CLIMATE CHANGE IMPACTS ON WOODLAND SPECIES: IMPLICATIONS FOR THE CONSERVATION OF WOODLAND HABITATS IN IRELAND

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ABSTRACT

Global climate is rapidly changing and, while many studies have investigated the potential impacts of climate change on the distribution of woodland species in the wider European context, few have focused on the impacts of climate change on the distribution of woodland species in Ireland. This study evaluates the potential impact of climate change on the distribution of species characteristic of woodlands and assesses the implications for the conservation of woodlands in Ireland. Only some 2% of the land area of Ireland is covered in semi-natural woodlands, including communities which are conservation priorities such as bog woodland, alluvial forests and *Taxus baccata* (Yew) woods. We applied an ensemble of species distribution modelling techniques, using atlas data for 104 vascular plant, bryophyte, bird and butterfly species from Ireland, baseline climate data (1961–1990) and projected future climate data (HadCM3 GCM; 2031–2060), at a 10km^2 resolution. Of the 104 species, 44 modelled well in at least 6 of the 8 models. Under a scenario of unlimited dispersal, almost 50% of species which modelled well were projected to lose climate space, with the largest range contraction projected for the butterfly *Aphantopus hyperantus* (Ringlet; −47.7%). The remainder were projected to have increased climate space, with *Thecla betulae* (Brown hairstreak) and *Frangula alnus* (Alder buckthorn) having the largest projected increases of 886% and 532% of their current ranges. When a scenario of limited long-range dispersal was considered, all species were projected to lose some of their current range, from a decrease of 52.4% for *Carex strigosa* (thin-spiked wood-sedge) to a decrease of 10.9% for *Saxifraga spathularis* (St Patrick's cabbage). These results have significant implications for the future of woodlands in Ireland. Conservation management plans for these habitats need greater focus on potential climate change impacts in order to ensure these communities' long-term survival.

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INTRODUCTION

It is now widely accepted that global climate is rapidly changing, with average temperatures rising at an unprecedented rate, by more than 0.7°C, over the past century (IPCC 2007). Global surface temperatures are projected to increase by between 1.1°C and 6.4°C by 2100 (IPCC 2007). Regional variation is evident in global climate change; for example, temperatures have increased in Arctic regions at almost twice the global rate, and precipitation has increased significantly in some areas while decreasing in others (IPCC 2007). These changes in climate are projected to have significant impacts on biodiversity and may lead to widespread changes in species distribution and community composition in many parts of the world (Walther *et al.* 2002; Parmesan and Yohe 2003; Root *et al.* 2003; Parmesan 2006). Evidence from the early Holocene has shown that changes in climate can cause rapid changes to community distribution and composition, leading to major biodiversity loss, within a matter of decades (Tinner and Kaltenrieder 2005). Impacts of climate change have already been detected in a wide range of taxa and communities, including changes in phenology (Roy and Sparks 2000; Donnelly *et al.* 2006), altitudinal range (Grabherr *et al.* 1994; Parolo and Rossi 2008) and geographical range (Araujo *et al.* 2006; Lenoir *et al.* 2008) of species, population density, community structure and species genetics and evolution (Rodriguez-Trelles and Rodriguez 1998; Thomas *et al.* 2001).

When faced with a change in their environment beyond their normal tolerance, such as climate change, species and populations can respond in one of two ways, either by adaptive evolution so that the new climate is tolerated, or movement to another area with a more suitable climate. Should either adaptive evolution or geographic dispersal prove too slow to keep up with a shifting climate, and should they lack sufficient

phenotypic plasticity to tolerate changing environmental conditions, these species will face local extinction (Thomas *et al.* 2004a, 2006; Pearson 2006). Global climate change has already led to the extinction of some species (Pounds *et al.* 2006), while the range of others has shifted commensurate with changes in climate (Parmesan and Yohe 2003; Walther *et al.* 2005). Range shifts towards the poles of up to 6.1km per decade have been reported by Parmesan and Yohe (2003). In a study on the effects of climate change on the distribution of European plants, Bakkenes *et al.* (2002) found a general trend for the climate envelopes of species to shift north-eastwards, although a wide range of individual responses was found.

Ireland is one of the least forested countries in Europe. Only *c.* 10% of Ireland is forested, and commercial conifer plantations comprise the majority of this figure (Forest Service 2007), so that only *c.* 2% of the land area is covered by semi-natural woodland (defined as woodland dominated by native species) (Gallagher *et al.* 2001). This relative paucity of woodland habitats makes the conservation of woodland in Ireland a priority, with special concern for the semi-natural woodlands. Under the EU Habitats Directive (EEC 1992), member states are obliged to conserve any habitats listed in Annex I; four Annex I woodland types occur in Ireland (Table 1; Perrin *et al.* 2008). Of these, three woodland types are priority habitats: bog woodland, alluvial forests with *Alnus glutinosa* and *F. excelsior*, and *Taxus baccata* (Yew) woods. Perrin *et al.* (2008) identified the main threats to Irish woodlands as deforestation, grazing and the spread of invasive alien species, but to this, the threat of climate change should be added. The native and semi-natural woodlands in Ireland are not only limited in area, but also those woodlands which do occur are generally highly fragmented and/or disturbed, making them particularly vulnerable to the effects of climate change (Noss 2002; Brook *et al.* 2008).

Table 1—EU habitats directive Annex I woodland types found in Ireland.

Code[a]	*Description*
91A0	Old sessile oak woods with *Ilex* and *Blechnum* in the British Isles
91D0	Bog woodland
91E0	Alluvial forests with *Alnus glutinosa* and *Fraxinus excelsior*
91J0	*Taxus baccata* woods of the British Isles

[a]Council Directive 92/43/EEC on the conservation of natural habitats and of wild fauna and flora.

While the effects of climate change on woodland species in Ireland have not been studied in detail, adverse effects of climate change on species distributions and abundances in English woodlands have already been found (Kirby *et al.* 2005). In southern England, Broadmeadow *et al.* (2005) found that the majority of native broadleaved trees were predicted to become unsuitable for commercial timber production. Furthermore, a study by Lindner *et al.* (2010) suggests that woodlands and forests within Europe's temperate oceanic zone (including Ireland) may have a greater incidence of mass outbreaks of insect herbivores, including bark beetles, as well as range shifts and expansions of tree pathogens.

The most commonly used methods to assess the impacts of projected climate change on the distribution of biodiversity are species distribution models (SDMs), which statistically relate current species distributions to climatic variables, enabling projections of distributions under future climate change scenarios (Pearson and Dawson 2003; Thuiller *et al.* 2005). SDMs have been used extensively to determine the potential impact of climate on both species and communities, and can be important in informing conservation strategies (Midgely *et al.* 2003; Carroll 2010). Because we have little knowledge on the physiological factors that govern the distribution of many species, SDMs can provide valuable insight into the potential impacts of climate change on these species using broader climatic and environmental variables as proxies for a variety of ecophysiological processes.

This study focused on Irish woodlands, and the aims were (1) to project the changes in the distribution of woodland species under a future climate change scenario and assess the potential implications for woodland communities, (2) to investigate the use of SDMs for predicting the distribution of woodland species, and (3) to discuss the results of these model projections in the context of future conservation management of woodland habitats in Ireland.

METHODS

STUDY AREA

The study area consisted of the whole island of Ireland (both the Republic and Northern Ireland), on the north-western fringe of Europe between 51°25′N and 55°25′N, and 5°26′W and 10°37′W. Ireland has a temperate oceanic climate, with mean monthly temperatures ranging from 6°C–6.5°C in January to 15°C–15.5°C in July (Rohan 1986) and relatively high (<800mm to >2500mm per annum) and frequent (150 to >220 days per annum) rainfall. Temperatures in Ireland are

projected to rise by 3°C–4°C by the end of this century; an increased seasonal variation in rainfall amounts is also projected, leading to lower summer and higher winter precipitation (McGrath and Lynch 2008; Sweeney and Fealy 2002).

SPECIES SELECTION

Species from four broad taxonomic groups (vascular plants, bryophytes, butterflies and birds) which were either confined to or characteristic of a variety of semi-natural woodlands were identified. The list of vascular plant and bryophyte species associated with woodlands was compiled from a variety of sources; in general, these were species listed in the literature as characteristic or indicator species of semi-natural woodland in Ireland. Butterfly species of interest were identified based on their use of woodland plant species as larval food sources. A small number of birds with known affinities for woodland habitats were also selected. Nomenclature of vascular plants follows Stace (2010), while that of bryophytes follows Atherton *et al.* (2010). Nomenclature of butterflies follows Bond *et al.* (2006) and that of birds (using vernacular common names) follows Dudley *et al.* (2006).

DATA SOURCES

Climate data from the 1961 to 1990 baseline period were obtained for the whole island of Ireland (Sweeney and Fealy 2002; 2003). Using daily climate data from 560 precipitation stations and 70 stations for temperature, 10 × 10km grid cell (Irish National Grid) resolution data were spatially interpolated using a polynomial regression method with an inbuilt adjustment for elevation.

The climate change data used in the current study include the mean values of the IPCC A2 and B2 scenario outputs (Nakicenovic *et al.* 2000), obtained by statistically downscaled outputs from the HadCM3 Global Climate Model (Sweeney and Fealy 2003). The B2 family of scenarios places more emphasis on the projected finding of local solutions to economic, social and environmental sustainability, whereas the A2 family of scenarios projects a greater increase in global carbon dioxide (CO_2) emissions associated with different development trajectory assumptions (Nakicenovic *et al.* 2000).

Species distribution data were obtained from a variety of sources. For vascular plants and bryophytes, species data were largely obtained from the National Biodiversity Network (NBN) Gateway (NBN Gateway 2008); while data for selected bryophytes were obtained from the National Parks and Wildlife Service. Data on bird species distribution were obtained from the Global Biodiversity Information Facility (GBIF), www.gbif.org. Butterfly distribution data were provided by Butterfly Ireland (Republic) and National Biodiversity Network (UK), http://www.nbn.org.uk/. The geographical distributions of plant species were classified into biome and eastern limit categories, following Hill *et al.* (2004) for vascular plants and Hill *et al.* (2007) for bryophytes.

Digital Elevation Models (DEMs) were used to calculate the elevation of each grid cell. Topographical data were extracted from the GTOPO30 DEM (U.S. Geological Survey), with data at a 30-arc seconds (approximately 1km^2) resolution projected to the Irish National Grid. A range of topographical variables were extracted from the DEM, based on the habitat and ecological requirements of the selected species. Data were extracted for each 10 × 10km grid cell. Data processing was undertaken in ArcGIS v9.3 (ESRI 2008). Hawth's Tools, an extension to ArcGIS, was used to carry out the polygon in polygon analysis (Beyer 2004).

VARIABLE SELECTION

A large range of climatic and topographic variables were considered for analysis. All were tested for collinearity, then selected to avoid this, using variance inflation factors (VIFs) (Zuur *et al.* 2007). VIFs were calculated between the variables. The variables with highest VIFs were eliminated until the VIFs for all variables were below a value of five, which is sufficiently low to avoid collinearity (Zuur *et al.* 2007). Knowledge of the species' ecological requirements informed the final selection of the most ecologically important variables. The variables used were minimum annual monthly temperature (which was always February), continentality index (difference between mean maximum and mean minimum temperatures), net annual precipitation and elevation (Table 2).

We predicted the distribution (current and future projections) of 104 target species using eight modelling techniques available in the BIOMOD library (Thuiller *et al.* 2009), run and calibrated within the R environment (R Development Core Team 2010): Generalized Linear Models (GLMs), Random Forests (RFs), Generalized Boosting Models (GBMs), Artificial Neural Networks (ANNs), Classification Tree Analysis (CTA), Multiple Adaptive Regression Splines (MARSs), Flexible Discriminant Analysis (FDA) and Generalized Additive Models (GAMs) (Thuiller *et al.* 2009). We implemented a split-sample cross-validation procedure to evaluate the models (i.e. different data portions are used to construct and to evaluate the models). Models were calibrated for each species on 80% of the initial data and then evaluated on the remaining 20% using the area under the curve (AUC) of the receiver-operating characteristic (ROC) (Swets 1988) and the True Skill Statistic

Table 2—Current mean, minimum, maximum and range values for climatic and topographic variables (elevation is metres above datum) and projected climate variables for 2055.

Variable		*Baseline*				*Projected*			
Abbreviation	*Description*	*Mean*	*Min*	*Max*	*Range*	*Mean*	*Min*	*Max*	*Range*
FebMin	Minimum February temperature (°C)	1.4	−2.0	3.8	5.8	2.7	−1.0	5.4	6.4
NAP	Net annual precipitation (mm)	1254	692	2114	1422	1183	528	2048	1520
CI	Continentality index	17.0	14.1	18.8	4.7	19.9	15.5	24.4	8.9
Elevation	Elevation (metres above datum)	110	1	480	479	110	1	480	479

(TSS) (Allouche *et al.* 2006). Thresholds used to evaluate model predictive performance are presented in Table 3 (Swets 1988). In this study, species were considered to have modelled well if they had an AUC of > 0.90 or a TSS value of > 0.60, or if AUC > 0.70 and TSS > 0.40.

ENSEMBLE FORECASTING

Buisson *et al.* (2010) accounted for the variation associated with predicting species ranges in terms of the species distribution data, the modelling technique, the global circulation model and the gas emission scenario used, and highlighted the importance of assessing deviance by including a range of modelling techniques. To overcome the difficulty of obtaining different results from different species distribution modelling techniques, we used the ensemble forecasting function in BIOMOD to analyse the resulting range of uncertainties from the eight modelling techniques using a consensus approach rather than comparing single modelling outcomes (Thuiller *et al.* 2009).

The data were not normally distributed, which limited the statistical tests for differences which could be carried out. Model comparisons were carried out using Friedman tests, with *post hoc* Wilcoxon signed ranks tests. Differences between model scores and range changes in different grouping categories were compared and analysed for significance with Kruskal–Wallis tests, with *post hoc* Mann–Whitney U tests to determine differences between groups. SPSS (Release 18.0.0) was used to carry out these tests and to produce boxplots. Corrections for multiple comparisons, where necessary, were made using the Dunn-Šidák correction.

The simulated current and future distributions of the species were compared for the models using both climate and topography variables, and the percentage decrease or increase in range for each species was calculated. Central to possible range changes of species under changing climate is the ability of those species to colonise new potentially suitable areas. This mostly depends on the dispersal ability of species. However, detailed dispersal distances are not available for most species; therefore, we examined two extreme scenarios:

1. Unlimited dispersal, where the entire projected future range of the species is taken to be the actual future distribution.
2. No long-range dispersal, where the future distribution results solely from the overlap between the current and projected future range of the species.

Table 3—Threshold values for classifying model prediction accuracy (after Thuiller *et al.* (2009)).

Accuracy	*AUC*	*TSS*
Excellent or high	0.9–1	0.8–1
Good	0.8–0.9	0.6–0.8
Fair	0.7–0.8	0.4–0.6
Poor	0.6–0.7	0.2–0.4
Fail or null	0.5–0.6	0–0.2

RESULTS

Mean AUC and TSS scores for all models were calculated for each species (Appendix I). Mean, minimum and maximum scores for each model for AUC and TSS are presented in Table 4. The models generally performed well, with mean AUC values of greater than 0.7 for all models except for CTA. Mean TSS scores were greater than 0.4 for all models except CTA. Of the 104 species modelled, 44 species modelled 'well' according to the AUC/

Table 4—Minimum, maximum and mean AUC and TSS scores from BIOMOD for each model, for all species.

	AUC			*TSS*		
	Min	*Max*	*Mean*	*Min*	*Max*	*Mean*
ANN	0.547	0.994	0.743	0.145	0.841	0.422
CTA	0.520	0.906	0.654	0.075	0.804	0.297
GAM	0.527	0.987	0.743	0.139	0.968	0.429
GBM	0.566	0.991	0.749	0.176	0.963	0.439
GLM	0.530	0.993	0.738	0.128	0.979	0.423
MARS	0.539	0.987	0.733	0.138	0.868	0.415
FDA	0.553	0.945	0.728	0.131	0.804	0.399
RF	0.541	0.991	0.730	0.143	0.977	0.411

TSS scores (i.e. AUC of > 0.90 or a TSS value of > 0.60, or if AUC > 0.70 and TSS > 0.40). Table 5 summarises the number and percentage of species which performed well for each model.

Distributions of AUC and TSS scores for each of the models were plotted as boxplots, with the species separated into different taxonomic groups (birds, bryophytes, butterflies and vascular plants) (Figs. 1 and 2). When corrected for multiple comparisons, median AUC scores were significantly higher ($p < 0.05$) for vascular plants than bryophytes in five models (GBM, GLM, MARSs, FDA and RF), while median TSS scores were significantly higher ($p < 0.05$) in four models (GLM, MARS, FDA and RF). Of the bryophytes, *Sematophyllum demissum* and *Sematophyllum micans* consistently produced higher AUC and TSS scores, shown as outliers in the boxplots, while *Telaranea nematodes* produced higher TSS scores. Of the vascular plants, *Euphorbia hyberna* and *Saxifraga spathularis* consistently produced higher AUC and TSS scores. *Glechoma hederacea* and *Hymenophyllum wilsonii* were also occasional outliers.

PROJECTED RANGE CHANGES

Model performances in BIOMOD were in broad agreement; ensemble forecasting results were therefore chosen to produce data on range changes. Range changes (for both the unlimited dispersal and no long-range dispersal scenarios) were calculated for those species that performed well in at least six of the eight BIOMOD models (Fig. 3). A mean increase in range of 65.9% was projected under the unlimited dispersal scenario, while a mean reduction in range (−26.9%) was projected under the no long-range dispersal scenario. Under a scenario of unlimited dispersal, the median range change of vascular plants was significantly lower than that of bryophytes ($p < 0.05$). Almost 50% of species which modelled well were projected to lose climate space, with the largest range contraction projected for the butterfly *Aphantopus hyperantus* (Ringlet) (−47.7%). The remainder were projected to have

Table 5—Number of species with 'satisfactory' or higher AUC and TSS scores from BIOMOD (i.e. AUC of > 0.90 or a TSS value of > 0.60, or if AUC > 0.70 and TSS > 0.40). Total number of species included in the models was 104.

Model	*No. of species which performed well*	*Percentage of species which performed well*
ANN	57	54.3
CTA	21	20.0
GAM	58	55.2
GBM	58	55.2
GLM	54	51.4
MARS	51	48.6
FDA	47	44.8
RF	49	46.7
Mean	49.4	47.0

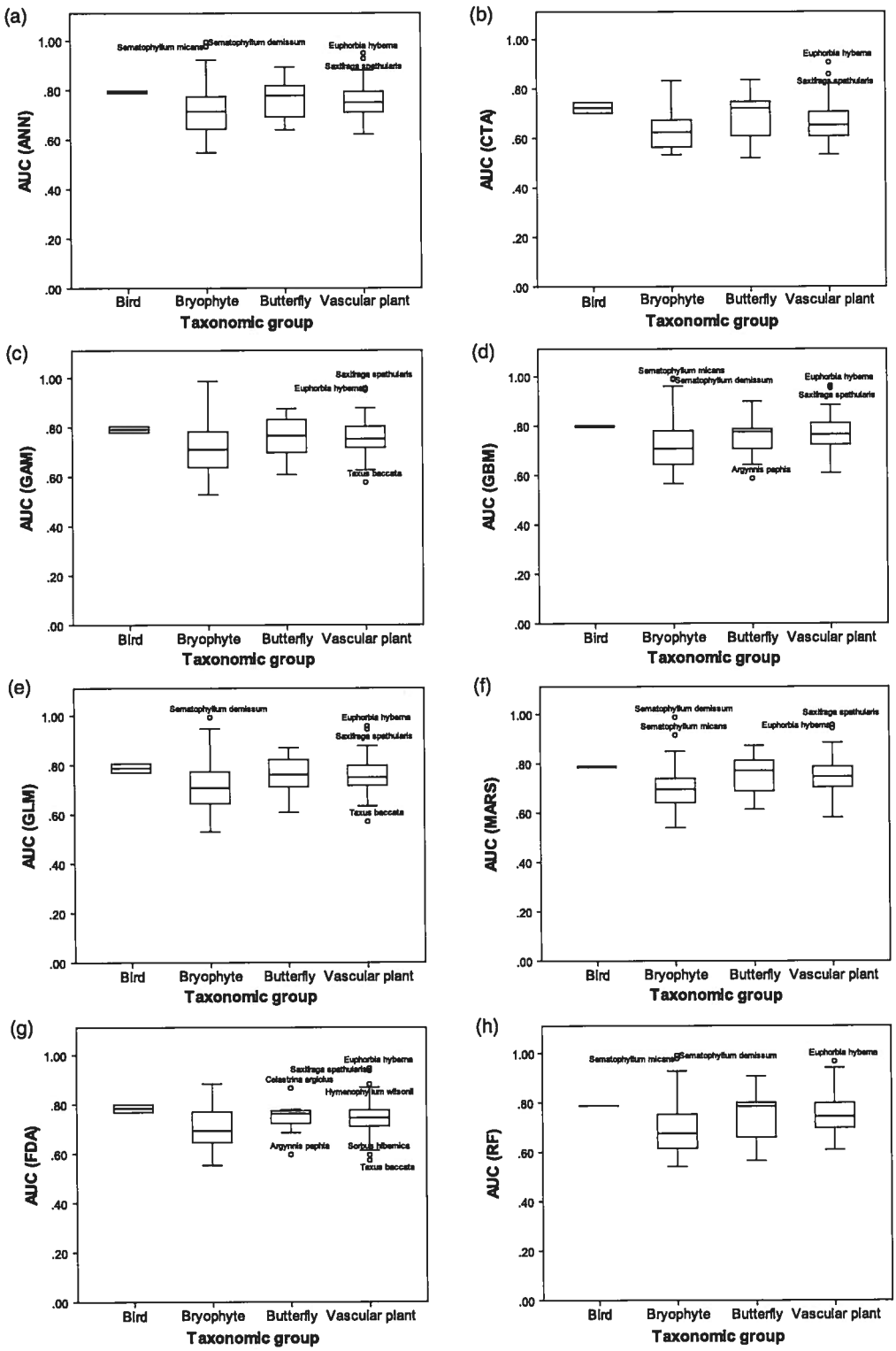

Fig. 1—Box plots showing values of AUC for species distribution models of 104 species, produced using (a) ANN, (b) CTA, (c) GAM, (d) GBM, (e) GLM, (f) MARS, (g) FDA and (h) RF in BIOMOD. Outliers are indicated by open circles, and labeled. (Note: only two bird and five butterfly species are presented here).

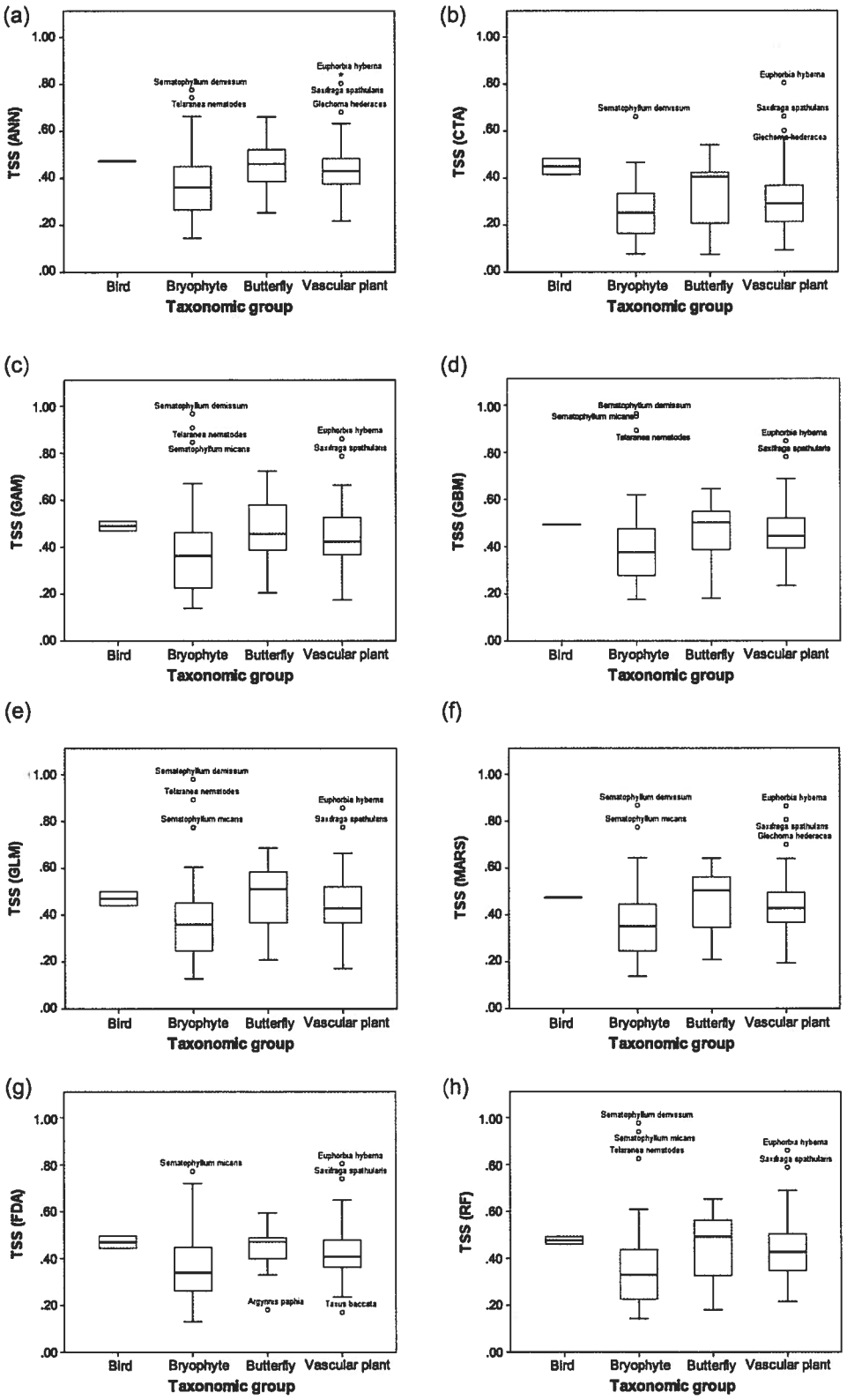

Fig. 2—Box plots showing values of TSS for species distribution models of 104 species, produced using (a) ANN, (b) CTA, (c) GAM, (d) GBM, (e) GLM, (f) MARS, (g) FDA and (h) RF in BIOMOD. Outliers are indicated by open circles, and labeled. (Note: only two bird and five butterfly species are presented here).

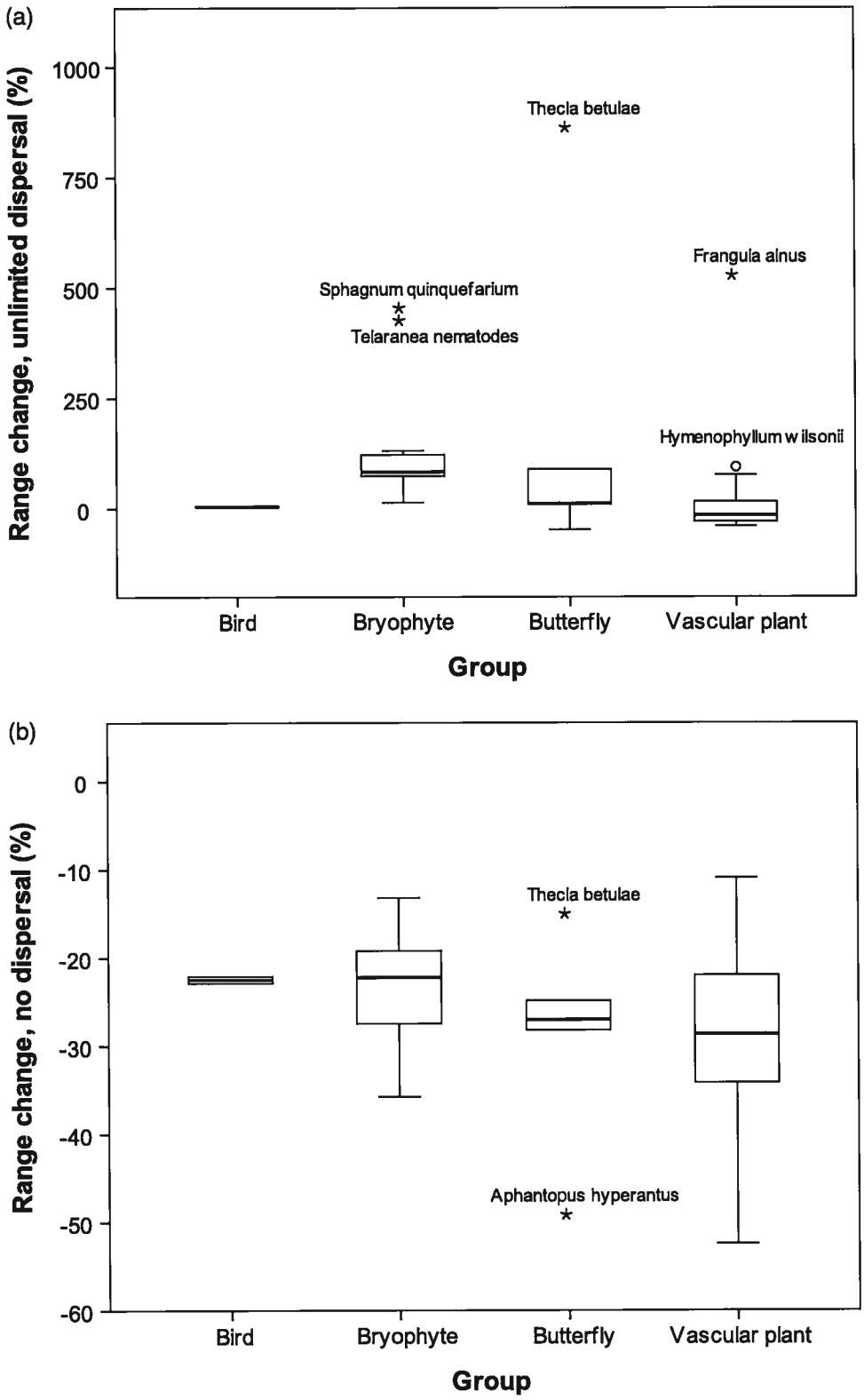

Fig. 3—Boxplots showing range changes for (a) unlimited dispersal and (b) no long-range dispersal for the species which modeled well, divided into taxonomic groups. Outliers are indicated by stars or open circles, and labeled. (Note: only two bird and five butterfly species are presented here.

increased climate space. Under the unlimited dispersal scenario, no significant differences were found between taxonomic groups, although some large increases in potential range can be seen (Fig. 3a). *T. nematodes*, a woodland liverwort which grows on peaty banks or rocks, is currently found in woodland in south-west Ireland (Atherton *et al.* 2010). This rare bryophyte (occurring in only 17 grid squares) is projected to have an increase in suitable climate space of over 400%, while *Sphagnum quinquefarium*, a moss of acidophilous woodland, is currently more widespread (Atherton *et al.* 2010) but is also projected to have increased climate space of over 450%. The actual potential for range increase of bryophytes, and indeed of most of the species modelled here, may be limited by availability of habitat.

Of the butterflies, only *A. hyperantus* was projected to lose climate space under the unlimited dispersal scenario. *Gonepteryx rhamnus* (Brimstone) was projected to have a potential range increase (unlimited dispersion) of almost 90%, but a limited dispersal range change of −27%. Larval food plants for *G. rhamnus* are primarily *Rhamnus cathartica* (Buckthorn) and *Frangula alnus* (Alder buckthorn). While *R. cathartica* did not model well, *F. alnus* was projected to have a 35% decrease in range under the limited dispersal scenario, which may result in a further decrease in suitable range for *G. rhamnus*. *Thecla betulae*, the Brown Hairstreak butterfly, was the species with the largest increase in potential range (866.7%).

Bryophytes showed a significantly greater increase in range than vascular plants under the unlimited dispersal scenario (145.9% ± 149.0 vs 17.4% ± 109.3; $p < 0.05$). Under the no long-range dispersal scenario, bryophytes are projected to show a mean range loss of 23.5% ± 6.5 compared to a loss of 28.4% ± 9.9 for vascular plants (Table 6).

No significant differences were found between range changes for the biome or eastern limit categories of plant species, although some trends were evident. Species in the boreal-montane and southern temperate biomes show the greatest increase in range under unlimited dispersal (218.8% and 167.3%), while species in the wide-boreal, boreo-temperate and temperate are projected to have the greatest losses in suitable climate space (Table 6).

While there is a general trend for an increase in suitable climate space under the unlimited dispersal scenario, this is not the case for those species in the European (e.g. *Blechnum spicant*), Eurasian (e.g. *G. hederacea*) and circumpolar (e.g. *Deschampsia cespitosa*) eastern limit categories, all of which show a mean decrease (Table 6). The hyperoceanic category is projected to gain the largest amount of suitable climate space, at 140.0% ± 164.3. Under the limited dispersal scenario, all categories are projected to have decreased ranges, with all but the hyperoceanic (e.g. *H. wilsonii*) and Eurasian eastern limit categories projected to have large (> 25%) mean decreases.

Table 6—Mean range changes for plant species (± standard deviation), under unlimited dispersal and no long-range dispersal, for plant type, biome and eastern limit categories.

	Number of species	*Range change (Unlimited dispersal)*	*Range change (No long-range dispersal)*
Bryophyte	11	145.9 ± 149.0	−23.5 ± 6.5
Vascular plant	27	17.4 ± 109.3	−28.4 ± 9.9
Biome			
Wide-boreal	1	−25.2	−29.0
Boreal-montane	2	218.8 ± 330.9	−19.1 ± 8.3
Boreo-temperate	14	29.1 ± 57.2	−27.0 ± 6.6
Temperate	17	34.5 ± 134.8	−29.5 ± 11.0
Southern-temperate	4	167.3 ± 175.0	−19.5 ± 5.8
Eastern limit			
Hyperoceanic	5	140.0 ± 164.3	−19.1 ± 5.7
Oceanic	4	52.7 ± 57.2	−26.3 ± 8.6
Suboceanic	10	89.8 ± 139.0	−29.1 ± 12.7
European	10	−11.9 ± 25.2	−30.1 ± 6.9
Eurosiberian	6	72.3 ± 225.5	−27.4 ± 7.8
Eurasian	1	−4.8	−14.8
Circumpolar	2	−22.0 ± 4.6	−26.6 ± 3.4
Overall mean		54.6	−27.0

When the no long-range dispersal scenario is considered, no species were projected to maintain their entire current range; all species were projected to lose suitable climate space (Appendix II). *S. spathularis* was the species with the smallest projected decrease in range, at 10%, while *Carex strigosa*, *A. hyperantus*, *Lysimachia nemorum* and *Cardamine flexuosa* were all projected to lose more than 40% of their current climate space.

PATTERNS OF DISTRIBUTION CHANGE

Changes in distribution fall into one of two main groups; for some species, suitable climate space is lost in the centre of the country, and ranges are either maintained or expanded around the periphery. The other pattern of range shift is for a loss of climate space in the west and south, with ranges maintained or gained in the north and east. This seemed to be linked to eastern limit categories, with hyperoceanic, oceanic and suboceanic eastern limit categories showing a decrease in the centre of the country and an increase near the coasts (e.g. *D. aemula* (hyperoceanic), *Saccogyna viticulosa* (oceanic) and *L. nemorum* (suboceanic); Fig. 4a–c), which reflect the projected change in continentality index (i.e. an increase in the difference between mean maximum and minimum temperatures; Fig. 4d). Species in the Eurosiberian, Eurasian and circumpolar categories showed a trend for a range shift to the north east (e.g. *Betula pubescens* (Eurosiberian), *G. hederacea* (Eurasian) and *Phalaris arundinacea* (circumpolar); Fig. 5a–c), which is similar to the projected change in minimum February temperature (Fig. 5d). Distribution maps for all other species that modelled well are presented in Appendix III.

DISCUSSION

Almost half of the species in this study modelled well, and the projected range changes for individual species can contribute to the understanding of the impacts of climate change on woodland species in Ireland. There is an overall picture of a loss of suitable climate space, although this varies greatly from species to species, with some species projected to gain large increases on their current range.

Model performance was good using just three climatic variables together with elevation. A range of biotic and abiotic factors affect species distribution; however, the models may be improved through the addition of further variables, for example interactions with other biota, soil type and dispersal ability. The potential for dispersal of the organisms modelled varies widely, and this has been addressed simply in this model, either in completely unlimited dispersal or in completely limited (no long-range) dispersal (i.e. no dispersal from one grid square to another). Neither of these scenarios is likely to accurately represent the species' true capacity for dispersal, which probably varies along a continuum from organisms capable of widespread dispersal (such as birds and bryophytes) to those with relatively limited dispersal abilities (such as trees). Consequently, some species which are projected to have an increase in suitable climate space, e.g. species of tree such as *A. glutinosa*, may not necessarily be able to migrate or disperse quickly enough or far enough to take advantage of their expanded climatic envelope. Some species may also have specific habitat requirements (e.g. soil type) which are not met by the areas projected to have suitable climate space in the future. One important assumption of the data used for the current, 'observed', distribution of species is that these current distributions are in equilibrium with the climate data, which is not always the case. A lag between climate change and species distribution is likely to be greater for long-lived, poor dispersers such as trees. One of the predictions regarding climate change in Ireland is that extreme weather events may become more frequent (Dunne *et al.* 2008), but this is difficult to quantify and was not included in the analyses. In addition to increased number and intensity of storm events, the wetter winters and drier summers predicted may result in increased winter flow in rivers and streams (with the potential for increased flooding) and decreased summer flow, both of which could have implications for woodlands near to waterbodies.

Under the unlimited dispersal scenario, a mean increase in range across all species is projected; this is similar to findings in a recent report on the implications of climate change for woodland biodiversity in the UK (Berry *et al.* 2012), although these authors did not consider a no long-range dispersal scenario. The majority of species modelled here are projected to experience a decrease in potentially suitable climate space (24 of 46 species under the unlimited dispersal scenario, with all species losing at least some of their current range under the no long-range dispersal scenario). Community composition may therefore change drastically, as individual species respond to climate change at different rates and in different ways. The composition of butterfly communities in the UK has been shown to become dominated by generalist species as the climate warms (Menendez *et al.* 2006). This pattern may be repeated across taxonomic groups, as dispersal limitations are likely to matter less to generalist species than to specialists. Generalists may also be more likely to find suitable habitat than specialists.

Butterflies may already be under threat from other anthropogenic processes, including habitat fragmentation. British butterflies were found to

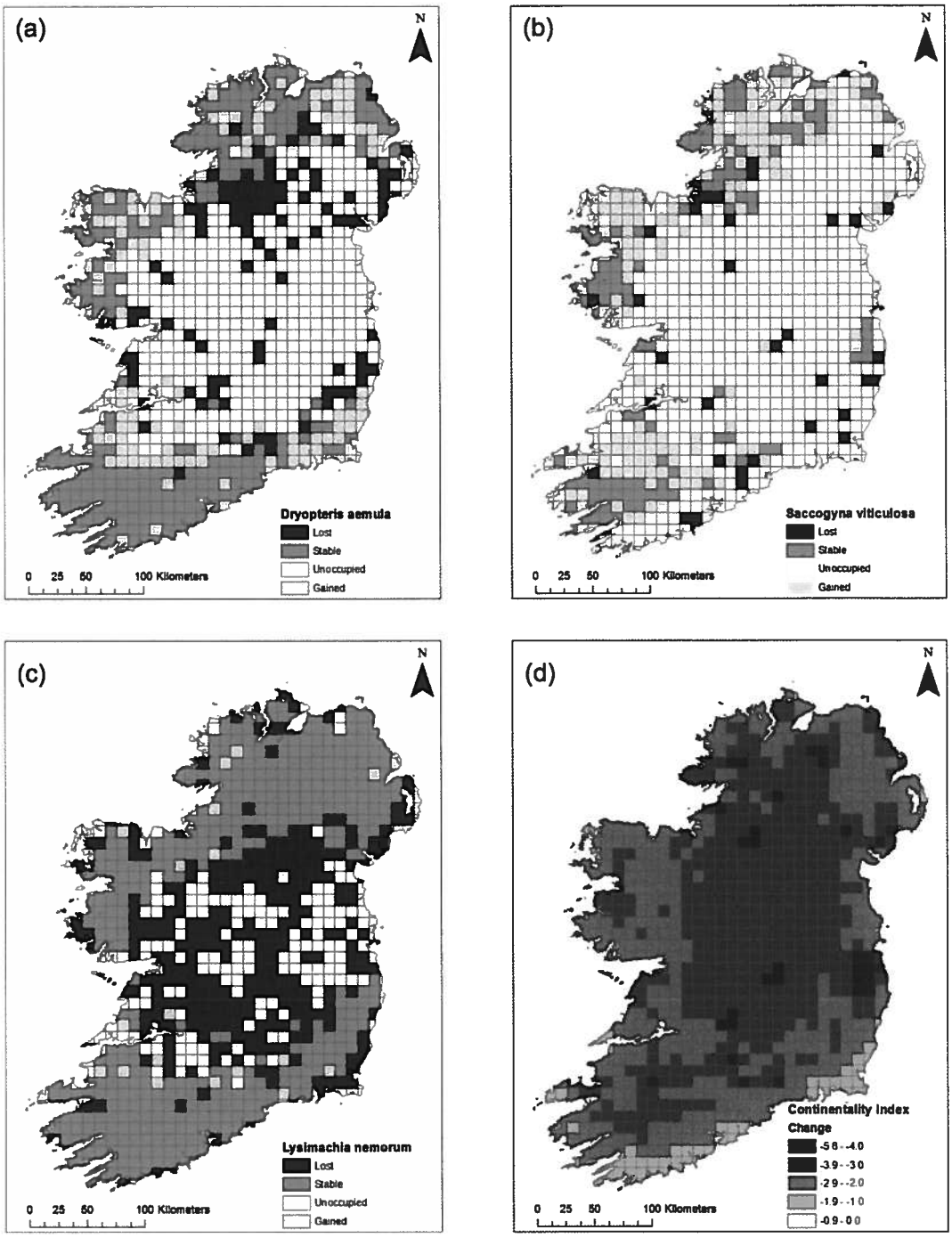

Fig. 4—Species distribution maps showing the projected change in distribution under unlimited dispersal for (a) *Dryopteris aemula*, a hyperoceanic species, (b) *Saccogyna viticulosa*, an oceanic species, and (c) *Lysimachia nemorum*, a sub-oceanic species. Projected change in continentality index is also shown (d), where the darker colours indicate the greatest decrease in continentality index (i.e. a larger difference between mean maximum and minimum temperatures).

have disappeared from 13% of the 10km squares occupied during the 1970–1982 census period (Thomas *et al.* 2004b). The average species richness of British butterflies, however, has increased since 1970–1982 (Menendez *et al.* 2006). In this study, all of the woodland butterfly species which modelled well were projected to lose large areas of suitable climate space under the no long-range dispersal scenario; *T. betulae* was projected to lose 14.8%, while all others projected to lose 25% or more of their current range. When the unlimited dispersal scenario was used, however, only *A. hyperantus* was projected to lose climate space. Of the other four species, two were projected to increase their

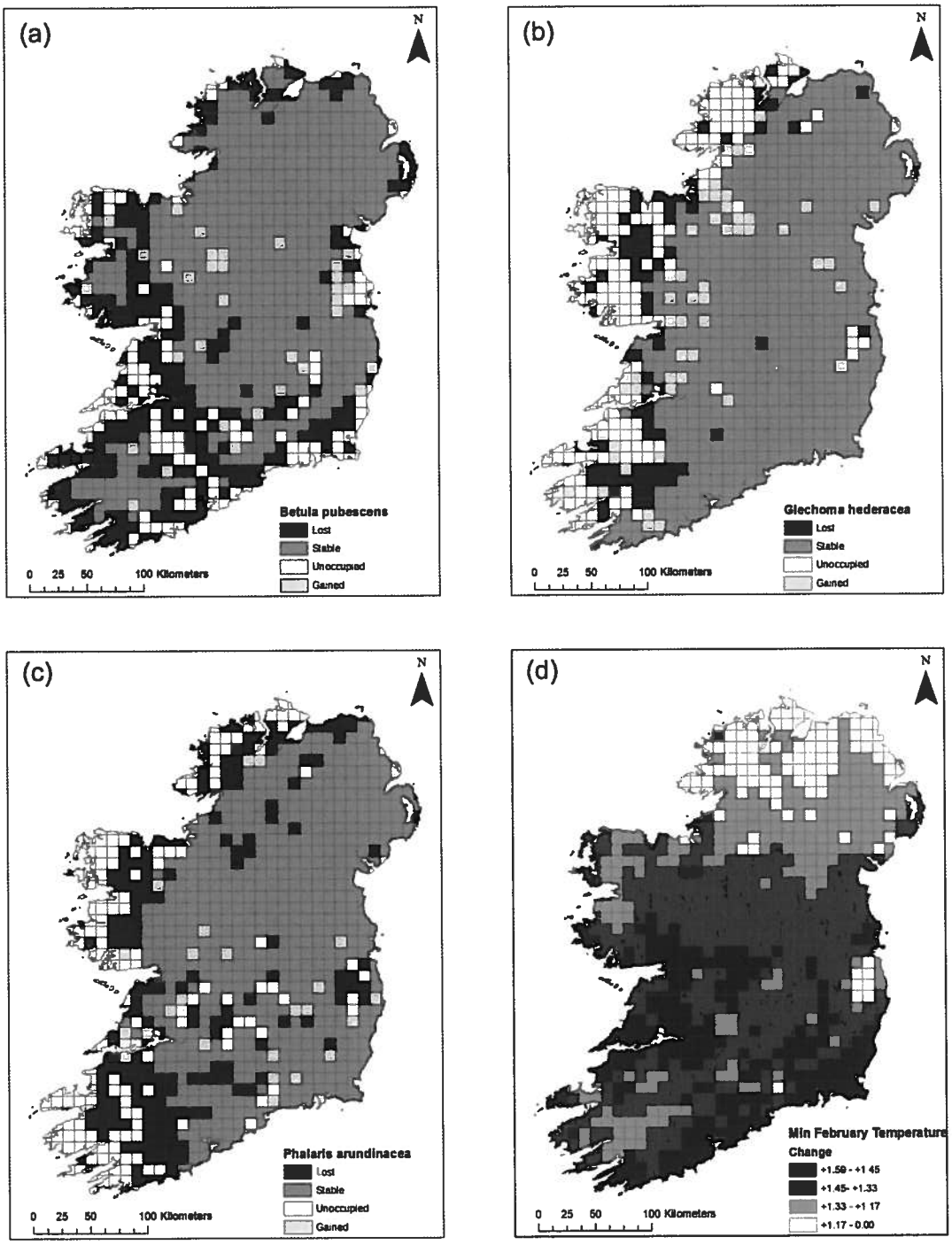

Fig. 5—Species distribution maps showing the projected change in distribution for (a) *Betula pubescens*, a Eurosiberian species, (b) *Glechoma hederacea*, a Eurasian species, and (c) *Phalaris arundinacea*, a circumpolar species. Projected change in minimum February temperature is also shown (d), where the darker colours indicate the largest increase in minimum February temperature.

current range by small amounts, while the range of *Gonopteryx rhamni* was projected to increase by 89.6%, and that of *T. betulae* was projected to increase by 866.7%. The differences between range change for the unlimited and no long-range dispersal scenarios can be large, and while the limited dispersal scenario may not be applicable to such mobile organisms as most butterflies, when the potential distribution of suitable food plants (*T. betulae* larvae, for example, feed primarily on *Prunus spinosa*) and any potential phenological mismatches (e.g. Buse and Good 1996; Visser and Holleman

2001) are taken into account, future range contractions may be even larger than projected.

Berry *et al.* (2003) found that oak woodlands and beech woodlands in Britain and Ireland were projected to have medium vulnerability. Of the oak woodland species studied by Berry *et al.* (2003), only *Dryopteris aemula* and *B. spicant* were included in this study. Berry *et al.* (2003) found that *D. aemula* gained climate space, while *B. spicant* showed no change. In this study, *D. aemula* was projected to expand by almost 20% of its current range (unlimited dispersal) or lose over a quarter (limited dispersal), while *B. spicant* was projected to lose a significant part of its range under both scenarios. In a more recent study, Berry *et al.* (2012) examined the impacts of climate change on a number of woodland species in the UK, and some of their results are at odds with the results in this study, for example while both *B. pubescens* and *Quercus robur* are projected to lose climate space here (at −30% and −6% of their current range under unlimited dispersal, respectively), in the Berry *et al.*'s study, *Q. robur* is projected to have an 'insignificant gain', and *B. pubescens* an 'insignificant loss'. These differences may reflect differences in modelling techniques, but it is likely that the larger area and more varied climate of the UK will provide more potentially suitable climate space under climate change than that of Ireland. Ireland's relatively depauperate flora means that woodland communities found here are subtly different to those found in the UK, and these communities may also respond differently to climate change, as community composition shifts in favour of species more suited to the changed climate. These differences underline the necessity of research into the impacts of climate change on Irish woodland species.

The projected expansions in distribution of hyperoceanic and oceanic plant species reflect the patterns of projected decrease in continentality index, i.e. a movement towards coastal areas where smallest changes in continentality index are projected (Fig. 4). The projected shifts in distribution of Eurosiberian, Eurasian and circumpolar species seem to reflect the patterns of projected change in minimum February temperature, with a general shift in distribution to the north and east (Fig. 5). The projected range shifts to the north east is a pattern which was also noted, at a European scale, by Bakkenes *et al.* (2002). Bryophytes show a greater mean increase in range under unlimited dispersal and a smaller decrease in range under limited dispersal than vascular plants, indicating that bryophytes and vascular plants are likely to respond to climate change at different rates and in different ways. Even within these broad taxonomic groups, differing projected responses to climate change were seen. These types of varied responses to climate change have been predicted/observed by many studies (for example Le Roux and McGeoch 2008; Lenoir *et al.* 2008) and suggest that range responses of individual species to climate change will lead to changes in the species composition of many communities.

The impacts of climate change on phenology (the timing of life cycle events in plants and animals) were not taken into account in this study. The onset of spring, as measured by timing of temperature increases, as well as biotic responses such as leafing, insect hatching and arrival of migrant birds, appears to be moving forward at a rate of 2.8 days per decade (Parmesan 2007), although some authors suggest a much greater rate of advancement (Root *et al.* 2005). Earlier leafing date in trees can cause a 'ripple effect' on other species in a woodland (Schwartz *et al.* 2006), for example by causing a mismatch between timing of insect hatching and availability of food (de Vries *et al.* 2011) or decreasing the level of light available for vernal species (Kirby *et al.* 2005). Changes in the phenology of some of the tree species in this study, therefore, could affect the distribution of insects and birds associated with them, e.g. the impact of the projected loss of range of *F. alnus* on *G. rhamnus* (the larvae of which feed on *F. alnus*) may be amplified if there are phenological mismatches between leafing and larval emergence. Earlier leafing may also be detrimental to the plant itself, for example exposing young leaves to late frosts. For some species, however, lack of winter chilling may lead to delayed budburst (Murray *et al.* 1989). Not all species respond to climate change and spring advancement with changes in the timing of life cycle events; Parmesan and Yohe (2003) found that between 20% and 70% of species in areas experiencing warming trends did not exhibit change in their phenological patterns. The variation inherent in phenological responses to climate change makes it difficult to predict the effects it might have on interspecific interactions.

The results presented here have a number of implications for woodlands in Ireland. Under the no long-range dispersal scenario, all of the species which modelled well were projected to have a decreased area of suitable climate space in 2055. The 'unlimited dispersal' scenario showed that, for some species, climate change will result in either an increased area of suitable climate or a shift in potential range; however, large range shifts over a short time period are very improbable. Ireland has a small area of woodland, much of the landscape being occupied by agricultural land. This means that the area available for colonisation by woodland plants is smaller than in many other European countries. Many of the dominant or characteristic species of Irish woodlands have limited dispersal

abilities, and long-range dispersal is likely to be further restricted by a lack of suitable habitat for colonisation. Modelling of the suitable climate space of these woodland species has shown that there are species-specific responses to climate, for example *B. pubescens* is projected to lose 30% of its current range under the unlimited dispersal scenario, while *Q. robur* is projected to lose just 6%. The species composition of the existing woodlands and woodland communities may therefore change, as some species will tolerate climate change more readily than others.

A number of the species included in this study are of conservation interest. *F. alnus* is listed as 'rare' in the Irish Red Data list for vascular plants (Curtis and McGough 1988), and the increase in potential range for this species (under the unlimited dispersal scenario) may aid in its conservation. Of the bryophytes, *S. demissum* is listed as 'near threatened' by Lockhart *et al.* (2012). *S. demissum* was projected to have a large increase in potential range (under the unlimited dispersal scenario), while *S. quinquefarium* was projected to more than quadruple of its current range, although the availability of suitable habitat will restrict any actual range expansion. *Leptidea sinapis*, the wood white butterfly, which is listed as 'near threatened' by Regan *et al.* (2010), is projected to experience a contraction of its current range under climate change.

There are a number of ways in which the impacts of climate change on the distribution of woodland species in Ireland might be mitigated. The most important is probably the maintenance and conservation of the existing woodlands, especially protecting them from other stressors (e.g. excessive grazing pressures) to increase the likelihood of survival of the species which are present. The existing woodlands of one type might also become suitable habitats for species which currently live in other types of woodland. The translocation of vulnerable species from areas which are projected to become inhospitable to areas within the new projected range could be attempted, a process known as 'assisted migration' (McLachlan *et al.* 2007) or 'assisted colonisation' (Hoegh-Guldberg *et al.* 2008). While this is an unpredictable and potentially expensive method of conservation, it has been used with some success to re-colonise areas with species formerly indigenous to that area and could potentially be an important part of climate change mitigation in Ireland. Managed, commercial woodlands could be made more profitable/viable through the use of plants of a more southerly provenance, e.g. plantations could be stocked with plants sourced from regions with climates currently similar to those projected (Broadmeadow *et al.* 2005). This type of management could help to maintain some species in the woodland, but the overall species composition is likely to change, due to changes in suitable climate space for other species.

CONCLUSION

This study has shown that, for many of the characteristic species of semi-natural woodland in Ireland, climate change is a real threat. For others, however, it may represent a real opportunity. The area of suitable climate space is projected to shrink for all species, given a no long-range dispersal scenario. While the reality has to be that actual dispersal lies between the unlimited and no long-range dispersal scenarios, other factors such as land use and biotic interactions will also impact on future distribution. Further information on responses to biotic and abiotic factors, dispersal ability and phenological responses will be required to determine appropriate conservation measures for woodlands and woodland species in Ireland.

The relatively small area and fragmented nature of Irish semi-natural woodlands makes their conservation a priority. Threats from climate change are high, as outlined above, and further investigations into the impact of climate change are required to gain an increased understanding of the potential range changes for these species and communities of high conservation value.

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Appendix I—Mean AUC (Area Under the Curve) and TSS (True Skill Statistic) scores for each species.

Species	*Group*	*Mean AUC*	*Mean TSS*
Ajuga reptans	Vascular plant	0.742	0.393
Allium ursinum	Vascular plant	0.638	0.254
Alnus glutinosa	Vascular plant	0.742	0.424
Anemone nemorosa	Vascular plant	0.747	0.418
Aphantopus hyperantus	Butterfly	0.747	0.491
Argynnis paphia	Butterfly	0.594	0.187
Betula pubescens	Vascular plant	0.760	0.436
Blechnum spicant	Vascular plant	0.804	0.529
Brachypodium sylvaticum	Vascular plant	0.730	0.407
Calliergonella cuspidata	Bryophyte	0.622	0.221
Calypogeia muelleriana	Bryophyte	0.696	0.328
Cardamine flexuosa	Vascular plant	0.718	0.403
Carex echinata	Vascular plant	0.749	0.420
Carex strigosa	Vascular plant	0.760	0.451
Carex sylvatica	Vascular plant	0.700	0.344
Celastrina argiolus	Butterfly	0.877	0.626
Cephalozia bicuspidata	Bryophyte	0.701	0.356
Certhia familiaris	Bird	0.786	0.478
Conopodium majus	Vascular plant	0.732	0.388
Corylus avellana	Vascular plant	0.754	0.440
Ctenidium molluscum	Bryophyte	0.635	0.285
Deschampsia cespitosa	Vascular plant	0.813	0.571
Dicranum scoparum	Bryophyte	0.659	0.287
Diplophyllum albicans	Bryophyte	0.765	0.432
Dryopteris aemula	Vascular plant	0.827	0.544
Dryopteris affinis	Vascular plant	0.806	0.529
Euonymus europaeus	Vascular plant	0.773	0.468
Euphorbia hyberna	Vascular plant	0.950	0.842
Eurhynchium praelongum	Bryophyte	0.551	0.146
Eurhynchium striatum	Bryophyte	0.593	0.183
Fissidens dubius	Bryophyte	0.628	0.244
Frangula alnus	Vascular plant	0.768	0.491
Frullania tamarisci	Bryophyte	0.707	0.370
Galium odoratum	Vascular plant	0.687	0.318
Galium palustre	Vascular plant	0.711	0.389
Garrulus glandarius	Bird	0.777	0.471
Geum rivale	Vascular plant	0.757	0.418
Glechoma hederacea	Vascular plant	0.872	0.667
Gonepteryx rhamni	Butterfly	0.784	0.509
Hyacinthoides non-scripta	Vascular plant	0.746	0.407
Hylocomium brevirostre	Bryophyte	0.695	0.354
Hymenophyllum tunbridgense	Vascular plant	0.705	0.364
Hymenophyllum wilsonii	Vascular plant	0.852	0.588
Hypericum androsaemum	Vascular plant	0.662	0.300
Hypericum pulchrum	Vascular plant	0.756	0.457
Hypnum cupressiforme	Bryophyte	0.583	0.173
Hypnum jutlandicum	Bryophyte	0.691	0.316
Ilex aquifolium	Vascular plant	0.699	0.352
Isothecium alopecuroides	Bryophyte	0.563	0.178
Leptidea sinapsis	Butterfly	0.761	0.451
Luzula sylvatica	Vascular plant	0.806	0.513
Lysimachia nemorum	Vascular plant	0.761	0.431

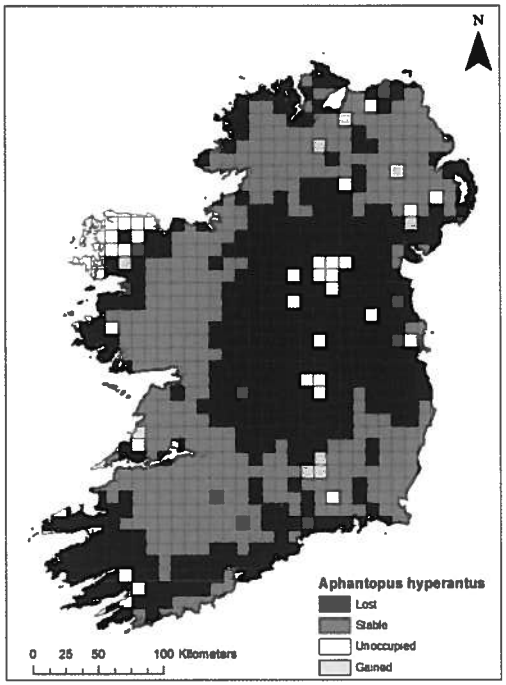
Appendix I (*Continued*)

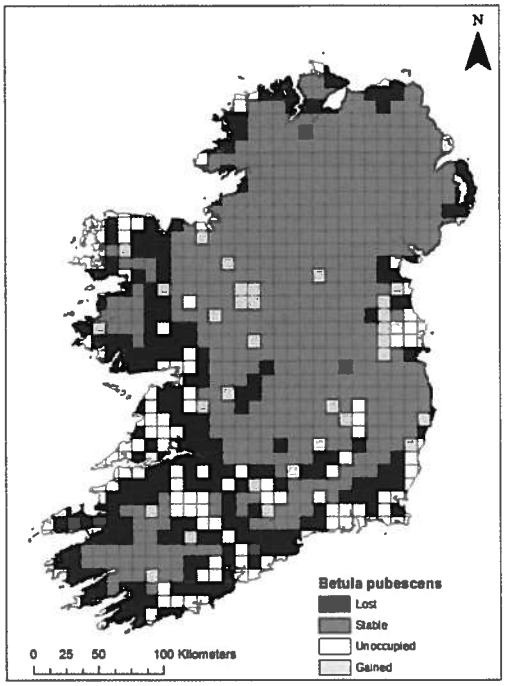
Species	*Group*	*Mean AUC*	*Mean TSS*
Malus sylvestris	Vascular plant	0.709	0.349
Marchesinia mackaii	Bryophyte	0.709	0.384
Metzgeria furcata	Bryophyte	0.578	0.170
Mnium hornum	Bryophyte	0.713	0.379
Molinia caerulea	Vascular plant	0.745	0.428
Neckera crispa	Bryophyte	0.687	0.335
Neozephyrus quercus	Butterfly	0.640	0.266
Oxalis acetosella	Vascular plant	0.710	0.340
Phalaris arundinacea	Vascular plant	0.797	0.528
Plagiomnium undulatum	Bryophyte	0.574	0.168
Plagiothecium undulatum	Bryophyte	0.826	0.561
Polypodium vulgare	Vascular plant	0.821	0.553
Polytrichum commune	Bryophyte	0.692	0.334
Polytrichastrum formosum	Bryophyte	0.676	0.306
Populus tremula	Vascular plant	0.703	0.371
Potentilla erecta	Vascular plant	0.722	0.399
Potentilla sterilis	Vascular plant	0.722	0.374
Prunus avium	Vascular plant	0.728	0.402
Pseudotaxiphyllum elegans	Bryophyte	0.753	0.433
Quercus petraea	Vascular plant	0.689	0.346
Quercus robur	Vascular plant	0.743	0.412
Ranunculus ficaria	Vascular plant	0.676	0.324
Rhynchostegiella tenella	Bryophyte	0.581	0.199
Rhytidiadelphus loreus	Bryophyte	0.831	0.553
Rhytidiadelphus triquetrus	Bryophyte	0.654	0.269
Rumex sanguineus	Vascular plant	0.709	0.373
Saccogyna viticulosa	Bryophyte	0.796	0.500
Salix cinerea	Vascular plant	0.629	0.274
Sanicula europaea	Vascular plant	0.650	0.263
Saxifraga spathularis	Vascular plant	0.932	0.768
Scapania gracilis	Bryophyte	0.790	0.520
Sematophyllum demissum	Bryophyte	0.944	0.843
Sematophyllum micans	Bryophyte	0.911	0.771
Silene dioica	Vascular plant	0.754	0.453
Sorbus aucuparia	Vascular plant	0.743	0.387
Sorbus hibernica	Vascular plant	0.618	0.266
Sphagnum fallax	Bryophyte	0.739	0.464
Sphagnum palustre	Bryophyte	0.708	0.376
Sphagnum quinquefarium	Bryophyte	0.782	0.530
Stellaria holostea	Vascular plant	0.842	0.604
Taxus baccata	Vascular plant	0.595	0.196
Telaranea nematodes	Bryophyte	0.870	0.757
Thamnobryum alopecurum	Bryophyte	0.586	0.184
Thecla betulae	Butterfly	0.802	0.545
Thuidium tamariscinum	Bryophyte	0.647	0.249
Tortella tortuosa	Bryophyte	0.700	0.355
Ulmus glabra	Vascular plant	0.686	0.321
Ulota bruchii	Bryophyte	0.683	0.345
Ulota crispa	Bryophyte	0.657	0.303
Vaccinium myrtillus	Vascular plant	0.801	0.485
Veronica montana	Vascular plant	0.670	0.291
Viola reichenbachiana	Vascular plant	0.735	0.382

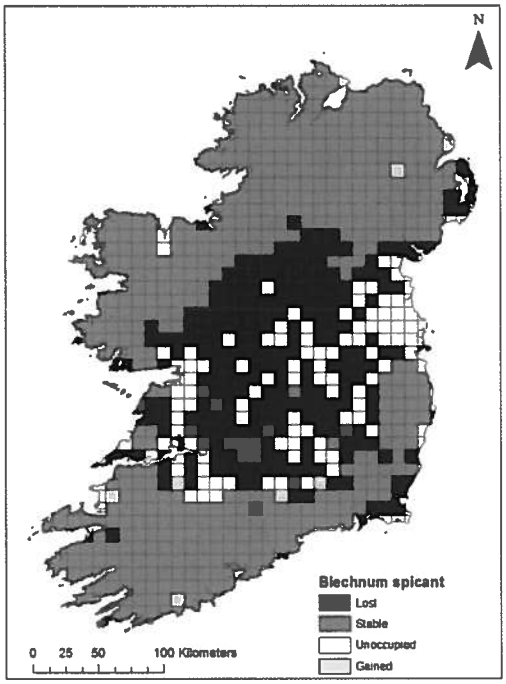
Appendix II—Percentage range change, from BIOMOD ensemble forecasting, under the unlimited and no long-range dispersal scenarios. No. pass scores indicates the number of models in BIOMOD in which the species modelled well.

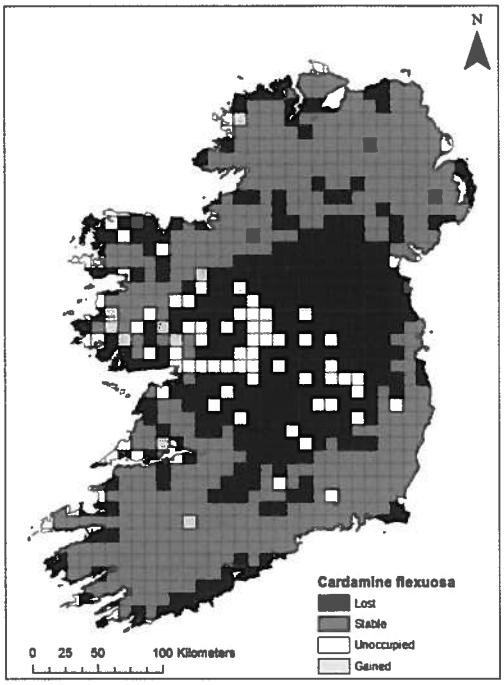
Species	Group	Current range (no. 1km grid squares)	% Range Change (Unlimited dispersal)	% Range Change (No long-range dispersal)	No. pass scores
Certhia familiaris	Bird	529	4.5	−22.1	7
Garrulus glandarius	Bird	529	4.9	−22.9	8
Diplophyllum albicans	Bryophyte	288	14.2	−35.8	7
Plagiothecium undulatum	Bryophyte	173	79.8	−19.7	8
Pseudotaxiphyllum elegans	Bryophyte	162	131.5	−29	7
Rhytidiadelphus loreus	Bryophyte	206	60.2	−23.8	8
Saccogyna viticulosa	Bryophyte	162	90.7	−25.9	8
Scapania gracilis	Bryophyte	186	80.1	−22	8
Sematophyllum demissum	Bryophyte	16	68.8	−18.8	8
Sematophyllum micans	Bryophyte	18	83.3	−22.2	7
Sphagnum quinquefarium	Bryophyte	53	452.8	−13.2	7
Telaranea nematodes	Bryophyte	17	429.4	−17.6	8
Aphantopus hyperantus	Butterfly	891	−47.7	−48.9	8
Celastrina argiolus	Butterfly	354	11.6	−24.9	8
Gonepteryx rhamni	Butterfly	222	89.6	−27	8
Leptidea sinapis	Butterfly	461	9.5	−28.2	8
Thecla betulae	Butterfly	27	866.7	−14.8	7
Betula pubescens	Vascular plant	762	−30.4	−34	7
Blechnum spicant	Vascular plant	809	−29.7	−32.4	8
Cardamine flexuosa	Vascular plant	846	−40	−42.1	6
Carex echinata	Vascular plant	771	−26.2	−32	7
Carex strigosa	Vascular plant	103	44.7	−52.4	6
Corylus avellana	Vascular plant	864	−24.3	−25.7	6
Deschampsia cespitosa	Vascular plant	794	−25.2	−29	8
Dryopteris aemula	Vascular plant	374	19.8	−26.2	8
Dryopteris affinis	Vascular plant	765	−31.9	−37.3	7
Euonymus europaeus	Vascular plant	478	11.9	−19.9	7
Euphorbia hyberna	Vascular plant	138	68.8	−12.3	8
Frangula alnus	Vascular plant	56	532.1	−35.7	6
Galium palustre	Vascular plant	885	−29.7	−31.8	6
Glechoma hederacea	Vascular plant	702	−4.8	−14.8	8
Hyacinthoides non-scripta	Vascular plant	747	−32.1	−38.4	6
Hymenophyllum wilsonii	Vascular plant	169	94.1	−18.9	7
Hypericum pulchrum	Vascular plant	867	−28.7	−30.2	7
Luzula sylvatica	Vascular plant	607	−14.5	−28.7	8
Lysimachia nemorum	Vascular plant	730	−38.8	−43.2	7
Molinia caerulea	Vascular plant	860	−18.4	−21.9	6
Phalaris arundinacea	Vascular plant	744	−18.7	−24.2	8
Polypodium vulgare	Vascular plant	514	−1.9	−26.8	8
Quercus robur	Vascular plant	661	−6.2	−22.1	6
Saxifraga spathularis	Vascular plant	128	76.6	−10.9	8
Silene dioica	Vascular plant	256	44.1	−34.4	7
Stellaria holostea	Vascular plant	666	−4.8	−15.8	8
Vaccinium myrtillus	Vascular plant	692	−15.2	−24.9	7

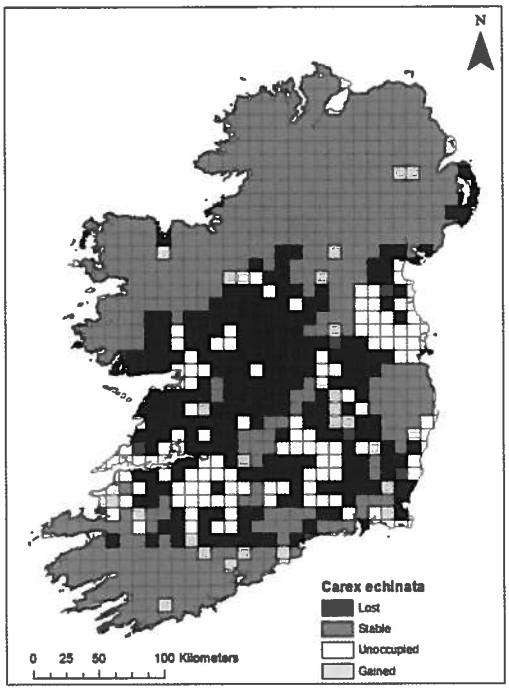
Appendix III—maps showing change in suitable climate space for species which modeled well, under the unlimited dispersal scenario.







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Lost
Stable
Unoccupied
Gained
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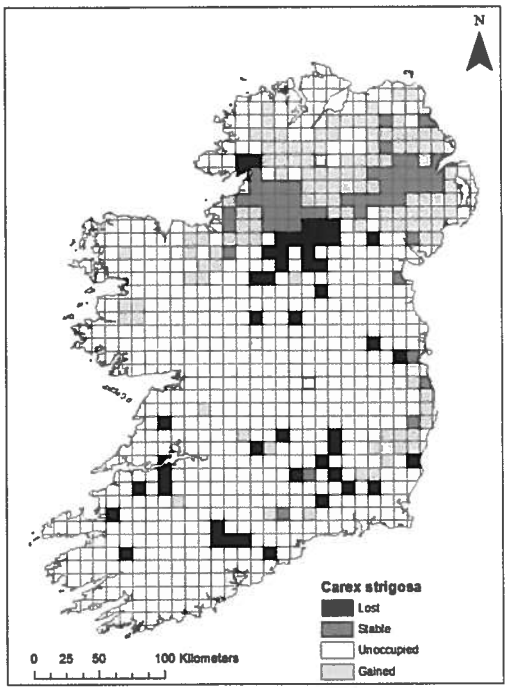
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Carex strigosa
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Stable
Unoccupied
Gained
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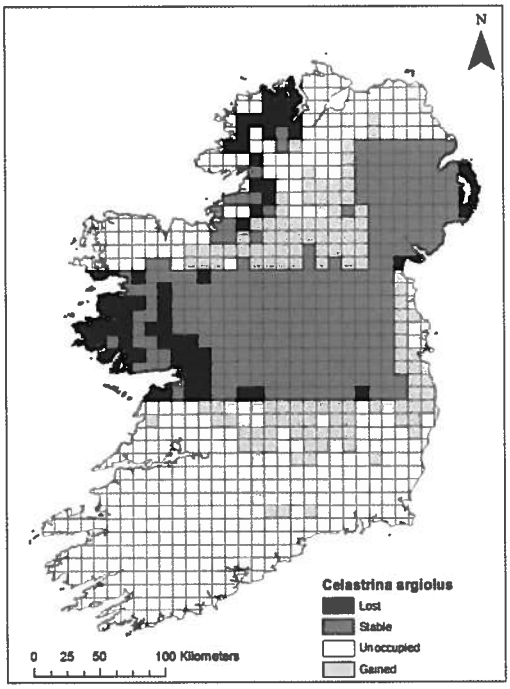
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Celastrina argiolus
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Stable
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Gained
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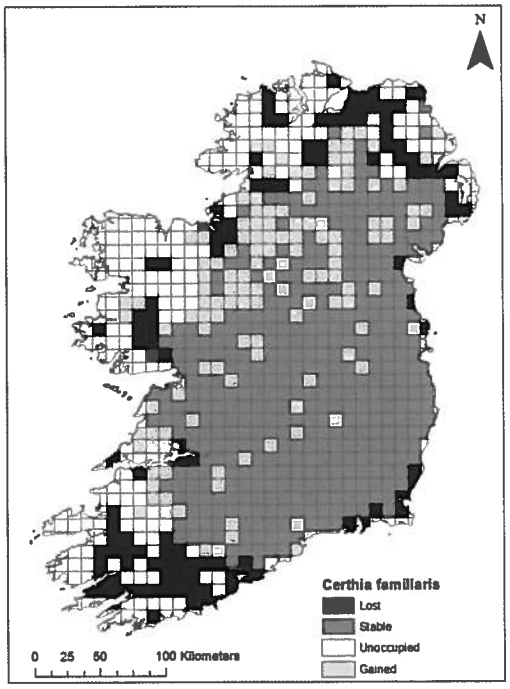
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Certhia familiaris
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Stable
Unoccupied
Gained
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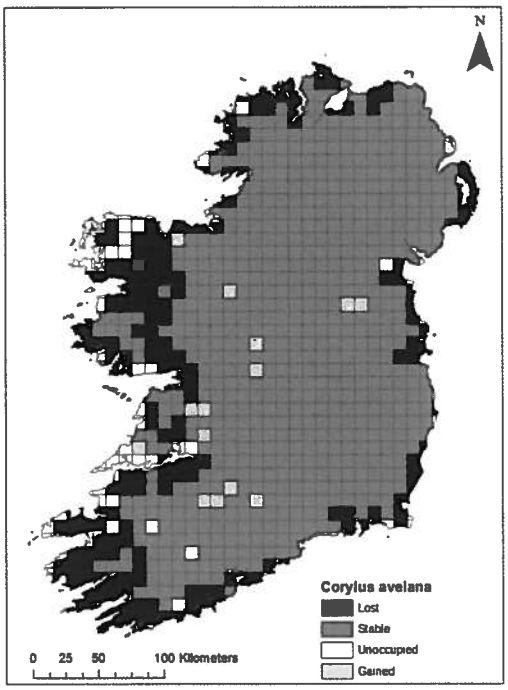
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Lost
Stable
Unoccupied
Gained
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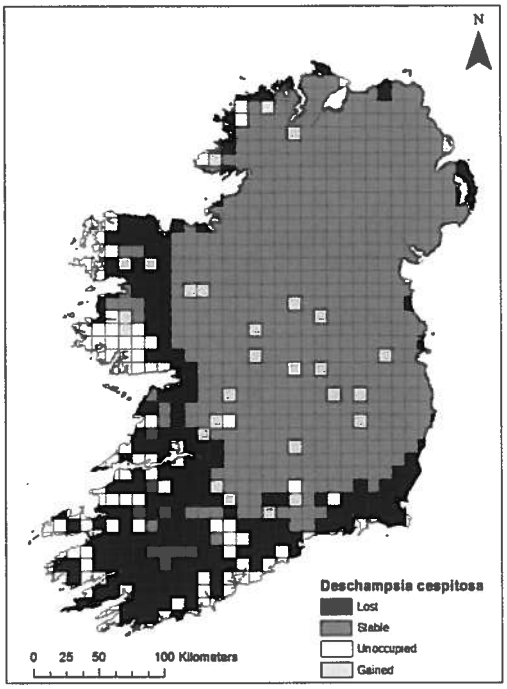
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Deschampsia cespitosa
Lost
Stable
Unoccupied
Gained
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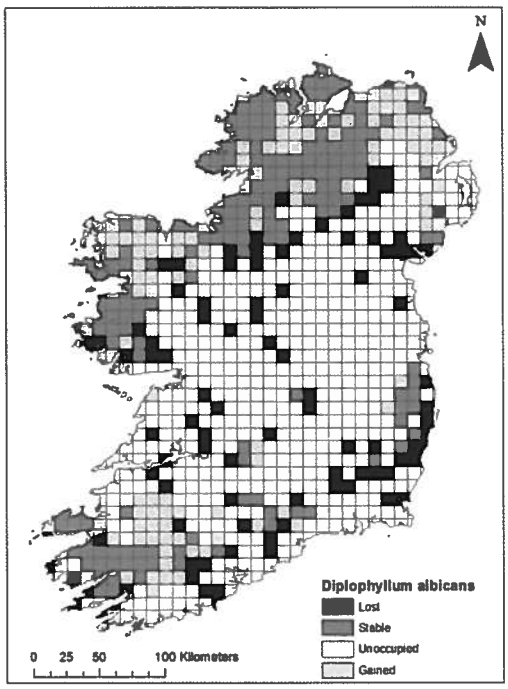
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Gained
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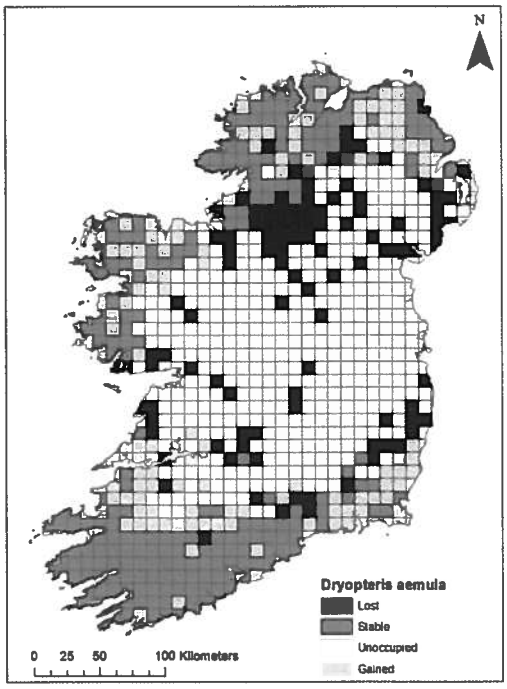
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Gained
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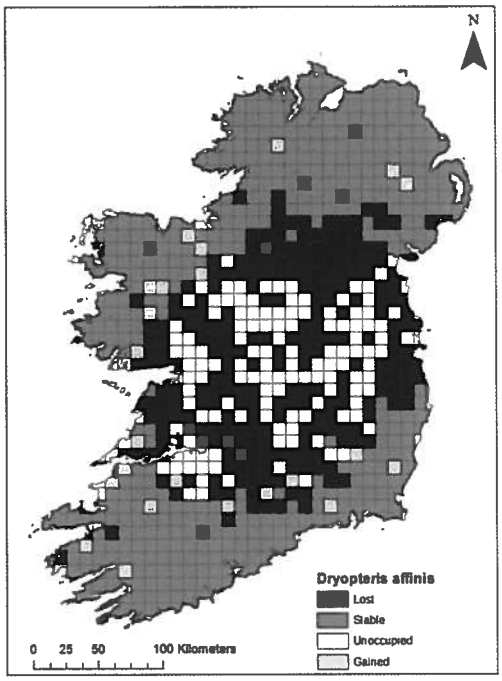
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Dryopteris affinis
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Stable
Unoccupied
Gained
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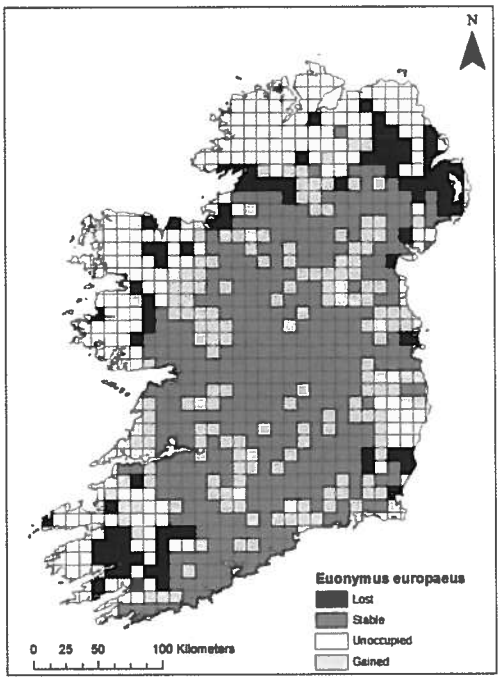
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Euonymus europaeus
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Unoccupied
Gained
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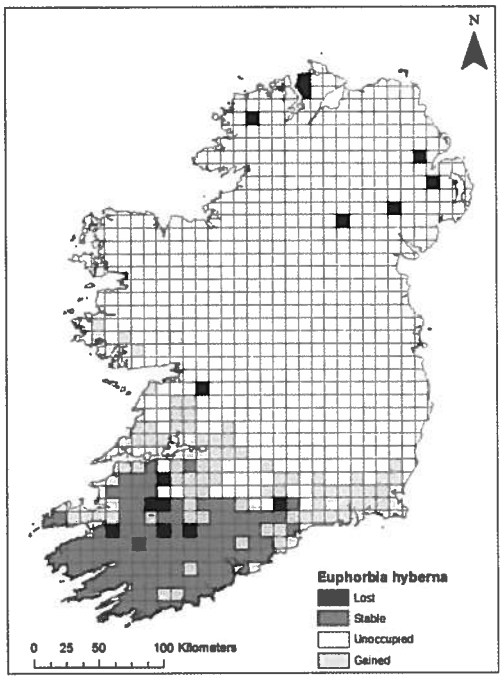
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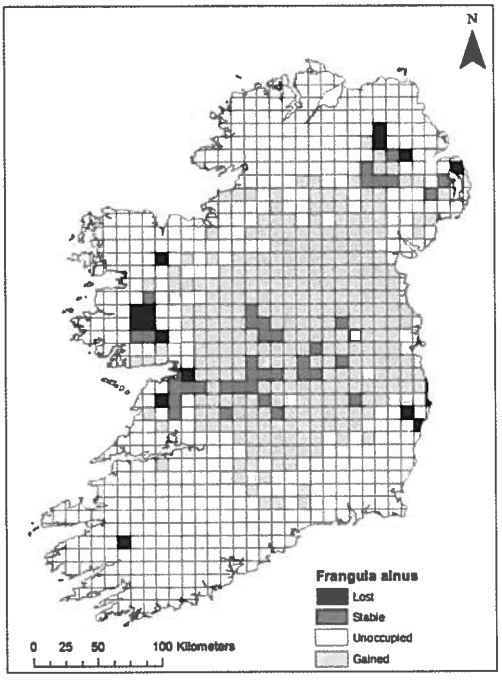
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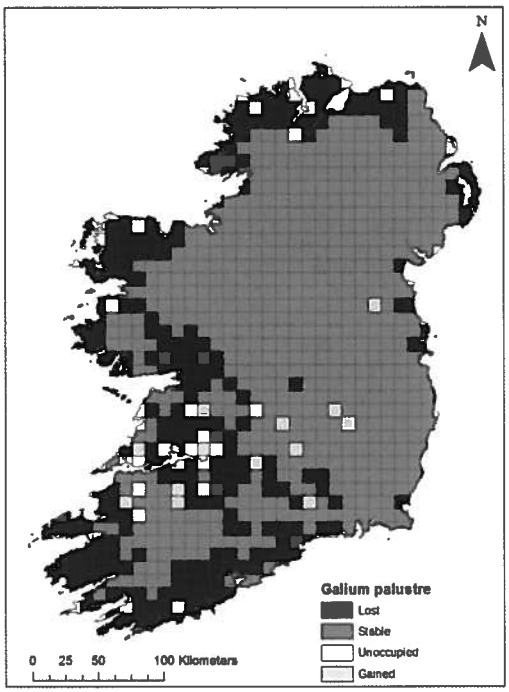
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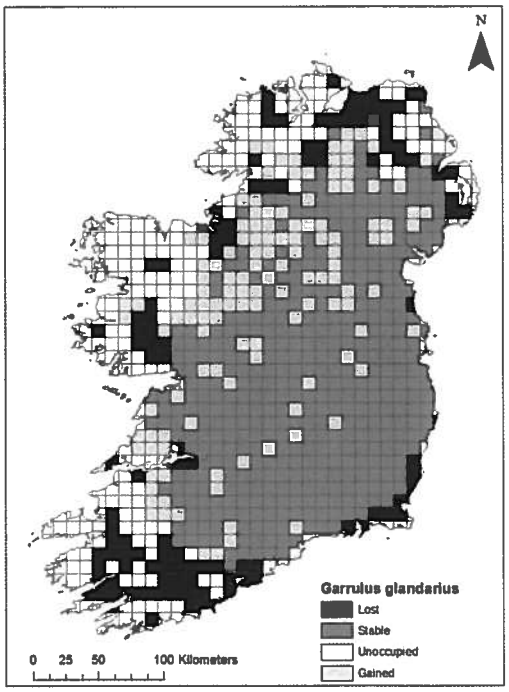
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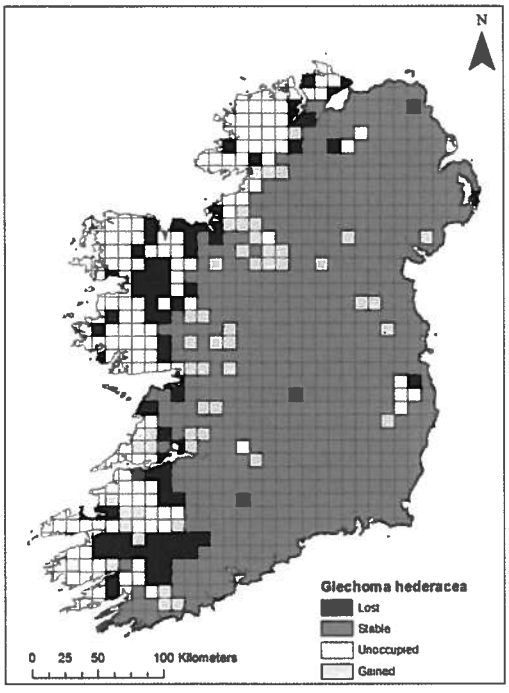
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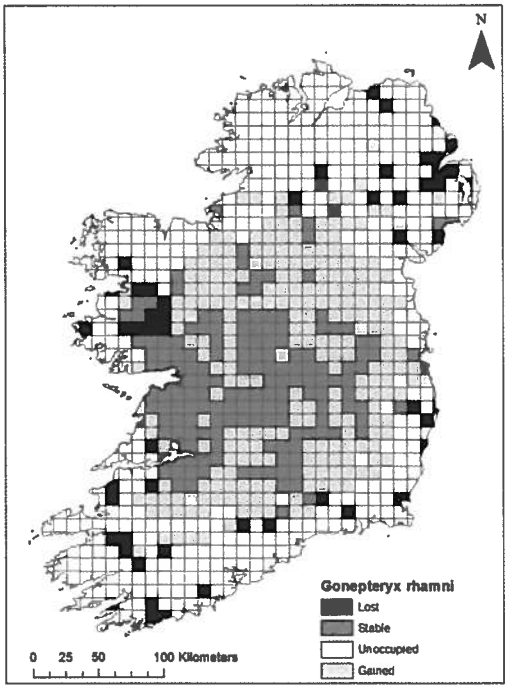
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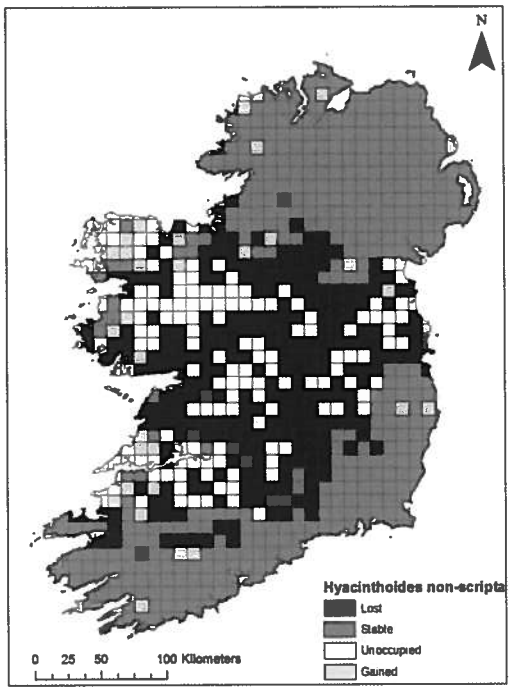
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Hyacinthoides non-scripta
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Stable
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Gained
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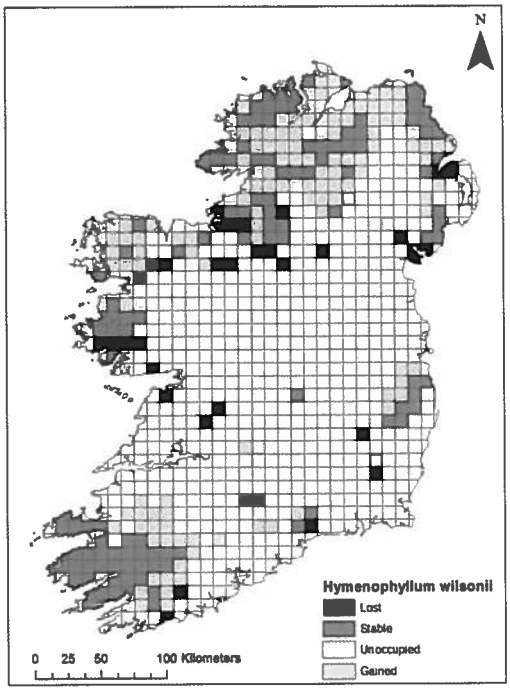
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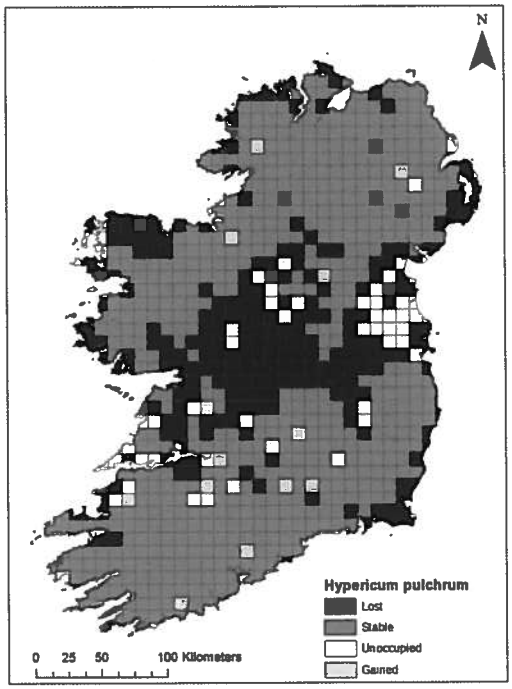
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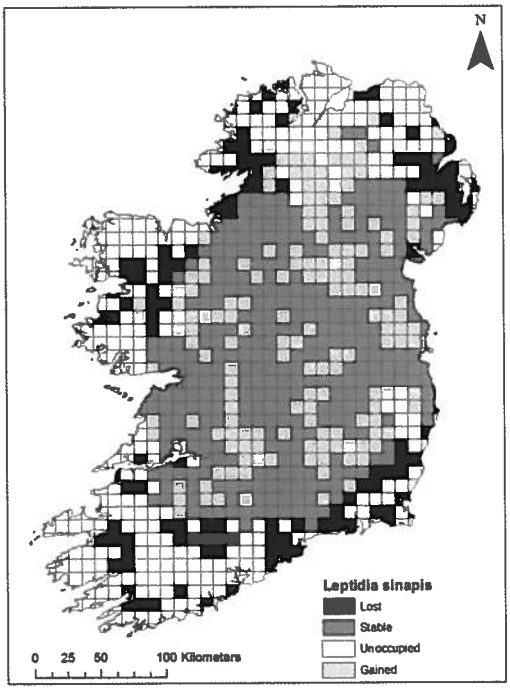
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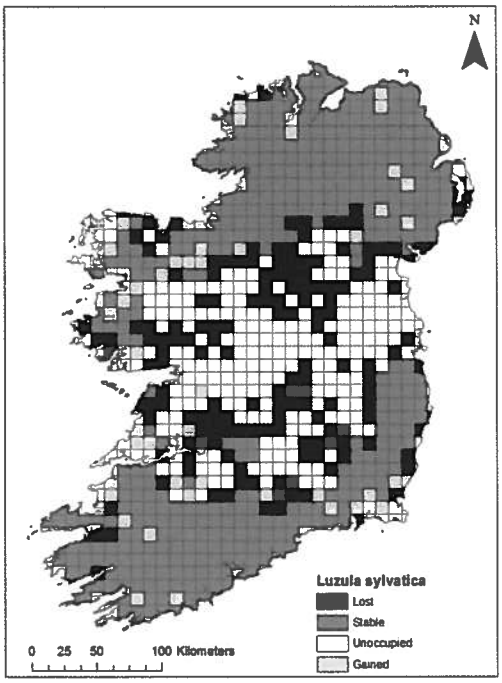
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Stable
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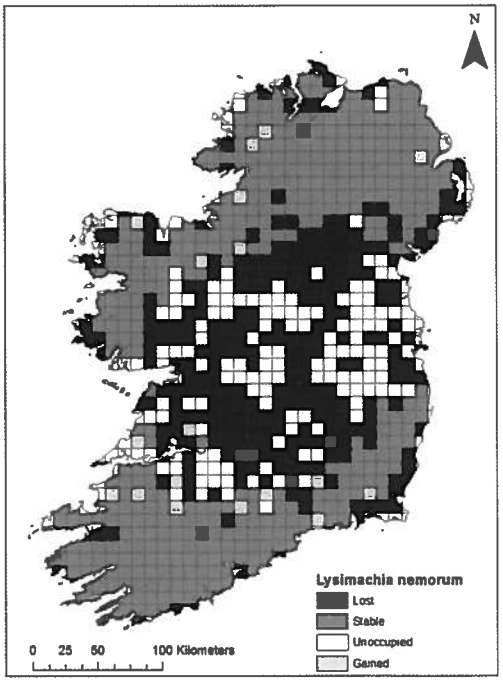
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Lysimachia nemorum
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Stable
Unoccupied
Gained
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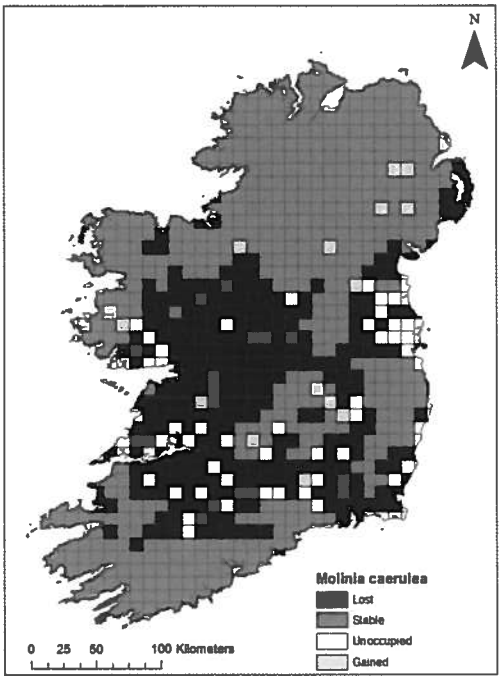
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Stable
Unoccupied
Gained
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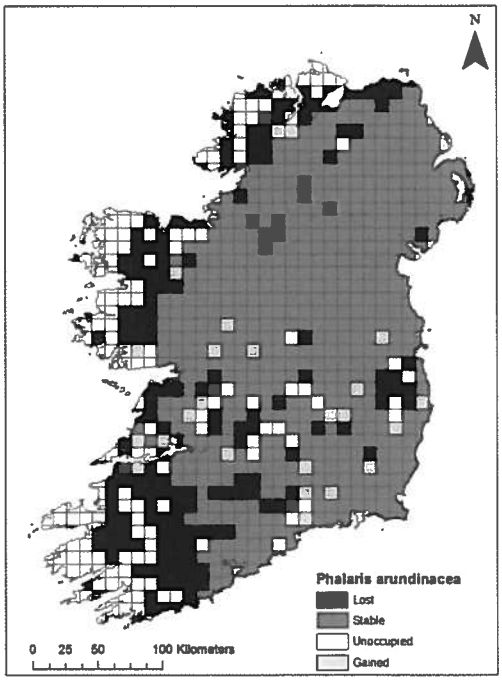
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Stable
Unoccupied
Gained
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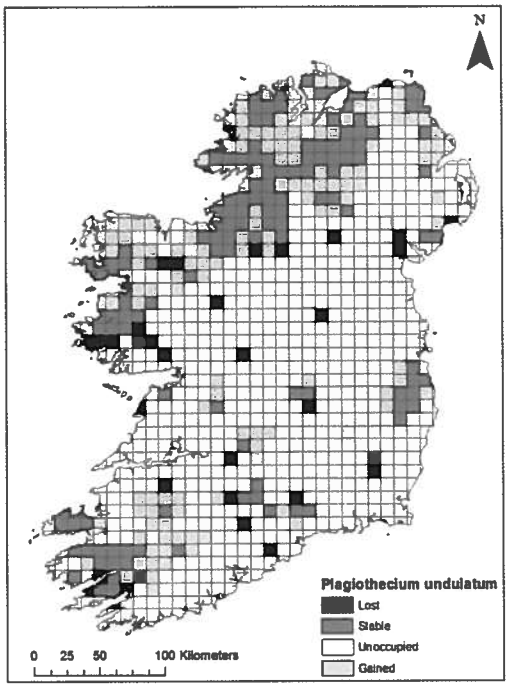
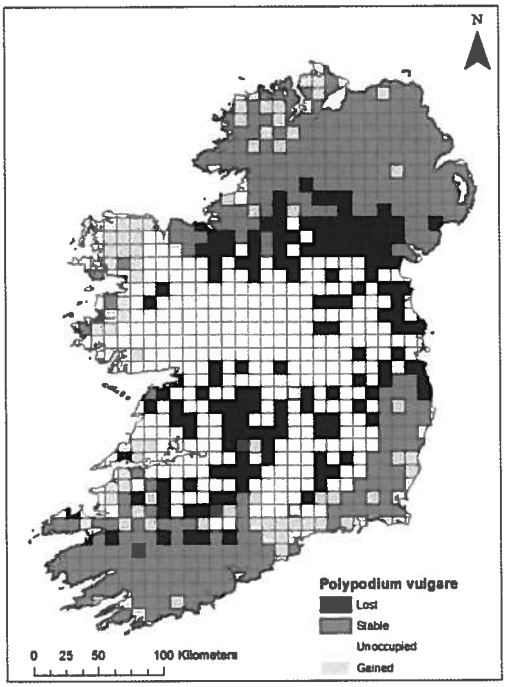
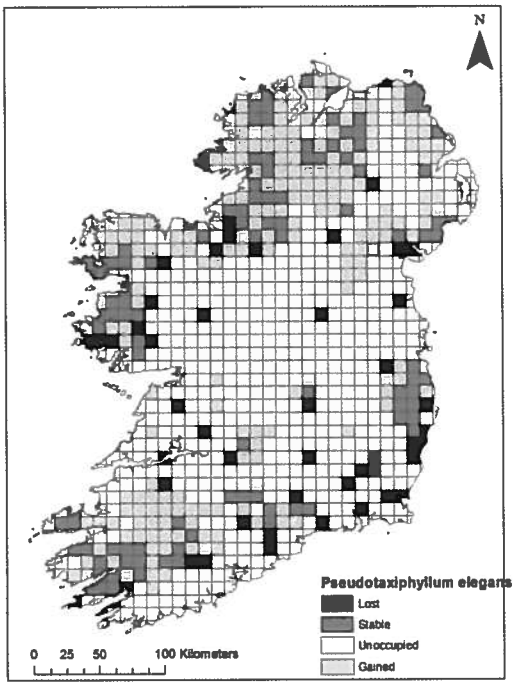
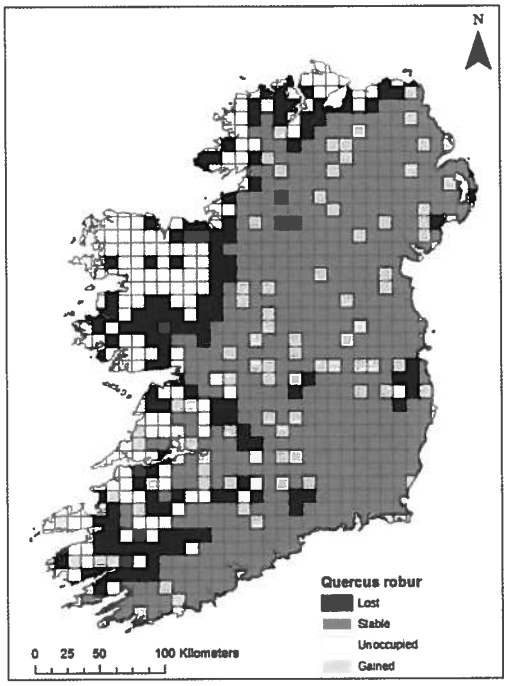
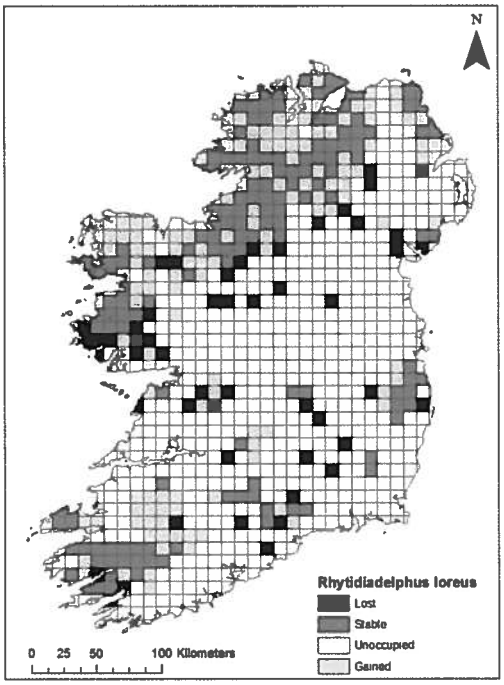
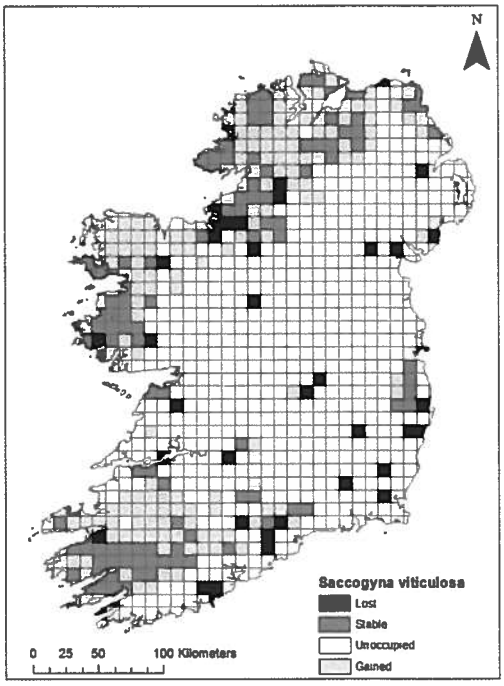

N
Plagiothecium undulatum
Lost
Stable
Unoccupied
Gained
0 25 50 100 Kilometers

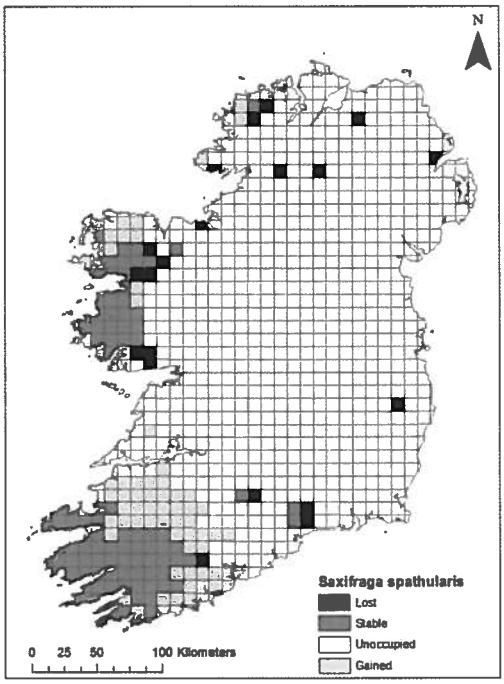

N
Polypodium vulgare
Lost
Stable
Unoccupied
Gained
0 25 50 100 Kilometers

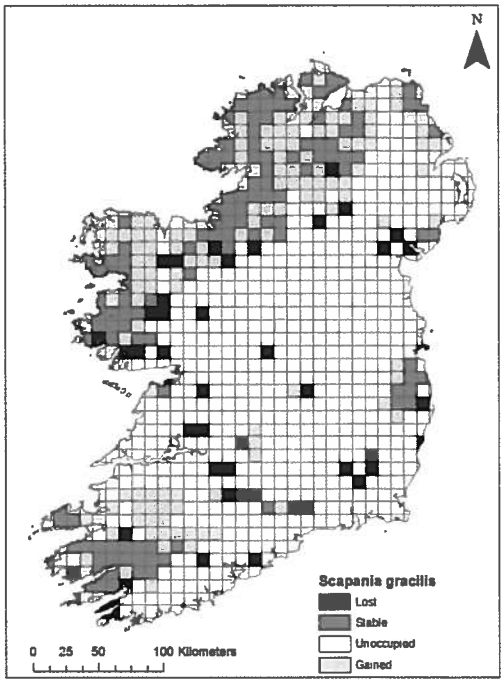

N
Pseudotaxiphyllum elegans
Lost
Stable
Unoccupied
Gained
0 25 50 100 Kilometers

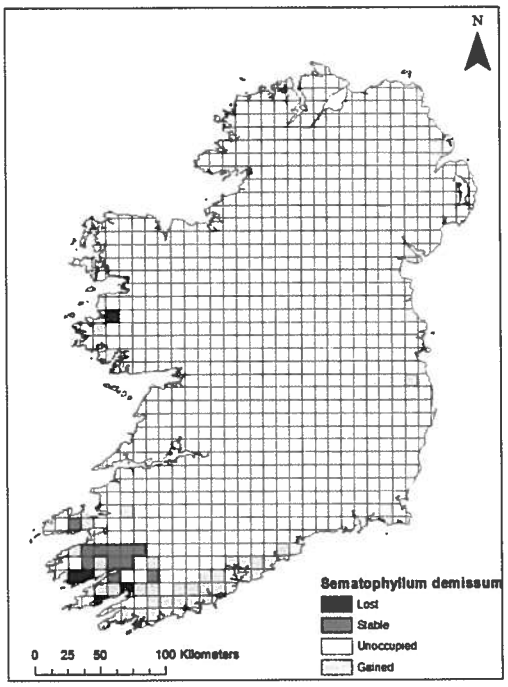

N
Quercus robur
Lost
Stable
Unoccupied
Gained
0 25 50 100 Kilometers

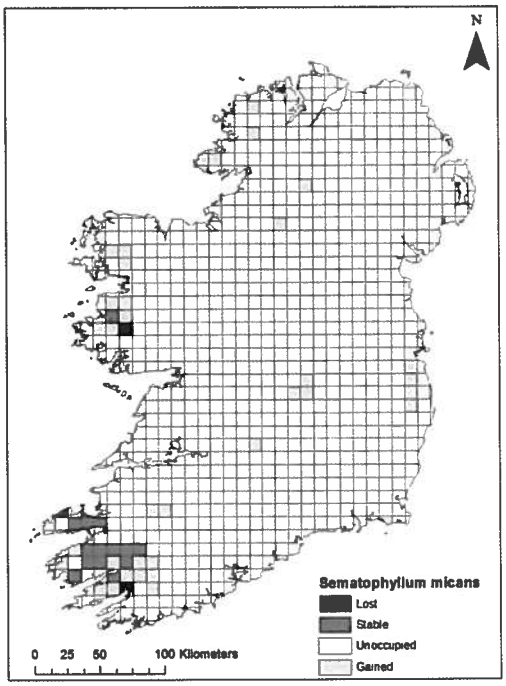

N
Rhytidiadelphus loreus
Lost
Stable
Unoccupied
Gained
0 25 50 100 Kilometers

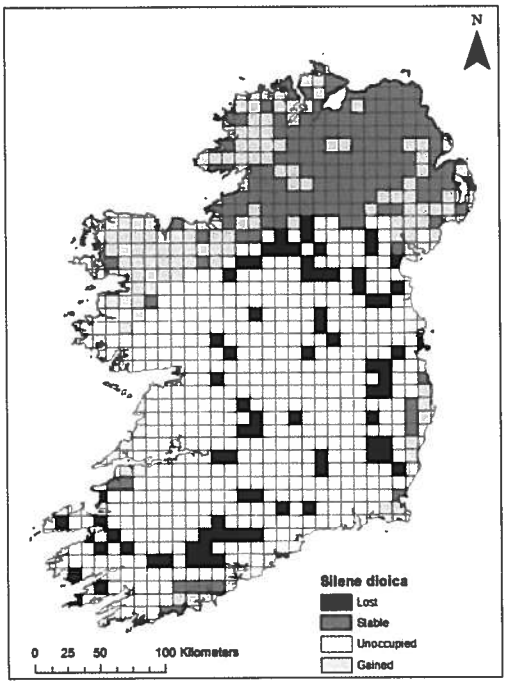

N
Saccogyna viticulosa
Lost
Stable
Unoccupied
Gained
0 25 50 100 Kilometers

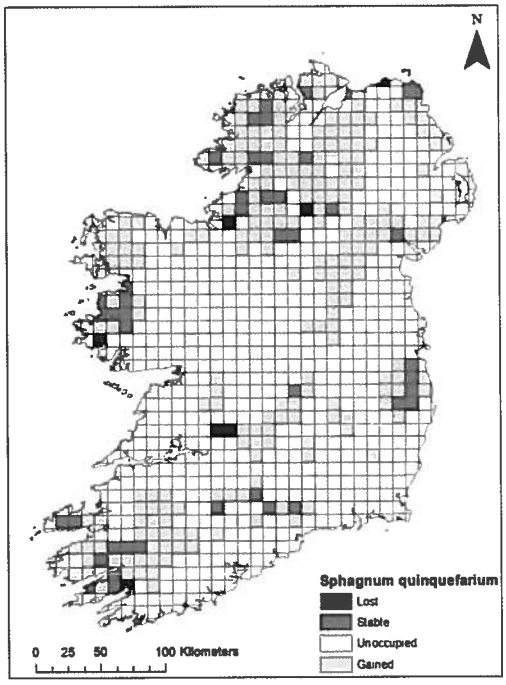

N
Saxifraga spathularis
Lost
Stable
Unoccupied
Gained
0 25 50 100 Kilometers

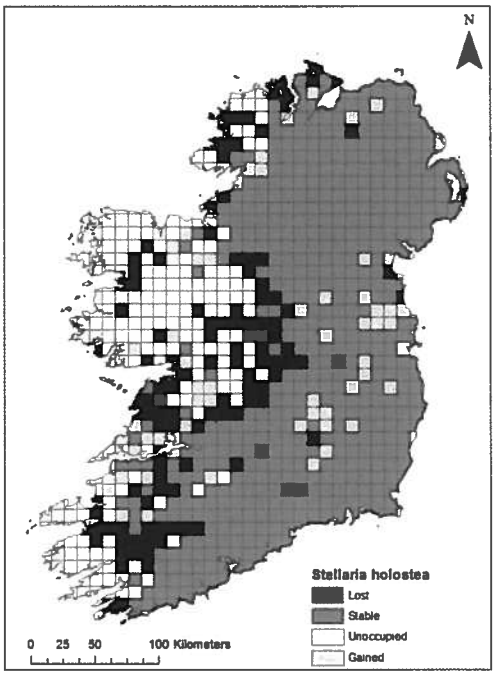

N
Scapania gracilis
Lost
Stable
Unoccupied
Gained
0 25 50 100 Kilometers

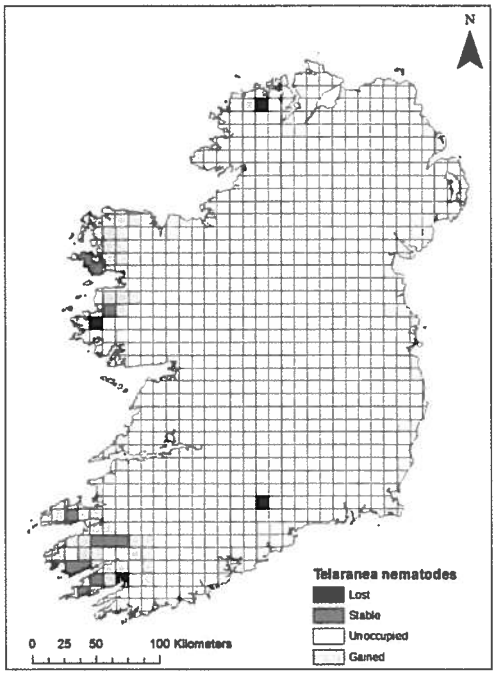

N
Sematophyllum demissum
Lost
Stable
Unoccupied
Gained
0 25 50 100 Kilometers

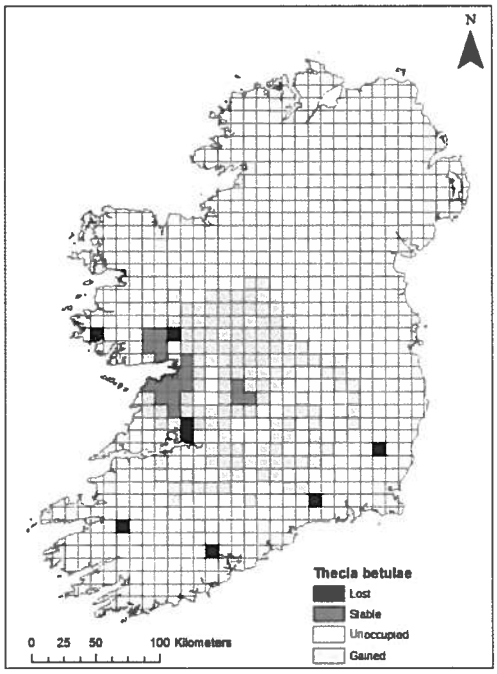

N
Sematophyllum micans
Lost
Stable
Unoccupied
Gained
0 25 50 100 Kilometers

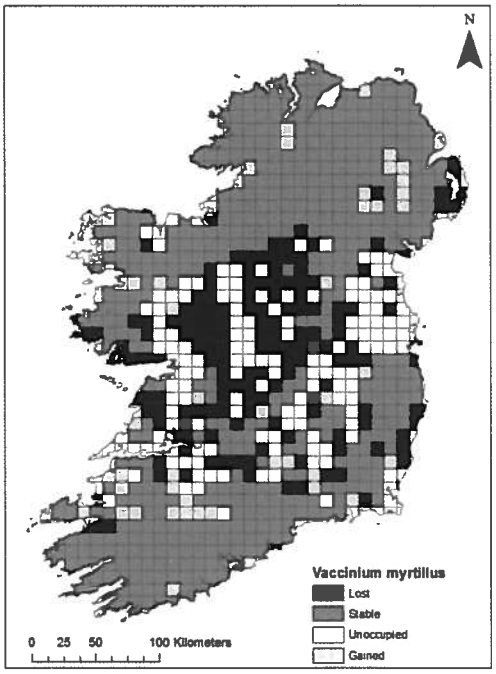

N
Silene dioica
Lost
Stable
Unoccupied
Gained
0 25 50 100 Kilometers


N
Sphagnum quinquefarium
Lost
Stable
Unoccupied
Gained
0 25 50 100 Kilometers


N
Stellaria holostea
Lost
Stable
Unoccupied
Gained
0 25 50 100 Kilometers


N
Telaranea nematodes
Lost
Stable
Unoccupied
Gained
0 25 50 100 Kilometers


N
Thecla betulae
Lost
Stable
Unoccupied
Gained
0 25 50 100 Kilometers


N
Vaccinium myrtillus
Lost
Stable
Unoccupied
Gained
0 25 50 100 Kilometers