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Differentiating the effects of climate and land-use change on European biodiversity: a scenario analysis

Jan E. Vermaat[1], Fritz A. Hellmann[2], Astrid J.A. van Teeffelen[3,7] , Jelle van Minnen[2], Rob Alkemade[2], Regula Billeter[4], Carl Beierkuhnlein[5], Luigi Boitani[6], Mar Cabeza[7], Christian K. Feld[8], Brian Huntley[9], James Paterson[10] and Michiel F. WallisDeVries[11,12]

[1] Department of Environmental Sciences, Norway's University of Life Sciences, P.O. Box 5003, NO-1432 Ås, Norway, jan.vermaat@nmbu.no; previous address: Section Earth Sciences and Economics, Faculty Earth and Life Sciences, VU University, Amsterdam, The Netherlands

[2] PBL Netherlands Environmental Assessment Agency, Bilthoven, The Netherlands

[3] Environmental Geography group, Department of Earth Sciences, Faculty Earth and Life Sciences, VU University, Amsterdam, The Netherlands

[4] Institute of Natural Resource Sciences, Zürich University of Applied Sciences, Wädeswil, Switzerland

[5] Department of Biogeography, BayCEER, University of Bayreuth, 95440 Bayreuth, Germany

[6] Department of Biology and Biotechnologies, Università di Roma La Sapienza, Roma, Italy

[7] Department of Biological and Environmental Sciences, University of Helsinki, Finland

[8] Department of Aquatic Ecology and Centre for Water and Environmental Research (ZWU), University of Duisburg and Essen, 45117 Essen, Germany

[9] School of Biological and Biomedical Sciences, Durham University, Durham, United Kingdom

[10] Land Use Research Group, School of Geosciences, University of Edinburgh, Drummond Street, Edinburgh, EH8 9XP, United Kingdom

[11] De Vlinderstichting / Dutch Butterfly Conservation, P.O. Box 506, 6700AM Wageningen, The Netherlands

[12] Wageningen University, Laboratory of Entomology, P.O. Box 16, 6700AA Wageningen, The Netherlands

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Abstract

Current observed as well as projected changes in biodiversity are the result of multiple interacting factors, with land use and climate change often marked as most important drivers. We aimed to disentangle the separate impacts of these two for sets of vascular plant, bird, butterfly and dragonfly species listed as characteristic for European dry grasslands and wetlands, two habitats of high and threatened biodiversity. We combined articulations of the four frequently used SRES climate scenarios and associated land use change projections for 2030, and assessed their impact on population trends in species (i.e. whether they would probably be declining, stable or increasing). We used the BIOSCORE database tool, which allows assessment of the effects of a range of environmental pressures including climate change as well as land use change. We updated the species lists included in this tool for our two habitat types. We projected species change for two spatial scales: the EU27 covering most of Europe, and the more restricted bio-geographic region of 'Continental Europe'. Other environmental pressures modelled for the four scenarios than land use and climate change generally did not explain a significant part of the variance in species richness change. Changes in characteristic bird and dragonfly species were least pronounced. Land use change was the most important driver for vascular plants in both habitats and spatial scales, leading to a decline in 50-100% of the species included, whereas climate change was more important for wetland dragonflies and birds (40-50%). Patterns of species decline were similar in continental Europe and the EU27 for wetlands but differed for dry grasslands, where a substantially lower proportion of butterflies and birds declined in continental Europe, and 50% of bird species increased, probably linked to a projected increase in semi-natural vegetation. In line with the literature using climate envelope models we found little divergence among the four scenarios. Our findings suggest targeted policies depending on habitat and species group. These are, for dry grasslands, to reduce land use change or its effects and to enhance connectivity, and for wetlands to mitigate climate change effects.

Key words: climate envelope modelling, SRES scenario articulation, species sensitivity database, land use change, wetlands, dry grasslands, habitat connectivity

Introduction

The effects of ongoing and anticipated climate change on European biodiversity are well studied (e.g. Harrison et al. 2006, Paterson et al. 2008, Huntley et al. 2010; Araujo et al. 2011, Fronzek et al., 2012, Jaeschke et al. 2014). A growing consensus converges on the following points: (a) Within distribution ranges, currently observed phenological changes are already substantial (Menzel et al. 2006). (b) Current distribution ranges of many species are observed to move northwards (up to several kilometres per year, e.g. Hickling et al. 2006, Campbell et al. 2009), although many species lag behind the moving isotherms (Devictor et al. 2012). European biodiversity conservation policy recognizes the importance of climate change (EEA 2012). Specific adaptation measures are beginning to be designed and evaluated (Van Teeffelen et al. 2015). This is a pressing issue, since bioclimatic envelope modelling (cf. Araujo & Townsend Peterson 2012) suggests that in the current network of conservation areas in Europe about two-thirds of the angiosperm and terrestrial vertebrate species concerned would lose suitable habitat by 2080 (Araujo et al. 2011). Similar dramatic changes were projected by Thuiller et al. (2005: 27-43% of all European angiosperm species would be lost by 2080) and Settele et al. (2008: 70% of butterflies lose more than half of their climatologically suitable range by 2080). Thus, protecting key 'retention areas' for conservation (Lung et al. 2014), and enhancing connectivity among protected habitats are important policy challenges (Cliquet et al. 2009, Dodd et al. 2010, Van Teeffelen et al. 2015).

However, Beale et al. (2008) suggest that land use change and biotic interactions exceed the effects of climate change as projected by climate envelope models (i.e. since these models did not perform better than properly designed random null models with current spatial autocorrelation; see also Suttle et al. (2007) and BISE (2012)). Projected trajectories of future land use change, however, are highly divergent, depending on the articulation of world economic development as well as changing socio-cultural constellations (Lorenzoni et al. 2000, Busch 2006). This divergence is generally grasped in scenarios, and the Special Report on Emission Scenarios (SRES) scenarios have become a benchmark set of scenarios for global change modelling (Lorenzoni et al. 2000, Berkhout et al. 2002, Busch 2006), and are the fundament for the next generation of climate change scenarios (Moss et al. 2010; Van Vuuren & Carter 2014).

Where species distribution modelling studies included socio-economic aspects, this has generally been restricted to the climatic consequences of socio-economic developments, such as differences in temperature increase and net water availability (Araujo et al. 2011, Hickler et al., 2012). The parallel changes in land use and human occupation that go along with such divergent scenarios (e.g. Busch 2006, Verboom et al. 2007, Verburg et al. 2008, Spangenberg et al. 2012), or the potential of successfully implemented near-future mitigation measures (e.g. reforestation, Dale et al. 2010, Fletcher et al. 2010, Hellmann and Verburg 2010, Pawson et al. 2013), have generally been ignored in biodiversity modelling (but see Verboom et al., 2007, Titeux et al., 2016). Both Olivier and Morecroft (2014) and De Chazal and Rounsevell (2009), argue that understanding the mechanisms underlying the interactive effects of climate change and land use change would overcome attribution errors in interpretation and help in a more robust design of adaptive conservation measures. All this suggests that the potentially interacting effects of climate and land use change should be studied in concert.

Quantifying the magnitude of this climate versus land use change interaction in Europe is hampered by the high geographical variability in both biodiversity (Anderson and Ferree, 2010) and land use patterns (Verburg et al. 2008, Kleijn et al. 2010). Also, foreseen climate change differs greatly in intensity across Europe (Christensen et al., 2007, Rajczak et al., 2013), hence biodiversity responses will not be uniform (Barbet-Massin et al. 2012). We chose to address the issue of high geographic variability in biodiversity by focusing on specific, comparatively homogeneous habitats: dry grasslands and wetlands. The issue of highly variable land use patterns was covered by using the highest resolution land use projection data available for the SRES scenarios (i.e. 1 km^2, from Verburg et al., 2008). Martin et al. (2013) argue for a finer spatial resolution than the 5 km they used to be able to track habitat suitability for a wetland specialist butterfly. We addressed geographic variation in the projected intensity of climate change by comparing responses across the whole of Europe with those from a more homogeneous biogeographic region, Continental Europe (Metzger et al. 2005, Verboom et al. 2007). Barbet-Massin et al. (2012) similarly coupled land use and three SRES scenarios to study their effects on European birds, but did not separate the effects of climate and land use. They concluded that for 70% of European birds the range would decrease due to a projected northward shift (median 335 km by 2050).

We focused on dry grasslands and wetlands, since these habitats are both well-studied and a European conservation target. They represent increasingly threatened habitats that once were widespread and common across Europe. Both habitat types are subject to pronounced decline and fragmentation (cf Fig. 1). They are considered particularly rich in angiosperms, insects and small vertebrates of which currently many are red-listed (Poschlod and WallisDeVries 2002, Veen et al. 2009, Ciskova et al. 2011, Heubes et al. 2011). Despite comparable physiognomy, these habitat types differ in species composition and taxonomic richness (Walker et al. 2004, Dengler 2005).

We used the BIOSCORE tool, a database of species sensitivity to a range of environmental pressures (including climate change) and habitat suitability for a wide range of European species (Delbaere et al. 2009, Eggers et al. 2009, Louette et al. 2010; see below).

Specifically, we asked the following questions:

(1) What are projected responses in species richness to climate change and land use change for the period up to 2030, and can the separate effects be disentangled?
(2) To what degree are species responses similar across the two studied habitat types of high conservation value?
(3) Does the regional restriction to Continental Europe lead to marked differences in species responses, compared to an analysis covering the whole of Europe (here represented by 27 European countries, the so-called EU27, because of data availability)?

Materials and methods

The BIOSCORE tool

BIOSCORE is a European biodiversity impact assessment tool (full presentation in Delbaere et al. 2009; applications in Eggers et al. 2009, Louette et al. 2010; www.bioscore.eu). It combines a database on species' sensitivities to a range of environmental pressures with habitat suitability using CORINE 2000 level 3 land cover types (Davies et al., 2004). It has a user interface that allows changing the impact of these pressures with a five point Likert scale, and has the possibility to generate outcomes for different bio-geographical breakdowns of Europe. User defined combinations of changes in (policy-related) environmental pressures are translated into impacts on a large number of species in nine species groups (birds, mammals, amphibians, reptiles, fish, butterflies, dragonflies, aquatic macro-invertebrates and vascular plants).

BIOSCORE includes expert-based sensitivity scores for each species and environmental pressure. These environmental pressures are labelled here 'input variable categories', and are grouped by the BIOSCORE expert group (Delbaere et al. 2009) into pollution, water related changes, climate change, disturbance regimes, direct pressures, species interaction and management.

The BIOSCORE sensitivity scores characterize a species' response to a relative increase or decrease of the environmental pressure and are thus representing a simplified species' response curve. The impact of a change in an environmental pressure category on a species is derived from a combination of the species' sensitivity score and the (projected) magnitude of change in that environmental pressure. Sensitivity is linked to the magnitude and direction of change. Species can respond positively (= population increase), negatively (= population decrease) or show no response (= stable).

The environmental pressures considered differ between species groups (cf. Delbaere et al., 2009). Land use serves as a practical indicator for habitat suitability by giving each CORINE land cover class a score expressing the probability of occurrence in this land cover type. Species respond to area changes of one land cover type according to this habitat's suitability score, and the effects of land use change can thus be traced. The simplified approach to sensitivity allows coverage of large numbers of species for which comparatively little detailed information is available (Delbaere et al., 2009).The BIOSCORE tool provides output such as tables or maps listing the number of species in a taxonomic group that will probably decline, remain stable or increase under the specified regime under focus. Next to the full effect of a combination it also tracks the separate effect of seven major input variable categories and of land use change if that is specified before the model run. It does not project extinction but indicates a probable trend.

Species groups used

Our analysis has been limited to three species groups in each habitat type: vascular plants, birds, dragonflies (wetlands) and butterflies (dry grasslands). In BIOSCORE, these groups contain a sufficient number of species characteristic for the two selected habitat types. These species are well studied, and their distribution is well known. We used two individual databases: one for dry grassland species and the other one for wetland species.

Characteristic dry grassland species were taken to be those for which the BIOSCORE database indicated a medium to high association with the CORINE land cover classes 3.2.1 ("Natural grasslands") or 3.2.3 ("Sclerophyllous vegetation"). Wetland species were those with a medium or high association with CORINE classes 4.1.1 ("Inland marshes"), 4.1.2 ("Peat bogs"), 5.1.1

("Watercourses") and 5.1.2 ("Water bodies"). Preliminary analyses revealed gaps in the BIOSCORE database for species lists as well as habitat suitability scores and pressure sensitivity scores for particular species groups and regions. Therefore, Hellmann, Vermaat and Alkemade revised and extended species lists of characteristic birds, butterflies, dragonflies and angiosperms for wetlands and dry grasslands, using expert judgment and published literature. Our revision is based on data in Van Swaay et al. (2006) and Lafranchis (2004) for butterflies, Svensson et al. (2013) for birds, Dijkstra and Lewington (2006) for dragonflies, and Van der Meijden (2005) for plants. For dry grasslands, this filtering procedure retained 41 vascular plant species, 28 butterfly species and 24 and 12 bird species for Europe and continental Europe, respectively. For wetlands, we retained 53 and 49 species of vascular plants, 102 and 51 species of dragonflies and 50 and 12 species of birds for Europe and continental Europe, respectively. Only four species of butterfly were associated to wetlands in the database, hence we decided to exclude these from the analysis. Occurrence in continental Europe is contained in the BIOSCORE database, as it is one of Europe's bio-geographical regions. The revised species lists are obtainable as excel files from the authors (FAH or JEV).

Climate change sensitivity of species as implemented in BIOSCORE

The BIOSCORE database was adjusted in two ways to better reflect the current state of understanding on how species respond to climate change. First, we adjusted the translation of species' climate sensitivity into population responses (Table 1). Species were allocated to one of four responses: species categorized as 'not vulnerable' to climate change are not expected to respond to any (reasonable) magnitude of climatic change because their (European) distributions are not primarily determined by climatic factors. Species categorized as having 'Low' climate sensitivity have a negative response (i.e. decrease) to only severe climatic changes. Species categorized with a 'Medium' or 'High' climate sensitivity also respond to moderate or limited climatic changes. Second, individual species' sensitivity to climate change was reviewed, and adjusted following expert knowledge and latest research insights. This procedure is documented in Annex 1. Since positive climate sensitivity is uncertain, we lumped the categories 'stable' and 'increase' into 'stable'.

Scenarios

We applied the four SRES scenarios (A1, A2, B1 and B2), which describe four divergent outlooks on global socio-economic development and their climate change impacts (Lorenzoni et al. 2000). They provide broad storylines, in which each scenario corresponds to an anticipated set of mutually consistent societal changes with corresponding climate change. Following Berkhout et al. (2002), Westhoek et al. (2006) and Spangenberg et al. (2012), we articulated the four SRES scenarios into separate qualitative storylines (Annex 2). These scenario storylines offer a framework allowing us to make assumptions on socio-economic developments and land use change and make specific articulations of their consequences for regional land use and the pressure indicators available in the BIOSCORE tool (Annex 2). For each scenario, the environmental pressures in BIOSCORE were set according to these assumptions (Table 2). We did a partial sensitivity analysis by successively setting the effects of continentality, eutrophication and soil moisture to zero, whilst all other settings remained as for the A1 scenario (cf Table 2).

Land use change projections from 2000 to 2030 are available from the EURURALIS project (Verburg et al., 2008) at 1 km^2 resolution for Europe (EU27 = EU25 + Norway and Switzerland, from 2007-2013) for each of the four SRES scenarios. Maps of these land use changes for each SRES scenario were used as input for BIOSCORE, alongside the other scenario assumptions (Table 2). Since the land use types defined in BIOSCORE do not exactly match those modelled by Verburg et al. (2008), a match-up operation was carried out (Annex 3). Species distribution data in the BIOSCORE tool reflect those in 'the late 1990s' (Delbaere et al., 2009), hence can be considered to correspond sufficiently with the initial year of the EURURALIS project.

Analysis of model outcomes

Our first question was addressed by comparing our BIOSCORE outcomes for the EU27 with the findings of Araujo et al. (2011). The contrast between climate change and land use change was addressed by firstly running BIOSCORE with the full scenario articulation for all seven input variable categories (Table 2), which has the full interaction, then secondly identifying the separate 'climate change' (one of the seven input variables) effect and thirdly 'land use change' effects. Question 2 was addressed by running the BIOSCORE tool with the two different species databases we had created for these two habitats, wetlands and dry grasslands. The effect of the high geographic heterogeneity of Europe (question 3) was assessed with a comparison to the more restricted biogeographical region continental Europe. Outcomes are presented in stacked bar charts as percentages of each species group that decrease, are stable or increase, and analysed with separate General Linear Model analyses of variance for each combination of 2 geographic extents x 2 habitat types times the 3 fractions (decline, stable, increase). This allowed us to test the effects of climate, land use and species group as well as the interactions between the climate versus land use contrast with species groups.

Results

Upon first visual inspection, the overall similarity in pattern among the four scenarios within each of the four geographic scale / habitat combinations is striking (Figs 2 and 3). Out of the 16 cases, only three show a distinctly different pattern. Generally, the fraction of species declining due to climate and land use together added up to the total (Figs 2 and 3). This was not the case in (a) dry grassland plants in continental Europe under the A1 scenario (Fig. 2), (b) wetland plant species in the EU27 under A2 and (c) continental wetland plants under A1 (Fig 3). Here also increased continentality and eutrophication (environmental input variables in Table 2) were responsible for substantial species decline. Across habitats, extents and scenarios, the estimated proportion of declining species was only substantial (50-100% when climate and land use taken together) for vascular plants. For the other species groups, the patterns were more variable: often at least half of the species will remain stable until 2030 (Figs 2 and 3). In the dry grasslands of continental Europe in contrast, characteristic birds are estimated to increase towards 2030, which may well be linked to a substantial increase in semi-natural vegetation (Annex 1).

In accordance, the scenarios did not explain a significant part of the variance in our overall GLM in addition to their influence through land use and climate change (Table 3). The contrast climate versus land use explained most of the variance for all species groups in dry grasslands of the EU27, but not in the other three scale-habitat type combinations, where the different responses among species groups, or the interaction caused most of the variation (Table 3a). This interaction and difference among species groups is clearly reflected in the estimated marginal means (Table 3b): the fraction of declining vascular plant species is mainly due to land use in all four combinations, whereas decline in wetland birds and dragonflies is coupled to climate change and continental birds and butterflies do hardly decline (Table 3, Figs 2 and 3).

The magnitude of the response of the characteristic species groups differed greatly, also between the four geographic scale – habitat combinations (Table 3b). Overall (Fig 2, 3), most characteristic vascular plants were found to decline, and this was mainly due to land use change. Dry grassland birds and butterflies were estimated to decline at the scale of the whole EU27, but this was much less pronounced in continental Europe. Wetland birds and dragonflies declined much less, and mainly due to climate change.

A partial sensitivity analysis for dry grasslands under the A1 scenario (Table 4) suggests that the BIOSCORE variables continentality, eutrophication and soil moisture do not have any additional effect on vascular plants. In contrast, butterflies were found to be quite responsive to changes in eutrophication and soil moisture in BIOSCORE (Table 4).

Discussion

Projected responses in species richness to climate change and land use change

Our modelling exercise suggests that by 2030, given land use change and climate change projections, notably many characteristic vascular plant species of dry grasslands and wetlands will have declined substantially (50-100% of them, Figs 2 and 3), and this decline appears to be mainly due to land use change (cf Titeux et al., 2016). For birds, butterflies and dragonflies, the pattern was more variable: substantial numbers of species appear stable. Particularly in wetlands (Figs 2 and 3) the (limited) decline in birds and dragonflies was largely driven by climate change (Table 3b). Given our articulation of the scenarios (Table 2), this may be aggravated by both reduced water availability and water quality. Many grassland bird species were found to increase in number, notably in continental Europe (Fig. 2). This may be due to the increase in semi-natural vegetation due to land abandonment (Westhoek et al. 2006). The latter may also imply that further forest expansion may ultimately lead to declines over longer time scales. These aggregate outcomes appear plausible given the overall ecology of the taxonomic groups and results of previous studies (e.g. Huntley et al. 2007, Settele et al. 2008). It should be noted, however, that we have not included specialist dependencies between butterflies and angiosperms: so this analysis cannot have fully grasped the secondary effect of plant decline on specialist insect fauna. The observed sensitivity of butterflies to eutrophication and soil moisture agrees with species trait analyses for this species group (WallisDeVries, 2014). It also parallels recent findings of Habel et al. (2016), who demonstrated a century-long decline in specialist butterflies of dry calcareous grasslands in Southern Germany coupled to habitat fragmentation and a decline in host plants due to land use intensification.

Within the four combinations of geographic scale (EU27 vs continental Europe) and habitat type, the response in the different species groups to the scenarios was highly similar: only 3 out of the 4x4 combinations of scale x habitat stood out visibly from the rest. This consistency among scenarios suggests that socio-economic development grasped by the SRES scenarios and its consequences for biodiversity has not yet diverged so much yet over the 3 decades covered by our modelling. Similarly, Araujo et al. (2011) found little contrast among the same four SRES scenarios, but estimated a much more pronounced decline across all species groups when modelling survival in conservation areas in Europe until 2080. Interestingly, our findings differ from those of Pompe et al. (2008), who used a detailed niche-based model projection of angiosperm species richness change across Germany by 2080, and found considerable difference among scenarios (corresponding to A1, A2 and B1), but only when dispersal was set to zero. However, when dispersal was included, the differences among scenarios remained but were less outspoken, hence in closer agreement with our results. This underpins the significance of dispersal, firstly for the survival of fragmented meta-populations (as reflected by many dry grassland vascular plants and butterflies, Pompe et al. 2008, Settele et al., 2008, Veen et al., 2009, Habel et al., 2016), and secondly for the design of viable biodiversity policy. Martin et al. (2013) found that climate was more important than land use in explaining the future distribution of a wetland specialist butterfly, but argued that this was because of insufficient spatial and thematic land use resolution. Geographical resolution of available species distribution and environmental data will be important in contributing uncertainty to the width and depth of our conclusions: this is obvious but not trivial and it should lead to caution in interpretation of model projections.

Overall, to answer our first question, our analysis suggests that the different species groups respond differently to land use and climate change, and that we can clearly separate their effects. Over the modelled time span of 30 years, vascular plants mainly decline due to land use, so plant diversity will probably decline, irrespective of habitat type or scenario. For birds and insects, however, the pattern is less straightforward, with winners and losers and a considerable contrast between dry grasslands and wetlands in the main driver responsible for this. For example, in continental Europe under the B1 and B2 scenarios, a substantial proportion of birds were estimated to increase, particularly due to land use change (Fig. 2), which is probably related to projected land abandonment.

Differences between habitat types

Our second question was whether the species of those two types of habitat would differ in their response, and they clearly did, but not in all aspects. In both habitats, vascular plant species declined more strongly than the other species groups. For birds and insects, however, land use was a stronger driver of species decline in dry grasslands of the EU27 (not in continental Europe), whereas in wetlands climate caused stronger declines for these species groups.

Differences between the larger and more restricted spatial extent (EU27 versus continental Europe)

For continental Europe we found a considerable difference in dry grassland species' responses compared to the whole EU27 (Fig 2), but the wetland species groups responded quite similarly. This implies that we have no single answer to our third question. Here, the importance of a homogeneous biogeographic region is overruled by that of the habitat: wetland or grassland is more important than biogeography. In continental Europe, grassland species may well have been estimated to increase due to the increase in semi-natural vegetation following considerable land abandonment. Subsequent forest development is probable (Delbaere et al. 2009) over longer time scales than modelled here and this suggests that this effect will be transient. It is tempting to speculate that wetlands are less fragmented than dry grasslands. To explain the more moderate decline of birds and butterflies in continental grasslands compared to the EU27 a relation with land use intensity appears plausible. Continental Europe excludes the intensively used agricultural areas of Denmark, Germany, The Netherlands, Belgium and Western France, where cattle density and nitrogen surpluses are high (Kleijn et al., 2009). Support can be found in the natural connectedness through river networks, and the importance of migratory wetland birds as dispersal vectors for plants (Amezaga et al. 2002, Santamaria 2002, Beltman et al. 2011), where once widespread transhumance has disappeared across most of Europe (Bruun and Fritzbøger 2002, Ozinga et al. 2009), thus greatly reducing the dispersal of dry grassland species.

Methodological constraints

As already outlined in the methods section, our approach has limitations. Firstly, the BIOSCORE database has been compiled using comparatively crude niche specifications and climate sensitivities (see also Annex 1), introducing uncertainty in species responses. Given the geographic extent, the large number of species included, the wide range of environmental pressures that could play a role, the variation in each species' responses to pressures and limited knowledge of these, this uncertainty is compounded and will not allow conclusions and generalisations at fine spatial or taxonomic resolution. For this reason we have selected only those species groups that are well studied and are comparatively rich in species to maximize eco-geographic articulation. Secondly, the database presumes fixed species preferences, similar to climate envelope models, and ignores possibilities for acclimation or selection of new genotypes within species (adaptation). This ignores the potential of evolutionary driven change. Thirdly, we use climate change projections and land use change deductions from EURURALIS as inputs that in themselves have considerable uncertainty – scenarios are plausible projections and confidence intervals are not straightforwardly derived. Fourthly, indirect effects through food web and competitive interactions among species have not been modelled. Notably for dry grasslands highly specialised insects have co-evolved with rare, vascular plants into tight host specificity under a probably extensive but age-old ruminant grazing regime (Bruun & Fritzbøger 2002, Suttle et al. 2007, Habel et al. 2016). Loss of these plants will lead to loss of the associated fauna, and this is not reflected in our outcome. Finally, our time horizon was constrained to 2030 by the land use projections done in EURURALIS. Other projective studies of biodiversity consequences of climate change have typically used a longer time horizon. IPCC (Kirtman et al. 2013) accordingly foresees that near-term (2016-2035) global temperature increase ranges between 0.3 and 0.7 °C, and witnesses a modest sensitivity to differences among scenarios. Thus, for the coming decades, this appears consistent with our findings, and it lends plausibility to our observed importance of land use change for species survival and local or regional biodiversity compared to climate change, despite the currently observed northward range extensions.

Implications for biodiversity policy and conservation practice

The implications of our scenario analyses for European biodiversity policy may appear sobering: by 2030 the difference between the four scenarios is fairly limited. Hence, also when climate policy will be effectively implemented and emissions are greatly reduced (the B1 and B2 scenarios used here, or similar RCPs, Moss et al. 2010), many characteristic plant species inhabiting these target habitats are projected to decline strongly, and this is mainly due to land use change. For insects and birds, the pattern is less straightforward and their decline is comparatively limited in wetlands, and in the continental dry grasslands.

Our findings suggest that until 2030 scenarios do not show substantial divergence in line with a.o. Araujo et al. (2011), but also that targeted policies for different habitat types and species groups are to be considered. These are for wetlands to reduce climate change effects, and for dry grasslands to reduce habitat loss due to land use change and to enhance connectivity, e.g. through the EU Green Infrastructure strategy. Hence, conservation of dry grasslands would benefit from simulating seasonal movements of herbivore flocks between different habitat fragments, a practice that is argued for in the literature (Fischer et al. 1996, Poschlod and WallisDeVries 2002, Manzano and Malo 2006) and is applied in Flanders with positive consequences (Couvreur et al. 2004). Fischer et al. (1996) demonstrated that sheep moving from grassland to grassland also disperse insects, such as grasshoppers in their fleece. In a review, Auffret (2011) argued that any measure inspired by traditional agricultural practice can be very effective. This author includes humans and their pets as a modern dispersal analogue which, when allowed to move freely as in the Scandinavian countryside where the freedom to roam is a lawful right, may also contribute to longer distance dispersal. A rejuvenation of a market for mutton and wool through focus on local and ecological production may contribute an economic incentive, notably under the B2 scenario, but this will not likely lead to cattle stocks of the size reported for the mid-nineteenth century (Bruun & Fritzbøger 2002, Poschlod and WallisDeVries 2002).

For wetlands, measures that reduce climate change effects can only be implemented through a careful consideration of the seasonal availability of water at or near the land surface, including flooding regimes, and the sustained connectivity of current river networks. Considerable practical guidance can be obtained from desiccation abatement programs where groundwater has been overexploited (for example Hinsby et al. 2008), from eutrophication abatement programs where external loading has been diverted and reduced, as well as from migration assistance programs for anadromous fish such as salmon.

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Figures and tables

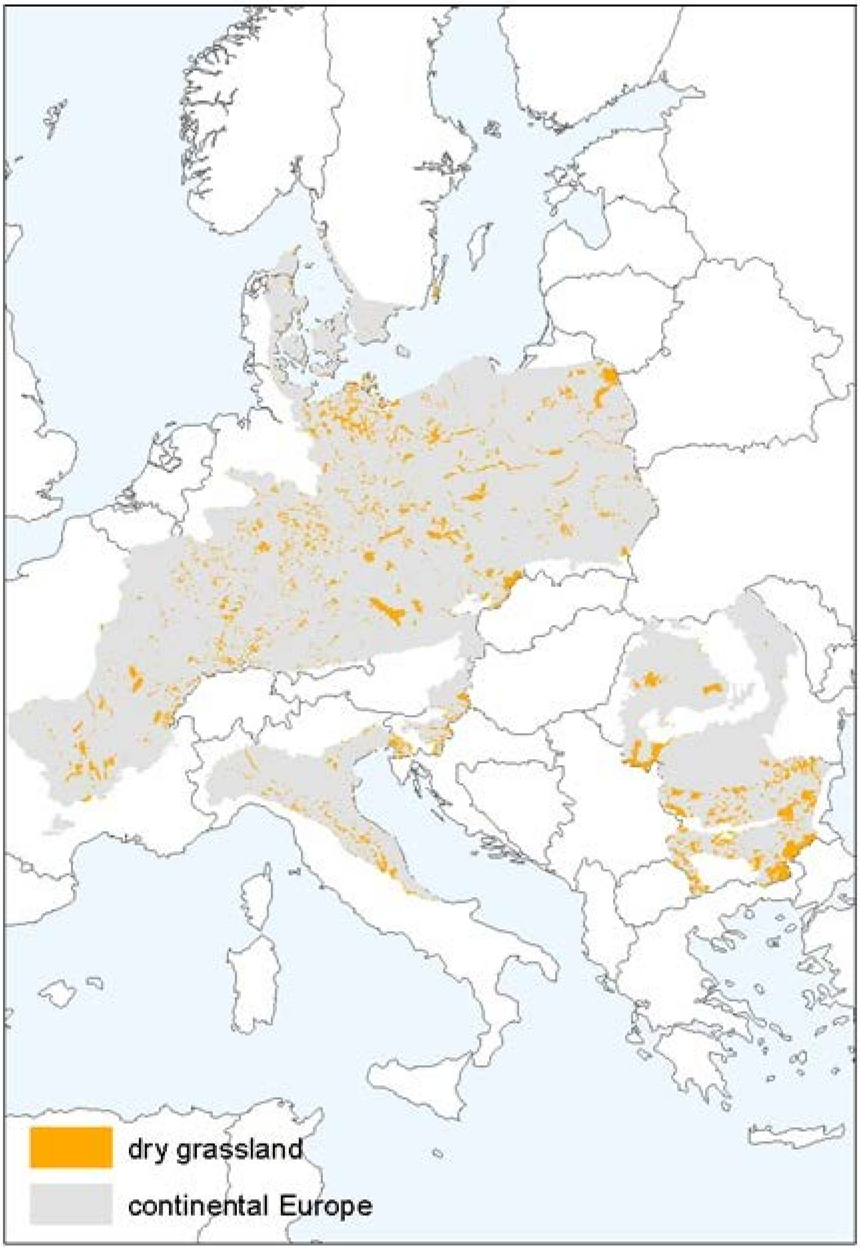
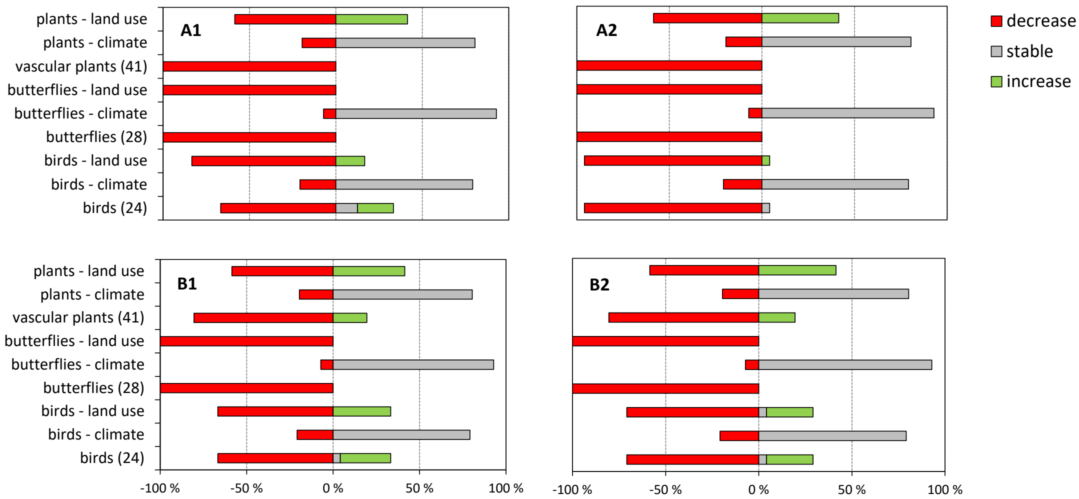


Figure 1. Distribution of dry grasslands across continental Europe. Data derived from the NATURA2000 database of the EEA from which "Dry grassland, steppes" was selected in, and, in the case of Poland and Romania the habitat classes 6110, 6120 and 6210 (i.e. calcareous grasslands).

(a) Europe



(b) Continental Europe

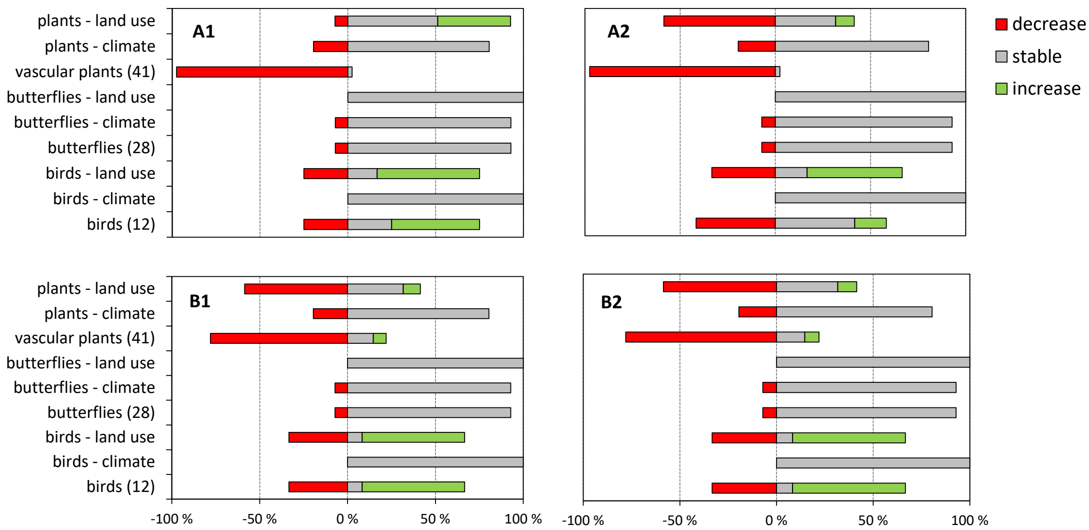
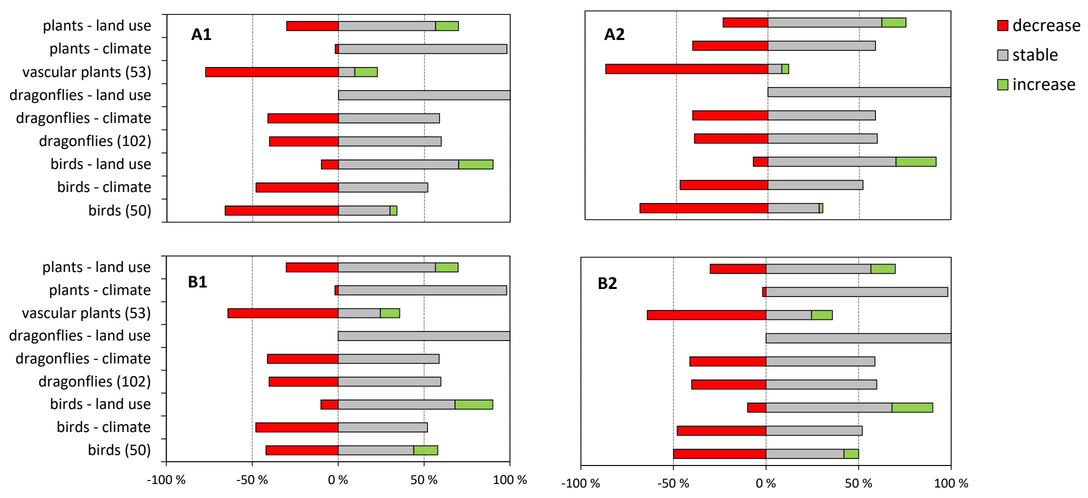


Fig 2. BIOSCORE outcome for dry grasslands in the EU27 (Europe) (a) and continental Europe (b). The percentage of species in a taxonomic group that is projected to decrease, remain stable or increase in occurrence; this is plotted bottom-to-top for the simultaneous effect of the full scenario articulation, for the separate effect of climate change, and for the separate effect of land use change, respectively. The first label has the number of species in the species group in parentheses. The full scenario articulation for BIOSCORE is presented in Table 1. Note that we use 'plants' in the chart labels only for brevity's sake, these are vascular plants. Note that in (b) continental Europe for vascular plants under A1 the percent declining species due to climate and land use do not add up to the total. Here increasing continentality and eutrophication also lead to substantial numbers of declining species.

(a) Europe



(b) Continental Europe

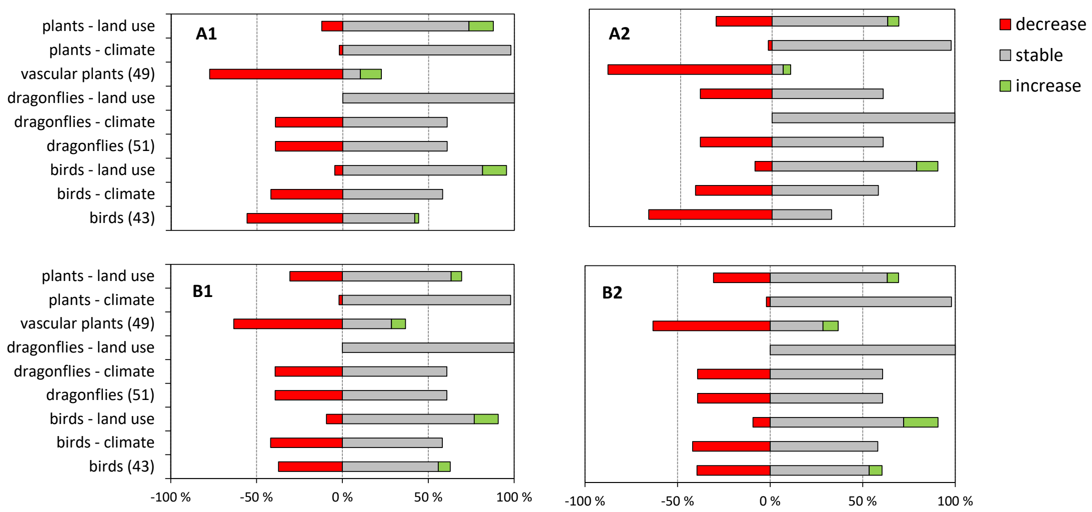


Fig 3. BIOSCORE outcome for wetlands. Further as Fig. 2. Note that where the percentage decline due to climate and land use does not add up to the total decline this is due to additional effects of continentality and eutrophication.

Table 1. Modelled population responses of species with different sensitivities for climate change to different levels of climate change in the BIOSCORE database. Left rows show species' climate sensitivity, top columns show the degree of climate change.

Climate change:	No	limited	moderate	severe
Species' climate sensitivity:				
Not sensitive	Stable	stable	stable	stable
Low	Stable	stable	stable	decline
Medium	Stable	stable	decline	decline
High	Stable	decline	decline	decline

Table 2. Articulation of SRES scenarios from Annex 2 in terms of BIOSCORE variables for 2030. The “+” indicate an improvement, and the “-” indicate a deterioration of the driving variable or pressure with respect to biodiversity (BIOSCORE uses a five point Likert-type scale). As an example, water temperature is thought to increase most under A2, and it is also thought to lead to the highest species decline. The zero sign means input variable not adjusted.

		Scenario			
BIOSCORE INPUT VARIABLES:		**A1**	**A2**	**B1**	**B2**
Pollution:	Eutrophication	-	--	+	+
	Acidification	0	0	0	0
	Salinisation	0	0	0	0
	Terrestrial pollution	-	--	+	+
	Water eutrophication & organic pollution	-	--	+	+
	Water pollution	-	-	+	+
	Water siltation	0	0	+	+
Water related changes:	Soil moisture	-	-	0	0
	Permanent water surface	-	-	-	-
	Temporary water availability	-	-	-	-
	Water quantity/flow (reduced)	0	0	0	0
	Water transparency	-	--	0	0
Climate change:	Climate change	-	-	-	-
	Continentality	-	-	-	-
	Temperature	-	--	-	-
	Water temperature	-	--	-	-
Disturbance:	Disturbance	-	-	0	0
	Powerlines	-	0	-	-
	Trampling	+	0	0	0
Direct pressures:	Harvesting of crops	-	-	0	0
	Hunting	0	0	0	0
	Harvesting of fish	0	0	0	0
Species interaction:	introduction of non-native species	-	-	-	+
	Disease organisms or parasites	0	0	0	0
Management:	Amount of dead wood	+	-	+	0
	Even aged forest	+	-	+	0
	Young felling age of forest	+	-	+	0

Table 3. Relative contribution of land use and climate change to variance in the fraction of species declining, remaining stable and increasing in each of the four cases modelled in BIOSCORE, respectively, dry grasslands and wetlands in the whole of Europe and continental Europe. Presented are (a) type 3 sums of squares for 4x3 (4 cases x fraction species declining, stable and increasing*) separate GLM analyses, and (b) marginal means of the fraction of species declining in a species group due to climate and land use (these correspond to the numbers presented in figs 2 and 3). Sums of squares are only presented when significant (mostly $p<0.001$, always $p<0.05$), otherwise NS is used. Degrees of freedom were 1 (climate versus land use), 2 (species groups), 2 (interaction), 18 (error) and 23 (corrected total). Bold printed are the sums of squares of factors contributing distinctly most to the total variance, and the major marginal means of proportionate species decline in a species group.

case	(a) Type 3 sums of squares	fraction of species group				(b) marginal means in the fraction declining due to:		
		declining	stable	increasing			climate	land use
Europe, dry grasslands	climate vs land use	**2.41**	**4.21**	**0.25**		birds	0.20	**0.79**
	species groups	0.09	0.02	0.17		butterflies	0.07	**1.00**
	interaction	0.30	0.03	0.17		vascular plants	0.20	**0.59**
	error	0.05	0.01	0.05				
	corrected total	2.90	4.26	0.64				
continental, dry grasslands	climate vs land use	0.17	1.03	0.36		birds	0.01	0.31
	species groups	**0.34**	0.82	0.33		butterflies	0.07	0.01
	interaction	0.17	0.90	0.33		vascular plants	0.20	**0.46**
	error	0.20	0.04	0.08				
	corrected total	0.89	2.78	1.11				
Europe, wetlands	climate vs land use	0.19	0.02	0.08		birds	**0.48**	0.10
	species groups	0.07	0.18	0.05		dragonflies	**0.41**	0.01
	interaction	**0.59**	**0.70**	0.05		vascular plants	0.02	**0.29**
	error	0.03	0.03	0.01				
	corrected total	0.86	0.90	0.18				
continental, wetlands	climate vs land use	NS	NS	0.03		birds	**0.42**	0.08
	species groups	NS	0.10	0.02		dragonflies	**0.29**	0.10
	interaction	**0.36**	**0.35**	0.02		vascular plants	0.02	**0.26**
	error	0.26	0.24	0.01				
	corrected total	0.73	0.70	0.08				

*The contribution of the four SRES scenarios was not estimated separately over and above 'climate versus land use' because of insufficient remaining degrees of freedom. In an overall GLM with the four cases pooled the scenarios did not explain a significant part of the variance over and above 'climate versus land use' and species groups.

Table 4. Partial sensitivity analysis of the BIOSCORE tool. Using the A1 scenario and the continental European dry grasslands subset, the effect of three BIOSCORE environmental switches was successively set to zero, and the outcome for all three species groups is compared with the run depicted in figure 2b and with BIOSCORE settings described in Table 2.

Run	Effect on vascular plants	Effects on butterflies	Effects on birds
(a) Continentality from '-' to zero	1 species moved from decline to stable	28 species moved from stable to increase due to a land use effect, but this was overshadowed by a negative climate effect so it is not reflected in the overall change	None
(b) Eutrophication from '-' to zero	3 species moved from decline to stable, and 1 to increase	28 species moved from stable to increase due to land use change, and for 26 this remained the case after incorporating the climate effect	None
(c) Soil moisture from '-' to zero	Same as (b)	Same as (b)	none

Differentiating the effects of climate and land-use change on European biodiversity: a scenario analysis - Annexes

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Annex 1. Revision of climate sensitivity of species in the BIOSCORE database.

Butterflies

We assigned a climate sensitivity to each dry grassland and wetland butterfly species in BIOSCORE based on Settele et al. (2008). Settele et al. compiled an atlas of climate sensitivity for the majority of European butterfly species through climate envelope modelling for 2051-2080 using HadCM3 climate data (table 2.1) and three of the four SRES scenarios (SEDG corresponds largely to B1, BAMBU=A2 and GRASS=A1, Spangenberg et al. 2012). Settele et al. (2008) classified butterfly species in different classes of climate vulnerability based on: a) fit of the climate envelope model with the species' present distribution and b) the geographical overlap of the modelled current and climate change distribution. We used the results of the SEDG scenario, equivalent to IPCC/SRES B1, since it is most similar to B2 available for birds and vascular plants and both scenarios project comparatively moderate changes and lead to acceptable consistency.

Area Under Curve, geographical overlap of modelled current and climate change distribution, and climate risk category according to SEDG-scenario in Settele et al. (2008) are available as excel sheet form the authors. Resulting BIOSCORE climate sensitivity scores are also given.

Table 1.1 Criteria for climatic risk categories of Settele et al. (2008), and conversion of these climatic risk categories into climate sensitivity scores in BIOSCORE. AUC = Area Under Curve, an indicator for goodness of model fit.

Climatic risk category Settele et al. (2008)			BIOSCORE
Category	AUC	Overlap	Climate sensitivity score
Potential risk	<= 0.75	-	Not
Low risk	> 0.75	>= 50%	Low
Risk	> 0.75	50% > AND >= 30%	Low
High risk	> 0.75	30% > AND >= 15%	Medium
Very high risk	> 0.75	15%> AND >= 5%	Medium
Extremely high risk	> 0.75	< 5%	High

Birds

Climate sensitivities of birds were assigned using the data of Huntley et al. (2008), who determined the climate sensitivity of the majority of European bird species through climate envelope modelling for the period 2070-2099 using HadCM3 climate data (IPCC/SRES B2 scenario). Huntley et al. (2008) do not directly classify bird species into climate change vulnerability classes, but instead give the overlap between the current and climate change distribution plus the AUC. Thus, like for butterflies, we used the overlap between the current and climate change distribution plus the AUC as presented by Huntley et al. (2008) to classify birds into climate sensitivity classes and we implemented these likewise in the BIOSCORE database (see table 1.1).

Vascular plants

We assigned climate sensitivities for plants in BIOSCORE using Thuiller et al. (2005), who determined the climate sensitivity of the majority of European plant species through climate envelope modelling for the period 2051-2080 using HadCM3 climate data. Similar to butterflies and birds, the geographical overlap between the current and climate change distribution was determined under the B2 scenario and used to classify plant species in climate sensitivity classes. Only the geographical overlap could be derived from Thuiller et al. (2005). Therefore, we dropped one category and assumed sufficient fit (i.e. AUC > 0.75).

Dragonflies

We assigned a climate sensitivity to each dragonfly species in BIOSCORE based on expert knowledge and current distribution (Dijkstra and Lewington, 2006). We decided whether a species would increase or decrease using the following assumptions:

- Species with alpine-boreal distributions will decrease.
- Species with southern European or North African distributions will –at the least- remain stable, as they have opportunities to increase.
- Species that are widespread and common throughout most of Europe will remain relatively stable.
- Species with Atlantic and continental distributions will decrease slightly.
- Species with very restricted or fragmented distributions are most vulnerable to climate change.
- Generalist species are less vulnerable to climate change than habitat specialists (e.g. bog species).

The resulting climate sensitivity plus assumptions are available from the authors.

Annex 2. Narrative articulation of the SRES scenarios for use in the BIOSCORE tool based on Berkhout et al. (2002), Lorenzoni et al. (2007), and Westhoek et al. (2006).

scenario	narrative
A1	This scenario has a focus on globalization and economic growth, with less attention for environmental sustainability. Overall, it foresees an affluent, wealthy world. European farmers have to compete in a global market, which favours agricultural intensification in highly productive regions and agricultural land abandonment in more marginal regions. Climate change and associated temperature rise is intermediate in this scenario. Technical progress is rapid in this world. Due to agricultural intensification in highly productive regions and little emphasis on environmental sustainability, eutrophication and pollution are expected to increase in this scenario. Water transparency is expected to deteriorate due to increased temperatures and nutrient inputs. Increased harvesting of crops and a reduced trampling of the soil (i.e. more cattle kept year-round in stables) is expected as part of a more efficient, industrial European agriculture. Climate change is intermediate in this scenario, and variables such as (water) temperature, continentality, temporary water availability, soil moisture and permanent water surface are expected to deteriorate. Overall, water quantity/flow is not expected to change, as extra drought in summer is expected to be offset by additional rainfall in winter. The global focus of this scenario is likely to result in more international transport and shipping, leading to more invasive species.
A2	This scenario also has a focus on economic growth, but with more resistance to globalization than the scenarios A1 and B1. Europe aims to be remain more self-reliant in its food production than in scenarios A1 and B1. As a result, European farmers are more protected by policies and do not compete in a global market. Because there is also little attention for environmental sustainability, this leads to on-going agricultural intensification and much less agricultural land abandonment than in the other scenarios. Climate change and associated temperature rise are high in this scenario. Eutrophication, pollution and the number of crop rotations (harvests) are expected to increase substantially in this scenario due to agricultural intensification. Water transparency is expected to deteriorate significantly due to increased temperature and nutrient inputs. No additional trampling of the soil is expected, as changing the entire agricultural production process (i.e. cattle kept year-round in stables) seems unnecessary as farmers do not have to compete on a global market. More marginal agricultural areas are kept in use. Climate change is high in this scenario, and variables such as (water) temperature, continentality, temporary water availability, soil moisture and permanent water surface are expected to deteriorate. Overall, water quantity/flow is not expected to change, as extra drought in summer is expected to be offset by additional rainfall in winter. Although not really global, this scenario does have a focus on economic growth requiring international transport and shipping. Increasing numbers of invasive species can therefore be expected.
B1	This scenario has a focus on sustainable economic growth. Due to a strong belief in globalization, important steps towards a (fair) global economic market have been taken but within certain boundary conditions to ensure sustainable growth. European farmers have to compete in a global market, which favours intensive agriculture in highly productive regions and agricultural land abandonment in more marginal regions. Nonetheless, environmental

	regulations regarding agricultural production are strict and aim to reduce the negative impacts of intensive agricultural production systems. Global environmental issues (i.e. global warming) are efficiently tackled through global cooperation and agreements. The resulting world is affluent and internationally oriented with less climate change than scenarios A1, A2 and B2. Technical progress is rapid in this world. Although agriculture remains intensive in this scenario, environmental regulations are assumed to change the agricultural production system in a way to limit its’ negative impacts. Things such as eutrophication, pollution and the number of crop rotations (harvests) are expected to improve or remain stable. Water siltation is expected to decrease due to less erosion-prone on-farm practices. Forestry practice is expected to comply with high environmental standards, resulting in older forests and more dead wood. Although climate change is less in this scenario than in the scenarios A1, A2 and B2, important variables such as (water) temperature, continentality, temporary water availability, soil moisture and permanent water surface are still expected to deteriorate to some degree. Overall, water quantity/flow is not expected to change, as extra drought in summer is expected to be offset by additional rainfall in winter. Water transparency is expected to deteriorate due to increased temperatures and nutrient inputs. The global focus of this scenario is likely to result in more international transport and shipping, leading to more invasive species.
B2	In this scenario there is more resistance to globalization than the scenarios A1 and B1, and there is an emphasis on sustainable economic growth. Instead of developing towards a global economic market, regional-scale production is supported as dependency on international markets is not favoured. European farmers are protected by policies and do not have to compete in a global market. But environmental regulations for farmers are strict in order to minimize the negative impacts of agricultural production. This results in changes in the agricultural production process, which will become less intensive. To reduce the dependency on global markets, demand and support for European agricultural products remains high. Therefore land abandonment is smaller in this scenario than in the others. Climate change and associated temperature rise is intermediate in this scenario. Although the demand for European agricultural products remains high in this scenario, agricultural production is expected to become less intensive due to environmental regulations promoting environmental sustainability. Things such as eutrophication, pollution and the number of crop rotations (harvests) are expected to improve or remain stable. Water siltation is expected to decrease due to less erosion-prone on-farm practices. Although high environmental standards will be put into place for forestry, the increased demand for European wood (i.e. less dependency on global markets) is expected to be a driving factor for more intensive use of European forests. This more intensive use will partly offset the beneficial environmental effects of high environmental forestry standards on forest biodiversity. Climate change is intermediate in this scenario, and variables such as (water) temperature, continentality, temporary water availability, soil moisture and permanent water surface are expected to deteriorate to some degree because of this. Overall, water quantity/flow is not expected to change, as extra drought in summer is expected to be offset by additional rainfall in winter. Water transparency is expected to deteriorate due to increased temperatures and nutrient inputs.

Annex 3. Land use changes from 2000 – 2030 derived from EURURALIS* and modelled in the relevant BIOSCORE scenario runs. Left as percentage and right in km^2.

	%				KM2			
(a) Europe	A1	A2	B1	B2	A1	A2	B1	B2
Urban	25%	7%	6%	3%	45,980	12,115	10,341	4,802
Arable	-11%	0%	-12%	-11%	-130,322	-4,024	-151,572	-130,539
Pasture	-5%	-6%	-13%	-11%	-29,476	-34,557	-72,465	-59,961
semi-natural vegetation	-15%	-27%	-21%	-22%	-70,619	-129,319	-99,954	-104,101
abandoned arable**					32,912	10,835	92,252	82,480
permanent crops	-12%	1%	-18%	-15%	-17,490	1,137	-25,738	-22,098
Forest	10%	10%	12%	13%	138,999	126,912	166,257	174,813
abandoned pasture**					30,016	16,901	80,879	54,604
(b) Continental Europe								
urban	20%	4%	4%	2%	14,649	2,636	2,696	1,451
arable	-10%	-2%	-12%	-13%	-54,572	-10,476	-63,474	-71,133
pasture	-1%	-8%	-11%	-15%	-2,316	-16,029	-22,830	-30,982
semi-natural vegetation	34%	-3%	33%	38%	15,265	-1,176	15,094	17,353
abandoned arable**					10,920	7,479	30,260	45,262
permanent crops	-21%	-11%	-25%	-32%	-3,543	-1,881	-4,302	-5,367
forest	3%	3%	4%	5%	9,564	10,399	14,211	17,276
abandoned pasture**					10,033	9,048	28,345	26,140

*Matchup of the land use types of the CLUE modelling framework (Verburg et al. (2008)) to the CORINE types available in BIOSCORE:

1. Moors, heaths, beaches, bare rocks and dunes have been kept constant in time in the simulations of Verburg et al. (2008) and are therefore kept constant in BIOSCORE.
2. Arable land, pasture, permanent crops, forest and urban are modelled by Verburg et al. (2008), and their percentage change was thus directly derived from Verburg et al. (2008). Subcategories in BIOSCORE (respectively urban fabric/green urban areas and broadleaved/coniferous/mixed forest), were assumed to change proportionally.
3. Verburg et al. (2008) includes (semi-)natural vegetation as a land use type. We assumed this to be equivalent to natural grasslands, sclerophyllous vegetation and transitional woodland-shrub in BIOSCORE, and presumed these to change proportionally.
4. Verburg et al. (2008) includes abandoned land as a land use type, which has no equivalent in BIOSCORE. We assumed that transitional woodland-shrub roughly corresponds (in terms of biodiversity) to abandoned land. As a next step, we therefore adjusted the area transitional woodland-shrub in BIOSCORE to match the increase in abandoned land estimated by Verburg et al. (2008).
5. We used heterogeneous agricultural land as a rest term to keep the above land changes consistent with the total land area, with the prerequisite that its' percentage change should be intermediate between the percentage changes of arable land and pasture. Verburg et al. (2008) does not distinguish heterogeneous agricultural land as a land use type and it is contained within the other agricultural land use types in their simulations.

** These land use types are not included in the input CORINE land use map, and therefore no percentage change could be calculated but only the absolute increase could be given.