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Current population trends mirror forecasted changes in climatic suitability for Swedish breeding birds

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Current population trends mirror forecasted changes in climatic suitability for Swedish breeding birds

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Capsule Swedish breeding bird species that are predicted to experience a more suitable climate by 2050 are currently increasing in numbers.

Aims To test, for a large set of breeding birds, if recent population trends mirror the changes in predicted climatic suitability across the Swedish distribution range, and to test if considering natal dispersal improves the fit of the predictive models.

Methods Recent decadal population trends of 131 species of birds breeding in Sweden were compared to forecasted change in their future national distribution range by 2050, as simulated by suitability distribution models using climate and natal dispersal scenarios. Two other potential predictors of recent demographic trends are controlled for – namely habitat specialization and generation time.

Results The 1998–2009 population trends were positively correlated with predicted changes in distribution range. Thus, forecasted changes in climatic suitability predict recent population trends. Accounting for the species-specific natal dispersal provided only a slightly better fit.

Conclusion Recent climate change has affected the population size of Swedish breeding birds. Climatic suitability models can be an efficient tool for predicting the impacts of climate change on the abundance of birds.

Species distribution models that couple observed geographical distributions to climatic variables are frequently used to forecast the potential impacts of ongoing climatic changes on the distribution and size of plant and animal ranges (Thomas *et al.* 2004, Thuiller *et al.* 2005, Araújo *et al.* 2006, Jetz *et al.* 2007, Huntley *et al.* 2008). However, their use for this purpose is difficult to validate. The classical validation is to see how well the models accurately predict the current observed distribution range. In some studies it has been shown how well models can explain recent distribution shifts (Hill *et al.* 1999), or recent changes in population size at the national (Green *et al.* 2008) or continental scale (Gregory *et al.* 2009).

Here we compare recent trends in breeding population size to predicted changes in climatic suitability by 2050 for 131 bird species. In other words, we compare recent changes in abundance to forecasted changes in distribution area. We focused on the situation in Sweden, where a large number of European species have their northern distribution limits. Accordingly, there is room for many species to expand their distribution range.

In Sweden, the effects of climate change on birds are likely to be high (Pigot *et al.* 2010, Jiguet, Devictor *et al.* 2010, Lindström *et al.* 2012). We obtained predicted Swedish climatic suitability distributions from climatic niche models combining Western Palaearctic species distributions and current or future climatic conditions from scenarios for 2050 of the Intergovernmental Panel on Climate Change (IPCC) fourth assessment (IPCC 2007). Estimates of recent population trends arose from the national breeding bird survey implemented across the whole country for the period 1998–2009. If bird population trends are effectively impacted by ongoing climate changes, they are expected to parallel climate-induced trends in

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predicted climatic suitability – under the hypothesis that changes in abundance would parallel changes in presence probability. This should be visible after having considered other traits known to influence species trends, such as habitat specialization and demographic strategy. As climate change is reported to impact European breeding bird populations, especially since the mid-1990s (Gregory *et al.* 2009), we expected a positive correlation between the recent abundance trends and predicted changes in climatic suitability. This would provide support for the efficiency of climatic suitability models to predict the impacts of climate change on the abundance of birds. Finally, because species-specific dispersal ability could prevent species from colonizing climatically suitable areas, we performed two analyses considering predicted changes in climatic suitability, assuming either a full dispersal from the current to the future range, or a more realistic scenario constrained by species-specific natal dispersal (Barbet-Massin *et al.* 2012).

METHODS

Bird population data

We considered 131 breeding bird species monitored by the national Swedish breeding bird survey (SBBS; Lindström *et al.* 2011; see Appendix 1 for a list of species). In 1996, the SBBS started a new monitoring scheme with 716 fixed routes systematically distributed over the whole of Sweden, 25 km apart in both N–S and W–E directions. The systematic distribution ensured representative coverage of all widespread habitats. A fixed route consists of 8-km line transect, formed as a 2 × 2-km square with a 5-minute point count every full kilometre. The route is walked at a speed of 30–40 minutes per kilometre, starting at 04:00. All birds seen or heard are recorded. The observer might deviate 200 m from the line or point, but outside this distance counting was suspended. Census date varied between mid-May and early July depending on latitude (earliest in the south, latest in the north).

Species-specific trends and associated standard-errors were calculated using Trends and Indices for Monitoring data (TRIM; Pannekoek & van Strien 2001), taking over-dispersion and serial correlation into account (Lindström *et al.* 2011). TRIM analyzes time-series of counts with missing observations using log-linear Poisson regression. We used the total number of birds observed along the lines as independent observations in trend analyses. We used 1998 as the starting year, because too few routes were surveyed in 1996–97.

Climatic distribution models

Changes in the Swedish distribution range size for each species were estimated from predicted distributions obtained by climatic niche modelling for the whole Western Palaearctic. Forecasted change was calculated as the log-ratio of future divided by current modelled climatic suitability in Sweden.

The presence–absence data of the current distribution ranges were obtained by geo-referencing and digitizing breeding distribution maps for the 131 species from the handbooks of the Birds of the Western Palaearctic (BWPi 2006), with a 0.5° × 0.5° resolution. For each species, we computed distribution models with eight climatic variables, obtained from the IPCC (2007) fourth assessment: (1) annual mean temperature; (2) mean temperature of the warmest month; (3) mean temperature of the coldest month; (4) temperature seasonality; (5) annual precipitation; (6) precipitation of the wettest month; (7) precipitation of the driest month; and (8) precipitation seasonality. The seasonality is the coefficient of variation of the monthly means. Future climate projections (for 2050) were derived from five general circulation models (GCMs) – BCM2, ECHAM5, HADCM3, MIROHIC3_2-HI and MK3 – and three recent special reports on emission scenarios (SRES) – A1B, B1 and A2 when available – using monthly mean predictions taken from IPCC (2007), resulting in 13 future climate projections for each species.

For the modelling of species distributions, we used seven different niche-based modelling techniques, performed with the BIOMOD computational framework (Thuiller *et al.* 2009): (1) generalized linear model (GLM), a regression method with polynomial terms for which a stepwise procedure is used to select the most significant variables; (2) generalized additive model (GAM), another regression method with four degrees of freedom and a stepwise procedure to select the most parsimonious model; (3) classification tree analysis (CTA), a classification method running a 50-fold cross-validation to select the best trade-off between the number of leaves of the tree and the explained deviance; (4) artificial neural networks (ANN), a machine learning method, with the mean of three runs used to provide predictions and projections, as each simulation gives slightly different results; (5)

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multivariate adaptive regression splines (MARS), a regression method; (6) generalized boosting model (GBM), a machine learning method which combines a boosting algorithm and a regression tree algorithm to construct an 'ensemble' of trees; and (7) Random Forest (RF), a machine learning method which is a combination of tree predictors such that each tree depends on the values of a random vector sampled independently and with the same distribution for all possible trees. In order to evaluate the predictive performance of a distribution model, for each species, we used a random subset of 70% of the data to calibrate the model and then used the remaining 30% for evaluation, using a threshold independent method, the area under the relative operating characteristic curve (AUC) (Fielding and Bell 1997). The data-splitting approach was then replicated five times, from which we calculated the mean AUC of the cross-validation. The final calibration of every model for making predictions uses 100% of available data.

We then used an ensemble forecast technique which aims to take into account the variability among species distribution models, climate models and climate scenarios, in order to get the central tendency (Araújo & New 2007). Indeed, for each species, we obtained 7 modelled current distributions and 91 (7 models × 13 [GCM × SRES]) modelled future distributions from climate variables. The current and future consensus distributions were obtained by calculating the weighted mean distributions: the 7 models were ranked according to their predictive performance, and a decay of 1.6 gave the relative importance of the weights (Thuiller *et al.* 2009), giving respective weights of 0.38, 0.24, 0.15, 0.09, 0.06, 0.04 and 0.02 to the models according to their ranking. The consensus between different GCMs and SRE scenarios was obtained by calculating the mean of the models consensus across GCMs and SRES. In order to transform the consensus distribution, obtained as continuous probabilities ranging between 0 and 1, to a presence–absence distribution, we preserved the occurrence probabilities for pixels above the sensitivity–specificity sum maximization threshold – these pixels are the presence distribution. We set to zero the occurrence probability for pixels under the threshold, which are considered as the areas where the species is absent (Liu *et al.* 2005).

By applying the threshold maximizing the sensitivity and specificity of the ensemble predictions, we produced the filtered (by presence–absence) distribution for each species. We further focused on the Swedish parts of the obtained presence ranges and summed the grid climatic suitability for the current and the future ranges, by summing the probabilities of the filtered distribution, weighting each pixel by its area to account for the latitudinal variations in pixel area. Then we estimated the log-ratio of the future (2050) divided by the current predicted climatic suitability, for each species.

We reiterated this estimation with ensemble predictions accounting for the ability of a species to disperse to the future range, based on species-specific natal dispersal. We followed the method proposed by Barbet-Massin *et al.* (2012) combining generation time and the distribution pattern of natal dispersal for each species. This method provides a dispersal correction value to apply to climatic suitability of pixels located outside the current range but within the predicted future range. This second approach provides estimates of future distribution ranges that account for species' ability to disperse and, hence, to colonize newly suitable areas effectively.

Other species traits

Generation time was considered as a proxy for most demographic traits (Jiguet, Gregory *et al.* 2010). Data on generation time were extracted from BirdLife International (2004). From this reference, values reported as <3.3 were set as 3.0 for non passerines and 2.0 for passerines.

Species habitat specialization was estimated as the coefficient of variation (standard deviation/average) of average species densities among 12 habitat classes (Julliard *et al.* 2006). Bird data were those collected by the SBBS on point counts along the fixed routes to calculate average bird densities among 12 habitat classes. Habitat data were collected from the Swedish Coordination of Information on the Environment (CORINE) Land Cover (SCLC) database, a more detailed product than the European CORINE Land Cover (CLC) database, and better suited to national requirements. The CLC has 44 classes, of which 35 are represented in Sweden, and the minimum mapping unit is 25 ha. Additional classes have been added to the SCLC and the minimum mapping units are 1, 2 or 5 ha, depending on the class. The National Land Survey of Sweden is responsible authority for the data (http://nils.slu.se/). For each point count of the fixed routes, the habitat with the largest area within a 400-m radius of the point was selected as the main habitat.

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Analysis of species trends and traits

Statistical analyses were performed using the R software. We fitted a linear model using phylogenetic generalized least squares (GLS function from NLME package) to explain observed population trends with predicted changes in climatic suitability, habitat specialization and generation time. We defined a within-group correlation structure referring to the phylogenetic tree of the 131 species (created with the APE package), using a CORGRAFEN function with no branch lengths. This tree was completed from the one used by Devictor *et al.* (2010) and is summarized in Appendix 2. We used the squared standard errors of the growth rate estimates as the VARFIXED function in the weighted model. We performed two models: the independent predictor related to the predicted changes in climatic suitability assuming either a full dispersal scenario from the current to the future range; or a more realistic scenario constrained by species-specific natal dispersal and generation time. We compared the log-likelihood values of the two models to determine if climate change models were improved by considering dispersal.

RESULTS

In the first model assuming a full dispersal scenario, the observed population trends were well predicted by forecasted changes in climatic suitability (see Fig. 1; mean = 0.091 ± 0.020 sd, $t_{127} = 4.5$, $P < 0.001$), beyond the strong effect of habitat specialization (mean = –0.020 ± 0.005 sd, $t_{127} = -3.8$, $P < 0.001$). There was no effect of demographic traits (generation time, $t_{127} = 0.1$, $P = 0.90$). In the second model assuming a more realistic dispersal scenario, these two significant effects were maintained (change in climatic suitability: mean = 0.097 ± 0.021 sd, $t_{127} = 4.7$, $P < 0.001$; habitat specialization, mean = –0.021 ± 0.005 sd, $t_{127} = -3.8$, $P < 0.001$). The model based on realistic dispersal scenarios had a higher log-likelihood than the model considering a full dispersal (226.4 versus 225.6). The model based on a realistic dispersal scenario was also run without using the squared standard errors of the growth rate estimates as weights. The effect of forecasted change in climatic suitability was maintained ($t_{127} = 3.6$, $P < 0.001$) but not the effect of habitat specialization ($t_{127} = -0.3$, $P = 0.74$). Overall, the forecasted changes in climatic suitability had a high predictive power on population trends, while habitat specialization was a factor correlated with population decline.

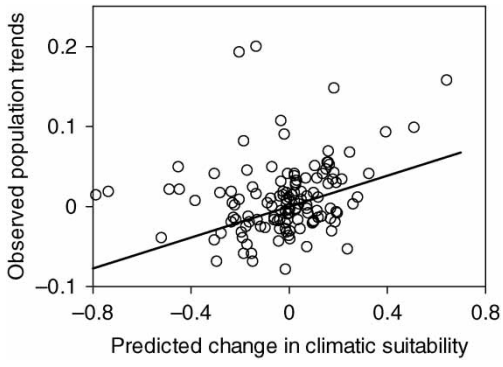

Figure 1. Effect of the predicted change in climatic suitability across the forecasted distribution range against residuals of recent observed trends (1998–2009 population trends, first adjusted to habitat specialisation, generation time and accounting for phylogenetic relatedness among species; see Appendix 2) in breeding populations of 131 common bird species of Sweden (see Appendix 1 for a list of species).

DISCUSSION

Bird distributions are well predicted by climate (Pigot *et al.* 2010). Therefore, the predicted impacts of global climate change on their future distributions, as modelled by climatic suitability models, are considered robust (Jetz *et al.* 2007, Huntley *et al.* 2008). This is supported by the ability of such climate models to model recent changes in bird species distribution, or even population size, retrospectively (Green *et al.* 2008). Recent trends in breeding bird populations are also related to ongoing climatic changes, from local to global spatial scales (Devictor *et al.* 2012, Le Viol *et al.* 2012, Lindström *et al.* 2012). The link between predicted trends in future climatic suitability and observed trends in recent population size has also been highlighted at a continental scale for European birds (Gregory *et al.* 2009). It is further supported here at a finer, national spatial scale, for a set of 131 common breeding bird species in Sweden. Trends of Swedish breeding birds are known to be partly driven by changes in land-use practices (Wretenberg *et al.* 2007), within the global framework of biotic homogenization and of declines of habitat specialists (Julliard *et al.* 2003, Le Viol *et al.* 2012). The contribution of habitat specialization to predicting recent population trends in the present study further supports this hypothesis.

Our results lend further support to using distribution range modelling to predict the fate of biodiversity (Bellard *et al.* 2012). We used presence–absence data

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at a continental scale to model current and future climatic suitability, where trends in suitability values do correlate with observed trends in the abundance of the corresponding species. Such links between climatic suitability and species abundance are not always straightforward, and previous studies have reported a mere correlation (Nielsen *et al.* 2005). Indeed, climatic suitability more likely correlates to the maximum possible abundance within the fundamental niche (van der Wal *et al.* 2009) than to the realized abundance when facing interactions with other species (Sagarin *et al.* 2006). Therefore, abundance *per se* does not necessarily correlate with climatic suitability obtained from species distribution models. To evaluate the effects of changes in climate suitability it may, therefore, be better to evaluate changes in abundance, as in the present study, since they are likely to be less sensitive to the dynamic equilibrium of bird populations and the true relationship between the local fundamental and realized niches of the species.

Adjusting the climatic suitability distributions to species-specific dispersal ability provided a slightly better fit to the current population trends, though the two models' log-likelihood values differed by less than two units. Earlier predictions of future distribution ranges have considered either a full or a null dispersal from current observed range to potential future colonized areas (Thomas *et al.* 2004, Thuiller *et al.* 2006, Huntley *et al.* 2008), although some recent studies tried to consider more realistic dispersal scenarios, for plants (Midgley *et al.* 2006, 2010) as well as for birds (Barbet-Massin *et al.* 2012).

Land-use change has driven the declines of habitat specialists in Sweden in various ways (Wretenberg *et al.* 2006), while climate warming probably became an increasing pressure on biodiversity only in the latest decade (Jiguet, Devictor *et al.* 2010, Lindström *et al.* 2012). There was a 1°C increase in average summer temperatures in Sweden between 1975 and 2009, with the largest increase taking place during the last decade (Lindström *et al.* 2012). Thus, recent climate warming has taken place, with the potential to affect bird distributions and numbers.

Most Swedish bird populations are at the northern end of the species' latitudinal distribution. These populations are, therefore, suspected to be more driven by current changing climate than their more southern counterparts, because projected impacts of climate change on birds increase with latitude (Jetz *et al.* 2007). At the very least, the potential impacts of climate change should be easier to detect at the edge of the gradual response of population dynamics along a species' thermal range (Jiguet, Devictor *et al.* 2010). As the current observed trends are proportional to the future predicted impacts of climate change, we confidently argue that current climate change is an important driver of recent bird population dynamics in Sweden, despite the effects of other drivers such as land-use changes (Robertson & Berg 1992, Wretenberg *et al.* 2006). In the present study, considering a colonization scenario constrained by species-specific natal dispersal and generation time provided only a slight improvement to explain recent population trends with predicted impacts of climate change on distribution ranges.

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APPENDIX 1. LIST OF THE 131 BREEDING BIRD SPECIES (SCIENTIFIC NAMES)

Anas crecca, *Anas penelope*, *Anas platyrhynchos*, *Aythya fuligula*, *Mergus merganser*, *Mergus serrator*, *Bucephala clangula*, *Somateria mollissima*, *Tadorna tadorna*, *Anser anser*, *Cygnus olor*, *Cygnus cygnus*, *Phasianus colchicus*, *Tetrao tetrix*, *Dendrocopos major*, *Dendrocopos minor*, *Picus viridis*, *Dryocopus martius*, *Jynx torquilla*, *Cuculus canorus*, *Apus apus*, *Columba palumbus*, *Columba livia*, *Columba oenas*, *Streptopelia decaocto*, *Botaurus stellaris*, *Adrea cinerea*, *Gavia stellata*, *Gavia arctica*, *Podiceps cristatus*, *Podiceps auritus*, *Accipiter nisus*, *Circus*

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aeruginosus, *Milvus milvus*, *Buteo buteo*, *Pernis apivorus*, *Pandion haliaetus*, *Falco tinnunculus*, *Larus ridibundus*, *Larus canus*, *Larus fuscus*, *Larus marinus*, *Larus argentatus*, *Sterna hirundo*, *Sterna paradisaea*, *Charadrius hiaticula*, *Pluvialis apricaria*, *Vanellus vanellus*, *Haematopus ostralegus*, *Gallinago gallinago*, *Scolopax rusticola*, *Numenius arquata*, *Actitis hypoleucos*, *Tringa totanus*, *Tringa nebularia*, *Tringa ochropus*, *Tringa glareola*, *Fulica atra*, *Grus grus*, *Lanius collurio*, *Corvus corax*, *Corvus cornix*, *Corvus frugilegus*, *Corvus monedula*, *Nucifraga caryocatactes*, *Pica pica*, *Garrulus glandarius*, *Luscinia luscinia*, *Phoenicurus phoenicurus*, *Oenanthe oenanthe*, *Saxicola rubetra*, *Ficedula hypoleuca*, *Muscicapa striata*, *Erithacus rubecula*, *Turdus merula*, *Turdus philomelos*, *Turdus viscivorus*, *Turdus pilaris*, *Turdus iliacus*, *Sturnus vulgaris*, *Certhia familiaris*, *Troglodytes troglodytes*, *Sitta europaea*, *Acrocephalus schoenobaenus*, *Acrocephalus palustris*, *Acrocephalus scirpaceus*, *Hippolais icterina*, *Sylvia atricapilla*, *Sylvia borin*, *Sylvia curruca*, *Sylvia communis*, *Phylloscopus collybita*, *Phylloscopus trochilus*, *Phylloscopus sibilatrix*, *Locustella naevia*, *Regulus regulus*, *Delichon urbicum*, *Hirundo rustica*, *Riparia riparia*, *Aegithalos caudatus*, *Parus caeruleus*, *Parus major*, *Parus ater*, *Parus cristatus*, *Parus palustris*, *Parus montanus*, *Alauda arvensis*, *Lullula arborea*, *Passer domesticus*, *Passer montanus*, *Anthus trivialis*, *Anthus pratensis*, *Motacilla alba*, *Motacilla cinerea*, *Motacilla flava*, *Prunella modularis*, *Emberiza citrinella*, *Emberiza schoeniclus*, *Emberiza rustica*, *Emberiza hortulana*, *Carduelis cannabina*, *Carduelis spinus*, *Carduelis carduelis*, *Carduelis flammea*, *Carduelis chloris*, *Loxia curvirostra*, *Carpodacus erythrinus*, *Pyrrhula pyrrhula*, *Coccothraustes coccothraustes*, *Fringilla coelebs*, *Fringilla montifringilla*.

APPENDIX 2. PHYLOGENETIC TREE OF THE 131 SPECIES USED TO DEFINE THE WITHIN-GROUP CORRELATION STRUCTURE

TREE < -"((((((((((Anas_crecca,Anas_penelope,
Anas_platyrhynchos),Aythya_fuligula),
Mergus_merganser,Mergus_serrator),
Bucephala_clangula),Somateria_mollissima),
Tadorna_tadorna),Anser_anser),(Cygnus_olor,
Cygnus_cygnus)),(Phasianus_colchicus,Tetrao_tetrix)),
(((((Dendrocopos_major,Dendrocopos_minor),
Picus_viridis),Dryocopus_martius),Jynx_torquilla),
(Cuculus_canorus,(Apus_apus,(((Columba_palumbus,
(Columba_livia,Columba_oenas)),
Streptopelia_decaocto),(((((Botaurus_stellaris,
Ardea_cinerea),((Gavia_stellata,Gavia_arctica),
(Podiceps_cristatus,Podiceps_auritus))),
(((((Accipiter_nisus,Circus_aeruginosus),
(Milvus_milvus,Buteo_buteo)),Pernis_apivorus),
Pandion_haliaetus),Falco_tinnunculus)),
((((Larus_ridibundus,(Larus_canus,Larus_fuscus,
Larus_marinus,Larus_argentatus)),(Sterna_hirundo,
Sterna_paradisaea)),(((Charadrius_hiaticula,
Pluvialis_apricaria),Vanellus_vanellus,
Haematopus_ostralegus),(((Gallinago_gallinago,
Scolopax_rusticola),Numenius_arquata),
(Actitis_hypoleucos,Tringa_totanus,Tringa_nebularia,
Tringa_ochropus,Tringa_glareola)))),(Fulica_atra,
Grus_grus))),((Lanius_collurio,(((Corvus_corax,
(Corvus_cornix,Corvus_frugilegus,Corvus_monedula)),
Nucifraga_caryocatactes),(Pica_pica,
Garrulus_glandarius))),((((((Luscinia_luscinia,
Phoenicurus_phoenicurus,Oenanthe_oenanthe),
(Saxicola_rubetra,(Ficedula_hypoleuca,
Muscicapa_striata))),Erithacus_rubecula),
(Turdus_merula,(Turdus_philomelos,
Turdus_viscivorus,Turdus_pilaris,Turdus_iliacus))),
Sturnus_vulgaris),((((Certhia_familiaris,
Troglodytes_troglodytes),Sitta_europaea),
(((((((((Acrocephalus_schoenobaenus,
(Acrocephalus_palustris,Acrocephalus_scirpaceus)),
Hippolais_icterina),((Sylvia_atricapilla,Sylvia_borin),
(Sylvia_curruca,Sylvia_communis))),
((Phylloscopus_collybita,Phylloscopus_trochilus),
Phylloscopus_sibilatrix)),Locustella_naevia),
Regulus_regulus),(Delichon_urbicum,Hirundo_rustica,
Riparia_riparia)),Aegithalos_caudatus),
((Parus_caeruleus,Parus_major),(Parus_ater,
(Parus_cristatus,Parus_palustris,Parus_montanus)))))),
((Alauda_arvensis,Lullula_arborea),
(((Passer_domesticus,Passer_montanus),
(((Anthus_trivialis,Anthus_pratensis),(Motacilla_alba,
(Motacilla_cinerea,Motacilla_flava))),
Prunella_modularis)),((Emberiza_citrinella,
Emberiza_schoeniclus,Emberiza_rustica,
Emberiza_hortulana),(((((((Carduelis_cannabina,
Carduelis_spinus),(Carduelis_carduelis,
Carduelis_flammea)),Carduelis_chloris),
Loxia_curvirostra),Carpodacus_erythrinus),
Pyrrhula_pyrrhula),Coccothraustes_coccothraustes),
(Fringilla_coelebs,Fringilla_montifringilla)))))))))))))
Root;