus, the species has successfully established under various biotic and abiotic environmental conditions. Beyond potential positive effects of soil eutrophication and mild winters, anthropogenic impact may directly facilitate seed dispersal and provide sites and resource conditions suitable for germination and establishment of *C. claviculata*, whereas a decrease of forest management may constrain the species.

Introduction

Range expansions have been observed in many species during recent decades (Le Roux & McGeoch 2008). In Central Europe, these may be a trace of ongoing post-glacial recolonization processes (Taberlet et al. 1998). However, most recent range expansions in cultural landscapes are probably facilitated by human activities such as transport of diaspores, nitrogen inputs, land-use changes and disturbance (Chauchard et al. 2010), as well as climate change (Walther 2004).

Range expansions imply the establishment of new species in extant communities. This process may be conceptualized as a series of filters selecting the species of a local community from a larger species pool (Integrated Community Concept *sensu* Lortie et al. 2004). Successful establishment may be achieved if a new species shows higher fitness than resident species (competitive dominance) or if it occupies a different niche (stabilizing processes) (MacDougall et al. 2009). Resource fluctuation (Davis et al. 2000) may be an important factor determining establishment success because new species may be able to colonize during periods of low competition through residents, which may occur after disturbance. Thus, the success of local establishment of new species may be driven by a group of features and factors such as (1) species traits (e.g. mode of dispersal), (2) community characteristics (e.g. vegetation type or resource use by residents), (3) disturbance and (4) abiotic environmental factors such as climate and resource availability (Stohlgren et al. 1999; Tilman 2004; Davis et al. 2005).

Ceratocarpus claviculata is an annual forest species of the family *Fumariaceae*. It grows on humic, acidic soils of the submeridional and temperate zone (Schultze-Motel 1986; Jäger & Werner 2005). As a result of its restriction to Western Europe, *C. claviculata* is regarded as an eu-oceanic species (Jäger & Werner 2005). However, during the last decades the species showed both an increase in frequency within its range (Buttler 1986; van der Eerden et al. 1998; Decocq 2000; Hill et al. 2004) and a rapid range expansion eastwards and northwards into sub-continental and northern-temperate regions (Benkert et al. 1995; Oredsson 2005). Currently, it occurs in N Portugal and NW Spain, France, Belgium, The Netherlands, NW Germany, UK, Ireland, Denmark and scattered in S Norway, S Sweden and NE Germany. The last two regions represent the newly invaded range where it was first detected about 25 years ago (Benkert et al. 1995; Oredsson 2005).

Several ideas have been proposed to explain the recent spread of *C. claviculata*. These are closely linked to the sequence of factors that determine the invasibility of a local community (Lortie et al. 2004; Davis et al. 2005). (A) Dispersal: because *C. claviculata* lacks structures for long-

distance dispersal, anthropogenic activities, such as transport of wood and forest management (clearcutting) are made responsible for the fast regional expansion and local spread, respectively (Buttler 1986; Benkert et al. 1995; Decocq 2000; Lethmate et al. 2002; Horstmann 2005; Oredsson 2005). (B) Increased winter temperatures: after seeds of the species have reached a new locality, mild winter temperatures, potentially a consequence of climate change, may facilitate seedling survival and the establishment of new populations (Folland & Karl 2001; Lethmate et al. 2002). (C) Nitrogen availability: increased atmospheric nitrogen inputs as a driving factor of floristic changes in forests of Central Europe (Kuhn et al. 1987; Thimonier et al. 1992; van Dobben et al. 1999) may increase the cover of this species after successful establishment (Pott & Hüppe 1991; Vannerom et al. 1994; van der Eerden et al. 1998).

Despite a wealth of knowledge concerning factors that govern plant invasions and range expansions, these still present an apparent paradox (Sax & Brown 2000): why are some organisms, which originate from distant localities and had no chance to adapt to the local environment and the extant communities of the new range, able to establish successfully? In order to gain deeper understanding of factors governing the range expansion of *C. claviculata*, we analyzed vegetation relevés at three different scales: (1) We analysed relevés across the entire range extracted from various databases to quantify the effects of different climatic zones and tree cover on the variation in community composition. Floristic patterns across the entire range were analysed using an Indicator Species Analysis. (2) Using own relevés from NW Germany (native range) and NE Germany and Sweden (invaded ranges), we tested whether abundance of *C. claviculata*, community composition and habitat characteristics differed between the invaded ranges and that part of the native range, which was presumably the source for colonization of the new range sites (Benkert et al. 1995; Oredsson 2005). (3) As the species has also increased within the native range during the past decades, we tested whether the abundance of *C. claviculata*, community composition and habitat characteristics differed between relevés from the period 'before 1970' and 'between 1990 and 2006' using data from the Dutch National Vegetation Database.

Community ecology of the study species

Ceratocarpus claviculata has been described as a constituent of various forest communities in different parts of its range and is considered a character species of the acidophytic oak birch forests of the order *Quercetalia roboris* Tx. 1931. Here, the species has its main occurrence in the

associations *Deschampsia flexuosa*–*Quercetum roboris* Pasarge 1966 and the *Betula pendula*–*Quercetum roboris* Tx. 1930 nom. invers. propos. Owing to its eu-atlantic distribution, it is further acknowledged as differential species for western variants of these communities in NW Germany, France and Benelux (Härdtle et al. 1997). In the UK, *C. claviculata* is part of similar acidophytic communities of the *Quercus robur*–*Pteridium aquilinum*–*Rubus fruticosus* woodland and the *Quercus* spp.–*Betula* spp.–*Deschampsia flexuosa* woodland (Rodwell 1998). In France and Belgium, the species is found in acidophytic, Atlantic beech forests of the alliance *Ilici*–*Fagion* Br.-Bl. 1966. In Spain, it grows in hyper-oceanic pedunculate oak forests, Orocantabrian NW Iberian birch–sessile oak forests and Cantabrian-Euskaldian mixed oak–ash forests (Bohn et al. 2003). In addition, *C. claviculata* occurs on poor acidic sands in NE Germany in more continental, dry, secondary spruce and pine forests of the alliance *Dicrano polyseti*–*Pinion sylvestris* (Libbert 1933) W. Matuszkiewicz 1962 nom. cons. propos. in the class *Vaccinio*–*Piceetea* Br.-Bl. in Br.-Bl. et al. 1939 (Berg et al. 2001). Within the same class, the species is also found on peat soils of disturbed bogs in secondary birch fen-woods of the *Betuletum pubescentis* Tx. 1937 (Pott 1995; Meyer & Voigtländer 1996).

Outside forests, the species is often found in ecotonal communities. Strongholds of *C. claviculata* occurrences across the entire geographic range are those in disturbed and sun-exposed situations of clearings. Within the acidophytic forest clearing communities, stands with *C. claviculata* comprise the association *Corydalido claviculatae*–*Epilobietum angustifolii* Hülbusch & Tx. 1968 (Berg et al. 2001, 2004; Dengler et al. 2007). Other ecotonal communities are along forest edges, hedges, roads, ditches, and tracks. These stands have been assigned to different syntaxa within the *Pruno-Rubion radulae* Weber 1974, *Origanetalia vulgaris* Th. Müller 1961, *Convolvulion sepium* Tx. 1947 and *Alliarion* Oberd. (1957) 1962 (Castroviejo 1975; Jäger & Werner 2005; BfN 2008).

Finally, the species occurs in dwarf-shrub heaths and sometimes even in pioneering, xerophilous communities on schist outcrops. In Brittany, these occurrences were attributed to the *Erico cinerea*–*Vaccinietum myrtilli typicum* (Gloaguen & Touffet 1973) Clément 1978 and the *Festuco-Sedetum anglici* Clément et al. (1980) (Clément & Touffet 1978; Clément et al. 1980).

Methods

Datasets

Entire range (= dataset 1)

We obtained vegetation relevés containing *C. claviculata* from the entire range, irrespective of habitat type, from

national, county and regional databases (denoted by their IDs from the Global Index of Vegetation Plot Databases (GIVD), Dengler et al. 2011): Spain (EU-00-004, Font et al. 2010), France (EU-FR-003, Brisse et al. 1995), Flanders (EU-BE-001, Vandenbussche & Hoffmann 2001), The Netherlands (EU-NL-001, Schaminée et al. 2006), the UK (EU-GB-001, Rodwell 2011), Germany (EU-DE-013, Ewald et al. 2010), Mecklenburg-Vorpommern (EU-DE-001, Berg & Dengler 2004), and NW Germany (EU-DE-010, Peppler-Lisbach 2011; EU-00-008 and EU-DE-019 Heinken 2011 a, b). These data were complemented with other published (Pollmann & Lethmate 2006) and unpublished (several volunteers) relevés from forests and woodlands. As the Dutch database contained 4481 relevés with *C. claviculata*, whereas there were, for example, only 45 relevés from Spain, we randomly selected 300 relevés from The Netherlands (all after 1970) to reduce geographical imbalance. However, in an attempt to improve the estimation of community composition and habitat characteristics within the centre of the species distribution range we retained more relevés from the UK, N Belgium, The Netherlands and NW Germany in the data set than from adjacent regions. All relevés were also filtered according to plausibility (location, species composition) and relevé size. The plot size of the filtered relevés ranged from 4 to 300 m² (median = 100 m², lower quartile = 100 m², upper quartile = 225 m²), reflecting the heterogeneity of data sets among and within different databases. The final data set contained 762 relevés (Denmark: two, Flanders: 128, France: 95, Germany: 186, Spain: 45, Sweden: 28, The Netherlands: 231, UK: 47). According to its geographic coordinates, each relevé was assigned to one of five climatic environmental zones defined by Metzger et al. (2005): (1) Atlantic North, (2) Atlantic Central, (3) Continental, (4) Lusitanian or (5) Alpine South s.l.; the last zone included the original zones Alpine South, Mediterranean Mountains and Mediterranean North. Because relevés of the defined groups varied considerably in mean plot size (ANOVA, $P < 0.001$), we included plot size as covariate in the analyses.

Invaded versus native range (= dataset 2)

In the invaded range, we selected the northernmost and easternmost regions and visited all currently known localities of the species that contained at least several populations. In the native range, we selected a landscape section of roughly the same dimension as in the invaded range and within the same forest type (conifer-dominated stands). Within this section we made random stops at every forest site and selected the first *C. claviculata* population we found.

Invaded and native range differed strongly with respect to continentality (Table 1). However, during the past years, temperature had increased and precipitation decreased, which has resulted in warmer winters but drier vegetation periods in all four regions (DWD 2010; SMHI 2010). The invaded range belongs to the Continental zone and was situated in S Sweden (= S-S; 12.95–14.63° E; 55.99–56.29° N) and NE Germany (= NE-G; 13.96–14.04° E; 52.24–52.30° N); the study sites in the native range belonged to the Atlantic North zone and were situated in NW Germany (= NW-G; 8.22–8.26° E; 52.94–53.05° N).

Substrate type differed only slightly between the three study regions with sand dominating in NW Germany and NE Germany and sand to silt in S Sweden. In all regions, the predominating humus types were moder and mor. Mean pH_{KCl} in the upper 10 cm of soil in selected sites was 3.2 (± 0.35 SD, $n=23$) in S Sweden, 3.2 (± 0.63 SD, $n=25$) in NW Germany and 3.3 (± 0.3 SD, $n=25$) in NE Germany (N. Voss, unpubl. data).

Using the ordinal scale of van der Maarel (1979, 2007), we recorded 73 relevés in the three regions (native range: NW-G, $n=25$; invaded range: NE-G, $n=25$; and S-S, $n=23$). The size of the plots varied between 25 and 100 m² (mean = 69.3 m², lower quartile = 36 m², upper quartile = 100 m²). Both, the varying size and shape of the plots were chosen to account for differences in the homogeneity of the forest vegetation and the patchy occurrence of the study species. There was, however, no significant difference in relevé size between the three regions (ANOVA, $P=0.090$). However, we also accounted for differences in relevé size in the analysis of this data set (see Statistical analyses).

We estimated the cover of the tree, shrub, herb and bryophyte layers as well as the proportion of litter and bare soil in the field. The height of the herb layer was estimated to obtain information on vegetation structure. We did this by approximating the height by measuring at the level of main biomass production. The impact of disturbance through silviculture was estimated by assigning an ordinal value (none = 0, little = 1, much = 2) for (a) logging, (b) woodpiles, (c) skid trails and other tracks. The

values were summed so that each plot obtained a score between 0 and 6.

Analysis of temporal variation (= dataset 3)

To compare vegetation composition within the native range between two time-periods, we selected relevés from mixed deciduous oak forests from the Dutch National Vegetation Database (ID EU-NL-001, Schaminée et al. 2006), which were sampled either in the period 1936 to 1970 (old relevés) or 1990 to 2006 (new relevés). All selected relevés contained information on the cover of bryophyte species. To improve homogeneity and comparability of data, old and new relevés were filtered according to the following criteria: (1) presence of *Quercus* spp. in the tree or the shrub layer; (2) cover of coniferous trees < 5%; (3) location in the same geographic region; and (4) plot size between 50 and 100 m². The final data set contained 181 relevés, 40 from 1936 to 1970 and 141 from 1990 to 2006. Plot size did not differ significantly between the two periods (mean_{1936–1970} = 91.7 m², mean_{1990–2006} = 92.4 m², *t*-test, $P=0.42$, total median = 100 m², lower quartile = 90 m², upper quartile = 100 m²). However, we accounted for differences in plot size in the analysis of this data set (see Statistical analyses).

Data management

Relevés were processed using the TURBOVEG software (Hennekens & Schaminée 2001). For datasets (1) and (2), species abundances were transformed to ordinal scale (van der Maarel 1979, 2007). In all datasets, species nomenclature was standardized according to the electronic taxonomic reference list GermanSL (Jansen & Dengler 2008); species lacking in this German reference list were added following the nomenclature of Flora Europaea (Tutin et al. 2001). Subspecies were subsumed on the species level. Because of the inconsistent determination of species of *Rubus fruticosus* agg. and *Rubus corylifolius* agg., the groups were treated as one taxon *Rubus* sp.

Using the JUICE software (Tichý 2002), the occurrence of a species in the shrub and in the herb layer was merged

Table 1. Average temperature in January (coldest winter month) and from March to June (main growth period of *Ceratocarpus claviculata*) and average precipitation from March to June for the study regions in the native (NW-G) and the invaded range (S-S and NE-G) for the past and the present (DWD 2010; SMHI 2010).

Region	Climate Station	$T_{\text{January}} (^{\circ}\text{C})$		$T_{\text{March-June}} (^{\circ}\text{C})$		Precipitation _{March–June} (mm)	
		1991–1990	2002–2009	1991–1990	2002–2009	1991–1990	2002–2009
S-S	Kristianstad	– 1.3	0.5	8.0	9.0	162	159
NE-G	Lindenberg	– 1.2	0.2	10.2	11.9	201	156
NW-G	Bremen	0.8	2.6	10.0	11.1	230	188

into one layer. The tree layer was excluded from ordination but was considered in all other analyses as an explanatory variable. To avoid the undue influence of rare species in data sets (2) and (3) we removed species that occurred in less than 3% of the relevés. In data set (1) we deleted only those species that occurred in less than three relevés in order to avoid a loss of too many species from regions with a small number of relevés (e.g. Alpine South or Lusitania with 34 and 22 plots, respectively). Thus, the total number of species was reduced in data set (1) from 582 to 300, in (2) from 188 to 81 and in (3) from 311 to 105 species.

For data sets (2) and (3), species richness and Shannon diversity index were calculated in TURBOVEG. Furthermore, using the cover values, we calculated the weighted mean Ellenberg indicator values (Ellenberg et al. 1992) for each relevé including all species of the herb and shrub layers with an assigned indicator value. The tree layer was excluded because many of the stands analysed were forest plantations and thus the tree layer may not reflect the environmental site conditions properly. Including all species, except *C. claviculata*, we further calculated the proportional cover of neophytic and therophytic species and the calibrated proportion of hemerobic species (Frank & Klotz 1990; Klotz & Kühn 2002a) and of ruderal strategy for each relevé (Klotz & Kühn 2002b). Hemerobic species were used as an indicator for human influence on vegetation. The hemerobic level (Klotz & Kühn 2002a) describes the degree of anthropogenic impact on a vegetation unit. Most species of the Central European flora have been assigned to one or more of the hemerobic levels defined by Frank & Klotz (1990) and Klotz & Kühn (2002a) and made available in the biological traits database BIOLFLOR (Klotz et al. 2002). In order to obtain numeric values for each species, we assigned a value of zero to all species, which were listed as either ahemerobic ('a') and oligohemerobic ('o'), i.e. species with a chief occurrence in natural vegetation units. Species listed as either 'm' (mesohemerobic), 'b' (β -euhemerobic), 'c' (α -euhemerobic), 'p' (polyhemerobic) or 't' (metahemerobic) received a value of one, indicating a higher occurrence and frequency in more human-dominated vegetation units. Species assigned to both groups of hemerobic levels received an intermediate value (e.g. 'aomb' = 0.5). In order to obtain an indicator for ruderal tendency we proceeded in a similar way with Grime's (1977) strategy types and assigned a value of one to the r-strategy, whereas c- and s-strategy were assigned a value of zero. Again, for intermediate strategy types proportions of the r-strategy were calculated. Species information for ruderal tendency was also extracted from BIOLFLOR (Klotz & Kühn 2002b).

To obtain percentage cover values for the herb and tree layer in data set (3), we summed up the percentage cover of the species in the herb and tree layer for each plot, respectively.

Statistical analyses

The analyses were carried out with PC-Ord 5.3 (Indicator Species Analysis; McCune & Grace 2002), CANOCO (DCA, CCA; ter Braak & Šmilauer 2002) and STATISTICA 8.0 (ANOVA, FA, multiple regression, HSD-test, MANCOVA, *t*-test; StatSoft Inc., 2008).

Entire range

In order to quantify the effects of different climatic environmental zones and tree cover on the variation in community composition we employed several CCAs for a variance partitioning procedure. We also included plot sizes in the analysis to account for their heterogeneity, which might cause size-dependent ordination patterns (Otýpková & Chytrý 2006). We used log (Area), percentage tree cover and climatic environmental zone (dummy coded) as environmental variables in CCAs. To obtain the effect of a variable, partial CCA was performed controlling for the other two variables (Legendre & Legendre 1998). For all CCAs, significance was tested by permutation tests (1000 permutations). The ratios of a given canonical Eigenvalue to the sum of all Eigenvalues (total inertia) and to the sum of all canonical Eigenvalues were used to estimate percentages of explained variation of the total inertia and of the total canonical Eigenvalue.

To describe species composition for the different groups, we calculated species constancies and performed Indicator Species Analysis (Dufrêne & Legendre 1997; McCune & Grace 2002). Tree species were considered both in the tree layer as well as in the herb/shrub layer and thus we obtained two indicator values in order to include information on the prevailing forest type. Statistical significance of the observed indicator value for a species was evaluated by a Monte Carlo test using 4999 permutations.

Invaded versus native range

In order to visualize the relationships among vegetation plots and to account for the effects of varying plot size in our data we ran partial DCA ordination with species cover abundance data. We applied detrending by second-order polynomials and used log (Area) as covariate. For interpretation purposes, we overlaid header data such as cover of trees and other derived variables such as proportions of neophytes, therophytes, hemerobic species, ruderal strategy, Ellenberg indicator values and vegetation structure.

As in dataset (1), we calculated constancies and performed Indicator Species Analysis (Dufrêne & Legendre 1997). Tree species were considered both in the tree layer as well as in the herb/shrub layer and thus we obtained two indicator values in order to include information on

the prevailing forest type. Statistical significance of the observed indicator value for a species was evaluated by a Monte Carlo test using 4999 permutations.

As a result of missing non-species information (e.g. disturbance, height of herbs) in 13 plots, the subsequent statistical analyses were performed using only 60 relevés (NW-G, $n = 18$; NE-G, $n = 21$ and S-S, $n = 21$). We carried out a MANCOVA to test for significant differences between regions using plot size as covariate (for respective variables see Table 3). Mahalanobis distance was calculated to detect multivariate outliers. To meet the assumptions of normality, the variables cover of shrubs, bryophytes, bare soil and litter as well as proportion of neophytes and hemerobic species were arcsine-square root-transformed and height of herbs was square root-transformed. Cover of *C. claviculata* was first back-transformed to percentage scale (van der Maarel 1979, 2007) and then Box-Cox transformed ($\lambda = -0.922$). Pillai's trace statistic was used because it is most robust to deviations from multivariate normality and the assumption of homogeneity of the variance-covariance matrices across groups with equal sample sizes and approximate univariate normality of response variables (Johnson & Field 1993). Furthermore, we applied HSD tests for unequal group size to assess significant differences of each variable between the regions.

We used stepwise-forward regression in multiple regression to analyse which of the environmental variables (predictors) were significantly associated with the abundance of *C. claviculata* (response variable). As there were many intercorrelated predictors, Factor Analysis (FA, standard varimax axis rotation) was employed for data reduction purposes to avoid problems with multicollinearity (Stevens 2002). The FA resulted in five independent, orthogonal factors (Eigenvalue ≥ 1.5). These were interpreted according to the factor loadings of the original predictors (Table 4). Subsequently, the factor scores obtained were used as independent surrogate variables in the multiple regression. Plot size was also included into the model.

Analysis of temporal variation

As in dataset (2), for visualization and to account for plot size effects we ran partial DCA ordination with species cover abundance data. We applied detrending by second-order polynomials, used log (Area) as covariate and overlaid header data.

We again calculated constancies and performed Indicator Species Analysis (Dufrêne & Legendre 1997). Tree species were considered both in the tree layer as well as in the herb/shrub layer and thus we obtained two indicator values in order to include information on the

prevailing forest type. Statistical significance was evaluated by a Monte Carlo test using 4999 permutations.

To test for significant differences between time-periods we carried out a MANCOVA using plot size as covariate (for respective variables see Table 5). Mahalanobis distance was calculated to detect multivariate outliers. Cover of *C. claviculata* was back-transformed to percentage scale (van der Maarel 1979, 2007) and then power-transformed with an exponent of -0.5 to meet assumptions of normality. To assess significant differences of each variable between the time-periods, we obtained *P*-values from the univariate results of MANCOVA.

Results

Entire range

Taking climatic environmental zones, tree cover and plot size into account as constraining variables in CCA, these explained only 5.9% of total variation in community composition (total inertia = 18.4). However, when controlling for the other two variables, each variable yielded a significant effect on floristic composition in partial CCA (Table 2). Climatic environmental zones explained 68.9% of total canonical Eigenvalue (4.1% of total inertia), whereas plot size explained only about 17.6% (1.0% of total inertia) and tree cover even less (8.9% of total canonical Eigenvalue, 0.5% of total inertia). The number of significant indicator species (see the Supporting Information, Appendix S1) with indicator values ≥ 14 for the climatic environmental zones differed strongly with ten species for the Atlantic-North (among them *Quercus robur* in the tree layer, *Sorbus aucuparia*, *Rubus* sp., *Ilex aquifolium*, *Dryopteris dilatata*, *Frangula alnus*), only four species for the Atlantic-Central (*Quercus rubra*, *Betula pendula*, *Prunus serotina*, *Molinia caerulea*), seven species for the Continental (e.g. *Deschampsia flexuosa*, *Pinus sylvestris*-tree layer, *Impatiens parviflora*, *Rubus idaeus*, *Robinia pseudoacacia* tree layer), 12 species for the Lusitanian (e.g. *Epilobium*

Table 2. Results of canonical correspondence analysis (CCA) with the explaining variables (Exp. var.) climatic environmental zone (C), log (Area) (A) and percentage cover of trees (T) as well as partial CCAs, each adjusted for two of the variables (Covar.). Canonical Eigenvalues (Eigen.), percentage of explained variance of total inertia (% Total inertia), percentage of explained variance of the total canonical Eigenvalue (% Can. Eigen.) and *F*-ratio (*F*) for the test of significance of all canonical axes and corresponding probability value (*P*) obtained by the Monte Carlo permutation test (1000 permutations). Total inertia = 18.36.

Exp. Var.	Covar.	Eigen.	% Total Inertia	% Can. Eigen.	<i>F</i>	<i>P</i>
C, A, T	–	1.085	5.91	100.0	7.466	0.001
C	A, T	0.747	4.07	68.9	7.709	0.001
A	C, T	0.191	1.04	17.6	7.890	0.001
T	C, A	0.096	0.52	8.9	3.970	0.001

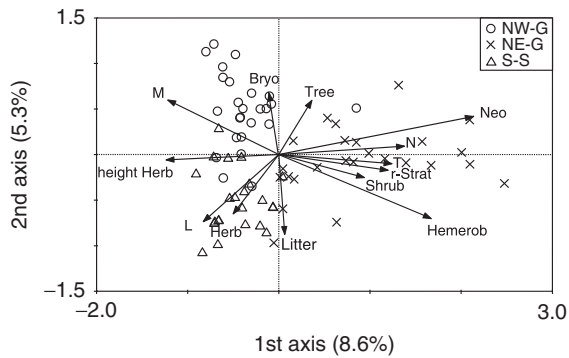


Fig. 1. Partial Detrended Correspondence Analysis (DCA) of native (NW-G, $n=25$) and invaded (S-S, $n=23$ and NE-G, $n=25$) range sites adjusted for the covariable plot size. Total inertia=4.38, cumulative explained variance=22%. Only the first two axes were plotted (explained variance=8.6 and 5.3%, respectively). Vectors ($-0.25 \leq r \leq +0.25$) indicate cover sum of litter (Litter), bryophytes (Bryo), herbs (Herb), shrubs (Shrub) and trees (Tree), proportions of hemerobic species (Hemerob), neophytes (Neo) and r -strategists r -Strat, Ellenberg indicator values for light (L), moisture (M) nutrients (N) and temperature (T), and the height of the herb layer (height Herb). The vector proportions of therophytes ($r=0.43$, not shown) goes parallel with proportions of r -strategists.

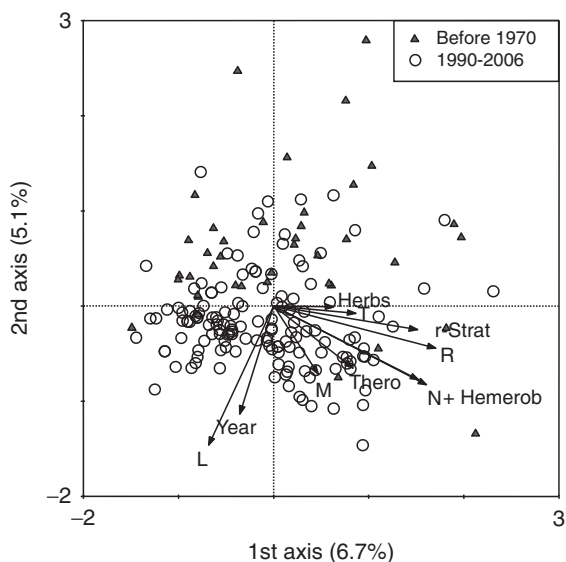


Fig. 2. Partial Detrended Correspondence Analysis (DCA) of relevés from old (before 1970, $n=40$) and new (1990–2006, $n=141$) Dutch relevés adjusted for the covariable plot size. Total inertia=5.52, cumulative explained variance=18.4%. Only the first two axes were plotted (explained variance=6.7 and 5.1%, respectively). Vectors ($-0.25 \leq r \leq +0.25$) indicate cover sum of herbs (Herbs), proportions of hemerobic species (Hemerob), r -strategists (r -Strat), and therophytes (Thero), sampling year (Year) and Ellenberg indicator values for light (L), moisture (M), nutrients (N) and temperature (T).

angustifolium, *Cytisus scoparius*, *Galium saxatile*, *Sambucus racemosa*, *Linaria repens*) and 19 species for the Alpine–South zone, some of which are endemic to the Iberian

Peninsula (e.g. *Erica arborea*, *Genista florida*, *Cytisus orome-diterraneus*). Across the entire range, the most constant species (mean constancy > 25%) occurring together with *C. claviculata* were *Q. robur* (37% mean constancy), *Lonicera periclymenum* (27%), *Agrostis capillaris* (26%), *Holcus mollis* (25%) and *Galeopsis tetrahit* (21%).

Native versus invaded range

Partial DCA ordination of the species abundances (Fig. 1) yielded a total inertia of 4.5 before, and 4.4 after fitting the covariable log (Area). Thus, plot size accounted for only 1.5% of total inertia.

There was a clear separation of the regions NW-G, NE-G and S-S along the first and second axis. Thus, on the one hand, we found floristic differences between native and invaded range sites, but on the other hand there were also large differences between the two invaded regions. The first axis was positively correlated with the cover of shrubs ($r=0.37$), open soil ($r=0.19$, not shown), proportion of neophytes ($r=0.85$), hemerobic species ($r=0.65$), r -strategists ($r=0.50$), therophytes ($r=0.43$, not shown), Ellenberg indicator values for nitrogen ($r=0.56$) and temperature ($r=0.50$), and negatively correlated with Ellenberg indicator value for moisture ($r=-0.49$) and the height of herbs ($r=-0.50$). The second axis was positively correlated with the cover of bryophytes ($r=0.31$) and trees ($r=0.27$) and negatively correlated with litter ($r=-0.40$), herbs ($r=-0.30$) and Ellenberg indicator value for light ($r=-0.34$).

The MANCOVA showed significant differences ($P < 0.001$) between the three regions in site conditions and habitat characteristics (Table 3). The comparison showed only few consistent differences between native and invaded range. In contrast, we often found either clinal variation from NW-G over NE-G to S-S or differences between the two German regions on the one hand and S-S on the other hand. The covariable plot size was not significant ($P=0.251$). The cover of *C. claviculata* was higher in the invaded range, increasing slightly from NW-G to NE-G and being significantly higher in S-S (HSD test, Table 3). Similarly, litter cover, proportions of hemerobic species, therophytes and r -strategists, as well as disturbance by forestry and tracks, tended to be higher in invaded range sites, whereas the cover of bryophytes tended to be lower.

Indicator Species Analyses (Appendix S2) was consistent with these results featuring nitrophilous species such as *Sambucus nigra*, *Moehringia trinerva* and *Chelidonium majus* and neophytic species such as *P. serotina*, *R. pseudoacacia* and *I. parviflora* in NE-G, indicators for moisture, such as *F. alnus* and *M. caerulea* in NW-G and species characteristic for clearings such as *S. racemosa*, *R. idaeus*,

Table 3. Habitat characteristics and cover of *Ceratocarpus claviculata* (mean \pm SD) in the native versus invaded range: Northwestern Germany (NW-G, native range, $n = 18$), Southern Sweden (S-S, invaded range, $n = 21$) and Northeastern Germany (NE-G, invaded range, $n = 21$). Letters indicate significant differences according to HSD test, ($P < 0.05$). MANCOVA was significant for the three regions with Pillai's trace = 1.593, $F_{34, 82} = 9.45$, $P < 0.001$ but not significant for the covariable plot size (log [Area]) with Pillai's trace = 0.353, $F_{17, 40} = 1.28$, $P = 0.251$. Pearson's regression coefficient is shown for significant relationships ($P < 0.05$) between variables and plot size.

	Native Range		Invaded Range	
	NW-G	S-S	NE-G	Pearson's r (log [Area])
Cover sum (%):				
Tree	49.2 ^a \pm 21.7	27.9 ^b \pm 28.8	42.4 ^{ab} \pm 16.6	
Shrub	7.2 ^a \pm 6.4	10.5 ^a \pm 17.9	22.8 ^b \pm 17.5	
Herb	43.3 ^a \pm 19.6	45.7 ^a \pm 21.7	33.1 ^a \pm 17.6	
Moss	38.1 ^a \pm 32.2	5.1 ^b \pm 6.5	28.8 ^a \pm 24.2	
Litter	61.8 ^a \pm 32.2	93.5 ^b \pm 6.7	69.8 ^a \pm 23.7	
Bare soil	0.0 ^a \pm 0.0	1.3 ^a \pm 2.6	1.5 ^a \pm 4.5	
<i>C. claviculata</i>	4.4 ^a \pm 1.7	9.5 ^b \pm 6.5	6.8 ^{ab} \pm 8.4	
Height herbs (cm)	53.4 ^a \pm 23.4	63.8 ^a \pm 36.9	23.3 ^b \pm 9.3	
Ellenberg IV				
Light	5.83 ^{ab} \pm 0.28	6.01 ^b \pm 0.41	5.67 ^a \pm 0.32	
Moisture	5.37 ^a \pm 0.31	5.18 ^a \pm 0.36	4.78 ^b \pm 0.25	
Nitrogen	4.94 ^a \pm 0.69	5.05 ^a \pm 0.66	5.69 ^b \pm 0.77	- 0.24
Temperature	4.77 ^a \pm 0.55	4.99 ^{ab} \pm 0.46	5.30 ^b \pm 0.45	
Disturbance	2.27 ^a \pm 1.23	4.76 ^b \pm 1.92	3.14 ^a \pm 1.53	
Proportion cover of:				
Neophytes	0.044 ^b \pm 0.038	0.007 ^a \pm 0.022	0.185 ^c \pm 0.110	
Hemerobic species	0.254 ^a \pm 0.101	0.377 ^b \pm 0.157	0.504 ^c \pm 0.127	
Therophytes	0.045 ^a \pm 0.055	0.055 ^{ab} \pm 0.071	0.098 ^b \pm 0.071	- 0.30
r-Strategists	0.039 ^a \pm 0.038	0.053 ^{ab} \pm 0.039	0.080 ^b \pm 0.049	- 0.38

D. flexuosa and *E. angustifolium* in S-S. These last findings were reflected by a higher proportion of light-demanding species in S-S.

The multiple regression on the cover of *C. claviculata* with the five surrogate predictor variables (from Factor Analysis, Table 4) showed a significant relationship with two factors ($r^2_{corrected} = 0.30$, $df = 2$, $F = 13.62$, $n = 60$, $P < 0.001$). Only factor 2 (surrogate: cover of bryophytes and litter) and factor 3 (surrogate: disturbance) correlated significantly with the cover of *C. claviculata*.

Comparison of old and new relevés

The partial DCA yielded a total inertia of 5.5 after fitting the covariable plot size (log [Area]). Without adjustment, total inertia was 5.6; thus, plot size accounted for only 1.9% of total inertia (Fig. 2). Using grouping according to time-period, a weak separation of plots from before 1970 and after 1990 was evident along the second axis (more pronounced on the plain of second and third axis). Vectors for Shannon index ($r = 0.15$, but -0.54 for third axis), cover of herbs ($r = 0.24$) and trees ($r = 0.13$), Ellenberg indicator values for temperature ($r = 0.33$), reaction ($r = 0.69$) and nutrients ($r = 0.65$), cover of herbs ($r = 0.24$ but with third axis -0.55), proportion of therophytes ($r = 0.32$) and r-strategists ($r = 0.59$) and hemerobic spe-

cies ($r = 0.59$) were correlated with the first axis. Ellenberg indicator values for light ($r = -0.61$) and for moisture ($r = -0.31$) and proportion of neophytes ($r = -0.22$) were correlated with the second axis.

Habitat characteristics differed significantly between the two time-periods and were in part significantly correlated with plot size (Table 5). Cover of *C. claviculata* was higher in plots from before 1970 than in plots after 1990. Shannon diversity was lower in the newer relevés. This corresponds to a more than eightfold higher number of indicator species (Appendix S3) for old plots. Furthermore, Ellenberg indicator values for light, temperature, moisture, and nutrients were slightly higher in current than in old plots. Also, the proportion of hemerobic species and neophytes was larger in the new relevés, as indicated by species such as *P. serotina*, *Amelanchier lamarkii* and *Q. rubra*.

Discussion

Entire range

The CCA yielded only a very low percentage of variance explained by the environmental variables used. Explained variance depends on the number of species, plots and further unknown environmental factors (we included only two in the ordination). Thus, rather than the ratio of

Table 4. Relationship between *Ceratocapnos claviculata* and environmental variables. (a) Factor loadings, Eigenvalues and explained variance of Factor Analysis, $n = 60$. The factors scores were used as independent surrogate variables in multiple regression for variables with loadings > 0.700 or < -0.700 (in bold). Variables transformed before analysis are labeled with[†]. (b) Results from stepwise-forward GRM with the five surrogate variables and plot size as predictors for the cover of *C. claviculata* (%). Only significant relationships ($P < 0.05$) are shown. Area was not significant. SS = sum of squares, df = degrees of freedom, F = F -ratio, P = error probability, β = regression coefficient, EV = explained variance.

(a)						
Variable	Factor 1	Factor 2	Factor 3	Factor 4	Factor 5	
Cover sum (%)						
Tree	0.208	0.113	0.619	-0.257	-0.112	
Shrub [†]	0.343	-0.154	0.444	0.196	0.401	
Herb	-0.373	0.058	-0.065	0.104	0.730	
Bryophyte [†]	0.056	-0.964	0.061	-0.085	0.022	
Litter [†]	-0.027	0.957	-0.031	0.005	0.049	
Bare soil [†]	-0.190	0.224	-0.103	0.534	-0.496	
Height herbs (cm) [†]	-0.763	0.132	0.025	-0.035	0.280	
Disturbance						
Tracks	-0.393	-0.036	0.566	-0.153	0.175	
Skid trails	-0.150	0.110	-0.745	0.048	-0.119	
Logging	0.026	0.072	-0.707	-0.145	0.300	
Ellenberg IV						
Light	-0.296	0.207	-0.117	-0.282	0.555	
Temperature	0.440	0.528	0.017	0.381	-0.012	
Moisture	-0.656	-0.173	0.091	0.029	-0.022	
Nutrients	0.453	0.230	0.162	0.478	0.044	
Proportion						
Neophytes [†]	0.743	-0.118	0.262	0.365	-0.140	
Therophytes	0.114	-0.053	-0.035	0.867	0.035	
<i>r</i> -Strategists	0.099	0.128	-0.042	0.919	-0.058	
Hemerobic species [†]	0.444	0.447	0.102	0.521	0.135	
Eigenvalue	2.789	2.608	2.106	2.912	1.521	
Proportion explained variance	0.155	0.145	0.117	0.162	0.084	
(b)						
Effect	SS	df	F	P	β	EV (%)
Intercept	39.72	1	3415.68	< 0.001		
Factor 2 (cover of litter/bryophytes)	0.05	1	4.20	0.045	0.223	5.1
Factor 3 (disturbance)	0.27	1	23.03	< 0.001	-0.523	28.0
Error	0.66	57				

explained to unexplained variance, the percentage of explained variance of the total canonical eigenvalue of each variable should be considered (Leyer & Wesche 2007). Despite the low number of variables included, our results reflect quite well the underlying patterns of vegetation composition and show the appropriateness of using the climatic environmental classification of Metzger et al. (2005) for interpretation of species composition. However, results of large datasets from various databases from across the entire range of a species should be interpreted with caution. Because the original authors usually applied various sampling techniques for various study aims, huge heterogeneity in the resulting dataset might be either associated with actual environmental heterogeneities or/and with differences in sampling method/intention. The

latter was shown by the wide range of plot sizes, which accounted for a low proportion of total variance but explained 17.6% of canonical variation.

In total, 68.9% of the explained variation resulted from the effect of the climatic environmental zones after accounting for the effects of tree cover and plot size. The climatic environmental zones largely depend on minimum and maximum temperature of the months January, April, July and October, on precipitation during these months and on oceanity. As expected, climatic stratification accounts for a large part of species composition. Relevés originating from the Atlantic Central zone yielded only a low number of significant indicator species, which indicates a large floristic heterogeneity. The Atlantic Central zone is the largest of the climatic geographic

Table 5. Comparison of old (before 1970, $n=40$) and new Dutch relevés (1990–2006, $n=141$). Mean \pm SD of habitat characteristics and cover of *Ceratocarpus claviculata* of the two time-periods (P values from ANOVA) and Pearson's correlation between the environmental variables and the plot size (Area) (only shown if $P < 0.05$). Time-period (Pillai's trace = 0.3875, $F_{13, 166} = 8.126$, $P < 0.001$) and the covariate "Area" (Pillai's trace = 0.209, $F_{13, 166} = 3.383$, $P < 0.001$) are significant in MANCOVA.

Variable	Before 1970	1990–2006	P	Pearson's r (Area)
Cover sum (%)				
Tree	60.7 \pm 41.6	64.2 \pm 29.2	0.538	
Herbs	296.2 \pm 95.1	282.9 \pm 131.6	0.552	– 0.26
<i>C. claviculata</i>	6.1 \pm 8.0	3.5 \pm 5.5	0.010	
Shannon Index	3.16 \pm 0.36	2.79 \pm 0.42	< 0.001	– 0.25
Ellenberg indicator values				
Light	5.35 \pm 0.44	5.65 \pm 0.42	< 0.001	
Temperature	5.05 \pm 0.44	5.20 \pm 0.43	0.049	
Moisture	5.35 \pm 0.47	5.55 \pm 0.48	0.020	– 0.21
Reaction	3.73 \pm 0.82	3.69 \pm 0.73	0.801	– 0.33
Nitrogen	4.15 \pm 0.89	4.79 \pm 0.92	< 0.001	– 0.27
Proportion of:				
Neophytes	0.012 \pm 0.026	0.046 \pm 0.045	< 0.001	
Therophytes	0.050 \pm 0.037	0.043 \pm 0.053	0.485	– 0.18
r -Strategists	0.059 \pm 0.037	0.048 \pm 0.039	0.098	– 0.27
Hemerobic species	0.419 \pm 0.090	0.461 \pm 0.098	0.018	– 0.21

regions and thus a variety of environmental habitat conditions are included within this zone. In addition, the low number of indicator species might result from the literal "central position": the large Atlantic Central zone is the centre of the range of many typical elements of the European flora and thus shares many of these species with the adjoining zones. In contrast, the Alpine South zone with relevés largely originating from Spain, because of its geographic isolation, showed the most differing species composition.

Native versus invaded range

The two study regions in the invaded range exhibited differences in vegetation composition as large as those between the native and invaded ranges. These results suggest that *C. claviculata* has successfully established in various vegetation types that differ among the three regions. However, there were no systematic differences in habitat characteristics between native and invaded range sites.

We found a higher mean cover of *C. claviculata* in the invaded range. This is surprising as the invaded regions are, despite milder winters during the past decade, still characterized by continental climate. Furthermore, in all regions many individuals were observed which germinated apparently in autumn and survived despite low winter temperatures, even after the long and cold winters in 2008 and 2009. These data and observations suggest that microclimatic conditions, which may be affected by the surrounding vegetation and litter, might be more important for germination, establishment and survival

than macroclimate (Buttler 1986; N. Voss, et al. unpubl. data). This is also in line with the positive impact of litter cover on *C. claviculata* abundance as revealed by the multiple regression.

The results of the multiple regression also suggested that abundance of *C. claviculata* was associated with disturbance through silviculture, which, in fact, was higher in the new range. A larger human impact in the new range might also be reflected by a higher proportion of hemerobic and ruderal species, indicating a higher availability of microsites for the establishment of short-lived species, and by higher proportions of neophytic and nitrophilous species (Lososová et al. 2006; Chytrý et al. 2008). These results are consistent with the novel niche theory (MacDougall et al. 2009), which claims that disturbed habitats, especially those altered by human activities, are often successfully colonized by new species because they represent novel conditions for residents. Many species entering disturbed habitats have weed-like traits, such as the annual, self-pollinating *C. claviculata*. It was suggested that the often-observed higher abundance of introduced species in their new range results from a higher rate of disturbance, which creates colonization gaps with higher substrate availability and low competition (Pickett & White 1985; Davis et al. 2000; Chmura & Sierka 2007; Fausch 2008).

In addition to the present impact of silviculture in conifer-dominated forests other past or recent disturbances may have promoted *C. claviculata*. Factors such as wild boars, game passes and human leisure activities may have positively affected both the dispersal of *C. claviculata* and the disturbance of forest sites (Buttler 1986; Pott 1995; Dzwonko & Loster 1997). Recently, L. Tandler & C.

Peppler-Lisbach (unpubl. results) showed that the occurrence of *C. claviculata* was correlated with the presence of forest roads or paths.

The question is prompted: How could a species like *C. claviculata*, which has no adaptation to long-distance dispersal, overcome large distances of tens or hundreds of kilometres prior to its successful establishment in the new range? Occurrences might be related to haul roads and/or seeds or fruits attached to timber bark that may be translocated through forestry machinery or shipping of wood (Buckley et al. 2003). Large amounts of pulpwood and sawtimber were transported to Swedish sawmills and paper plants after severe storms in NW Germany and The Netherlands in 1972. These transports most probably facilitated the introduction of *C. claviculata* to Sweden (Oredsson 2005). Moreover, expansion in the new range might be related to an expansion within the native range. An increased propagule pressure in the native range caused by, for example, more favourable nutrient supply or climate, may result in an increased dispersal probability and thus provides a further explanation for successful expansion.

However, our results suggest that beyond the proposed effects of increased nutrient availability and mild winter temperatures (Pott & Hüppe 1991; Vannerom et al. 1994; van der Eerden et al. 1998; Lethmate et al. 2002), anthropogenic impact may directly facilitate seed dispersal and provide sites and resource conditions suitable for germination and establishment of *C. claviculata*.

Comparison of old and new Dutch relevés

Plots from deciduous oak forests from before 1970 and after 1990 differed with respect to community composition and species diversity. Cover of *C. claviculata* decreased significantly between the two periods despite an increase of Ellenberg indicator values for nutrients and an increased anthropogenic impact on the studied forest community, as indicated by an increase of neophytic and hemerobic species. In contrast, van Dobben et al. (1994) found that the cover of *C. claviculata* increased in The Netherlands by 17% between 1984 and 1993 in parallel with strong changes of understory species composition probably owing to increased ammonia deposition (van Dobben et al. 1994). However, in contrast to our data from acidophytic oak forests, van Dobben et al. (1994) focused on pine forests, which are more intensively managed than deciduous forests. Furthermore, traditional deciduous woodland management techniques (featuring coppicing, canopy opening, litter removal, grazing, natural treefalls and soil disturbance), which favoured germination and establishment of ruderal and therophytic species, have largely been abandoned (Brunet et al. 1996; Förster

1998; Rodwell 1998). The demise of traditional management techniques and conversion from more open canopies to dense timber forests caused a general decline in herb cover, which in turn may have negative impacts on therophytic and ruderal species (Brunet et al. 1997; Diekmann et al. 1999; Strandberg et al. 2005; Gondard et al. 2007; Spitzer et al. 2008). Hence, lacking traditional management and disturbance may have caused the observed decrease of *C. claviculata* and Shannon index in oak forests, which are considered as the species main habitat in its northwest European range (Härdtle et al. 1997). As we used data from vegetation databases, the relevés of the two periods compared did not come from identical locations, which would have been the case in a permanent plot study. Although the database approach is valuable for temporal comparisons in a given vegetation type (Wildi 1989; Holeksa & Wozniak 2005), results should be interpreted with caution. Observed changes might result from sampling bias, if, for example, relevés from before 1970 were from ancient oak forest whereas the younger relevés originated from younger stands. Land-use history data might be useful to solve this problem but were not available in this dataset. However, we tried to reduce potential sampling bias by using several selection criteria for the extraction of relevés from the database.

Conclusions

Our analyses suggest that *C. claviculata* occupies a relatively broad ecological niche as it occurs in a wide range of vegetation types. Across its entire range, macroclimatic conditions are a significant driver of vegetation composition. Vegetation composition and structure differ significantly between the two regions of the new range, indicating that the species has successfully established under different biotic and abiotic environmental conditions. However, our analyses suggest that, in general, anthropogenic disturbance of resident vegetation and soil surface play an important role for local dispersal and population establishment by providing sites and suitable conditions for germination of *C. claviculata*. In contrast, for habitats in open oak–birch forests, our temporal comparison showed a decrease of abundance of *C. claviculata*. This decrease might reflect changes in forest management during the past century that resulted in a closure of tree canopies in recent forests.

Acknowledgements

We thank Lars Fröberg, Peter Gutte, Heinz Henker, Jörg Hoffmann, Thomas Homm, Kjell-Arne Olsson, Alf Oredsson, Hans Sonnenberg and Frank Zimmermann for information on localities with *C. claviculata*, Jupp Scholz-vom Hofe for help during field work, Lander Baeten,

Michel Botineau, Stephen Bungard, Guillaume Decocq, Norbert Hölzel, Rebecca Johnson, Jack Lighten, Peter Llewellyn, Alex Lockton, Olivier Plantard, Alex Prendergast, Andreas Prinzing, Pete Steward, Jan Thiele, Kevin van den Hof, Kris Verheyen and Matthias Wichmann for vegetation data, Marcos Mendez for support during a field trip in Spain, Stephan Hennekens for help with the software TURBOVEG, Erik Welk for help with the transformation of geographic coordinates and Regine and Gert Schumann for their hospitality in Oldenburg. Finally, we thank Jürgen Dengler as editor and two anonymous reviewers for valuable comments that improved the quality of the manuscript. The study was funded by the Deutsche Forschungsgemeinschaft (DFG, EC 209/6-1).

References

- Benkert, D., Hoffmann, J. & Fischer, W. 1995. *Corydalis claviculata* (L.) DC. – ein Neubürger der märkischen Flora. *Schriftenreihe für Vegetationskunde* 27: 353–363.
- Berg, C. & Dengler, J. 2004. Von der Datenbank zur Regionalmonografie – Erfahrungen aus dem Projekt “Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung”. *Berichte der Reinhold-Tüxen-Gesellschaft* 16: 29–56.
- Berg, C., Dengler, J. & Abdank, A. (eds.) 2001. *Die Pflanzengesellschaften Mecklenburg-Vorpommerns und ihre Gefährdung – Tabellenband*. Weissdorn-Verlag, Jena, DE.
- Berg, C., Dengler, J., Abdank, A. & Isermann, M. (eds.) 2004. *Die Pflanzengesellschaften Mecklenburg Vorpommerns und ihre Gefährdung – Textband*. Weissdorn-Verlag, Jena, DE.
- BfN [Bundesamt für Naturschutz]. (ed.) 2008. VegetWeb. Bonn, DE. Available at: <http://www.floraweb.de/vegetation/aufnahmen.html> (accessed March 19 2008)
- Bohn, U., Neuhäusl, R., Gollub, G., Hettwer, C., Neuhäuslová, Z., Raus, T., Schlüter, H. & Weber, H. 2003. *Karte der natürlichen Vegetation Europas/Map of the natural vegetation of Europe. Maßstab/Scale 1:2 500 000*. Landwirtschaftsverlag, Münster, DE.
- Brise, H., de Ruffray, P., Grandjouan, G. & Hoff, M. 1995. The phytosociological database “SOPHY” – part I: calibration of indicator species – Part II: Socio-ecological classification of the relevés. *Annali di Botanica* 53: 177–223.
- Brunet, J., Falkengren-Grerup, U. & Tyler, G. 1996. Herb layer vegetation of south Swedish beech and oak forests – effects of management and soil acidity during one decade. *Forest Ecology and Management* 88: 259–272.
- Brunet, J., Falkengren-Grerup, U., Ruhling, A. & Tyler, G. 1997. Regional differences in floristic change in South Swedish oak forests as related to soil chemistry and land use. *Journal of Vegetation Science* 8: 329–336.
- Buckley, D.S., Crow, T.R., Nauertz, E.A. & Schulz, K.E. 2003. Influence of skid trails and haul roads on understory plant richness and composition in managed forest landscapes in Upper Michigan, USA. *Forest Ecology and Management* 175: 509–520.
- Buttler, K.P. 1986. Über das Vorkommen des Rankenden Lerchensporns in Hessen und Thüringen. *Natur und Museum* 116: 33–43.
- Castroviejo, S. 1975. Algunos datos sobre las comunidades nitrofilas vivaces (*Artemisietea vulgaris*) de Galicia. *Anales del Instituto Botanico A.J. Cavanilles* 32: 489–502.
- Chauchard, S., Beilhe, F., Denis, N. & Carcaillet, C. 2010. An increase in the upper tree-limit of silver fir (*Abies alba* Mill.) in the Alps since the mid-20th century: a land-use change phenomenon. *Forest Ecology and Management* 259: 1406–1415.
- Chmura, D. & Sierka, E. 2007. The invasibility of deciduous forest communities after disturbance: a case study of *Carex brizoides* and *Impatiens parviflora* invasion. *Forest Ecology and Management* 242: 487–495.
- Chytrý, M., Jarošík, V., Pyšek, P., Hájek, O., Knollová, I., Tichý, L. & Danihelka, J. 2008. Separating habitat invasibility by alien plants from the actual level of invasion. *Ecology* 89: 1541–1553.
- Clément, B. & Touffet, J. 1978. Les pelouses xerophiles autour de quelques affleurement schisteux en Bretagne interieure. *Colloques Phytosociologique* 6: 177–189.
- Clément, B., Gloaguen, J.C. & Touffet, J. 1980. Une association originale de lande de Bretagne occidentale: l’*Erico cinerea*–*Vaccinietum myrtilli*. *Documents Phytosociologiques* 5: 167–176.
- Davis, M.A., Grime, J.P. & Thompson, K. 2000. Fluctuating resources in plant communities: a general theory of invasibility. *Journal of Ecology* 88: 528–534.
- Davis, M.A., Thompson, K. & Grime, J.P. 2005. Invasibility: the local mechanism driving community assembly and species diversity. *Ecography* 28: 696–704.
- Decocq, G. 2000. Un problème de phytogéographie forestière: la présence de *Ceratocapnos claviculata* (L.) Lidén dans le Nord de la France. *Acta Botanica Gallica* 147: 143–150.
- Dengler, J., Eisenberg, M. & Schröder, J. 2007. Die grundwasserfernen Saumgesellschaften Nordostniedersachsens im europäischen Kontext – Teil II: Säume nährstoffreicher Standorte (*Artemisietea vulgaris*) und vergleichende Betrachtung der Saumgesellschaften insgesamt. *Tuexenia* 20: 91–136.
- Dengler, J., Jansen, F., Glöckler, F., Peet, R.K., De Cáceres, M., Chytrý, M., Ewald, J., Oldeland, J., Finckh, M., Lopez-Gonzalez, G., Mucina, L., Rodwell, J.S., Schaminée, J.H.J. & Spencer, N. 2011. The Global Index of Vegetation-Plot Databases (GIVD): a new resource for vegetation science. *Journal of Vegetation Science* 22 doi: 10.1111/j.1654-1103.2011.01265.x.
- Diekmann, M., Brunet, J., Ruhling, A. & Falkengren-Grerup, U. 1999. Effects of nitrogen deposition: results of a temporal-spatial analysis of deciduous forests in South Sweden. *Plant Biology* 1: 471–481.

- Dufrène, M. & Legendre, P. 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345–366.
- DWD [Deutscher Wetterdienst]. 2010. Klimadaten ausgewählter deutscher Stationen, Zeitreihen an Stationen. Offenbach a. Main, DE. Available at: <http://www.dwd.de> (accessed on June 20 2010)
- Dzwonko, Z. & Loster, S. 1997. Effects of dominant trees and anthropogenic disturbances on species richness and floristic composition of secondary communities in southern Poland. *Journal of Applied Ecology* 34: 861–870.
- Ellenberg, H., Weber, H.E., Düll, R., Wirth, V., Werner, W. & Paulißen, D. 1992. Zeigerwerte von Pflanzen in Mitteleuropa. *Scripta Geobotanica* 18: 1–248.
- Ewald, J., Conrad, S., May, R. & Kleikamp, M. 2010. Neues von VegetWeb. *Tuexenia* 30: 493–494.
- Fausch, K.D. 2008. A paradox of trout invasions in North America. *Biological Invasions* 10: 685–701.
- Folland, C. & Karl, T. 2001. Observed climate variability and change. In: Houghton, J.T., Ding, Y., Griggs, D.J., Noguer, M., van der Linden, P.J., Dai, X., Maskell, K. & Johnson, C.A. (eds.) *Climate change 2001: the scientific basis*. pp. 99–181. Cambridge University Press, Cambridge, UK.
- Font, X., Rodríguez-Rojo, M.P., Acedo, C., Biurrun, I., Fernández-González, F., Lence, C., Loidi, J. & Ninot, J.M. 2010. SIVIM: an on-line database of Iberian and Macaronesian vegetation. *Waldökologie, Landschaftsforschung und Naturschutz* 8: 15–22.
- Förster, A. 1998. Wild und Vegetation im Reichswald Kleve. *Zeitschrift für Jagdwissenschaft* 44: 66–77.
- Frank, D. & Klotz, S. 1990. *Biologisch-ökologische Daten zur Flora in der DDR*. Martin-Luther-Universität Halle-Wittenberg, Halle, DE.
- Gondard, H., Santa-Regina, I., Salazar, S., Peix, A. & Romane, F. 2007. Effect of forest management on plant species diversity in *Castanea sativa* stands in Salamanca (Spain) and the Cevennes (France). *Scientific Research and Essays* 2: 62–70.
- Grime, J.P. 1977. Evidence for existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169–1194.
- Härdtle, W., Heinken, T., Pallas, J. & Welß, W. 1997. *Quercus-Fagetia* (H5) – Sommergrüne Laubwälder, Teil1: *Quercion roboris* – Bodensaure Eichenmischwälder. *Synopsis der Pflanzengesellschaften Deutschlands* 2: 1–51.
- Heinken, T. 2011a. Deciduous forests on acidic soils (Germany). *Biodiversity & Ecology* 4 (in press).
- Heinken, T. 2011b. Pine forests on acidic soils (Germany). *Biodiversity & Ecology* 4 (in press).
- Hennekens, S.M. & Schaminée, J.H.J. 2001. TURBOVEG, a comprehensive data base management system for vegetation data. *Journal of Vegetation Science* 12: 589–591.
- Hill, M.O., Preston, C.D. & Roy, D.B. 2004. *Plantatt – attributes of British and Irish plants: Status, size, life history, geography and habitats*. Biological Records Centre, NERC Centre for Ecology and Hydrology, Monks Wood, UK.
- Holeksa, J. & Wozniak, G. 2005. Biased vegetation patterns and detection of vegetation changes using phytosociological databases. A case study in the forests of the Babia Gora National Park (the West Carpathians, Poland). *Phytocoenologia* 35: 1–18.
- Horstmann, D. 2005. Zur Ausbreitung des Rankenden Lerchensporns (*Ceratocarpus claviculata* (L.) Lidén) in Ostwestfalen-Lippe. *Berichte des Naturwissenschaftlichen Verein für Bielefeld und Umgegend* 45: 91–96.
- Jäger, E.J. & Werner, K. (eds.) 2005. *Exkursionsflora von Deutschland. Band 4: Gefäßpflanzen: Kritischer Band*. 10th ed. Fischer, Jena, DE.
- Jansen, F. & Dengler, J. 2008. GermanSL – Eine universelle taxonomische Referenzliste für Vegetationsdatenbanken in Deutschland. *Tuexenia* 28: 239–253.
- Johnson, C.R. & Field, C.A. 1993. Using fixed-effects model multivariate analysis of variance in marine biology and ecology. *Oceanography and Marine Biology* 31: 177–221.
- Klotz, S. & Kühn, I. 2002a. Indikatoren des anthropogenen Einflusses auf die Vegetation. *Schriftenreihe für Vegetationskunde* 38: 241–246.
- Klotz, S. & Kühn, I. 2002b. Ökologische Strategietypen. *Schriftenreihe für Vegetationskunde* 38: 197–202.
- Klotz, S., Kühn, I. & Durka, W. 2002. BIOLFLOR – Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenreihe für Vegetationskunde* 38: 1–334.
- Koperski, M., Sauer, M., Braun, W. & Gradstein, S.R. 2000. Referenzliste der Moose Deutschlands. *Schriftenreihe für Vegetationskunde* 34: 1–519.
- Kuhn, N., Amiet, R. & Hufschmid, N. 1987. Veränderungen in der Waldvegetation der Schweiz infolge Nährstoffanreicherungen aus der Atmosphäre. *Allgemeine Forst- und Jagdzeitung* 158: 77–84.
- Legendre, P. & Legendre, L. 1998. *Numerical ecology*. Elsevier Science, Amsterdam, NL.
- Le Roux, P.C. & McGeoch, M.A. 2008. Rapid range expansion and community reorganization in response to warming. *Global Change Biology* 14: 2950–2962.
- Lethmate, J., Ebke, K. & Pollmann, W. 2002. Zur Ausbreitung des Rankenden Lerchensporns *Ceratocarpus claviculata* (L.) Lidén. *Osnabrücker Naturwissenschaftliche Mitteilungen* 28: 117–135.
- Leyer, I. & Wesche, K. 2007. *Multivariate Statistik in der Ökologie*. Springer, Heidelberg, DE.
- Lortie, C.J., Brooker, R.W., Choler, P., Kikvidze, Z., Michalet, R., Pugnaire, F.I. & Callaway, R.M. 2004. Rethinking plant community theory. *Oikos* 107: 433–438.
- Lososová, Z., Chytrý, M., Kuhn, I., Hájek, O., Horáková, V., Pyšek, P. & Tichý, L. 2006. Patterns of plant traits in annual vegetation of man-made habitats in central Europe. *Perspectives in Plant Ecology, Evolution and Systematics* 8: 69–81.
- MacDougall, A.S., Gilbert, B. & Levine, J.M. 2009. Plant invasions and the niche. *Journal of Ecology* 97: 609–615.

- McCune, B. & Grace, J.B. 2002. *Analysis of ecological communities*. MjM Software Design, Gleneden Beach, OR, US.
- Metzger, M.J., Bunce, R.G.H., Jongman, R.H.G., Mucher, C.A. & Watkins, J.W. 2005. A climatic stratification of the environment of Europe. *Global Ecology and Biogeography* 14: 549–563.
- Meyer, N. & Voigtländer, U. 1996. Zur Verbreitung und Soziologie des Rankenden Lerchenspornes (*Corydalis claviculata* (L.) Lam. et DC.) in Mecklenburg-Vorpommern. *Botanischer Rundbrief für Mecklenburg Vorpommern* 29: 73–78.
- Oredsson, A. 2005. Blekinges första barkbjörnbär: saxiskt björnbär. *Svensk Botanisk Tidskrift* 99: 269–272.
- Otýpková, Z. & Chytrý, M. 2006. Effects of plot size on the ordination of vegetation samples. *Journal of Vegetation Science* 17: 465–472.
- Peppler-Lisbach, C. 2011. Forests of the Oldenburg Region (NW Germany). *Biodiversity & Ecology* 4 (in press).
- Pickett, S.T.A. & White, P.S. (eds.) 1985. *The ecology of natural disturbance and patch dynamics*. Academic Press, Orlando, FL, US.
- Pollmann, W. & Lethmate, J. 2006. Räumliche Variabilität der Vegetation in bodensauren Kiefernbeständen – Untersuchungen zur Ausbreitung von *Ceratocapnos claviculata*. *Osnabrücker Naturwissenschaftliche Mitteilungen* 32: 59–73.
- Pott, R. 1995. *Die Pflanzengesellschaften Deutschlands*. 2nd ed. Ulmer, Stuttgart, DE.
- Pott, R. & Hüppe, J. 1991. Die Hudelandschaften Nordwestdeutschlands. *Abhandlungen des Westfälischen Museums für Naturkunde* 53: 1–314.
- Rodwell, J.S. 1998. *British plant communities – woodlands and scrub*. Cambridge University Press, Cambridge, UK.
- Rodwell, J.S. 2011. UK National vegetation classification database. *Biodiversity & Ecology* 4 (in press).
- Sax, D.F. & Brown, J.H. 2000. The paradox of invasion. *Global Ecology and Biogeography* 9: 363–371.
- Schaminée, J.H.J., Janssen, J.A.M., Haveman, R., Hennekens, S.M., Heuvelink, G.B.M., Huiskes, H.P.J. & Weeda, E.J. 2006. *Schatten voor de natuur – Achtergronden, inventaris en toepassingen van de Landelijke Vegetatie Databank*. KNNV Uitgeverij, Utrecht, NL.
- Schultze-Motel, W. 1986. Berberidaceae, Lauraceae, Papaveraceae, Cruciferae, Capparidaceae, Resedaceae. In: Conert, H.J., Hamann, U., Schultze-Motel, W. & Wagenitz, G. (eds.) *Gustav Hegi: Illustrierte Flora von Mitteleuropa* 4(2), Part 1. 3rd ed.. Verlag Paul Parey, Berlin, DE.
- SMHI [Swedish Meteorological and Hydrological Institut]. 2010. Dataserier från svenska observationsstationer. Norrköping, SE. Available at: <http://www.smhi.se> (accessed June 20 2010)
- Spitzer, L., Konvicka, M., Benes, J., Tropek, R., Tuf, I.H. & Tufova, J. 2008. Does closure of traditionally managed open woodlands threaten epigeic invertebrates? Effects of coppicing and high deer densities. *Biological Conservation* 141: 827–837.
- Stevens, J. 2002. *Applied multivariate statistics for the social sciences*. Erlbaum Associates, Mahwah, NY, US.
- Stohlgren, T.J., Schell, L.D. & van den Heuvel, B. 1999. How grazing and soil quality affect native and exotic plant diversity in rocky mountain grasslands. *Ecological Applications* 9: 45–64.
- Strandberg, B., Kristiansen, S.M. & Tybirk, K. 2005. Dynamic oak-scrub to forest succession: effects of management on understorey vegetation, humus forms and soils. *Forest Ecology and Management* 211: 318–328.
- Taberlet, P., Fumagalli, L., Wust-Saucy, A.G. & Cosson, J.F. 1998. Comparative phylogeography and postglacial colonization routes in Europe. *Molecular Ecology* 7: 453–464.
- ter Braak, C.J.F. & Šmilauer, P. 2002. *CANOCO reference manual and Cano draw for Windows user's guide: Software for canonical community ordination (version 4.5)*. Microcomputer Power., Ithaca, NY, US.
- Thimonier, A., Dupouey, J.L. & Timbal, J. 1992. Floristic changes in the herb-layer vegetation of a deciduous forest in the Lorraine Plain under the influence of atmospheric deposition. *Forest Ecology and Management* 55: 149–167.
- Tichý, L. 2002. JUICE, software for vegetation classification. *Journal of Vegetation Science* 13: 451–453.
- Tilman, D. 2004. Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Science of the United States of America* 101: 10854–10861.
- Tutin, T.G., Heywood, V.H., Burges, N.A., Valentine, D.H., Walters, S.M. & Webb, D.A. (eds.) 2001. *Flora Europaea. Volumes I–V. Digital version*. Cambridge University Press, Cambridge, UK.
- Vandenbussche, V. & Hoffmann, M. 2001. De Vlaamse Vegetatie Databank (VLAVEDAT): eerste aanzet tot een overzicht van natuurtypen en plantengemeenschappen in Vlaanderen. *Stratiotes* 22: 36–44.
- van der Eerden, L., de Vries, W. & van Dobben, H. 1998. Effects of ammonia deposition on forests in the Netherlands. *Atmospheric Environment* 32: 525–532.
- van der Maarel, E. 1979. Transformation of cover-abundance values in phytosociology and its effects on community similarity. *Vegetatio* 39: 97–114.
- van der Maarel, E. 2007. Transformation of cover-abundance values for appropriate numerical treatment – Alternatives to the proposals of Podani. *Journal of Vegetation Science* 18: 767–770.
- van Dobben, H.F., Vocks, M.J., Jansen, E. & Dirkse, G.M. 1994. *Veranderingen in de ondergroei van het Nederlandse denbos over de periode 1985–1993* [IBN Rapport 085]. Instituut voor Bos- en Natuuronderzoek, Wageningen, NL.
- van Dobben, H.F., ter Braak, C.J.F. & Dirkse, G.M. 1999. Undergrowth as a biomonitor for deposition of nitrogen and acidity in pine forest. *Forest Ecology and Management* 114: 83–95.

- Vannerom, H., De Jaeck, H., Monnens, J. & Verbruggen, F. 1994. Over de uitbreiding van *Ceratocapnos claviculata* (L.) Lidén en de expansie van enkele andere stikstoffinnende soorten in Noord-Belgie. *Dumortiera* 58–59: 42–43.
- Walther, G.R. 2004. Plants in a warmer world. *Perspectives in Plant Ecology Evolution and Systematics* 6: 169–185.
- Wildi, O. 1989. Analysis of the disintegrating group and gradient structure in Swiss riparian forests. *Vegetatio* 83: 179–186.
- Wisskirchen, R. & Haeupler, H. 1998. *Standardliste der Farn- und Blütenpflanzen Deutschlands*. Ulmer, Stuttgart, DE.

Supporting Information

Additional supporting information may be found in the online version of this article:

Appendix S1. Indicator species and common species for the climatic environmental zones.

Appendix S2. Indicator species and common species of native and invaded range sites.

Appendix S3. Indicator species and common species of old and recent vegetation relevés.

Please note: Wiley-Blackwell are not responsible for the content or functionality of any supporting materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.