RESEARCH ARTICLE

Assessing continental-scale risks for generalist and specialist pollinating bee species under climate change

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Abstract

Increased risks of extinction to populations of animals and plants under changing climate have now been demonstrated for many taxa. This study assesses the extinction risks to species within an important genus of pollinating bees (*Colletes*: Apidae) by estimating the expected changes in the area and isolation of suitable habitat under predicted climatic condition for 2050. Suitable habitat was defined on the basis of the presence of known forage plants as well as climatic suitability. To investigate whether ecological specialisation was linked to extinction risk we compared three species which were generalist pollen foragers on several plant families with three species which specialised on pollen from a single plant species. Both specialist and generalist species showed an increased risk of extinction with shifting climate, and this was particularly high for the most specialised species (*Colletes anchusae* and *C. wolfi*). The forage generalist *C. impunctatus,* which is associated with Boreo-Alpine environments, is potentially threatened through significant reduction in available climatic niche space. Including the distribution of the principal or sole pollen forage plant, when modelling the distribution of monolectic or narrowly oligolectic species, did not improve the predictive accuracy of our models as the plant species were considerably more widespread than the specialised bees associated with them.

Keywords

Introduction

There is general consensus that the most pressing environmental problem that faces the world today is climatic change and it is widely acknowledged that this change is likely to have major impacts both on biodiversity (Green et al. 2003) and on human society in general (Stern 2007). Many animal and plant species are expected to show major shifts in abundance, distribution and phenology and this could lead to extinctions at the local, regional, continental or even global scale (Flenner and Sahlen 2008; Graham-Taylor et al. 2009; Hegland et al. 2009; Settele et al. 2008). Accurate prediction of likely risks under a shifting climatic regime is essential to enable conservation priorities to be set and assist in directing mitigation actions (Santos et al. 2009).

A number of recent studies have considered the effects of observed climatic shifts on various taxa, and in addition to more general studies such as Parmesan and Yohe (2003), Root et al. (2003) and Menzel et al. (2006), these include butterflies (Sparks and Yates 1997; Parmesan et al. 1999; Roy and Sparks 2000; Menéndez et al. 2008), flowering plants (Sparks et al. 2000) and birds (Sanz 2003; Sergio 2003). More recent work has used current distributions of European birds (Huntley et al. 2007) and butterflies (Schweiger et al. 2008; Schweiger et al. 2012; Settele et al. 2008) to forecast likely future ranges, and to consider the possible conservation implications of shifts in distributions.

In addition to work on butterflies, there are increasing numbers of studies on other insect groups, and these include Odonata (Dingemanse and Kalkmann 2008), Coleoptera (eg Molina-Montenegro et al. 2009), Diptera (eg Graham-Taylor et al. 2009), invertebrate disease vectors (e.g. Wilson and Mellor 2008) and pest species (e.g. Hoffmann et al. 2008). Among pollinators, Williams et al. (2007) have assessed the vulnerability of three species of bumblebee (*Bombus*) to extinction by studying climatic niches that determine their ranges at a regional scale.

The number of large scale multi-taxa studies on insect species other than Lepidoptera has been restricted because detailed data on the biology and distribution of most insects in general, and pollinator species in particular, are available at fine resolutions for only a few places. Risk of local extinctions can, therefore, be assessed quite accurately given detailed information on local population, habitat size and climatic conditions (e.g. Franzén et al. 2009). However, assessing extinction risks of these species at the regional, continental or global scale is hampered by lack of appropriate data.

A risk analysis should, ideally, be based on complete data on the species' distribution in conjunction with knowledge on both the abiotic requirements (e.g. climate, geomorphology, soil) and the biotic requirements (e.g. principal forage plants). Then, using scenarios for changes in climate and land use, a model can be built to predict potential range shifts and extinctions. Some existing studies have based their analyses on a climate only model (e.g. Huntley et al. 2007; Settele et al. 2008) and others (e.g. Luetolf et al. 2009) on a habitat only model. A smaller number of studies link both habitat and climate models (e.g. Santos et al. 2009; Schweiger et al. 2008; 2012).

We make use of one of the few available pollinator datasets for which comprehensive European-scale distribution is currently known: a number of specialist and generalist *Colletes* bee species, some of which are endemic to Europe. We ask:

1) What are the levels of risk associated with shifts in climatic conditions at locations where the pollinator species currently occur?

2) Can we predict the current distribution of specialist and generalist pollinator species at a continental scale based on climate and host plant distribution variables?

3) Is it likely that the ranges of principal forage plants and specialist bees can become uncoupled under climate change with the possible threat of extinction to one or both species?

4) What are the likely future European distributions of the investigated species under the projected shifts in climatic conditions?

The aim of our study is to provide a continental-scale assessment of the risk a pollinator species is likely to face under future climate change and to determine if specialised species are at greater risk as a result of their narrow pollen forage requirements.

Methods

Species distribution and climate data

From a dataset containing distribution data on all 59 species of bees in the genus *Colletes* occurring in Europe (Kuhlmann, unpublished data) we selected six species for which there were sufficient data to cover adequately their entire European ranges (Appendix A). Three of these are polylectic species, i.e. pollen forage generalists (*Colletes albomaculatus*, *C. impunctatus*, *C. nigricans*) and three monolectic or narrowly oligolectic, i.e. forage specialists (*C. anchusae*, *C. hederae*, *C. wolfi*). Pollen foraging in *Colletes anchusae* and *C. wolfi* is restricted to *Cynoglottis barrelieri* (Boraginaceae) (Müller and Kuhlmann 2003; 2008) whereas *C. hederae* generally restricts its foraging to *Hedera helix* (Araliaceae) (Schmidt and Westrich 1993; Bischoff et al. 2005), although occasionally it will forage for pollen at various Asteraceae if *Hedera helix* flowers are not available (Müller and Kuhlmann 2008; Westrich 2008). Distribution records of these species from the last 125 years (with 61% of data from the last 40 years) across Europe were collated and transformed into a presence/absence map at 10' grid resolution. For the majority of 10' grid cells, there was no record, but in total, 1,549 or 4.9 % of all 10' grid cells had at least one record for one of the six species. Prevalence of the six species ranged from 10 to 150 occupied 10' grid cells (Table 1). We have assumed that all records represent the current distribution (cf. Williams et al 2007). Although many areas have had poor coverage, the problem is reduced by mapping at a relatively coarse 10' resolution. The presence/absence matrix of these 1,549 grid cells was used to build distribution models of the species.

Table 1. Model specification and model fit. Percent variation of present-day distribution explained and model fit of distribution models for the six species.

species	number of 10' cells recorded	model	Percent variation in distribution explained by model
generalists			
C. albomaculatus	110	climate	31.7
C. impunctatus	102	climate	64.2
C. nigricans	150	climate	23.1
specialists			
C. anchusae	16	climate	44.7
		climate + hostplant	45.5
C. hederae	76	climate	12.0
		climate + hostplant	12.2
C. wolfi	10	climate	65.0
		climate + hostplant	65.8

Current (1961–1990 average) and future (2041–2050 average, henceforth "2050") climate conditions at the same resolution were taken from Mitchell et al. (2004) and we used the following five climate variables to predict the distribution of our target species: mean annual temperature, mean minimum temperature of the coldest months, mean annual precipitation, annual water deficit and growing degree days > 5°C. These variables represent a set of biologically meaningful factors which, given the lack of detailed knowledge of climate requirements of individual species, aims to cover the relevant climate conditions for our six species. We restrict our analyses to a low greenhouse gas emission scenario (B2) which represents a socio-economic storyline focussing on local and regional solutions to economic and environmental problems and projects a global average temperature increase by the end of this century of between 1.4 and 3.8°C (IPCC 2007). We use this as a best case scenario of the lowest risk so that these underpin the minimum conservation action responses.

The known distribution (both historic and current) of the genus *Cynoglottis* is mapped in Müller & Kuhlmann (2003) who based the map on a synthesis of various regional, national and European floras (see references therein). The known distribution of *Hedera helix* is mapped by Meusel (1978) modified by Kuhlmann et al. (2007). All distributions were digitised as shape files in ArcGIS and converted to a presence/absence grid at the same resolution as the climate grid.

Distribution modelling

Generalised Linear Models (GLMs) with binomial errors and with linear and quadratic terms for all variables were used to predict the current distribution of the *Colletes* species. For the generalist species, we predicted their current distributions across Europe based on all six climate variables, while for the specialist species, we used the six

climate variables plus the host plant distribution as a binary predictor variable. For all models, we compared the model fit between the full model (including all possible predictor variables) and the most parsimonious minimal adequate model (including only the most significant variables retained after stepwise variable selection allowing for addition and deletion of variables at each step). The difference in model fit between the two methods was generally small and so we present the outcomes of the full models. All models and variable selection procedures were performed in S-Plus 6.2. Predictive power of the full model was assessed by quantifying the percentage of variation in species presence/absence explained by the full set of variables (Table 1). We used the models fitted on the current climate data to predict climatic suitability of the six species under future (2050) climate conditions. For the three specialist species, we assumed that the distribution of the host plants will not change substantially between now and 2050 seeing that the species are almost ubiquitous in Europe. Comparing current observed, current modelled and future modelled distributions of the six species allows us to assess likely shifts in suitable climate space under changing climate conditions. For each species we compare the local (within a 100 km radius from each observed location) and continental-wide change in climatically suitable area between current and future climate conditions (Fig. 1).

Results

Current distributions and suitable climate space

Within the genus *Colletes*, we have selected six species with a well recorded European distribution. We were able to explain between 12% (*C. hederae*) and 65% (*C. wolfi*) of the variation in their current distribution with the climate variables chosen here (Table 1). Overall, our bioclimate models were able to reproduce the observed current European distribution of our species accurately (Table 1; Fig. 1a–f). In particular, the suitable climate space of the two southern European generalist species *C. albomaculatus* and *C. nigricans*, for instance, was captured very well by our models. When modelling the distribution of the specialist species, including the distribution of the principal forage plants as an additional predictor, does not improve the model fit of the models. The percent variation in distribution with the food plants included in the model only increases very slightly (Table 1). *C. impunctatus* (Fig. 1b), shows that it occurs in most of its current suitable climate space, occurring in the clearly defined boreal climatic area in northern Europe, with a second centre of distribution in the montane region of the Alps in the south. *Colletes hederae*, on the other hand, appears to be the species which has least filled its suitable climatic space (Fig. 1e). Large areas in Italy, France and Spain have highly suitable climate but no, or only few, occurrences of the species have thus far been reported.

Under present-day climate conditions, species with a predominantly Mediterranean distribution are occupying areas with the highest climatic rarity, i.e., the climatic
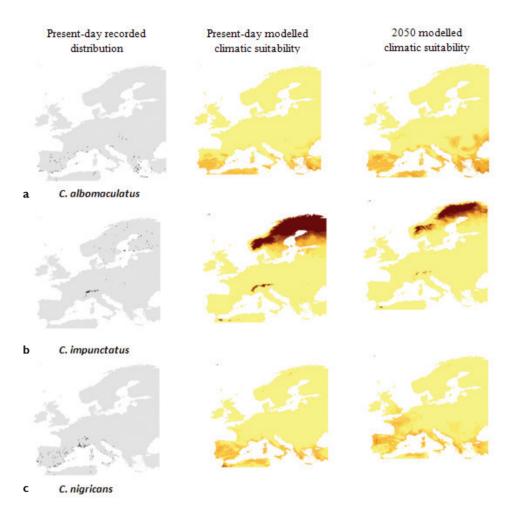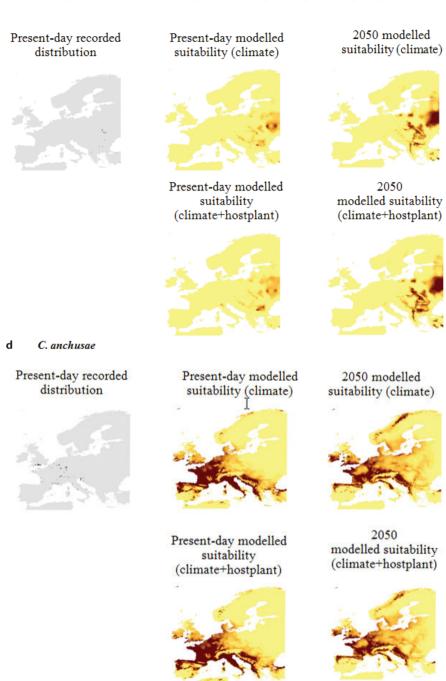
Figure 1 (a–c). Potential future European distribution of three investigated generalist *Colletes* species based on climate. [Present day recorded distribution; present day modelled distribution, and 2050 modelled climatic suitability of **a** *Colletes albomaculatus* **b** *C. impunctatus* and **c** *C. nigricans*]

conditions of the locations where the species is currently found are not found in many areas elsewhere in Europe. *C. nigricans*, with a south-western Mediterranean distribution, has the rarest suitable climate envelope of our six species (Fig. 1c). *C. albomaculatus*, which exploits suitable climatic space more widely across the Mediterranean region, extends into south eastern Europe (Fig. 1a).

Future suitable climate space

We calculated the change in climatically suitable area for each species between current and future climatic conditions locally (within a 100 km radius) and Europe-

Present-day recorded
distribution

Present-day modelled
suitability (climate)

2050 modelled
suitability (climate)

Present-day modelled
suitability
(climate+hostplant)

2050
modelled suitability
(climate+hostplant)

d   *C. anchusae*

Present-day recorded
distribution

Present-day modelled
suitability (climate)

2050 modelled
suitability (climate)

Present-day modelled
suitability
(climate+hostplant)

2050
modelled suitability
(climate+hostplant)

e   *C. hederae*

Figure 1 (d–e). Potential future European distribution of two investigated specialist *Colletes* species based on climate and host plant distribution. [Present day recorded distribution; present day modelled suitability (climate); present day modelled suitability (climate & hostplant); 2050 modelled suitability (climate); and 2050 modelled suitability (climate & hostplant) of **d** *Colletes anchusae* and **e** *C. hederae*]
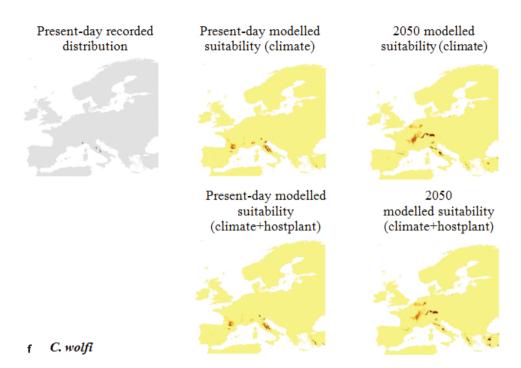
Figure 1 (f). Potential future European distribution of the specialist *Colletes wolfi* based on climate and host plant distribution. [Present day recorded distribution; present day modelled suitability (climate); present day modelled suitability (climate & hostplant); 2050 modelled suitability (climate); and 2050 modelled suitability (climate & hostplant)]

wide. Plotting the two against each other allows us to assess which species are going to be affected by loss of climatically suitable area locally vs. at the continental scale (Fig. 2). For instance, for *C. impunctatus* (generalist), close to 100% of grid cells with 100 km radius of current occurrences and in Europe as a whole are predicted to become less climatically suitable for that species in 2050 than they are now. This species is therefore likely to face difficulties locally where it currently occurs but also in terms of finding new areas to colonise in Europe. For *C. wolfi* (specialist) on the other hand, over 70% of grid cells locally are predicted to become climatically less suitable between now and 2050, where in the rest of Europe only less than 10% of grid cells in Europe will be less suitable for this species than they are now. This indicates that this species is likely to face difficulties locally, however, if it manages to disperse and migrate beyond its local environment, there are large areas elsewhere in Europe that will be climatically suitable in 2050. For the other two specialist species (*C. anchusae*, *C. hederae*), only ca. 20% of grid cells both close to where the species are currently found and Europe-wide are predicted to become less climatically suitable. This indicates that these species should be able to find suitable climatic conditions locally as well as farther afield (Figs 1d–e, 2).
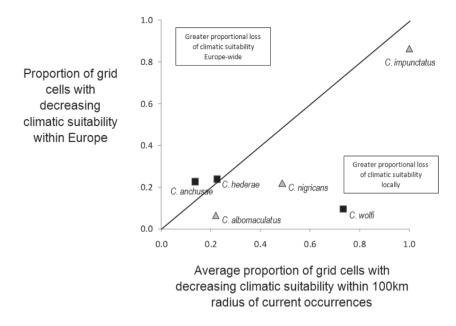
Figure 2. Local vs. continental scale change in climatic suitability between current and future climatic suitability of six *Colletes* species. For each species, we calculated the average number of grid cells within a 100 km radius that show decreasing climatic suitability for the species between current and future conditions. We also calculated for each species the proportion of grid cells with decreasing climatic suitability for the species in the whole of Europe. Black squares indicate specialists, grey triangles indicate generalists. The solid line indicates the 1:1 line.

Discussion

There are threats to all six studied *Colletes* species under predicted climate change, but the threats are not related to forage plant specialisation. In general, we predict that the trends will be towards a decrease in overall range of our species in Europe caused by a combination of a reduction in suitable climatic space, compounded by an increase in isolation between climatically suitable areas. The addition of principal forage plant distribution as an additional predictor, however, does not improve the power of the models, as the specialist forage plants are very widely distributed across the continent. This reflects findings by Schweiger et al. (2012) who found that the majority of investigated butterfly species in Europe are not limited by their larval host plants.

Of the generalist species, those currently showing a predominantly southern European distribution are predicted to exhibit only relatively minor decreases (*C. nigricans*) or no decrease in climatically suitable area (*C. albomaculatus*) under climate change. Both species, however, are predicted to experience an increase in isolation of their future suitable climate space. These changes may appear relatively small, but they represent net changes, and there is a clear movement northwards of the future climatic space, away from the current centres of distribution. *C. nigricans*, already well

established in the Mediterranean areas of France, may be able to expand into much of central and northern France along major river valleys. The projected situation in the drier parts of its current range suggests future significant declines in southern Iberia. The predicted suitable climatic envelope maps (Fig. 1a–f) suggest that *C. albomaculatus* looks well positioned to be able to expand into eastern central Europe, and possibly also in the steppic environments to the north west of the Black Sea (for map of European biogeographic regions see Appendix B). In both cases, expansion of range would be aided by their ability to exploit a broad diet spectrum.

Colletes impunctatus is a member of the Boreo-Alpine element in the European bee fauna, and is the generalist species that appears to be under the greatest threat from projected climate change. The area suitable for this species will be severely reduced in the Alps (currently a stronghold), and disjunctions will appear in Fennoscandia. These reductions in area will negatively affect this species.

The two restricted species which are monolectic on *Cynoglottis barrelieri*, (*Colletes anchusae* and *C. wolfi*) appear to be at risk from both a reduction in suitable climatic space as well as increased isolation (Fig. 1d, f). This is particularly significant for *C. anchusae*, which moves from being a species with a relatively low risk of negative climatic impacts, to one with a high risk. *C. wolfi* is currently very restricted in range and has a disjunct bicentric distribution, with centres in central Italy and again in the north of that country. This study indicates that the northern Italian population is under severe threat, with the suitable climatic envelope being eliminated by 2050, with distance, coupled with topography (the Alps and Appenine mountains acting as a dispersal barrier), making colonisation of new areas unlikely.

The third specialist species, *Colletes hederae* (Fig. 1e), might derive some benefits from the projected changes in climate. *C. hederae* is widely distributed in much of lowland western Europe, and is the most widespread of the specialist species. It is postulated that the species has expanded from centres south of the Alps with ameliorating climate (Kuhlmann, unpublished data). *C. hederae* has undergone a very rapid expansion of range in the last twelve years, reaching The Netherlands in 1997 (Peeters et al. 1999), and both Luxembourg (Feitz 2001) and the UK in 2001 (Cross 2002). The range has also expanded eastwards across northern Switzerland and southern Germany (Herrmann 2007) into central Germany (Frommer 2008). The principal forage plant, *Hedera helix*, is known to be strongly climate limited. Iversen (1944) demonstrated that the plant reproduces vegetatively in the northern parts of its range and that flowering is associated with areas of greater warmth. The northern boundaries of flowering of *Hedera helix* are likely to move northwards, creating new colonisation opportunities for *Colletes hederae* in the future.

We can say with confidence that although projected climate change may, in part, negatively impact on the studied bee species, it is most unlikely that declining populations of the most specialised *Colletes* will cause a serious reduction in pollination services to the principal forage plants. Waser et al. (1996) demonstrated that specialist pollinators tend to pollinate generalist plants, and this is certainly the case for *Hedera helix* (Ollerton et al. 2007) which attracts a wide range of insect visitors from several

orders. No data is available on the species that visit *Cynoglottis barrelieri*, but the flowers of the related plant *Anchusa strigosa* are known to attract a diverse assemblage of long-tongued bees of the genera *Eucera* and *Anthophora* in Israel (Kadmon and Shmida 1992) and so it is likely that *C. barrelieri* also attracts species other than *C. anchusae* and *C. wolfi* as visitors.

One of the possible consequences for both generalist and specialist *Colletes* species under climate change is that future shifts in range and distribution may be accompanied by changes in abundance. *Colletes* are known to support a number species of brood parasitic bees in the genus *Epeolus* which specialise on *Colletes* (Westrich 1989; Amiet et al. 1999) and future shifts are particularly likely to affect brood parasites, which need well established host populations to support them. In the case of *E. alpinus*, whose host (*C. impunctatus* (Amiet et al. 1999)) is restricted to boreo-alpine habitats, these risks are likely to be greater as the host habitats are predicted to diminish in area. Of our other modelled species, *Colletes hederae* is cited as a host of *Epeolus cruciger* (Kuhlmann et al. 2007), and believed to be a host of *E. fallax* (P. Westrich pers. comm.). In populations of *C. hederae* in northern Italy, Slovenia and southern Switzerland, nests are subject to parasitism by the bee *E. cruciger*, whereas no parasitism has been noted away from these core areas (Kuhlmann et al. 2007). Changing climate appears to have allowed the *C. hederae* to expand rapidly, without the cleptoparasite following at present.

Climate change presents a number of challenges for conservation. To the bees themselves, the plants they visit, and pollination services in general. In order to understand how climate shifts may affect plants and pollination more generally, a wider ranging study would be necessary, as this work deals with only 6 species out of an estimated European bee fauna of about 2,250 species (Polaszek 2004). However, given the likely loss of suitable climatic space and increased isolation of areas for these six species, it is likely that many other European bees may also be subject to similar increases in extinction risk under climate change. For effective bee conservation under environmental change, it is necessary to ensure that as the suitable climate envelopes move, that suitable habitat is available for the bees to exploit. For those bees that are forage specialists, this will clearly also involve the provision of the specialised forage itself.

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Appendix A

Summary data at 10' grid cell resolution (UTM WGS84) used for mapping the 6 species of *Colletes* in this study

Abbreviations used:

alb   *Colletes albomaculatus*
anc   *Colletes anchusae*
hed   *Colletes hederae*
imp   *Colletes impunctatus*
nig   *Colletes nigricans*
wol   *Colletes wolfi*

For further information on the dataset, contact M. Kuhlmann.

alb							
29RMP46	29RPQ56	29SMC68	29SMC78	29SNA09	29SNB00	29SNB01	29SNB10
29SNB20	29SNB40	29SNB51	29SNB90	29SPB10	30RYP76	30STB32	30STB53
30SUB31	30SUB51	30SUB60	30SUB69	30SUF08	30SUF44	30SUF65	30SVA86
30SVC56	30SVD63	30SVG10	30SVG42	30SVG80	30SVK72	30SVK82	30SWF09
30SWJ92	30SXG39	30SYH14	30TTK96	30TUK17	30TUM00	30TUM39	30TUM51
30TVK09	30TVK39	30TVK47	30TWK53	30TWL64	30TXM71	31SED17	31SED39
31TBF96	31TBH77	31TCF24	31TDH52	31TDH87	31TEH95	31TEJ40	31TFJ54
32SME66	32SME69	32SMF72	32SNF03	32TKN98	32TLN08	32TLP00	32TLP10
32TLQ07	32TPN59	32TPP14	33SVB35	33TUF66	33TVK28	33TVK39	33TYN17
33UXP35	33UXQ42	34SEF68	34SEG56	34SEH92	34SFF49	34SFF75	34SFF83
34SFG20	34SFG56	34SFG57	34SFG65	34SFG66	34SFG93	34SFH26	34SFH29
34SFH60	34SFH81	34SFJ76	34SGE61	34SGG15	34SGH26	34SGH44	34SGH52
34SGJ03	34SGJ14	34TCS18	34TCT54	34TCT56	34TEL01	34TEL47	34TEM53
34TEM61	34TFM90	34TGK34	35SKC30	35SKV43	35SKV61	35SLB30	35SLU09
35SLU98	35SLV40	35SLV80	35SMA96	35SNB27	35SNC15	35TNG67	35TNH52
35TPJ27	36RYA43	36SUG87	36SVG59	36SWG14	36SXG44	36SXH11	36SXH69
36SXH95	36SXJ84	36TWL53	36TWQ43	36TWR20	36TWR91	36TXQ15	36TXQ28
36TYL30	37SBR69	37SCE71	37SED09	37SED78	37SFD01	37SFD90	37TCL02
37TEE37	37TFE68	37TGE16	37TGE19	37TGE59	37TGF12	38SLH56	38SLJ39
38SLJ91	38SMG43	38SMH02	38TKK84	38TMK44	38TMK55	39STC68	39STD50
39SWV85	39SXV17	39TTG75	42SVJ72				
anc							
34TCS18	34TDL83	34TGN08	35TLH39	35TLL95	35ULP69	35ULP79	35ULP89
35ULQ25	35ULQ47	35ULR41	35ULR42	35UMP08	35UMP39	35UMP47	36SUG90
36SWG14	36SXG41	36SXH47	36SXH67	36SYG15	36TTL81	37SCE91	37SED08
hed							
30TXR38	30TYQ02	30UVA46	30UVB91	30UVU29	30UWA49	30UWB01	30UWB30
30UWB36	30UWB40	30UWB41	30UWB50	30UWB51	30UWB52	30UWB60	30UWB61
30UWB70	30UWB71	30UWB72	30UWB74	30UWB81	30UWB82	30UWB92	30UWV00
30UWV27	30UWV37	30UWV38	30UWV47	30UWV48	30UWV64	30UWV65	30UWV97

30UXB42	31TDG56	31TEJ25	31TEJ68	31TFJ06	31TFJ34	31TFJ85	31TFJ95
31TFJ96	31TFL50	31UCS23	31UCS33	31UDR06	31UDR91	31UES58	31UFS10
31UFS82	31UFS83	31UFS93	32TKS61	32TKS62	32TKS96	32TLS16	32TLS18
32TLS72	32TMK49	32TMS12	32TMS93	32TNK35	32TNM46	32TNR29	32TPM59
32TPP24	32TPS67	32TPS75	32ULU92	32ULV08	32ULV09	32UMA23	32UMA51
32UMA52	32UMA54	32UMV39	32UMV43	32UMV49	32UMV62	33TUG02	33TUK99
33TUL93	33TUL97	33TVK76	33TVL07	33TVL14	33TVL16	33TVL67	33TWG71
imp							
32TKQ82	32TLQ25	32TLQ47	32TLR33	32TLR58	32TLR59	32TLR69	32TLR89
32TLS40	32TLS60	32TLS61	32TLS71	32TLS72	32TLS80	32TLS81	32TLS82
32TLS83	32TLS90	32TLS91	32TLS92	32TMR09	32TMS00	32TMS04	32TMS10
32TMS12	32TMS21	32TMS22	32TMS26	32TMS31	32TMS33	32TMS45	32TMS66
32TMS74	32TMS75	32TMS78	32TMS86	32TMS97	32TNS12	32TNS13	32TNS64
32TNS65	32TNS67	32TNS68	32TNS69	32TNS73	32TNS75	32TNS76	32TNS83
32TNS87	32TNS96	32TNS98	32TPS08	32TPS15	32TPS25	32TPS49	32TPS59
32TPT32	32VNJ99	32VNP42	32VPN35	33UUA74	33UVC10	33UVR08	33UVV78
33VUD71	33VWG72	33VWH24	33VWH70	33VWK64	33WVN26	33WWN93	33WWR88
34UCF46	34UDG81	34UDV34	34VCJ47	34VDM26	34VDM27	34VDM36	34VDM37
34VDM45	34VDM46	34VDM48	34VDM65	34VEM17	34VEM27	34VEM35	34VEM47
34VEM57	34VEM99	34VEQ11	34VEQ38	34VER86	34VFM03	34VFM06	34VFM09
34VFM13	34VFM14	34VFM17	34VFM23	34VFM24	34VFM58	34VFP42	34VFR08
34WDB85	34WDB95	34WDV53	34WEA04	34WFS10	34WFT20	34WFT31	35VLG67
35VLG77	35VLG87	35VLH56	35VLH57	35VLH59	35VLJ61	35VMH05	35VMH40
35VMH62	35VNG45	35VNH26	35VNH30	35VNH31	35VNH76	35VNH77	35VNJ49
35VNJ68	35VNK04	35VNK11	35VNK28	35VNK37	35VNK39	35VNL12	35VNL13
35VNL99	35VPH15	35VPJ32	35VPJ33	35WLM77	35WLN81	35WLN88	35WLN89
35WLN91	35WMM75	35WMN05	35WMN21	35WMN22	35WMN24	35WNM25	35WNM32
35WNM72	35WNN90	35WNP19	35WNP91	35WNS11	35WPP06	36VUQ67	36VVP03
46UBU77	46UBU96	46UCA84	46UCA94	46UDA00	46UDA12	46UDA13	46UDA21
46UDA22	46UDV87	46UFA57	46UFA68	46UFV08	47TKM94	47TLH38	47TPK58
47TPL85	47UNQ89	48TUS28	48TWU10	48TXT21	48TXU40	48TXU41	48TXU60
48TXU80	48TXU81	48TYU21	48UWU97	48UXD28	48UXU05	48UXU26	48UXU27
48UXU41	48UXV00	49TBP70	49UBQ70				
nig							
29RMN00	29RMP40	29RMP46	29RNP17	29RNP89	29RNQ72	29RNQ85	29RPQ56
29RPQ64	29RQQ02	29SMC68	29SMC69	29SMC87	29SMC88	29SMC89	29SMC97
29SMD87	29SNA09	29SNB79	29SNB81	29SNC16	29SNC32	29SNC96	29SPB82
29SQD31	29TNF70	29TNF78	29TNF85	29TNF95	29TPE24	29TPE26	30STB32
30STB99	30STC90	30SUA57	30SUB15	30SUB69	30SUC01	30SUD07	30SUF06
30SUF44	30SVC56	30SVF36	30SVF58	30SVF77	30SVF89	30SVG60	30SVG80
30SVH43	30SVH54	30SVJ64	30SVK11	30SVK82	30SWF09	30SWF18	30SWG00
30SWG77	30SWG86	30SWH50	30SXG05	30SXG38	30SXG39	30SYH14	30SYH56
30SYH57	30SYJ27	30TTL92	30TTL95	30TUL09	30TUM00	30TUM41	30TUM52
30TVK39	30TVM48	30TWK02	30TWK53	30TWL47	30TWM32	30TXK28	30TXK66
30TXL37	30TXM01	30TXM08	30TXM98	30TYL46	30TYM01	30TYN30	31SBC48
31SBC59	31SCD41	31TBE77	31TBF55	31TBG61	31TBH77	31TCF18	31TCF24
31TCF55	31TCG00	31TCG01	31TCG34	31TDH51	31TDH69	31TDH87	31TEG17
31TEG28	31TEH00	31TFJ11	31TFJ44	31TFJ46	31TFJ54	31TFJ63	31TFJ67
31TFJ69	31TFJ75	31TFJ76	31TFJ84	31TFJ85	31TFJ92	31TFJ96	31TFK62

31TFK65	31TFL46	31TGJ21	32SMD78	32SMF78	32TKN88	32TKP74	32TKP95
32TKS62	32TLN08	32TLP10	32TLP11	32TLP13	32TLP23	32TLP27	32TLP28
32TLP33	32TLP43	32TLP75	32TLP95	32TLQ03	32TLR66	32TLS50	32TLS51
32TLS71	32TLS72	32TLS81	32TLS82	32TLS83	32TLS91	32TLS92	32TLS93
32TLT40	32TMM80	32TMN71	32TMP37	32TMP59	32TMR09	32TMS02	32TMS03
32TMS12	32TMS22	32TNK45	32TNK57	32TNM13	32TNN22	32TNQ81	33SUC10
33SWB08	33SWB28	33SXD29	33TTG93	33TUF66	33TUL14	33TUL56	33TUL87
33TUL93	33TVF32	33TVG06	33TVK39	33TVK76	33TWG74	33TXF90	33TXJ11
33TXJ21	34SEF99						
wol							
32TMQ21	32TMQ23	32TMQ24	32TMQ42	33TTH66	33TUG88	33TUG92	33TUG98
33TUH05	33TUH06	33TVG02					

Appendix B

Indicative map of the European biogeographical regions, 2005 (baseline map: ©EEA, Copenhagen, 2007).