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Vliv klimatických podmínek a změn v krajině na ptačí společenstva
The impact of climate and land-use changes on birds

Disertační práce

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Prohlášení:

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Poděkování

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Úvod:

Ptačí populace jsou ovlivněny mnoha vnějšími faktory, které způsobují jejich změny. Citlivost jednotlivých druhů na měnící se podmínky pak určuje, zda určitý druh na daném místě přibývá, či ubývá (Donald et al. 2006). Pro odhalení faktorů působících na ptáky, které jsou zároveň relevantní z hlediska jejich ochrany, je nutné použít data zachycující vývoj ptačích populací a zajisté nejvhodnější jsou ta dlouhodobá, jelikož odfiltrují krátkodobé výkyvy a přesněji vymezí ty faktory, které pozitivně i negativně působí na populační trendy (Keith et al. 2015). Co nejpřesnější identifikace vlivů, které při dlouhodobém působení potenciálně vedou k lokální extinkci, je zásadní pro stanovení ochrannářských priorit a následné zacílení praktické ochrany (Donald et al. 2007).

Při bližším pohledu na problematiku zjistíme, že nejčastěji jsou v kontextu populačních změn zmiňovány dva faktory, a sice klima a habitat (Reif 2013). Důkazy o tom, že měnící se klima ovlivňuje ptactvo, se množí po celém světě (Stephens et al. 2016). Klimatické změny zahrnují komplexní procesy, jejichž dopady se liší v různých částech světa (Loarie et al. 2009). V některých regionech dochází k nárůstu průměrných teplot, či naopak poklesu srážek a globálně byl zaznamenán i nárůst klimatických anomálií (IPCC 2013). V Evropě se tyto procesy projevují zejména na posunu fenologie ptačích druhů způsobené časnějším nástupem jara (Pautasso 2012). Nízká schopnost zareagovat na tento posun vede k poklesům hnízdní úspěšnosti či eventuelně k nárůstu mortality dospělých jedinců (Julliard et al. 2003), výsledkem čehož je populační pokles dotčených druhů, konkrétně dálkových migrantů, kteří nereagují na časnější nástup jara a vzniká u nich nesoulad se zahájením hnízdění a vrcholem potravní hojnosti v hnízdišti (Sanz et al. 2003, Both et al. 2006). Radikální změny jarního počasí tedy znevýhodňují dálkové migranty a mírnější zimy jsou naopak prospěšné pro některé rezidentní druhy (Knudsen et al. 2011), kterým nárůst teplot může prospívat. Ne všechny mechanismy ale postihují jen druhy s určitou migrační strategií skrze potravní řetězec, či fenologický cyklus. Změny klimatu mohou mít i přímý vliv na ptáky. Neočekávané klimatické anomálie, jako například vlny horka, sucha, či srážek bezprostředně ovlivňují ptačí populace a způsobují vyšší úmrtnost (Van Franeker et al. 2001, Julliard et al. 2004).

Měnící se podmínky vlivem klimatických změn nutí ptáky reagovat na nově vzniklé situace. Ti se pak na nové podmínky adaptují, nebo se potenciálně nevyhovujícím okolnostem snaží vyhnout tak, že doposud obývanou oblast opustí a osídlí jinou. Druhy se posouvají ve snaze následovat posuny své klimatické niky, v důsledku čehož se ale mění i celé ekosystémy a vazby mezi druhy (Devictor et al. 2008, 2012). Důkazů o vlivu klimatických změn na ptačí populace se napříč Evropou objevuje velké množství, přesto není úplně zřejmé, jak přesně tento mechanismus na ptáky působí (Pearce-Higgins et al. 2015).

Reakce druhů na změnu prostředí, ve kterém žijí, se dá do určité míry předpovídat v závislosti na vlastnostech druhu, které poukazují, jak daný druh interaguje s prostředím (Webb et al. 2010). Analýzy populačních trendů založené na zkoumání vlastností druhů jsou v celku zajímavým přístupem, jak nahlédnout na to, do jaké míry klimatické změny druhů zasahují (Reif 2013). Vlastnosti druhu ovlivňují, jak bude daný druh na vzniklou změnu reagovat, ovšem nejen na klimatickou, ale například i na změny v krajině nebo ve využívání půdy (Garcia et al. 2014). Je ale zřejmé, že druhy, které své areály posouvají podobným způsobem, sdílejí určité vlastnosti (Goodenough and Hart 2013).

Habitat zásadně ovlivňuje rozšíření druhů, protože druhy se nemohou dlouhodobě vyskytovat v prostředí, které pro ně není příznivé (Gaston and Blackburn 2000). S vývojem lidské společnosti je neodmyslitelně spjatý i vývoj životního prostředí, ať už jde o expanzi a rozvoj měst, nebo dochází ke změnám ve využívání krajiny (Sádlo et al. 2005). Přičemž tento vývoj neprobíhá ve všech zemích ani stejným způsobem, ani stejnou rychlostí. V západní Evropě je v souvislosti s ptáčimi populacemi nejčastěji zmiňovaná intenzifikace zemědělství (Donald et al. 2001). Na jihu Evropy dochází k opouštění půdy a sukcesi dřevin (Laiolo et al. 2004). Podobná situace, ale ne tolik výrazná se odehrává i na severu Evropy (Wretenberg et al. 2006) a ve východní části kontinentu, v postkomunistických zemích, došlo po vstupu do EU též k nárůstu intenzity hospodaření (Sanderson et al. 2013). Mezi další procesy patří například fragmentace původně celistvých prostředí, nebo zalesňování (Sklenička and Šálek 2008). Přestože jsou alespoň někteří ptáci na nově vzniklé změny méně choulostiví a zvládají se přizpůsobit (cf. Møller et al. 2015), tak stále nemáme kompletní informace o tom, jak se jejich populace v budoucnu reálně budou vyvíjet například v kontextu změn v potravním zastoupení (v nově vzniklých podmínkách nemusí žít ti samí bezobratlí, růst stejné rostliny apod.), v rozdílných mezidruhových vztazích, přítomnosti rozdílných patogenů atd.

Díky své popularitě zejména mezi amatérskými přírodovědci byla v mnoha evropských zemích nashromážděna celkem robustní data o početnosti ptáků pokrývající celé dekády (Greenwood 2003). Zásobárna takovýchto dat poskytla badatelům náhled, jak se populace ptáků měnily v dlouhodobých horizontech (Jiguet et al. 2012). V přístupech, jak daný materiál uchopit, ale chtě nechtě vznikla další rozmanitost. Mnoho studií se snažilo objasnit variabilitu v populačních trendech, k čemuž byly použity různé metodické přístupy, a i proto se význam jednotlivých ekologických proměnných mezi různými studiemi liší (Říhová 2015). Rozdílné závěry lze najít často i v rámci regionů (Říhová 2015). Je tak velice obtížné vyvodit obecné zákonitosti aplikovatelné například na celé areály rozšíření.

Tato disertační práce představuje vyhodnocení dopadu dvou nejvíce diskutovaných faktorů na ptáčí společenstva, a to sice klimatu a habitatu, v makroregionálním a kontinentálním měřítku.

Klima a jeho vliv na distribuci a početnost ptáků:

Změny distribuce a posun areálů rozšíření

Z globálního pohledu na distribuci byl pozorován celkový posun areálu rozšíření směrem do chladnějších oblastí, a to nejen u ptáků, ale i u jiných organismů, jako například u motýlů, či brouků (Bowler et al. 2015). Jelikož jsou ptáci velmi mobilní a jsou schopni relativně rychle reagovat na měnící se podmínky, posouvají své areály rozšíření z míst, která pro ně přestanou být vhodná do oblastí, ve kterých pro ně vznikají příhodné klimatické podmínky (Devictor et al. 2008).

Posun ale neprobíhá u všech druhů stejně. Jelikož se jednotlivé druhy mezi sebou liší v klimatických nárocích, a navíc klimatická změna nepůsobí napříč prostorem rovnoměrně, vzniká i variabilita v reakci na tyto podmínky (Huntley et al. 2006, 2008, **Příspěvek II**). Jednotlivé druhy se tedy mezi sebou liší v míře a směru posunu. A právě daná variabilita by mohla najít uplatnění v praktické ochraně. Například druhy, u kterých předpokládáme, že v průběhu 21. století zmenší rozlohu areálu rozšíření, v současné době vykazují největší populační pokles (Gregory et al. 2009). Předpokládané změny v rozloze areálu byly též spojovány s preferovaným habitatem (Angert et al. 2011) či mírou endemismu (Goodenough and Hart 2013).

Habitat je velmi důležitým ekologickým faktorem, který ovlivňuje výskyt a početnost (Reif 2008). Bylo zjištěno, že druhy s podobnými habitatovými nároky reagují přibližně stejným způsobem a podobně posouvají své areály (Goodenough and Hart 2013). Korelace mezi vlivem habitatových proměnných a klimatickou nikou není u ptáků ničím překvapujícím (Barnagaud et al. 2012). Některé skupiny druhů podle toho, jaký habitat obývají, mohou mít na klima shodnou reakci. Například druhy vázané na mokřadní habitaty posouvají své areály nejvíce, a to severovýchodním a severozápadním směrem (**Příspěvek II**) v souvislosti s narůstajícími srážkovými úhrny v severní části kontinentu (IPCC 2013).

Největší posun k severu vykazují lesní druhy a malé druhy obývající otevřenou krajinu (**Příspěvek II**). Velký posun lesních druhů by mohl být vysvětlen vztahem k chladnějším oblastem, zatímco druhy otevřených habitatů jsou teplomilnější. Zjištěné rozdíly v posunech druhů by mohly být vysvětleny tím, že klimatická změna probíhá rychleji právě na chladném severu (IPCC 2013, Massimino et al. 2015). Můžeme tedy říci, že lesní ptáci jsou proto náchylnější ke klimatickým změnám. Zároveň je zajímavé pozorovat, co se vlastně děje s areály lesních druhů, protože druhy z jehličnatých lesů vykazují spíše zmenšování areálu, kdežto druhy opadavých lesů zaznamenávají expanzi (Reif et al. 2008a, Jongsomjit et al. 2013). Nedá se tedy ani říci, že všichni lesní ptáci ubývají. U některých druhů byl dokonce

zaznamenán i přírůstek (**Příspěvek III**). V mnoha Evropských zemích dochází k rozšiřování lesních biotopů a je nepravděpodobné, že by všechny lesní druhy byly na ústupu (Gregory et al. 2007, Reif 2013). Největší posun k severu vykazují habitatoví specialisté, naproti tomu nejmenší generalisté (**Příspěvek II**). Generalisté se mnohem snáze vyrovnávají s dopadem klimatických změn než specialisté (Jiguet et al. 2007, Pearce-Higgins et al. 2015), a proto jsou pod vlivem klimatických změn ekologicky specializované druhy mnohem více tlačeny k posunu areálů na sever. Oproti tomu generalisté jsou klimatem ovlivněni daleko méně a méně na ně též reagují (**Příspěvek I, Příspěvek II**).

V naší studii (**Příspěvek II**) jsme zjistili, že právě dálkoví migranti vykazují nejvyšší míru posunu areálu. Nepředpokládáme, že daný jev vzniká vlivem jejich větší mobility, protože ta se v použitých datech nemohla projevit, ale kvůli latitudinální distribuci druhů s rozdílnou migrační strategií. S rostoucí latitudou počty dálkových migrantů klesají. Dálkoví migranti se tedy v Evropě soustředí spíše do nižších a středních zeměpisných šířek (Lemoine and Böhning-Gaese 2003) a mají tak prostor pro potenciální posun, než migranti na krátkou vzdálenost, či rezidentní druhy, kteří naopak tvoří hlavní část severských populací (Lemoine and Böhning-Gaese 2003).

Populační změny související s posunem areálu

Předpovídaný posun odráží míru tlaku, jakým klima na ptáky působí. Lze předpokládat, že druhy posouvající své areály nejméně vykazují určitou odolnost vůči nastávající klimatické změně, na druhou stranu čím více druhy posouvají své areály, tím více jsou na klima citlivé (Renwick et al. 2012).

Největší posun je v Evropě predikován pro druhy posouvající areál rozšíření severním směrem (**Příspěvek II**) a zároveň druhy s areálem rozšíření poblíž severní hranice kontinentu mají menší potenciál k posunu. Vzhledem k tlaku, kterým na ně klima působí, je otázkou, jak se změny v distribuci podepíší na jejich populacích.

Mnoho studií se z toho důvodu následně zaměřilo na prozkoumání vztahu mezi populačními trendy a latitudinální distribucí a zjistilo se, že chladnomilné druhy ubývají, kdežto u teplomilných druhů byl v Evropě zaznamenán nárůst populací (Gregory et al. 2009, Jiguet et al. 2010, **Příspěvek I**). Takové zjištění podporuje názor, že druhy, které posouvají areál více, jsou spíše citlivé na klima a následně jejich populace vykazují vesměs negativní reakci. Na evropském kontinentu pak právě severní druhy vykazují mnohem negativnější trendy, než druhy z jižní části kontinentu (**Příspěvek III**).

Heterogenita v míře posunu a rozdílné reakce populací na klimatické změny budou pak zásadně měnit druhové složení ptačích společenstev v prostoru. Středoevropské druhy nevykazují tak výrazný posun, jako druhy jižní a severní (Reif et al. 2010). V budoucnu můžeme předpokládat radikální populační pokles severských druhů, kdežto jižní druhy budou přibývat (Lemoine et al. 2007, **Příspěvek I**). Díky čemuž se zřejmě změní druhové bohatství ve střední Evropě. Ovšem jakým způsobem se změní, je v současné době obtížné předpovídat. Vzhledem k současné podobě latitudinálního gradientu druhové bohatosti ptáků v Evropě (Huntley et al. 2007), kdy ve středních šířkách je druhů nejvíce a v severních i jižních méně (zřejmě v souvislosti menší úživností prostředí směrem k severní i jižní hranici kontinentu), lze předpokládat, že druhová bohatost na jihu pravděpodobně vlivem „odlivu“ jižních směrem na sever a omezenému „přilivu“ druhů ze severu Afriky poklesne, a naopak v severní části kontinentu se v důsledku posunu druhově bohatých středoevropských společenstev zvýší (Barbet-Massin et al. 2012). Empirické studie zaměřující se na současné projevy klimatických změn ve změně distribuce ptačí druhové bohatosti tyto predikce víceméně potvrzují (např. Lindström et al. 2013).

Další jev spojený s narůstajícími teplotami, který byl pozorovaný nejen u ptáků, je posun horských druhů směrem do vyšších nadmořských výšek (Popy et al. 2010). Ten se v drtivé většině dosavadních studií zaměřených na latitudinální posuny areálu zanedbával, ačkoliv je logicky může „brzdit“, a proto v oblastech s různorodějším reliéfem můžeme očekávat omezenější posunu než na rovných nížinných plochách. Nejnovější studie zohledňující výškový posun skutečně zjišťují jeho výrazný dopad na míru latitudinálního posunu (Auer and King 2014), a proto by měl být v budoucích projekcích brán také v úvahu.

Dopad změn habitatu na ptačí populace:

Vliv změn v krajině na ptáky

Asi nejsnadněji zhodnotitelnou situaci vidíme u druhů otevřené krajiny, u kterých je pozorován napříč evropským kontinentem pokles (**Příspěvek III, Příspěvek IV**). V minulosti byly nejdramatičtější populační změny zaznamenány u západoevropských ptáků obývajících vysoce intenzivně využívanou zemědělskou krajinu, kde už po desetiletí populace tamních druhů vykazují prudký pokles (Gregory et al. 2005). Znatelně mírnější úbytek byl zaznamenán v bývalých komunistických zemích východní Evropy (Donald et al. 2001), kde po změně režimu dokonce trendy zaznamenaly mírný nárůst, než opět klesly (Reif et al. 2008b). V současné době ale pokles už není na Západě tak prudký (Inger et al. 2015) a naopak východní populace po vstupu do EU a změně hospodářské politiky zaznamenaly intenzivnější úbytek (Sanderson et al. 2013). Navzdory rozdílům v mikrohabitatových nárocích

jednotlivých druhů, byl populační úbytek ptáků zemědělské krajiny zaznamenán napříč celým kontinentem, nejméně však u druhů vázaných na ornou půdu (Chamberlain and Fuller 2001). Obecně je snižování počtu přisuzováno hospodářské politice států (Pe'er et al. 2014), přičemž asi největší roli hraje intenzifikace zemědělství (Donald et al. 2001), a to zejména přechod z jarní na zimní setbu spojený s absencí strnišť a aplikací pesticidů, což se projevuje nedostatkem potravy ke konci zimního období (Chamberlain et al. 2000). Negativní dopad má též redukce marginálních habitatů. Zasaženy tak jsou nejen druhy otevřené krajiny, ale i ty, které se na polích přizívají (Reif et al. 2014).

Obdobným příkladem může být i opouštění orné půdy, díky kterému dochází ke zhoršení kvality prostředí. K opouštění od orby dochází plošně napříč Evropou, v různých regionech má ale tento proces rozdílné příčiny. V České republice se v 90. letech rozmohl trend rozšiřování pastvin na úkor orné půdy (Hanzelka et al. 2015). V severní Evropě se naopak ustupuje od orby z důvodu zalesňování, které následně vede k poklesu populací polních ptáků (Wretenberg et al. 2006). Vzhledem k tomu, že populace obývající části areálů obhospodařované intenzivním způsobem, mají dle zmíněných poznatků tendenci klesat, tak v oblastech, kde dochází ke zhoršení podmínek vlivem opouštění půdy, vlastně vzniká na druhy dvojitý tlak (Reif 2013). Oproti tomu ekologičtí generalisté mohou z nově vzniklé situace profitovat a opuštěné plochy a nově zalesněné oblasti kolonizovat, díky čemuž jejich počty stoupají (Shultz et al. 2005).

Oproti strmému poklesu polních druhů si ptáci lesů stojí všeobecně dobře (Reif 2013). Navzdory tomu byl v některých regionech zaznamenán pokles, například u populací některých lesních druhů, a to z různých mikrohabitatů v celé Evropě (Gregory et al. 2007). Zejména u lesních specialistů je pravděpodobně zapříčiněn nahrazováním starších a původních porostů mladými jehličnatými monokulturami (Schulte et al. 2005, Reif et al. 2014, Fraixedas et al. 2015). Nejen habitatové změny, ale i fragmentace lesních ploch by mohly vysvětlovat vztah mezi lesními druhy a habitatovými proměnnými (Böhning-Gaese et al. 1993). Fragmenty totiž často podléhají vyššímu predančnímu tlaku a právě predančnímu tlaku je připisován za vinu například pokles hmyzožravých pěvců (Böhning-Gaese et al. 1993).

Trendy vodních ptáků nejsou v Evropě v různých regionech shodné, ve většině oblastí jsou ale spíše pozitivní (**Příspěvek III, Příspěvek IV**, Musilová et al. 2015) a obzvláště pak v jižní a západní Evropě (Seoane and Carrascal 2008). Vzhledem k rostoucím úhrnům srážek v severní části kontinentu a poklesu na jihu (IPCC 2013), posouvají vodní ptáci své areály rozšíření na sever. Zároveň tato skupina vykazuje největší posun severním a severozápadním směrem ze všech skupin ptáků a i v budoucnu můžeme tento trend očekávat. (**Příspěvek III**).

Mnoho vodních ptáků v různých částech kontinentu své areály zvětšuje (Van Turnhout et al. 2007, Lemoine et al. 2007).

Zhoršování kvality vodních habitatů, konkrétně například pokles kvality vod a eutrofizace, se v minulosti značně negativním způsobem podepsaly na populacích mokřadních druhů (Van Turnhout et al. 2010). Čistota vody, zejména množství polutantů a pH se sice zlepšilo, míra eutrofizace ale ne, přičemž množství živin ve vodě značnou měrou ovlivňuje celý potravní řetězec s dramatickými dopady na ptačí populace (Lehikoinen et al. 2015). V krajním případě pak můžeme pozorovat nárůst populací ryb, který sice svědčí rybožravým ptákům (Musil and Fuchs 1994), ale na druhou stranu zhoršuje průhlednost vod, což je naopak překážkou pro druhy orientující se pod vodou vizuálně (Cepák and Musil 1996).

I přesto v současné době vykazují vodní druhy populační přírůstek. Nárůst mokřadních druhů, zejména těch ohrožených může být vysvětlen zejména pozitivním dopadem ochrany jak druhové, tak i habitatové (**Příspěvek IV**), ovšem nezanedbatelný vliv může mít i zmírňování klimatu (Musilová et al. 2015).

Migrační strategie je jednou z nejdůležitějších druhových vlastností, u nichž byla zjištěna souvislost s trendem početnosti (Thaxter et al. 2010). Dálkoví migranti patří mezi skupiny ptáků všeobecně brané jako ubývající (Knudsen et al. 2011). Přičemž pokles jejich populací je přisuzován hlavně fenologickému nesouladu vznikajícím v důsledku klimatické změny (Both et al. 2006) v interakci se zhoršením kvality habitatu na zimovišti (Mantyka-Pringle et al. 2012). Pokud se ale podíváme na oblast Sahelu, kde v současnosti dochází k poklesu srážkových úhrnů a desertifikaci a tím pádem i zhoršení kvality prostředí, která přímo souvisí i s rapidním zvyšováním místní lidské populace následně spojené se zvýšeným tlakem na přírodní biotopy (Zwarts et al. 2009), je pak těžké od sebe tyto dva faktory striktně oddělit. Nové studie také ukazují, že zachycení vlivu faktoru působícího na zimovišti je metodicky obtížnější než u faktoru působícího v hnízdním období (Cresswell 2014). Proto je nyní ještě brzy dělat závěry ohledně toho, co rozhodujícím způsobem zapříčiňuje úbytek dálkových migrantů (Vickery et al. 2014).

Mění se klimatické podmínky a habitat

Debata o tom, jestli ptačí populace ovlivňují více klimatické nebo habitatové změny, je stále živá (Reif 2013).

Ráz krajiny se mění jak z důvodu změn v obhospodařování, tak i kvůli spontánním transformacím, ke kterým v krajině dochází (Pokorný 2011). Ačkoliv dopad změn v krajině na lokální populace lze celkem snadno vyjádřit, ale v kontinentálním měřítku vyhodnocování již tak snadné není, protože neumíme dostatečně dobře uchopit, v jakých habitatech jednotlivé

druhy žijí (Keil et al. 2012). Naopak zachycení klimatické niky jednotlivých druhů je na velkých škálách poměrně jednoduché a i přes řadu zjednodušení se pokládá za překvapivě přesné (Araújo et al. 2009), což může vést k dojmu, že klimatická změna formuje vývoj ptačích populací více než změny habitatů (Lemoine et al. 2007). Právě proto jsme u běžných druhů očekávali užší vazbu na klimatické faktory a kromě toho jde obecně o druhy s širší nikou a tedy vyšší tolerancí, co se prostředí týče. Překvapivě se však ukázalo, že u nich je hlavním ovlivňujícím faktorem právě habitat (**Příspěvek IV**).

V praxi může být obtížné od sebe jednotlivé faktory rozpoznat a třeba pokles široce rozšířených druhů nemusí být jednoznačně spjatý pouze s jedním faktorem (**Příspěvek I**, Gregory et al. 2005). Je také otázkou, zda dopad klimatických změn může být ovlivněn změnami probíhajícími v krajině, které jsou vlastně nepřímo indukované právě klimatem (Davey et al. 2012).

Konkrétní příklad najdeme v České republice, kde byla v posledních desetiletích zhruba pětina jehličnatého porostu nahrazena tradičním listnatým lesem, a zároveň zde byl zaznamenán pokles druhů vázaných na tento konkrétní typ prostředí (Reif et al. 2008b). V případě, že severské druhy preferují jehličnaté lesy více, než ostatní ptáci, pak změny v krajině zapříčiněné člověkem jen maskují souvislost mezi klimatickou změnou a populační dynamikou. Je možné, že indikátory klimatické změny generované na základě klimatické niky souvisí s habitatovými proměnnými. Tedy že změny, ke kterým v krajině dochází, jsou zcela indukované klimatickou změnou (Clavero et al. 2011).

(Ne)možnost odlišení vlivu klimatické od habitatové změny a jejich časté interakce mají významné dopady pro praktickou ochranu přírody. Na rozdíl od možnosti plánovat hospodářské a ochranné aktivity, můžeme klima cíleně ovlivnit jen velice obtížně a pro účely ochrany druhů prakticky vůbec ne. To však neznamená, že se klimatickou změnou nemá smysl z ochranného hlediska zabývat. Z hlediska jeho budoucího vývoje máme k dispozici modely, pomocí nichž můžeme třeba odhadnout, kam bude vhodné v budoucnu nasměrovat ochranné snahy, např. zřídit chráněná území, což by mohlo druhům pomoci se vyrovnat s důsledky klimatické změny. Identifikace vhodných oblastí však závisí na kvalitě predikce, kterou modely poskytují. Klimatické modely predikující posun totiž často nezohledňují vlivy jiných faktorů, které by mohly eventuelně posun distribuce zkomplikovat, nebo dokonce znemožnit. Takovým faktorem může být třeba zánik, či změna habitatu, nebo neschopnost disperze – například u druhů s lokálním výskytem, u kterých se potenciálně vhodný habitat nepřekrývá se současným výskytem (Barbet-Massin 2012), nebo zde vstupují do hry biotické interakce (Suttle et al. 2007).

Proto lze z hlediska ochrany přírody doporučit, aby se (i) pokud možno eliminoval vliv těch faktorů, které dále zesilují negativní účinky klimatickým změn na ptáky (např. úbytek

vhodného prostředí nebo zhoršená konektivita populací). (ii) Je třeba lépe porozumět vztahům mezi klimatickou a habitatovou nikou jednotlivých druhů, což umožní přesněji modelovat budoucí dopady klimatických změn na ptačí populace.

Tato práce se snaží k výše popsané debatě přispět několika konkrétními studiemi, které:

1) ukazují, že i v měřítku posledních dvou desítek let lze zaznamenat rozpoznatelný dopad klimatické změny na populace českých ptáků, který je v souladu s do budoucna predikovanými posuny areálů (**Příspěvek I**),

2) podrobněji zkoumají druhové vlastnosti pojící se s různě výraznými klimaticky indukovanými predikovanými posuny areálů a novým způsobem vyjadřují citlivost vůči klimatické změně jako délku tohoto predikovaného posunu (**Příspěvek II**),

3) testují, zda takto vyjádřená citlivost vůči klimatické změně skutečně signifikantně souvisí s populačními dopady doteď zjištěných klimatických změn (**Příspěvek III**),

4) pokouší se na robustním datovém materiálu shromážděném na evropské úrovni rozřešit, jestli v současné době ovlivňuje ptačí populace více klimatická nebo lidskou činností způsobená habitatová změna (**Příspěvek IV**).

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Příspěvky:

Příspěvek I.

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Příspěvek III.

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Příspěvek IV.

Koschová M. and Reif (rukopis): Species' habitat use, and not climatic niche, predicts population trends in European birds. *Ecological Indicators*.

The impact of climate change on long-term population trends of birds in a central European country

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Abstract

Numerous studies have shown that climate changes associated with increasing global temperature affect bird species. For instance, long-distance migrants are not able to respond adequately to rapid advances in spring phenology, and thus their populations decline due to lower breeding performance. Moreover, many species in the Northern Hemisphere have shifted their northern breeding range boundaries further north. However, studies focusing on bird populations at the scale of individual countries, which are responsible for creating environmental policies, are rather scarce. We hypothesized that bird species with different European latitudinal breeding distributions would have different long-term population trends in the Czech Republic, a small central European country, as a result of range dynamics caused by increasing spring temperature. In accordance with this prediction, the results of an analysis based on large-scale monitoring data (from 1982 to 2006) showed that species with more northern latitudinal distributions had more negative population trends in the Czech Republic. However, the strength of the relationship depended on the approach used for characterization of the species latitudinal distributions. When a phylogenetic regression was applied, the only significant explanatory variable was the latitudinal distribution expressed in categories defined by species range areas in different latitudinal bands. A more detailed analysis showed that southern and northern species groups have opposite population trajectories: the former increased and the latter declined throughout the study period. The effect of climate change remained significant when habitat association and the migratory strategy of each species were taken into account. However, it is difficult to determine whether climate change or habitat change is the more important driver of long-term trends in bird populations as the effects of both factors are dependent on interspecific variability in levels of species specialization.

Introduction

Climate change is recognized as one of the most important forces affecting whole ecosystems and its magnitude is predicted to increase in the coming decades (IPCC, 2007). Many studies have demonstrated its pervasive effects on bird populations at various spatial scales (Crick, 2004; Lehikoinen, Sparks & Zalakevicius, 2004; Drent, 2006; La Sorte & Thompson, 2007). For instance, climate change adversely affects breeding performance locally due to mismatches between the timing of breeding and peaks of major food resources (Visser *et al.*, 1998; Both & Visser, 2001; Sanz *et al.*, 2003; Both *et al.*, 2006) or the phenology of vegetation growth (Martin, 2007). The arrival dates of many bird species, especially short-distance migrants, advance (Ahola *et al.*, 2004; Gordo & Sanz, 2006; Jonzén *et al.*, 2006; Jonzén, Hedenstrom & Lundberg, 2007), and some species stay

longer at their breeding grounds (Thorup, Tottrup & Rahbek, 2007). At both the regional and global scales, it is predicted that changing climate will cause shifts in the distribution of main habitats, resulting in the movement of species' ranges (Peterson *et al.*, 2002; Böhning-Gaese & Lemoine, 2004; Huntley *et al.*, 2006, 2008; Jetz, Wilcove & Dobson, 2007). Moreover, species can face the consequences of unexpected anomaly events, such as the heat wave in France in 2003 (Julliard, Jiguet & Couvet, 2004) or the movement of ice cliffs in Antarctica in 1996, which directly affect bird populations (Van Franeker *et al.*, 2001).

Climate change involves complex processes having different consequences in different regions across the globe (IPCC, 2007). Average temperatures are rising in some areas (most substantially in Arctic regions), the frequency and magnitude of weather perturbations are increasing worldwide, and at the same time, precipitation is decreasing in the

arid subtropics (IPCC, 2007). In regions situated in centres of huge land masses (e.g. central Asia), the impacts of changing climate could be rather minor. However, there is wide agreement among climatologists that global temperature as well as temperature in all major biogeographic regions has been increasing for more than a century, and that this increase will continue during the 21st century despite differing in magnitude locally (IPCC, 2007). Therefore, we focus on the impacts of increasing temperature on breeding bird distributions and population trends, though we acknowledge the simplicity of this approach.

Despite considerable progress in understanding the effects of climate change on patterns of bird distribution at the continental scale (Schwartz *et al.*, 2006; Hitch & Leberg, 2007; Jetz *et al.*, 2007), long-term population changes at the level of individual countries has received much less attention (Böhning-Gaese & Lemoine, 2004; Lemoine *et al.*, 2007a). This situation may be problematic from the conservation perspective, because legislative tools creating conditions for effective conservation actions are mostly passed by parliaments of particular countries (Watzold & Schwerdtner, 2005). Even international legislation, for example EU directives, is largely under the influence of national governments. Therefore, deeper understanding of the effects of climate change on bird populations at the country level is urgently needed. However, this scale of spatial resolution is too coarse to detect local consequences such as poor breeding performance on the one hand, and at the same time, too small to detect marked distributional shifts (Peterson, 2003; but see Thomas & Lennon, 1999; Brommer, 2004). More direct driving forces inducing bird population changes probably overwhelm the effects of climate change at this spatial scale. For example, land-use change (e.g. agricultural intensification) directly affects species' population sizes by constraining the area of habitats available for breeding, passage and wintering or by altering habitat qualities which influence the carrying capacities of particular habitats (Chamberlain *et al.*, 2000; Fuller *et al.*, 2005; Bolliger *et al.*, 2007). Despite this, a recent study (Lemoine *et al.*, 2007a) showed that climate change could have a significant effect on bird populations in a central European landscape, even when controlling for habitat-based factors. How can we explain the influence of climate change at this level of spatial resolution?

We suggest that the mechanisms operating at the central European scale would be similar to those affecting continental-wide species' distributional shifts, but that their effects on bird populations are less conspicuous. Central Europe shows a high diversity of vertebrate species (Hewitt, 2000), including birds (Storch *et al.*, 2003). This results from the overlap of breeding ranges for species with northern- and southern-centred distributions (Storch & Šizling, 2002). If climate change is associated with an increase of average temperature, we would predict movement of species' ranges to the north, tracking shifts of their climatic optima (Huntley *et al.*, 2007). Unfortunately, we cannot see such range shifts within the area of central Europe, because it covers only a small part of the geographic ranges of particular

species. However, range movement is closely connected to local population dynamics, due to dispersal of individuals (Holt, Gaston & He, 2002; Gaston, 2003). Therefore, even if the spatial scale is too small for range shifts to be observed, one might be able to detect local population changes underlying broad-scale range dynamics. In the central European landscape, such effects would have different population consequences on species with different latitudinal distributions in Europe. Central European populations of species with southern-centred distributions should increase, and on the other hand, populations of birds with northern-centred distributions should decline. Therefore, the central European region can be viewed as a window into species' breeding range dynamics caused by climate change.

The Czech Republic, lying in the centre of Europe, is an ideal such window. Its avifauna consists of a mixture of species differing in their latitudinal distributions (Storch & Šizling, 2002; Št'astný, Bejček & Hudec, 2006). Moreover, there are high-quality data quantifying population changes of more than a hundred species in the Czech Republic, covering almost 25 years of continuous monitoring (Reif *et al.*, 2006, 2007). If climate change has affected populations of Czech birds, we would expect the following evidence in this monitoring data: (1) a negative correlation between the latitudes of centres of species' distributions in Europe and their population trends in the Czech Republic. Species with southern-centred distributions should have more positive population trends and species with northern-centred distributions should have more negative population trends in the Czech Republic. This pattern should hold true after controlling for differences in the habitat requirements of particular species and their migration strategies. (2) Annual species' population changes should be associated with annual changes in average temperature. Specifically, population indices of species with southern-centred distributions should correlate positively with increasing temperature, and the reverse should be true for species with northern-centred distributions.

Material and methods

Bird abundance

We used data on bird abundances from the Breeding Bird Monitoring Programme (BBMP) in the Czech Republic (Janda & Št'astný, 1984). The BBMP is a large-scale generic monitoring scheme focused on long-term population changes of common bird species. Its aims and methods are similar to other projects (e.g. the Breeding Bird Survey in the UK, Newson *et al.*, 2005) connected in the Pan-European Common Bird Monitoring network (Vorisek & Marchant, 2003). The BBMP is based on the work of skilled volunteers, who have performed annual bird censuses using a standard point-count method at 335 sites scattered throughout the Czech Republic. These data cover a continuous time series from 1982 to 2006. For a more detailed description of data from the BBMP used in our analysis, see Reif *et al.* (2007, 2008). We transformed the abundance of each species into

annual indices using log-linear models in TRIM 3.51 (Pannekoek & Van Strien, 2001). The value of the index was set at 100% in 1982 as the first year. The trend is the slope of the regression line through the logarithm of the indices across sample sites in 2 consecutive years. The computation of this slope takes into account the variances and covariances of the indices. The overall trend is the average of annual trends (mean relative population change) over the whole study period (i.e. 1982–2006 in our case). See Supporting Information Table S1 for detailed information on population trends (with standard errors) of particular species.

Bird distribution

We used the EBCC Atlas of European Breeding Birds (Hagemeyer & Blair, 1997) to assess the attributes of European breeding ranges of particular species. We calculated the latitudinal midpoint of each range (see Lemoine *et al.*, 2007a), that is the difference between the latitudes of the northernmost and southernmost points of the range divided by two and subtracted from the northernmost point. In addition, we recognized four groups of species according to their European distribution (specifically, northern, southern, central and widespread species) by the following assessment procedure. We first defined three European latitudinal regions with respect to the midpoint of the latitudinal range of the Czech Republic: the northern region has its southern boundary five geographical degrees north of the latitudinal midpoint of the Czech Republic, the southern region has its northern boundary five degrees south of the midpoint of the Czech Republic and the central regional lies in the central part of the continent between the northern and southern regions. In fact, these regions broadly correspond to the biogeographical division of Europe, that is to the Mediterranean region in the south, the boreal region in the north and the continental region in the central part of Europe (European Environmental Agency, 2006). In the next step, we measured the area of the breeding range of each species in each region, and calculated the proportion of a region covered by the range of a focal species. We omitted from these calculations territories for which no data were available (i.e. grid cells depicted as grey symbols on the EBCC Atlas maps). Based on these proportions, we defined four species groups differing in the latitudinal distributions of their breeding ranges in Europe. As nearly all species have large breeding ranges distributed in all three latitudinal regions, we could not use strict criteria such as 'northern species are those confined solely to northern region'. Instead we used a criterion focused on the avoidance of a region in which a species has the lowest proportion of its range. We thus recognized: (1) northern species whose ranges cover <30% of the southern region (e.g. *Turdus pilaris*); (2) southern species whose ranges cover <30% of the northern region (e.g. *Luscinia megarhynchos*); (3) central species whose ranges cover <30% of southern and northern regions (e.g. *Parus palustris*); (4) widespread species whose ranges cover more than 30% of the area of each region (e.g. *Passer domesticus*). Although such species sorting is arbi-

trary to some extent, and indeed 30% has no biological meaning, we argue that it mirrors the real latitudinal preferences of particular species.

Climatic data

The Czech Hydrometeorological Institute provided data on annual changes of mean spring temperature (April–June) from 1982 to 2006 in the Czech Republic (Fig. 1). Previous studies have found that spring temperature has the most important impact on breeding bird populations, which can be attributed to the effects of the climate change (Visser *et al.*, 1998; Winkler, Dunn & McCulloch, 2002; Möller & Szép, 2005; Laaksonen *et al.*, 2006). Spring temperature has significantly increased in the Czech Republic during this period ($r_s = 0.47$, $n = 25$, $P = 0.018$).

Data analysis

From 152 species counted in the BBMP, we excluded 43 species with uncertain trends. To identify these uncertain trends, we followed criteria introduced by Gregory *et al.* (2007), who recognized six categories of population trends based on their 95% confidence limits: a strong increase (lower limit of confidence interval ≥ 1.05); a moderate increase ($1.00 < \text{lower limit of confidence interval} < 1.05$); stable (confidence interval encloses 1.00 but lower limit ≥ 0.95 and upper limit ≤ 1.05); a moderate decline ($0.95 < \text{upper limit of confidence interval} < 1.00$); a strong decline (upper limit of confidence interval ≤ 0.95); and an uncertain trend (confidence interval encloses 1.00 but lower limit < 0.95 or upper limit > 1.05). We further excluded six species which were detected at <30 sites, as their trends and indices could be markedly affected by local fluctuations (Fox, 2004). In total, we used 103 species with high-quality population change data for the analysis. Throughout the text, we refer to those trends with values less than one as 'negative trends' and those trends with values greater than one as 'positive trends'. There were no trends of value exactly one in our data.

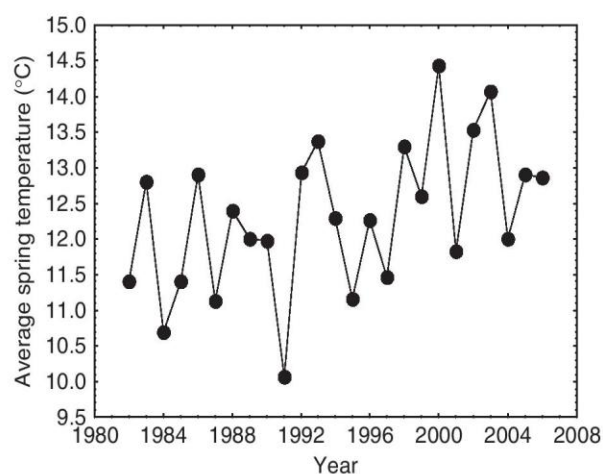


Figure 1 Changes in the average spring temperature (April–June) from 1982 to 2006 in the Czech Republic.

We related species' population trends to the latitudinal midpoints of their distributions using linear regression, and compared population trends between range-defined species' groups using one-way ANOVA. A number of studies have shown that both habitat association and migratory strategy affect bird population trends (Sanderson *et al.*, 2006; Lemoine, Schaefer & Böhning-Gaese, 2007b; Valiela & Martinetto, 2007). Therefore, we repeated the previous analyses using analysis of covariance, taking into account these potential confounding factors. Habitat requirements were extracted from Reif *et al.* (2006) sorting species into four groups (forest, farmland, urban and wetland species). Information about species' migratory strategy (long-distance migrant, short-distance migrant, resident) was provided by J. Cepák (*in litt.*) from the forthcoming Czech and Slovak Bird Migration Atlas. See Supporting Information Table S1 for data on the habitat association and migratory strategy of particular species. Finally, we calculated the geometric mean of indices for each range-defined species' group (Gregory *et al.*, 2005). These multi-species indices were correlated with mean annual spring temperatures.

Bird species are evolutionarily related through a phylogenetic scheme, and therefore they should not be treated as independent sample units (Harvey & Purvis, 1991). To overcome this problem, we applied the phylogenetic regression developed by Grafen (1989). This method is based on generalized least squares and adjusts the statistical analysis for non-independence among species. This method is very flexible and enables the fitting of standard statistical models including both categorical and continuous predictors. We used the Phyreg macro for SAS written by Grafen (2006), and applied the phylogenetic regression in all analyses testing the interspecific differences in population trends. However, some authors claim that controlling for phylogeny is not appropriate for analyses focused on recent bird population changes, having no relationship to the evolutionary history of particular species (Seoane & Carrascal, 2008). Therefore, we provide the results of both phylogenetically unconstrained analyses and analyses controlled for phylogeny (these statistics are marked with *).

We assembled a working phylogeny of the focal species based on Sibley & Ahlquist (1990), Leisler *et al.* (1997), Voelker (2002), Gill, Slikas & Sheldon (2005), Olsson *et al.* (2005), Alström *et al.* (2006), Benz, Robbins & Peterson (2006), Ekman & Ericson (2006), Arnaiz-Villena *et al.* (2007) and Päckert *et al.* (2007). Because the phylogeny was assembled from many sources, and therefore we had no consistent estimates of branch lengths, we adopted uniform branch lengths, which are reasonable for use in phylogenetic regressions (Remeš, 2006).

Results

The latitudinal midpoint explained a small proportion of the variability in species population trends (linear regression: $R^2 = 0.061$, $F_{1,101} = 6.61$, $P = 0.011$, $F^* = 2.15$, $P^* = 0.146$). As predicted, the relationship was negative illustrating that

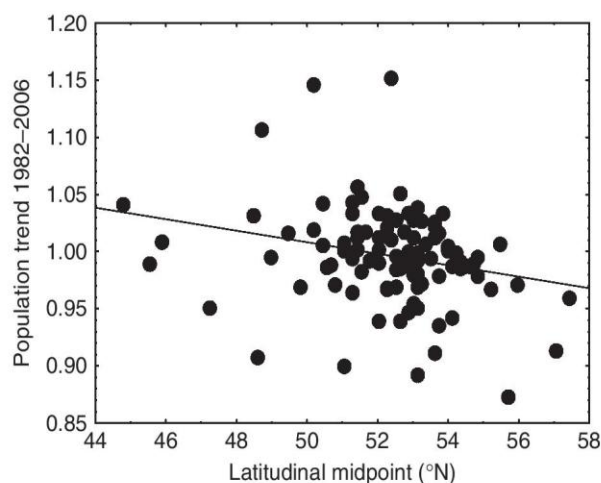


Figure 2 Relationship between the midpoint of European latitudinal breeding distribution and the population trend from 1982 to 2006 of 103 bird species in the Czech Republic.

Table 1 The effects of European latitudinal breeding distribution (expressed by the latitudinal midpoint), habitat association and migratory strategy on population trends of 103 bird species from 1982 to 2006 in the Czech Republic tested by analysis of covariance

	d.f.	<i>F</i>	<i>P</i>	<i>F</i> *	<i>P</i> *
Latitudinal midpoint	1	6.76	0.011	2.35	0.128
Habitat	3	1.45	0.234	2.34	0.078
Migratory strategy	2	1.45	0.239	1.00	0.370
Residuals	96				

Columns marked with * show results of phylogenetic regression applied in the same design as the previous analysis. See 'Materials and methods' for a more detailed description of particular variables.

Czech populations of more southerly distributed species increased on average, whereas populations of more northerly distributed species showed a general decline (Fig. 2). After controlling for the effects of habitat use and migratory strategy, the latitudinal midpoint was the sole significant predictor of population trend (Table 1). However, the effect of latitudinal midpoint on bird population trends was not significant when the phylogenetical relatedness of species was taken into account (Table 1).

Annual changes in geometric means of species' indices differed between particular species' groups defined by their European distributions (Fig. 3). Whereas northern species revealed a marked decline ($\beta = -1.68$, $r_s = -0.94$, $n = 25$, $P < 0.001$), the population increase of southern species was of lower magnitude ($\beta = 1.26$, $r_s = 0.60$, $n = 25$, $P = 0.002$). The population changes of central species were similar to those of southern species, while the population changes of widespread species resembled those of northern species (central: $\beta = 2.12$, $r_s = 0.81$, $n = 25$, $P < 0.001$; widespread: $\beta = -0.51$, $r_s = -0.58$, $n = 25$, $P = 0.002$). A comparison of population trends between the breeding range-defined species' groups showed significant differences between groups, both when phylogeny was and was not taken into

account (ANOVA: $F_{3,99} = 3.30$, $P = 0.024$, $F^* = 2.76$, $P^* = 0.046$). Trends of northern species were more negative than trends of southern species (Tukey's test: $P = 0.050$;

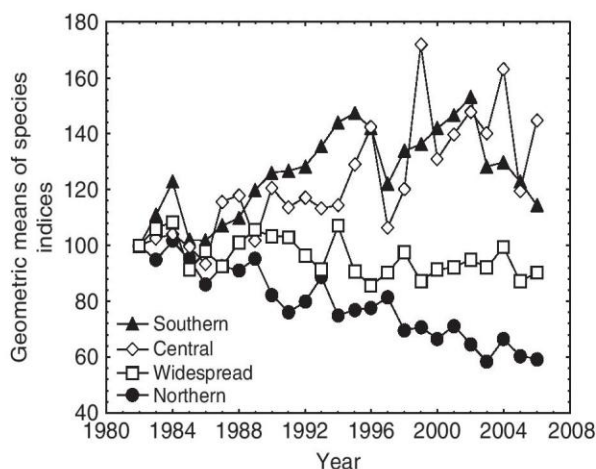


Figure 3 Changes of the geometric mean of species' population indices in four species' groups defined by their European latitudinal breeding distributions. Population indices express annual population changes in abundance of 103 bird species from 1982 to 2006 in the Czech Republic.

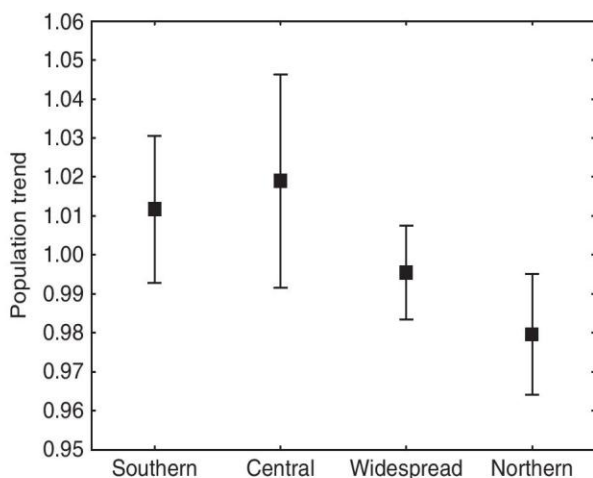


Figure 4 Differences in population trends ($\pm 95\%$ confidence intervals) between groups of 103 bird species with different latitudinal breeding distributions in Europe. The population trend expresses the average annual population change of a species from 1982 to 2006 in the Czech Republic.

Fig. 4). The effect of European distribution remained significant after including species' habitat use and migratory strategy into the model and explained the largest part of the variability in data compared with the other variables (Table 2).

Breeding range-defined species' groups differed in the relationships between their population indices and annual changes in spring temperature. These relationships were insignificant in southern species ($r_s = 0.27$, $n = 25$, $P = 0.183$), central species ($r_s = 0.33$, $n = 25$, $P = 0.111$) and widespread species ($r_s = -0.25$, $n = 25$, $P = 0.226$). Northern species showed a significant negative correlation ($r_s = -0.53$, $n = 25$, $P = 0.007$).

Discussion

Population trends describing changes in the abundance of 103 bird species from 1982 to 2006 in the Czech Republic were negatively related to latitudinal midpoints of the European breeding distributions of these species. Moreover, population trends differed between species' groups defined by their European distribution, with northern species having more negative population trends than southern species. These results confirm our first prediction stating that populations of species with different latitudinal ranges in Europe could significantly respond to changing climate even in the limited area of a small central European country. Similarly, Lemoine *et al.* (2007a) showed that species with more northern latitudinal midpoints have declined in southern Germany, supporting our view of central Europe as a window through which range dynamics are visible via species' population processes. Moreover, our results show that the projections of species' distributions in Europe under various scenarios of future climatic changes (Huntley *et al.*, 2006, 2007) have a reasonable basis in the current population trends of central European birds.

After controlling for the effect of phylogeny, the relationship between the European latitudinal distribution and population trend disappeared when we used the latitudinal midpoint as an explanatory variable. When we expressed latitudinal distribution as categories defined by the areas of species' ranges in different latitudinal bands, the relationship remained significant. We realize that latitudinal midpoint is a rather crude measure of a species' latitudinal distribution and therefore its biological meaning is limited. On the other hand, areas covered by a species' range in different latitudinal bands probably provide a better surrogate for the examination of the effects of climate on changes

Table 2 The effects of European latitudinal breeding distribution (expressed by the range-defined latitudinal category), habitat association and migratory strategy on population trends of 103 bird species from 1982 to 2006 in the Czech Republic tested by factorial analysis of variance

	d.f.	F	P	F^*	P^*
European distribution	3	4.14	0.008	2.66	0.052
Habitat	3	1.21	0.309	2.26	0.087
Migratory strategy	2	1.79	0.172	0.88	0.419
Residuals	94				

Columns marked with * show results of phylogenetic regression applied in the same design as the previous analysis. See 'Materials and methods' for a more detailed description of particular variables.

in species' abundance. Distributional limits of many species are determined by the occurrence of remote isolated populations, even though the bulk of the range of a species may be distributed in latitudes far apart from one of the limits (e.g. see the map of *Carduelis spinus* in Hagemeyer & Blair, 1997). Therefore, a latitudinal midpoint which is based on differences between the distributional limits may only weakly mirror the latitude where most of the species' range occurs and thus other measures (e.g. the centroid of the distribution) should be used (Huntley *et al.*, 2007, 2008).

Why does the European breeding distribution of a species predict its population trend in the Czech Republic? We suggest that the dispersal of juveniles plays a principal role. Although such dispersal is undirected (Greenwood & Harvey, 1982), we suppose that changing climatic conditions have caused lower survival or breeding performance of individuals of northern species that disperse towards lower latitudes. As a result, the populations breeding in lower latitudes decline and, at the same time, populations breeding in higher latitudes increase. A species' range thus moves north on a longer time scale. Because the territory of the Czech Republic, situated in the centre of the continent, samples southern populations of species with relatively northern European distributions and, at same time, northern populations of species with southern European distributions (Hagemeyer & Blair, 1997), these two groups of species differ in their average population trends in this country. Nevertheless, this pattern could also result from other factors, such as the direct effect of hot weather on the survival of adult individuals (Julliard *et al.*, 2004). Species widely distributed in southern latitudes would be more tolerant to such heat waves than species distributed in higher latitudes (Jiguet *et al.*, 2006). Moreover, migratory species could continue their migration further north in years with warmer springs, although Czech ringing data do not support this possibility (J. Cepák, *in litt.*).

The magnitude of population changes differed between groups defined by their European breeding ranges. Northern species showed the steepest population decline, but southern species revealed rather a slow population increase. This pattern could be caused by latitudes of the Czech Republic being closer in proximity to the range margins of northern species compared with that of southern species (J. Reif *et al.*, unpubl. data). The above-mentioned mechanisms could have impacts that are stronger near range edges and lower in core areas of species' ranges. Interestingly, central and widespread species also showed different population trajectories, the former resembling those of the southern species and the latter those of the northern species. Therefore, the same mechanisms of population change could apply to these species groups as in the case of southern and northern species, respectively, but with lower intensity. However, we propose that the decline of widespread species, as well as the increase of central species, need not be related to climate. There are only a few species in the central group and thus each species has a large influence on the average group performance (Gregory *et al.*, 2005). The highly positive trends of *Circus aeruginosus* or *Anas strepera*,

attributable to changes in fishpond management (Musil *et al.*, 2001), probably caused the overall increase of the central species group. On the other hand, the decline in widespread species, the group with the highest species richness in our sample, could have more complex causes connected to their continental-wide population decline (Gregory *et al.*, 2005).

Northern species had the most negative population trends and, at the same time, they were the only group with a significant (and negative) correlation with spring temperature. Although this result should be treated with caution, as time-series correlations could have no relationship to the real processes behind them (Sokal & Rohlf, 1994), we can speculate that northern species in the central European region are indeed those that are the most susceptible to the climatic change. However, the revealed pattern could be also connected to habitat changes in the Czech Republic. About 20% of coniferous forests have been replaced by deciduous broad-leaved forests during last decades (Anonymous, 2005) and many species associated with coniferous forest declined between 1982 and 2003 (Reif *et al.*, 2007). If northern species would favour coniferous forests more than other species' groups, human-caused landscape changes could mask their climate-related population trends.

Several studies have found poor breeding performance as a result of climate change in some bird species, especially long-distance migrants (e.g. Both & Visser, 2001; Sanz *et al.*, 2003; Martin, 2007). The most important factor was a mismatch between the times of rearing nestlings and peaks in prey abundance (Visser *et al.*, 1998; Laaksonen *et al.*, 2006). Birds did not sufficiently adjust their start of breeding to respond to the faster development of insects caused by warmer temperatures (Visser, Both & Lambrechts, 2004). This factor should have a particularly adverse effect on populations of long-distance migrants with genetically determined migration timing (Both *et al.*, 2006; Lemoine *et al.*, 2007b). Moreover, migratory species could suffer also from the deterioration of environmental conditions on their wintering grounds (Saether *et al.*, 2006). However, we have not found population declines of long-distance migrants in the Czech Republic (Reif *et al.*, 2006, 2007, 2008; this study). A local study performed in the southern part of the country showed that the long-distance migrant *Ficedula albicollis* was able to shift its egg-laying date proportionally to shifts in the leaf bud bursting of most tree species (Bauer, 2006a,b). However, it is impossible to generalize results from one local study to the whole-country level. Detailed examination of long-term data on the breeding performance of various bird species (using, e.g. a nest record scheme or constant-effort site trapping) would bring deeper insights into factors responsible for a relationship between temperature and population changes. Unfortunately, such data are not yet available in sufficient quality and quantity in the Czech Republic (Remeš, 2003; Jelínek, 2006).

Our analysis taking into account the habitat use of particular species corroborates the findings of Lemoine *et al.* (2007a). Their results showed that climate change was a more important factor than land-use change in shaping

differences in the abundance of bird populations between two census periods near Lake Constance in southern Germany. Our results show a similar pattern based on long-term monitoring data. However, in line with our above-mentioned interpretations, we argue that landscape change could markedly affect the observed patterns in at least some species (e.g. the population increase in wetland species). In addition, the effect of habitat approached the 0.05 significance level in all phylogenetic regressions. Therefore, one should be cautious regarding the interpretation of such results (Seoane & Carrascal, 2008). Jiguet *et al.* (2007) showed that the relationships between bird population trends and climate change are strongly affected by habitat specialization of particular species. Generalist species are more capable of tracking the effects of changing climate than specialist species (Jiguet *et al.*, 2007), which are strongly affected by habitat alteration (Archaux, 2007). Indeed, our previous work on Czech forest and farmland birds (Reif *et al.*, 2007, 2008) showed that population trends of specialists (either forest or farmland) were tightly linked to changes in their habitat. At the same time, population changes of generalist species revealed a weak association with habitat change. Therefore, to test directly whether climate change or landscape change is the more important determinant of bird population changes, it would be necessary to express the habitat specialization of each species quantitatively, and include this variable into the model. Although our BBMP data do not provide such detailed information, one could try to compile such data from published local studies or an atlas of breeding distribution (Št'astný *et al.*, 2006). Such further analysis would reveal with higher certainty whether climate change or land-use change is the more important threat to central European bird populations.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1. A list of 103 bird species used in the analyses with their population trends in the Czech Republic from 1982 to 2006 (Trend) and standard errors (SE), number of

sites where each species was censused (Sites), midpoints of their European latitudinal distribution in °N (Latitude), zones of their European latitudinal distribution centre (Zone: N - northern, S - southern, C - central, W - wide-spread; see Methods for further explanation), migratory strategy (Migration: L - long-distance migrant, S - short-distance migrant, R - resident) and habitat association (Habitat: A - farmland, F - forest, U - human settlements, W - wetlands).

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Species' ecological traits correlate with predicted climatically-induced shifts of European breeding ranges in birds

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Abstract: Climatically induced shifts of species' geographic ranges can provide important information about the potential future assembly of ecological communities. Surprisingly, interspecific variability in the magnitude and direction of these range shifts in birds has been the subject of few scientific studies, and a more detailed examination of species' ecological traits related to this variability is needed. Using maps in the Climatic Atlas of European Breeding Birds (Huntley et al. 2007) we calculated the potential shifts of European breeding ranges in 298 bird species, and explored their relationships with breeding habitat, dietary niche, migration strategy, life history and geographic position of the current breeding range. Breeding habitat type showed the strongest relationship with the potential range shifts, with forest and wetland species showing the largest magnitude of shift. At the same time, ecological specialists showed a larger magnitude of shifts than generalists. In addition, we found that species with current ranges situated near continental borders and species with lower migratory capacity are more limited in their potential to shift due to climate change. Our analyses thus indicate which ecological groups of birds will be most likely forced to move their ranges under predicted climate change. This knowledge can help to adopt proper conservation actions. These actions will be particularly important in the case of specialist species, which have been shown to be the most sensitive to climate change impacts.

Introduction

Some recent studies have shown that climate plays a key role in the population changes of many bird species (Crick 2004, La Sorte and Thompson 2007, Jiguet et al. 2010). Climate influences bird populations both directly, for instance, an increase of precipitation in spring may cause higher mortality of nestlings (Fairhurst and Bechard 2005), and indirectly, through particular components of the trophic chain (Sanz et al. 2003, Both et al. 2006, 2010).

Since population processes are closely linked to range dynamics, climatically induced population changes might result in the geographic range shifts of bird species (Araujo and New 2006, Pautasso 2012). There is an increasing body of evidence that these already occur in nature, as many species have moved their range boundaries poleward (e.g. Thomas and Lennon 1999, Hitch and Leberg 2007, Brommer 2008). That climate can play a key role in driving species' range dynamics has been confirmed by a study showing a close correspondence between past bird ranges modelled using bioclimatic variables capturing conditions of the Last Glacial Maximum and locations of sites with fossil record of the same bird species (Smith et al. 2013), as well as by bioclimatic modelling of current distributions of bird species (Jiménez-Valverde et al. 2011, Rapacciolo et al. 2012). Several recent studies have

found that species' ecological traits explain a significant proportion of the interspecific variability of these climatically induced range shifts observed over the last decades (Pöyry et al. 2009, Angert et al. 2011, Chessman 2012, Kharouba et al. 2013). Those specific traits associated with the largest range shifts observed in birds are a small geographic range size and broad ecological niche (Angert et al. 2011).

As climate change is expected to proceed with accelerating rate in the 21st century (IPCC 2007), it is expected that range shifts will be much larger in the future (Huntley et al. 2008, Barbet-Massin et al. 2012). Future range shifts under conditions of ongoing climate change have been estimated using climate envelope models (Araujo et al. 2009). Climate envelope is defined by the climatic conditions in the geographic range of a given species and can be expressed by using various measures such as thermal range, thermal optimum, mean precipitation or latitudinal midpoint (Jiguet et al. 2007). The climate envelope models are thus based on the relationships between current species distribution and climatic conditions in species geographic ranges (Huntley et al. 2007). Using these relationships and projected climatic scenarios for a focal time period in the future, we can model potential species ranges expected under given climatic conditions. The difference in geographic position between the current and modelled future species ranges is called the potential range

shift. Because climatic envelopes markedly differ among species (Chessman 2012) and, moreover, patterns of climate change vary across space, potential shifts show strong variability among species (Huntley et al. 2006, 2008). This variability can have important biological and conservation implications. For instance, Gregory et al. (2009) have shown that European bird species whose ranges are predicted to contract the most during the 21st century currently show the steepest population declines. A similar exercise was performed by Goodenough and Hart (2013) using the same dataset, but relating the changes in range size, range margins and overlap to a larger set of species' traits. Similarly to studies focusing on the changes in bird distribution observed over the past few decades (Angert et al. 2011), they found that the predicted changes in range size were related to species' habitat use, current range size and endemism (Goodenough and Hart 2013).

The aim of this study is to further explore the variability in climatically induced potential range shifts of European birds from a perspective of species' ecological characteristics. We do not focus on changes in range size, range margins or overlap, since this work has already been performed in some recent studies (Gregory et al. 2009, Goodenough and Hart 2013). Instead, we focus on the magnitude and direction of potential shifts of range centres. These variables provide information on distance by which the range of a given species has moved as a whole. There is thus a straightforward link to the intensity of the potential pressure of future climate change on a given species (Huntley et al. 2007). At the same time, the magnitude and direction of potential shifts has to date remained unexplored from the perspective of interspecific variability. Specifically, we ask which traits are typical for species shifting their ranges further, in contrast to species with smaller range shifts. Even though we may be unable to resist the impacts of climate change, if we reveal which ecological groups of species are predicted to be under the highest pressure (here expressed as the potential range shift), we can better focus on means of effective mitigation (Pearce-Higgins et al. 2011). For example, water birds seem to be significantly shifting their ranges as a result of climate change, therefore clear focus should be on the protection of wetlands in order to avoid a double threat – climate change accompanied by the disappearance of breeding habitats. The interaction between climatic processes and land use change has been recently recognized as one of the most important threats for biodiversity (Butchart et al. 2010). Several studies showed that land use change is a dominant driver in trends of species' abundance and distribution even under the conditions of recent climatic changes (Reif et al. 2010, Eglinton and Pearce-Higgins 2012, Beale et al. 2013). However, the climate change can seriously increase the risk species' extinction when the habitats are deteriorated by human exploitation (Matyka-Pringle et al. 2012). For example, in Sahel hunting pressure in wetlands is highest and has the most negative impact on water bird populations in years with the lowest rainfall (Zwarts et al. 2010).

Here we focus on traits that have been found in previous studies to be importantly related to changes in European bird distributions and abundances (Lemoine et al. 2007, Jiguet et al. 2010, Koleček and Reif 2011): breeding habitat

preference, dietary niche, migration strategy and life history. Since current changes in bird distribution and abundance are linked to species' potential range shifts (Gregory et al. 2009), we expect that these traits could also be significantly related to variability in the magnitude of potential range shifts. Specifically, we formulate the following predictions. First, species breeding in forest habitats will show larger shifts than open habitat species because forests are confined to colder areas that are undergoing a higher rate of warming (Barnagaud et al. 2012). Second, species breeding near humans will show smaller shifts than other species because their distribution is less limited by climate (Møller et al. 2012). Third, species with narrow ecological niches (either habitat or dietary) will show larger shifts, as their distributions are more determined by climatic factors than the distribution of ecological generalists (Hernandez et al. 2006). Together with ecological traits, we test for the limiting effects of the current latitudinal and longitudinal geographic range position on potential range shifts in the future. In association with this, we predict that species breeding closer to continental borders will show a smaller magnitude of shifts than other species (La Sorte and Jetz 2010).

Material and methods

Potential range shifts

We assessed potential shifts in the breeding ranges of European birds by using maps in A Climatic Atlas of European Breeding Birds (Huntley et al. 2007). These maps were constructed using bioclimatic modelling of current breeding bird distribution in Europe (Hagemeyer and Blair 1997). The species' breeding ranges were expressed as presences and absences in a 50-km square Universal Transverse Mercator (UTM) grid over the continent, excluding most of Russia. Huntley et al. (2007) first modelled the present climatic ranges of every species as a function of observed breeding distributions in Europe and the values of three bioclimatic variables in the UTM squares by a locally weighted regression. They applied the following bioclimatic variables: coldest-month mean temperature, annual temperature sum above 5°C and the annual ratio of actual to potential evapotranspiration; all expressed as means for the time period 1961-1990. In the next step, Huntley et al. (2007) predicted future climatic ranges of bird species given the relationships revealed in the first step and climatic projections for the period 2070 – 2099. The climatic projections were based on the HadCM3 model (Hadley Centre Coupled Model, version 3) from the IPCC (2001). See Huntley et al. (2007) for more details on the generation of species' breeding climate range maps.

We digitalized the maps of current climatic breeding ranges and predicted future climatic breeding ranges of 298 bird species recorded as breeding in Europe from Huntley et al. (2007) into ArcGIS 9.2 (Esri 2006). Huntley et al. (2007) provide data on 363 species but we excluded 65 marine and/or extremely rare species whose potential range shifts were not estimated reliably according to Huntley et al. (2007). We calculated the mean centre of the respective climatic ranges for every species (i.e. mean latitude and mean longitude). We

then calculated the potential range shift as the distance between the mean centres of the current and predicted future climatic breeding range in each species (Appendix). These distances were taken as the response variable for further analyses. We also estimated the direction of the shift as an azimuth expressed in degrees.

We sorted the species into three distinct groups according to the direction of the potential shift: (i) species shifting their range northward with a degree range from 337.5 to 22.5, where 0 degrees is north (157 species), (ii) species shifting their range north-eastward with a degree range from 22.5 to 90, where east is 90 degrees (52 species), and (iii) species shifting their range north-westward with a degree range from 270 to 337.5, where 270 degrees is west (89 species); see Appendix. These groups were used in further analysis.

Defining explanatory variables

We defined the following seven trait variables to explain the interspecific variability in potential range shifts. All trait variables were extracted from Cramp (2006), an extensive database assembling trait information for the entire European avifauna. Here we briefly describe their calculation [see Koleček and Reif (2011) for more details]. Habitat niche was based on the classification of each species into one or more habitat classes according to Böhning-Gasese and Oberrath (2003): closed forest (1), open forest (2), forest edge (3), woodland, orchard, garden (4), scrubland (5), open country with solitary trees or shrubs (6), and open country without solitary trees or shrubs (7). For each species the mean value of its habitat classes defines its (i) habitat niche position, while the difference between the largest and smallest values defines its (ii) habitat niche breadth. (iii) Species position along the humidity gradient was based on the classification of each species into categories according to Böhning-Gasese and Oberrath (2003): non-humid (1), wetland (2) or water (3). (iv) Dietary niche breadth was based on the classification of species by Böhning-Gaese et al. (2000) as obligatory herbivorous or obligatory insectivorous/carnivorous (1), herbivorous and insectivorous/carnivorous (2), or omnivorous (3). (v) Relation to built-up areas was assessed using information on the habitat use of particular species, sorting bird species as either non-urban (0) or urban (1). (vi) Migration strategy classified species as residents (1), short-distance migrants (2), or long-distance migrants (3). (vii) Life history ordinated species along a slow-fast life history axis. This axis was calculated using principal component analysis on a correlation matrix of six species' life-history traits: body mass, egg mass, number of broods per year, laying date (Julian date of the beginning of laying in the first breeding), clutch size and length of incubation, expressed as mean values from published data (Cramp 1977–1994), and represents the first principal component accounting for 55.6 % of the variability in life history traits across bird species (Hořák et al. unpublished data).

Moreover, we used two explanatory variables quantifying the geographic position of species' ranges because this position can limit the potential range shift. For this purpose, we used the (i) latitude and (ii) longitude of the mean centres

of current species' climatic ranges based on maps in Huntley et al. (2007).

Statistical analysis

First, we explored possible differences in the magnitude of potential range shift among groups of species defined by the shift direction using analysis of variance (ANOVA) and the Tukey HSD post hoc test.

Then, we focused on predictors of the potential range shift. We first related the explanatory variables to the potential range shifts for all species together to find a general pattern. In the next step, we performed the analysis for each of the three groups defined by the shift direction separately. By these separate analyses we wanted to take the differences between latitudinal and longitudinal climatic gradients into account. The latitudinal gradient is characterized by decreasing temperature from south to north, while degree of continentality in climate increases from west to east (Hoffman 1983). Therefore, we suggest that a potential range shift of the magnitude of 1000 km in northern direction has to some extent different biological interpretation from, for example, the eastward shift of the same magnitude. At the same time, the shift directions also differed in possible effects of limitation by continental borders: the limitation should be more evident in northward and westward direction than in eastward direction.

We ran linear models to test whether the magnitude of potential shift (response variable) is related to the above mentioned ecological characteristics and the latitudinal and longitudinal position of each species' range (explanatory variables). The variable longitudinal position was not included into the models for those species with northward directional shifts because we do not expect longitudinal limitation in these species. We first defined a full model which included all explanatory variables, and this model was subsequently simplified by using the "step" function in R 2.12.0 (R Development Core Team 2010). This function performs automatic backward elimination of variables from a model based on Akaike Information Criterion (AIC). The elimination stopped when dropping a variable would decrease the model fit as indicated by AIC. These models we call "final models". The accuracy of the estimates of predicted future climatic ranges modelled by Huntley et al. (2007) differed among species. Therefore, we used species-specific squared areas under curve (AUC) from Huntley et al. (2007) as model weights in our analyses to give more importance to species with more accurate estimates of potential range shifts.

Finally, closely related species can show similar climatically-induced range shifts (Buckley and Kingsolver 2012). Therefore, we tested the potential impact of a common evolutionary history in the examined species on the observed relations by quantifying the degree of phylogenetic autocorrelation at the species, genus, family and order levels, respectively, in the residuals of the respective final models using Moran's I in the R package "ape" (Paradis 2009). Non-significant autocorrelation would indicate no influence of species taxonomy on the observed relationships.

Table 1. The effects of habitat niche position (on a gradient from closed forest to open landscape), habitat niche breadth, habitat humidity, dietary niche breadth, relation to built-up areas, migration strategy, life history (gradient from slow to fast life histories) and latitudinal and longitudinal range position on predicted shifts of European breeding ranges for (a) all 298 bird species, (b) 157 species shifting their range northward, (c) 52 species shifting their range north-eastward and (d) for 89 species shifting their range north-westward, tested by linear models. Significant results are printed in bold.

a) All species				
variable	estimate	standard error	t	p-value
Habitat niche position	-27.61	7.30	-3.55	< 0.001
Habitat niche breadth	-15.73	7.98	-1.97	0.049
Habitat humidity	64.05	17.69	3.62	< 0.001
Relation to built-up areas	-74.14	47.32	-1.57	0.118
Migration strategy	31.50	15.22	2.07	0.039
Latitudinal range position	-1.57	0.78	-2.01	0.045
b) Northward shifting species				
variable	estimate	standard error	t	p-value
Habitat niche position	-27.79	10.02	-2.77	0.006
Habitat niche breadth	-27.87	10.55	-2.64	0.009
Habitat humidity	46.06	24.44	1.88	0.061
Dietary niche breadth	-64.79	29.51	-2.20	0.030
Relation to built-up areas	-93.88	65.14	-1.44	0.152
Migration strategy	31.10	20.76	1.54	0.125
Latitudinal range position	-1.08	0.78	-1.40	0.165
c) North-eastward shifting species				
variable	estimate	standard error	t	p-value
Habitat niche position	-24.20	13.75	-1.76	0.085
Habitat humidity	80.93	31.74	2.55	0.014
d) North-westward shifting species				
variable	estimate	standard error	t	p-value
Habitat humidity	39.41	20.64	1.91	0.060
Relation to built-up areas	-95.32	58.91	-1.62	0.109
Latitudinal range position	-7.40	2.01	-3.67	< 0.001
Longitudinal range position	5.69	3.12	1.83	0.071

Results

The groups defined by their potential range shift direction significantly differed in the mean magnitudes of their shifts (ANOVA: $F = 5.81$, $p < 0.001$; Tukey HSD test: $p < 0.001$ for all pairwise comparisons). The largest mean shift was found for the group shifting northward ($491.5 \text{ km} \pm \text{SD } 195.3 \text{ km}$), then for the group shifting north-eastward ($383.5 \text{ km} \pm 174.7 \text{ km}$), and the smallest shift was found for the group shifting north-westward ($246.3 \text{ km} \pm 167.0 \text{ km}$).

For all species together, habitat niche position, habitat niche breadth, habitat humidity gradient, migration strategy and latitudinal range position explained significant part

of variability in potential range shifts according to the final model (Table 1a). Species breeding in more forested habitats showed larger magnitude of shifts than species breeding in more open habitats (Table 1a). Habitat specialists showed larger magnitude of shifts than habitat generalists (Table 1a). Larger magnitude of shifts was also expressed by wetland species and species migrating on longer distances (Table 1a). Finally, species with more northern latitudinal range position showed smaller magnitude of shifts than the species with ranges in lower latitudes (Table 1a).

In northward shifting species the final model resulted in three variables with significant effects on the magnitude of potential range shifts: habitat niche position, habitat niche

Table 2. The amount of phylogenetic autocorrelation at the species, genus, family and order levels, respectively, quantified by Moran's I in residuals of the final models shown in Table 1.

Taxonomic level	All species		Northward shifting species		North-eastward shifting species		North-westward shifting species	
	Moran's I	p-value	Moran's I	p-value	Moran's I	p-value	Moran's I	p-value
Species	0.09	0.667	0.01	0.970	0.06	0.767	0.15	0.779
Genus	0.10	0.156	0.02	0.828	0.07	0.807	0.01	0.900
Family	-0.06	0.149	-0.07	0.292	0.19	0.246	-0.05	0.691
Order	0.03	0.233	0.00	0.855	0.10	0.252	-0.01	0.988

breadth and dietary niche breadth (Table 1b). The effects of these variables show that forest species express a larger magnitude of potential range shifts than open habitat species, and both habitat and dietary generalists showed smaller shifts than specialists (Table 1b).

For north-eastward shifting species, the final model found that an association with humid habitats was the only trait explaining a significant proportion of the variability in potential range shifts. Specifically, species with tighter associations with this habitat showed larger potential shifts (Table 1c).

In north-westward shifting species, the magnitude of their potential range shift was related to habitat humidity, with the species breeding in wetter habitats shifting more than species of drier habitats, and to latitudinal range position, where more northerly distributed species showed smaller shifts (Table 1d). However, whereas the effect of latitude was significant, the effect of habitat humidity was marginally insignificant ($p = 0.06$).

Residuals of all final models did not reveal any significant phylogenetic autocorrelation at any taxonomic level (Table 2).

Discussion

Our examination of climatically induced potential shifts in the breeding ranges of 298 bird species breeding in Europe revealed several important patterns. First, species shifting their potential ranges north-westward showed smaller shifts than species shifting their ranges north or north-eastward. Second, species' habitat requirements were strong predictors of the interspecific variability in the magnitude of potential range shifts within the groups of species defined by shift direction. Third, species with narrow habitat or dietary niches showed larger magnitudes of potential range shifts than ecological generalists. Fourth, the current latitudinal range position acts as a strong limiting factor in the species' potential range shifts.

The first and last patterns stress the importance of continental borders on a species' ability to track changing climate. Clearly, species breeding in northern latitudes and western longitudes have less space to shift their ranges than species breeding in southern and eastern regions. These limitations are important from a conservation perspective, because the lack of space available for shifts will result in a contraction of a species' range and thus a higher extinction risk (Gregory et al. 2009). Although this threat is more serious in the case

of the altitudinal ranges of montane species that can simply lose their habitat due to a warming climate (La Sorte and Jetz 2010), a similar effect can affect species breeding in the highest latitudes. Moreover, climate change is predicted to proceed at the highest rate in the northernmost latitudes (Jetz et al. 2007), and this factor can further strengthen the limitation effect of continental borders.

The effect of space limitation could also produce a potential bias in our results since species with ranges in the western part of the continent have less land mass available for potential range shift than the species breeding in the eastern part. As a consequence, the bioclimatic models can estimate smaller potential range shifts for the former species just due to the lack of sites with suitable climatic conditions. However, we do not think this bias is substantial because vast majority of species used for the analysis occupy wide range of longitudinal bands and is thus not confined to the western part of the continent (note that we excluded the species with extremely small ranges from data prior to the analysis because of high uncertainty in the potential range shift estimates, see Huntley et al. 2007). Moreover, taking longitudinal position into account did not show its significant effect on potential range shift in our model. Despite of a strong limiting effect of latitudinal range position and significantly smaller magnitude of range shift in westward shifting species (see above), we do not suggest that the longitudinal position of species' range *per se* hampers the revealed relationships between ecological traits and potential range shifts described below.

Our results indicate that the magnitude of potential range shifts is strongly related to species' habitat niche. This concurs with the findings of Goodenough and Hart (2013), who also analysed maps of climatic ranges of European birds in Huntley et al. (2007) but focused on changes in range size, range margins and overlap, and not on shifts of range centres. The dominance of habitat-related ecological traits among the significant explanatory variables is not surprising given the recently described correlation between habitat and the climatic niches of European birds (Barnagaud et al. 2012). For species shifting their ranges north-eastward or north-westward, we found the largest shifts in species dependent on humid habitats. This pattern can be explained by the predicted increase in rainfall due to climate change in northern parts of the continent in contrast to a decrease in rainfall in southern parts (IPCC 2007). As a result, the ranges of species associated with humid habitats are predicted to move further north and, at the same time, the future distribution of those

species might be affected by a shortage of humid habitats in southern parts of the continent. The predicted relationship between shift magnitude and humid habitat specialization may be, however, obscured by human impacts. As has recently been reported, many water and wetland birds observed in various European countries are undergoing a range expansion (Van Turnhout et al. 2007, Lemoine et al. 2007, Koleček et al. 2010). These species have possibly wider climatic ranges than they currently occupy because their distribution may have been strongly limited in recent history by human pressures such as hunting (Van Turnhout et al. 2007). After the recent establishment of legal protections in Europe, these species have started to colonize additional suitable sites (Donald et al. 2007). Climatic models do not reflect human activities (such as hunting pressure, habitat modification etc.), and therefore future predictions inform us rather about changes in geographical ranges under conditions which favour the wider distribution of birds living in wet habitats.

Concerning those species with northward shifts, a larger magnitude of potential shifts was found in habitat specialists and forest species than in habitat generalists and open-habitat species, respectively. These patterns confirm our initial expectations. Forest species breed in colder areas than open habitat species (Barnagaud et al. 2012), and these areas will shift further according to climatic projections due to a higher magnitude of warming in northern latitudes (IPCC 2007, Buckley and Kingsolver 2012). It is possible that forest species would be generally more sensitive to future climatic changes than species breeding in open habitats, because similar patterns to those in our results have also been observed in birds of California (Jongsomjit et al. 2013). There, the largest changes in breeding distribution caused by climatic factors were predicted for forest species, while climate contributed only slightly to the distribution changes of grassland and desert species (Jongsomjit et al. 2013). It is interesting that species of coniferous forests were predicted to contract their ranges, whereas species of broad-leaved woodland were predicted to enlarge their ranges (Jongsomjit et al. 2013). Unfortunately, we did not classify the habitat use of forest species in such detail, but it would be interesting to perform such an analysis for European birds as well.

The effect of habitat specialization observed in our results suggests that ecologically specialized species will be under higher pressure to move northward under the conditions of future climate change. In contrast, the geographical ranges of ecological generalists will be less affected. This result is alarming, as specialized species seem to be sensitive to both human-induced habitat alteration and range shifts due to predicted climate change (Jiguet et al. 2007). Consequently, their populations might be under substantial threat in the future.

We found a correlation between potential range shifts and species' migration strategy: species migrating on longer distances showed larger magnitude of shifts. This pattern cannot be explained by better dispersal ability of long-distance migrants (Barbet-Massin et al. 2012) because this trait was not considered in the models estimating the potential range shifts (Huntley et al. 2007). Instead, we suggest that the larger shift of long-distance migrants can be connected with latitudinal

distribution of bird species with different migration strategies across Europe. With increasing latitude, both number and proportion of long-distance migratory species in bird communities decrease, i.e. these species are mostly confined to lower or mid-latitudes (Lemoine and Böhning-Gaese 2003) and have thus more space to shift their range in response to climate change than the short-distance migrants and residents, which form majority in bird species in northern regions (Lemoine and Böhning-Gaese 2003). However, the significant effect of migration strategy was found only in the model analysing all species together and the separate analyses for the species groups defined by shift direction did not maintain this effect. This suggests that the relationship of migration strategy to species' climatic niche is probably weaker than the effect of habitat niche variables which were significant in both kinds of models.

The predictions of future ranges modelled by Huntley et al. (2007) solely using climatic scenarios and assuming no effects of dispersal limitation, biotic interactions or land use, have recently been challenged by studies pointing out the importance of these factors constraining the species' geographic ranges (Rapacciolo et al. 2012, Pigot and Tobias 2013). Although there have been attempts to incorporate these factors into predictions of species' future geographic ranges (Barbet-Massin et al. 2012), we used the maps from Huntley et al. (2007) because these were appropriate for purposes of our study. Our aim was not to predict the exact locations of species' ranges in the future for purposes of, for instance, assessment of their coverage by current protected areas (Hole et al. 2009, Virkkala et al. 2010). Instead, we aimed to link the intensity of the pressure posed by climate change, as expressed by the potential range shift of a given species, to species' ecological traits. For this purpose, the range shifts based solely on climatic models were sufficient.

Our study provides more detailed insights into the observations of Huntley et al. (2006, 2008), whose predictive models suggest radical spatial reorganization of European bird communities in the second half of the 21st century as a consequence of global warming. We have shown that the variability in potential shifts of European climatic breeding ranges of bird species are closely linked with species' ecology, most notably their habitat preferences and ecological niche breadth. The importance of this link has been confirmed by other studies focusing on patterns in the future changes of species ranges (Goodenough and Hart 2013, Jongsomjit et al. 2013), and indicates which ecological groups of birds will be forced to most move their ranges under predicted climate change. As different ecological groups of birds definitely have different abilities to cope with predicted changes, this knowledge is important for adopting proper conservation strategies (Buckley and Kingsolver 2012). It is important to note that these inferences do not deal with other potential changes not linked to climate, e.g. habitat alteration caused by changes in human land use. These non-climatic factors can effectively inhibit the species from tracking their climatic optima (Reif et al. 2010, Devictor et al. 2012), resulting in an interaction between the habitat and climate change effects (Mantyka-Pringle et al. 2012). Therefore, we suggest that those species

whose ecological characteristics correlate with the largest magnitude of potential range shifts caused by climate, i.e. forest species, wetland species and ecological specialists, should be the central focus of ecologists and conservationists. The conservation strategies should include securing population in their current ranges by, for example, enforcement of existing protected areas, thus providing enough individuals to disperse (Thomas et al. 2012, Beale et al. 2013). At the same time, it is worth to start the process of establishment of new protected areas to conserve the habitats (e.g. wetlands) in regions where such species can possibly move their range and along the dispersal routes (Hole et al. 2009).

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Appendix

Data used for the analysis of the relationships between potential range shifts and ecological traits of European birds. The file may be downloaded from www.akademai.com

Potential range shifts predict long-term population trends in common breeding birds of the Czech Republic

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Abstract. Breeding ranges of European bird species will probably shift as a result of the climate change in forthcoming decades. Although it is unclear whether these shifts will come true, one perceives the magnitude of these shifts as a measure of the intensity of the pressure of climate change on particular species. From this perspective, it is interesting to ask how these shifts relate to current species' population trends. For this purpose, we related the data on potential northward shifts of European breeding ranges based on projections of climate change to the long-term population trends for the period 1982–2011 of birds breeding in the Czech Republic. We predicted that the relationship between the magnitude of range shift and the population trend will vary according to the geographic position of species' distribution in relation to the position of the Czech Republic. The results indicated support for this prediction. After accounting for the effects of various ecological traits like habitat association, migration and life history strategy, populations of the species with the largest shift declined, if the centre of their distribution was in the northern Europe, but increased if their distribution centre was on the south of the continent. These results suggest that the climate change is among the main factors causing recent changes in bird populations but its effects strongly depend not only on species sensitivity to these changes but also on geographic context.

Key words: birds, climate change, range shift, population trends, climatic niche

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INTRODUCTION

Long-term population trends are directional changes in species population sizes and reflect their responses to the most important environmental pressures (Greenwood 2003). From a conservation perspective, data on population trends give us the information about potential threats to population of common species: if a negative trend lasts over sufficiently long time period, an originally common species becomes rare and vulnerable (Reif 2013). Therefore, determining factors significantly associated with long-term population declines or increases helps us to set priorities in practical conservation of the focal species (Gregory et al. 2005, 2007). Although human-caused habitat alteration is the key factor causing the decrease or increase of bird populations (Reif 2013, Vickery et al. 2014), the increasing importance of the climate change (Pautasso 2012) and the interactions between these two factors (Mantyka-Pringle et al. 2012) have recently been recognized.

The impact of recent changes in climate on birds is still hotly debated (Jetz et al. 2007, Sekercioglu et al. 2008). Species show a variety of responses to warming climate including physiological adaptations, phenological changes and changes in distribution (Bellard et al. 2012). It is thus difficult to express their sensitivity to the climate change using one metric comparable over a wide range of species. In this respect, one possibility offers the climatic envelope modelling. Under this framework, the current distribution of a species is related to the climatic conditions in its breeding range, which provides a possibility to obtain a statistical description of its climatic niche (Araujo et al. 2009). This can be used for the prediction of its future climatic breeding range based on projections of future climate (Huntley et al. 2007). In the next step, one can calculate differences in locations between this predicted future climatic range and the current climatic range of that species (Huntley et al. 2007). This difference informs us about the magnitude of potential range shift of a given species (Goodenough &

Hart 2013, Koschová et al. 2014). We must be aware that this potential does not need to be realized due to the influence of other factors such as habitat destruction and dispersal potential (Barbet-Massin et al. 2012). However, this potential range shift also quantifies the strength of the pressure of the climate change on a given species. Species showing short range shifts can be viewed as those with high resilience to the climate change, while species with large magnitude of shift should be those under the highest climatic impact (Renwick et al. 2012). For instance, the endemic species with an absence of overlap between the current and predicted future geographic range will be presumably under the highest risk of extinction (Huntley et al. 2008, Goodenough & Hart 2013).

A study by Gregory et al. (2009) focused on the relation between the area of predicted future ranges of European birds, calculated by Huntley et al. (2007), and their current population trajectory observed over last decades. The species whose ranges will reduce due to climatic warming during the 21st century show the most negative population development at the same time (Gregory et al. 2009). This study suggests that the climatically induced potential range shifts modulate even the present abundance of birds. However, this study did not focus on the effect of the magnitude of the potential range shifts. We suggest that this measure can be also significantly related to recent bird population changes because it quantifies the intensity of the climatic pressure upon species ranges. For this purpose, we use data on common bird population trends in the Czech Republic, whose central-European location makes this country particularly suitable to test this idea.

Several studies have found that the climate change probably affects central European populations of birds when southern species are increasing significantly more than the northern species (Lemoine et al. 2007, Reif et al. 2008a). It is possible that this is caused by species' tracking their climatic optima in space (Devictor et al. 2012). From the perspective of potential range shifts, we assume that within the southern species, the Czech populations of those with larger magnitude of shift will experience higher colonization rate from the southern source than the Czech populations of species with shorter shifts. Therefore, we predict that the southern species with larger potential range shifts will increase more than the southern species with shorter shifts. The opposite should be true for northern species, when the larger magni-

tude of potential range shift would refer to the higher rate of withdrawal from the Czech Republic. Of course, these predictions apply for central Europe with a latitudinal gradient of decreasing temperature.

The aim of this study is to test these predictions of climate change effects on population trends of birds in the Czech Republic. Specifically, we compare the trends of species with different latitudinal positions of European breeding ranges and different magnitudes of potential range shifts using multipredictor statistical models. There are numerous other factors besides the climate change driving bird population trends such as breeding habitat loss or changes in wintering quarters (Reif 2013). To control for their effects, we include relevant species' ecological traits such as habitat association, migration and life history strategy into the models.

MATERIALS AND METHODS

Bird population trends

To detect long-term trends in abundance of breeding bird populations in the Czech Republic, we used data from the Breeding Bird Monitoring Programme in the Czech Republic (BBMP) for the period 1982–2011. BBMP is based on fieldwork performed by skilled volunteers who count birds using standardized methodology. Each volunteer visited usually two times per breeding season (from mid-April to mid-June) a transect containing 20 points in 300–500 m intervals. During one visit, all birds were recorded for 5 min both visually and acoustically on a given point. Although both transects and points were selected by free choice of volunteers, the large number of transects, their regular distribution throughout the country (Reif et al. 2013) and their habitat coverage corresponding to country-wide proportions of the main land cover types (Reif et al. 2008a) suggest that the BBMP provides reliable sample of population trends for common bird species breeding in the Czech Republic (see e.g. Janda & Štátný 1984, Reif et al. 2006).

For each species recorded in the BBMP we estimated its population trend by using log-linear models in the program TRIM 3.51 (Pannekoek & Van Strien 2005) taking both site and year effects into account and correcting for serial correlation over time (Van Strien et al. 2001). Because some sites deviated from the prescribed two-visits rule being visited once or three times per breeding

season, we used the mean count across all visits at a given site in a given year as the input values for the models. The log-linear models provided an estimate of the population trend on a logarithmic scale for each species together with standard error. The trends were classified according to their values and confidence intervals (revealed from the standard errors) using the framework of Gregory et al. (2007). A trend value higher than 1.00 with its confidence interval not including 1.00 is considered as a population increase, a trend value between 0.00 and 1.00 with its confidence interval not including 1.00 is considered as population decline. When the confidence interval encloses 1.00 but its upper limit is lower than 1.05 and its lower limit is above 0.95 (i.e. the interval is narrow), the population of a given species is considered as stable. Finally, species' trends whose confidence intervals contained 1.00 and overlapped 0.95 or 1.05 at the same time (i.e. the interval is wide) were considered as "uncertain". From further analyses we excluded the species for which BBMP did not sample their populations reliably (e.g. aerial feeder, raptors, owls) or provided uncertain trends. In total, we used the trends of 106 species for further analyses.

For statistical analyses, it is recommended by the authors of TRIM to back-transform the trends of particular species from the logarithmic to arithmetic scale (Pannekoek & Van Strien 2005). Therefore, the values of the trends used in our analysis are less than zero for negative population change, more than zero for positive change and zero in the case of the absence of change (see Appendix 1).

Potential range shifts

We calculated the potential shift of the geographic range of every species from maps of "A Climatic Atlas of European Breeding Birds" (Huntley et al. 2007). These maps were constructed using bioclimatic modelling on current breeding bird distribution in Europe (Hagemeyer & Blair 1997). The breeding ranges expressed the presence or absence of species in a 50-km square UTM grid except most of Russia. Huntley et al. (2007) first modelled the present climatic range of every species breeding in Europe for the time period 1961–1990 using three bioclimatic variables: coldest-month mean temperature, annual temperature sum above 5 °C and annual ratio of actual to potential evapotranspiration. The model was computed with the locally weighted regression in the UTM squares. The revealed relationship

between species distribution and climatic variables was applied in the next step to predict the future climatic ranges of bird species under the climatic projection for the period 2070–2099. For this purpose, Huntley et al. (2007) used the projection of the climatic model HadCM3 published in the IPCC (2001). These data were already used in numerous studies focused on the effects of climate change on birds (e.g. Huntley et al. 2008, Gregory et al. 2009, Jiguet et al. 2010, Goodenough & Hart 2013) and are considered as reliable estimates of the intensity of climate change pressure on bird populations (Araujo et al. 2009).

We converted the maps from Huntley et al. (2007) into a digital form in program ArcGIS 9.2 (ESRI 2006) and calculated the mean centre (mean longitude and mean latitude), for both the current and the predicted climatic range. The potential range shift is the difference between these mean centres in kilometres (Koschová et al. 2014). These potential range shifts, together with the latitudinal position of the centre of the current breeding range, were taken as explanatory variables for further analyses (see Appendix 1). Although some variability in direction of shifts is present when one considers all European species in Huntley et al. (2007), the species in our dataset, i.e. the common birds breeding in the Czech Republic, showed shifts solely in the northern direction.

Species' traits

Bird populations are affected by a suite of environmental factors that mirror the relationships between population trends and species' ecological traits (Reif 2013). These effects can confound the contribution of the focal explanatory variables and thus need to be taken into account in a statistical analysis. For this purpose, we expressed the following ecological traits whose influence on bird population trends were described in previous studies (e.g. Jiguet et al. 2010, Koleček & Reif 2011): habitat niche position, habitat niche breadth, species position along the humidity gradient, dietary niche, migration strategy and life history (see Appendix 1). Values of these traits for each species were extracted from Koleček & Reif (2011) who excerpted the local literature on these traits for Czech birds. Here we briefly summarize the core information about each trait, see Koleček & Reif (2011) for more details.

Habitat niche position was expressed as a mean position along a gradient of habitats from forest interior (position of 1) to open treeless landscape (position of 7) by expert classification.

Habitat niche breadth was expressed as a difference between the values of extremes in a range of habitats occupied along the gradient described above. Classification of species' position along the humidity gradient discriminated species of non-humid (1), wetland (2) and water habitats (3). Dietary niche was defined according to Böhning-Gaese et al. (2000) into obligatory herbivorous or obligatory insectivorous/carnivorous (1), herbivorous and insectivorous/carnivorous (2) and omnivorous (3). Migration strategy classified species as residents (1), short-distance migrants (2) and long-distance migrant (3). Life history described species along a fast-slow life history axis. This axis was calculated by Koleček & Reif (2011) using a principal component analysis on correlation matrix of six species life-history traits: body mass, egg mass, number of broods per year, laying date, clutch size and length of incubation. As result, the species are ordinated along the axis from the species with slow life histories (sometimes also called as "K-selected" species) to species with fast life histories ("r-selected" species). Species with slow life histories have large bodies, large eggs and long incubation time, species with fast life histories are small, have small eggs and short incubation time (Koleček & Reif 2011).

Statistical analysis

We related the predictor variables (i.e. potential range shift, current latitudinal position and particular species' traits) to bird population trends using linear models. In the line with our prediction, we included the interaction between the predicted range shift and the current range position, interactions among other variables were not included due to a limited sample of 106 species and high number of explanatory variables. We applied an information theoretic approach to assess the rela-

tive importance of respective predictors. Using the R-package MuMIn (Barton 2013), we computed Akaike Information Criterion corrected for small sample sizes (AIC_c) for models containing all possible combinations among predictor variables (Burnham & Anderson 2002). Model averaging of the parameter estimates and their standard errors across all candidate models using the Akaike weights provided the model-averaged estimates with confidence intervals (Johnson & Omland 2004).

Since the species may not be fully independent statistical units due to their common evolutionary history (Harvey & Purvis 1991), we have checked for the presence of phylogenetic autocorrelation in model residuals. Specifically, we have calculated the degree of autocorrelation at the species, genus, family and order level, respectively, for the full model containing all explanatory variables, as well as for the model composed from the terms found as important using the information-theoretic approach. Non-significance of the autocorrelation would suggest that the results are not affected by common evolutionary history of the species. These calculations were performed using R-package 'ape' (Paradis et al. 2009).

RESULTS

From 106 species used for our study, populations of 57 increased, whereas 49 species had declining populations within the study period. The mean potential range shift across species was 375 km (\pm SD = 177 km).

Three best performing models ($\Delta AIC_c < 2$) accounted for 19–23 % of variability in bird population trends in Czech Republic (Table 1). All these models contained variables: habitat niche

Table 1. Explanatory variables included into the best performing linear models (according to the Akaike Information Criterion corrected for small sample sizes, AIC_c) relating population trends from 1982 to 2011 to the traits of 106 bird species in the Czech Republic (top) and characteristics of these models (bottom).

model	explanatory variables				
1	habitat niche position + position along a humidity gradient + migration strategy + life history + potential range shift + latitudinal position of the centre of the current breeding range + potential range shift \times latitudinal position of the centre of the current breeding range				
2	habitat niche position + migration strategy + life history + potential range shift + latitudinal position of the centre of the current breeding range + potential range shift \times latitudinal position of the centre of the current breeding range				
3	habitat niche position + position along a humidity gradient + migration strategy + life history				
model	AIC_c	No. of params	ΔAIC_c	AIC_c weight	Adjusted R^2
1	-306.6	9	0	0.14	0.23
2	-304.9	8	1.692	0.06	0.21
3	-304.6	6	1.964	0.05	0.19

Table 2. Effects of species' traits on population trends from 1982 to 2011 for 106 bird species in the Czech Republic obtained by model averaging based on information theory. The traits with confidence limits (CL) not overlapping zero are printed in bold. Importance of particular variables was calculated as a sum of Akaike weights of the models containing a given variable.

trait variable	coefficient	lower 95% CL	upper 95% CL	importance
dietary niche position	-0.0004	-0.0136	0.0128	0.236
position along a humidity gradient	0.0197	0.0007	0.0387	0.714
habitat niche position	-0.0117	-0.0197	-0.0038	0.924
habitat niche breadth	0.0017	-0.0071	0.0106	0.256
latitude of mean centre	0.0098	-0.0005	0.0201	0.630
migratory strategy	0.0147	-0.0009	0.0303	0.619
life history	0.0285	0.0135	0.0435	0.985
range shift	0.0014	0.0001	0.0028	0.632
latitude of mean centre × range shift	-0.00003	-0.00005	-0.00001	0.501

position, migration strategy and life history. Two of these models also contained the variable position along a humidity gradient. Our focal climatic variables, i.e. potential range shift, latitudinal position of the centre of the current breeding range and their interaction, were included in the two best performing models, but not in the third model. When considering a full model with all explanatory variables, excluding the interaction from this model resulted in marked increase in AIC_c from to -301.7 to -296.3 suggesting importance of this interaction effect.

Model averaged coefficients and confidence intervals indicated the direction and significance of the effects mentioned above (Table 2). Specifically, species breeding in more humid habitats

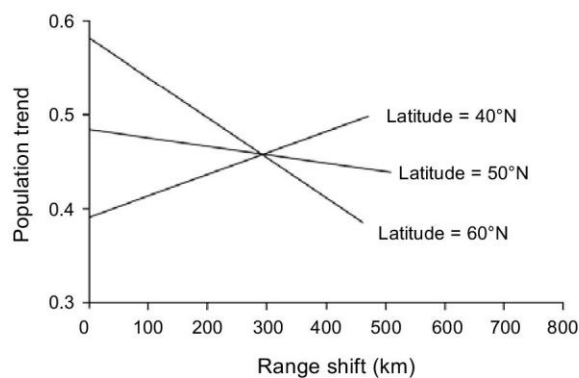


Fig. 1. Relationships between bird population trends and their potential range shifts in the interaction with the latitude of the species' mean range centre. The relationships were calculated by model averaging based on information theory (see Table 2). Shown are three different regression lines of population trend on the potential range shift (Range shift) for different latitudes of the mean range centre (Latitude). Population trends were estimated for 106 species counted in the Czech Republic from 1982 to 2011 using log-linear models in TRIM software. Negative values of trends indicate declining populations, positive values indicate increasing populations.

had more positive trends than species breeding in dry habitats; species breeding in more forested habitats had more positive trends than species breeding in more open habitats; species with slow life history had more positive trends than species with fast life history. These variables had also the highest importance according to Akaike weights of the models containing these traits (Table 2). Our focal climatic variables were related to the bird population trends in the way we predicted. The species with the potential shifts of larger magnitude increased in the Czech Republic, if their range centres were situated in lower latitudes, but the trends were less positive and even declined for species breeding in higher latitudes in Europe (Fig. 1). The importance of these climatic variables (measured by Akaike weights of models they appeared in) was lower than in the case of the most important habitat and life history traits, but higher than the importance of the remaining trait variables whose confidence intervals overlapped zero (Table 2).

The phylogenetic analysis confirmed that the residuals of the full model (containing all explanatory variables), as well as the residuals of the model composed from terms whose confidence intervals do not overlap zero after model averaging, do not show any significant autocorrelation at particular taxonomic levels (Table 3). These results justify no need to account for phylogeny in the analyses presented above.

DISCUSSION

Our results were in accord with the prediction that the relationship between population trends of birds in the Czech Republic and the potential shifts of their breeding ranges estimated by bioclimatic models depends on the location of the range centres in Europe. Specifically, species with

Table 3. The degree of phylogenetic autocorrelation calculated at particular taxonomic levels for the model containing all explanatory variables (full model) and for the model containing term whose confidence intervals do not overlap zero according to model averaging (reduced model), respectively. Non-significant autocorrelation indicates no effect of phylogeny on the results of statistical modelling.

	species		genus		family		order	
	Moran's I	p	Moran's I	p	Moran's I	p	Moran's I	p
full model	-0.09	0.848	0.13	0.381	-0.07	0.473	0.02	0.363
reduced model	-0.08	0.865	0.20	0.161	-0.07	0.466	0.03	0.384

large magnitude of shift have more increasing Czech populations, if the centre of their breeding distribution is located in southern Europe than species with range centres in northern Europe. We also found increasing populations of forest birds, water birds and species with slow life histories.

We assume that the potential range shift is connected with the climate change effects and quantifies the sensitivity of species to the climate change (Huntley et al. 2008). Specifically, the species for which bioclimatic models estimate larger magnitude of range shifts are probably under higher pressure to move northwards due to warmer climate. It is interesting that this pressure translates into a species' population trend according to the latitudinal position of its current breeding range. We suggest this relationship is shaped by the position of the Czech Republic within Europe. Specifically, it is possible that the climate change facilitates colonization of the Czech Republic by southern species, when the species most affected by climatic change show the highest rate of increase of Czech populations. By contrast, the same mechanism could affect population trends of the northern species but in opposite direction. It means that the climate change causes withdrawal of individuals of the northern species from the territory of the Czech Republic and its rate is higher for species more sensitive to the climate change effects. These results are in accord with some previous observations of differences in population trends between the northern and southern species observed in Europe (Lemoine et al. 2007, Jiguet et al. 2010, Devictor et al. 2012) including the Czech Republic (Reif et al. 2008b), but provide deeper insights into these patterns.

Our results develop an earlier study of Gregory et al. (2009) who described a relationship between the predicted change of breeding distribution in Europe and current population trend. The species whose ranges are predicted to contract had more negative European long-term population trends than the species whose ranges are predicted to expand. We suggest this pattern is

caused by the limitation effect of northern continental border. Species breeding currently close to continental border have less space to shift their ranges to the North and, as a consequence, their range is predicted to contract. Results of our study indicate that the limiting effect of northern continental border does probably not influence populations of birds in the Czech Republic strongly: it would result in more negative trends in northern species with smaller predicted range shifts, but the opposite was true according to our data. We suggest that this difference between European and Czech population trends is caused by the central-European location of the Czech Republic. The limiting effect of the northern continental border is thus not detectable in Czech populations breeding 2000 km from the northern range edge. Therefore, although the whole European population of such species may decline, central European subpopulation may not (see also Díaz et al. 2014).

We used the predicted shifts calculated by Huntley et al. (2007) who considered only climatic drivers but did not include the habitat change effects or species' dispersal ability into the models. Several studies have shown these factors can seriously modify outcomes of climatic influence on species' ranges, reducing the realized range shifts compared to the climatically driven projections (Tyre et al. 2001, Reif et al. 2010, Barbet-Massin et al. 2012). However, in our study, we use the magnitude of the range shifts estimated by bioclimatic models as a surrogate for intensity of the influence of the climatic change on bird species, and thus we were not interested in testing whether the predicted shifts will really happen with the magnitude estimated by the bioclimatic models (see also Koschová et al. 2014). Moreover, a recent study comparing breeding bird distribution during the Last Glacial Maximum inferred by bioclimatic models with the fossil record found marked congruence between the results of both methods of the past range reconstruction suggesting that the climate is the principal driver of breeding bird distribution in long-term (Smith et al. 2013).

The effects of other trait variables were in accord with the findings already described in other studies. Species' position along forest-open country and humidity gradients, respectively, confirm important influence of the habitat changes on populations of European birds (Böhning-Gaese & Bauer 1996, Lemoine et al. 2007, Desrochers et al. 2010). These habitat changes include forest expansion on abandoned agricultural land resulting in increase of forest bird species, agricultural intensification resulting in population decline of farmland birds, and more strict legal protection of some previously hunted large water birds resulting in increase of wetland species (Reif 2013). Of course, exceptions from such general patterns can be observed at the species level. For example, Tryjanowski et al. (2005) showed that White Stork *Ciconia ciconia* benefited from the loss of arable land in the Tatra Mountains. Moreover, population increase was not observed in many rare wetland species not covered by the BBMP data (Št'astný et al. 2006). Moreover, our results suggest that species' life history has the significant effect on bird population trends when species with slow life histories have more positive trends than the species with the fast life histories. Although this pattern seems rather counter-intuitive, we suggest that under the conditions of human-caused environmental perturbations, the slow life history can be indeed an advantage (see also Koleček et al. 2014). The slow life history species are long lived and they have thus higher probability to meet optimal conditions for reproduction during their life time than the shorter lived species with fast life histories (Sol et al. 2012).

In conclusion, our study provides further insights into previously described climate change effects on long-term trends in bird populations. Indirectly estimated sensitivity of species to the climatic changes shows an important effect in an interaction with latitudinal position of species' European breeding range. Future studies could search for relationships between the climatically driven predicted shifts of species' breeding ranges, observations of the current climate change impacts on the recent geographic range shifts and then link these relationships to the population trends. We suggest these links can uncover the mechanisms how the climate change causes the population changes, which is crucial for setting conservation strategies for the most adversely affected species.

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STRESZCZENIE

[Potencjalne zmiany zasięgu lęgówisk prognozują długoterminowe trendy populacyjne pospolitych gatunków ptaków w Czechach]

Przewiduje się, że w wyniku zmian klimatycznych mogą ulec zmianie zasięgi lęgówisk ptaków. W pracy powiązано prognozowane zmiany zasięgu lęgówisk w kierunku północnym z długoterminowymi trendami populacji 106 pospolitych gatunków lęgowych Czech. Zakładano, że badany związek może zależeć od położenia centrum zasięgu danego gatunku. W analizach uwzględniono także takie czynniki jak: środowisko życia, wilgotność siedliska, nisza pokarmowa, strategia migracji i historia życiowa (apendyks 1).

Stwierdzono, że oprócz zmiennych związanych z ekologią gatunków także potencjalna zmiana zasięgu oraz obecnego położenia centrum zasięgu były powiązane z trendami populacyjnymi badanych gatunków (Tab. 1, 2). Gatunki o największych potencjalnych zmianach zasięgu lęgówisk wzrastają liczebnie, gdy ich centrum zasięgu położone jest na południu, zaś znacznie mniejszy wzrost lub nawet spadek liczebności obserwowany jest, gdy ich centrum zasięgu znajduje się bardziej na północ (Fig. 1).

Appendix 1. Data used for relating population trends from 1982 to 2011 to the traits of 106 bird species in the Czech Republic. Legend: Habitat niche position — mean position along a gradient of habitats from forest interior (1) to open treeless landscape (7); Habitat niche breadth — difference between the values of extremes in a range of habitats occupied along the gradient described above; Habitat humidity — position along a humidity gradient with species of non-humid (1), wetland (2) and water habitats (3); Diet — dietary niche classifying species as obligatory herbivorous or obligatory insectivorous/carnivorous (1), herbivorous and insectivorous/carnivorous (2) and omnivorous (3); Migration — migration strategy classifying species as residents (1), short-distance migrants (2) and long-distance migrant (3); Life history — position along a fast-slow life history axis (see Methods section for details); Range shift — difference (km) between centres of current climatic European breeding range and climatic European breeding range predicted by bioclimatic models for the second half of 21st century (see Methods section for more details); Latitude — latitude of the centre of the species' current climatic breeding range in Europe.

Species	Trend	Habitat niche position	Habitat niche breadth	Habitat humidity	Diet	Migration	Life history	Range shift (km)	Latitude (degrees)
<i>Accipiter gentilis</i>	-0.0351	2.33	3	1	1	1	1.35	420	53.176
<i>Accipiter nisus</i>	-0.0234	2.67	3	1	1	2	0.66	319	51.372
<i>Acrocephalus scirpaceus</i>	0.0054	7	0	3	2	3	-1.06	401	48.849
<i>A. arundinaceus</i>	0.0301	7	0	3	1	3	-0.75	509	47.813
<i>A. schoenobaenus</i>	-0.0071	5.5	1	2	1	3	-1.10	395	51.571
<i>Aegithalos caudatus</i>	-0.0136	3	2	1	1	1	-1.53	455	49.724
<i>Alauda arvensis</i>	-0.0119	7	0	1	2	2	-0.93	277	57.801
<i>Alcedo atthis</i>	0.0805	7	0	3	1	2	-0.60	278	47.575
<i>Anas platyrhynchos</i>	0.0438	7	0	3	2	2	0.64	280	52.042
<i>Anas strepera</i>	0.1188	7	0	3	1	2	0.60	690	51.029
<i>Anser anser</i>	0.0686	5	5	3	1	2	1.34	529	53.683
<i>Anthus pratensis</i>	-0.0950	7	0	2	2	2	-1.08	525	56.111
<i>Anthus trivialis</i>	-0.0328	4.5	3	1	1	3	-1.02	311	53.443
<i>Ardea cinerea</i>	0.1222	4.5	3	3	1	2	1.24	458	50.677
<i>Aythya ferina</i>	0.0384	7	0	3	2	2	0.72	662	51.930
<i>Aythya fuligula</i>	0.0144	7	0	3	2	2	0.64	579	57.040
<i>Buteo buteo</i>	0.0129	4	4	1	1	2	1.29	362	49.765
<i>Carduelis cannabina</i>	-0.0131	5	2	1	2	2	-1.27	254	48.749
<i>Carduelis carduelis</i>	-0.0021	4.33	3	1	2	2	-1.18	301	47.953
<i>Carduelis flammea</i>	0.0133	3.67	3	1	2	1	-1.39	67	60.391
<i>Carduelis chloris</i>	-0.0071	4.33	3	1	2	2	-1.00	198	50.455
<i>Carduelis spinus</i>	-0.0364	3	2	1	2	2	-1.24	446	55.728
<i>Certhia brachydactyla</i>	-0.0072	2	2	1	2	1	-1.26	637	45.347
<i>Certhia familiaris</i>	-0.0001	2	2	1	2	1	-1.31	301	54.431
<i>Ciconia nigra</i>	0.0716	3.5	5	2	1	3	1.70	674	50.227
<i>Circus aeruginosus</i>	0.0635	7	0	3	1	3	0.98	372	61.736
<i>C. coccyzoides</i>	-0.0182	2.5	3	1	2	2	-0.70	542	49.417
<i>Columba oenas</i>	0.0222	1	0	1	1	2	-1.41	771	50.921
<i>Columba palumbus</i>	0.0315	2.5	3	1	1	2	0.36	138	51.274
<i>Corvus corax</i>	0.1169	2	2	1	3	1	0.58	117	52.287
<i>Coturnix coturnix</i>	0.1496	7	0	1	2	3	-0.43	334	47.591
<i>Cuculus canorus</i>	-0.0168	4	4	1	1	3	-0.82	127	51.006
<i>Delichon urbica</i>	0.0133	6	0	1	1	3	-1.01	133	50.723
<i>Dendrocopos major</i>	0.0126	2.5	3	1	2	1	-0.68	314	51.578
<i>Dendrocopos minor</i>	0.0181	3	2	1	1	1	-1.11	419	53.808
<i>Dryocopus martius</i>	0.0223	1	0	1	1	1	-0.09	370	53.755
<i>Emberiza citrinella</i>	-0.0105	4.67	3	1	2	1	-0.93	251	52.835
<i>Emberiza schoeniculus</i>	0.0048	6	0	3	2	2	-1.06	169	54.371
<i>Erithacus rubecula</i>	0.0050	2.5	3	1	2	2	-1.11	329	51.740
<i>Falco tinnunculus</i>	0.0071	5	2	1	1	2	0.42	114	50.679
<i>Ficedula albicollis</i>	0.0205	2.5	3	1	1	3	-1.08	618	49.169
<i>Ficedula hypoleuca</i>	-0.0153	2	0	1	1	3	-1.07	758	56.345
<i>Fringilla coelebs</i>	-0.0094	3.67	5	1	2	2	-1.06	129	50.395
<i>Fulica atra</i>	0.0303	7	0	3	2	2	0.42	394	50.075
<i>Galerida cristata</i>	-0.3316	7	0	1	2	1	-0.80	219	45.988

Continued on the next page

<i>Gallinago gallinago</i>	-0.1151	7	0	2	1	2	0.14	621	56.155
<i>Gallinula chloropus</i>	-0.0108	7	0	3	2	2	-0.01	335	48.741
<i>Garrulus glandarius</i>	0.0271	2.5	3	1	3	1	-0.22	167	50.549
<i>Hippolais icterina</i>	-0.0165	3.5	1	1	2	3	-1.02	751	53.420
<i>Hirundo rustica</i>	-0.0143	5	2	1	1	3	-0.92	116	50.960
<i>Charadrius dubius</i>	-0.0070	7	0	2	1	3	-0.07	341	50.395
<i>Jynx torquilla</i>	-0.0281	3.5	1	1	1	3	-1.14	349	52.934
<i>Lanius collurio</i>	0.0289	6	0	1	2	3	-0.70	376	50.937
<i>Lanius excubitor</i>	0.0015	4.5	3	1	1	2	-0.54	463	54.319
<i>Locustella fluviatilis</i>	-0.0118	3.5	2	2	1	3	-0.92	680	51.436
<i>Locustella luscinioides</i>	0.0617	7	0	3	1	3	-1.06	467	49.091
<i>Locustella naevia</i>	0.0022	6	0	2	1	3	-1.24	736	52.781
<i>Loxia curvirostra</i>	-0.0159	1	0	1	2	2	-0.80	532	55.195
<i>Luscinia megarhynchos</i>	0.0223	4	2	2	2	3	-0.85	315	45.211
<i>Milvus milvus</i>	0.2108	3	2	1	1	2	1.25	438	47.603
<i>Motacilla alba</i>	-0.0090	5	2	2	1	2	-1.11	99	51.820
<i>Motacilla cinerea</i>	-0.0073	4	4	3	2	2	-1.22	413	47.519
<i>Motacilla flava</i>	-0.1792	7	0	2	1	3	-1.10	196	51.632
<i>Muscicapa striata</i>	0.0211	3	2	1	1	3	-0.95	170	51.567
<i>Oenanthe oenanthe</i>	-0.1156	7	0	1	2	3	-1.02	160	51.867
<i>Oriolus oriolus</i>	0.0111	3	2	2	2	3	-0.30	259	48.163
<i>Parus ater</i>	-0.0007	2	2	1	2	1	1.36	527	51.364
<i>Parus caeruleus</i>	0.0089	3	2	1	2	1	-1.42	138	49.865
<i>Parus cristatus</i>	-0.0142	1	0	1	2	1	-1.15	621	52.315
<i>Parus major</i>	0.0022	3	2	1	2	1	-1.31	68	50.871
<i>Parus montanus</i>	0.0119	2	0	1	2	1	1.08	472	55.547
<i>Parus palustris</i>	-0.0079	2	2	1	2	1	-1.39	549	49.950
<i>Passer domesticus</i>	-0.0261	5	2	1	2	1	-1.01	197	51.516
<i>Passer montanus</i>	-0.0081	4.33	3	1	2	1	-1.12	197	48.987
<i>Perdix perdix</i>	-0.0700	7	0	1	1	1	0.01	505	50.017
<i>Phasianus colchicus</i>	-0.0017	5	2	1	2	1	1.25	419	49.047
<i>Phoenicurus ochruros</i>	0.0149	5	2	1	2	2	-1.02	487	48.104
<i>P. phoenicurus</i>	0.0320	3	2	1	2	3	-1.15	236	53.254
<i>Phylloscopus collybita</i>	0.0087	3.5	3	1	2	2	-1.37	198	52.076
<i>Phylloscopus sibilatrix</i>	-0.0298	2	0	1	1	3	-1.25	430	53.405
<i>Phylloscopus trochilus</i>	-0.0264	3.5	3	1	2	3	-1.28	674	54.867
<i>Picus viridis</i>	0.0407	2.5	3	1	1	1	-0.26	699	51.738
<i>Pica pica</i>	0.0263	5	2	1	3	1	-0.13	119	52.267
<i>Picus canus</i>	0.0425	2.5	3	1	1	1	-0.20	545	48.501
<i>Podiceps cristatus</i>	0.0135	7	0	3	1	2	0.93	387	51.528
<i>Prunella modularis</i>	-0.0332	3	2	1	2	2	-1.13	365	53.866
<i>Pyrrhula pyrrhula</i>	-0.0273	2.5	3	1	2	2	-0.89	421	53.807
<i>Regulus ignicapillus</i>	-0.0042	1	0	1	1	2	-1.55	555	46.636
<i>Regulus regulus</i>	-0.0439	1	0	1	1	1	-1.57	363	53.930
<i>Remiz pendulinus</i>	-0.0974	4.5	3	2	2	2	-1.34	346	48.350
<i>Saxicola ubetra</i>	0.0287	6.5	1	1	2	3	-1.04	260	53.403
<i>Serinus serinus</i>	-0.0392	3	2	1	2	2	-1.22	402	45.753
<i>Sitta europaea</i>	0.0174	2.5	3	1	2	1	-0.90	512	49.394
<i>Streptopelia decaocto</i>	0.0159	4	0	1	1	1	-0.09	296	49.847
<i>Streptopelia turtur</i>	-0.0262	4	4	1	1	3	0.00	289	47.263
<i>Sturnus vulgaris</i>	0.0246	4.33	3	1	2	2	-0.57	207	52.838
<i>Sylvia atricapilla</i>	0.0324	3.33	3	1	2	2	-1.11	323	50.332
<i>Sylvia borin</i>	-0.0204	2.5	1	1	2	3	-1.09	384	53.151
<i>Sylvia communis</i>	0.0092	5.5	1	1	2	3	-1.12	141	50.567
<i>Sylvia curruca</i>	0.0205	4.5	1	1	2	3	-1.26	359	52.942
<i>Tachybaptus ruficollis</i>	0.0139	7	0	3	1	2	-0.01	456	48.142
<i>Turdus merula</i>	0.0163	2.67	3	1	2	1	-0.50	134	49.655
<i>Turdus philomelos</i>	0.0116	4	4	1	2	2	-0.70	304	54.214
<i>Turdus pilaris</i>	0.0048	3.5	1	1	2	2	-0.51	551	55.681
<i>Turdus viscivorus</i>	0.0195	2.67	3	1	2	2	-0.34	299	52.310
<i>Vanellus vanellus</i>	-0.0701	7	0	2	1	2	0.48	337	54.086

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Abstract: Birds are among the most important organisms for indicating state of environmental health. It is thus important to learn what are the factors driving changes in bird population sizes. Although various possible drivers were determined to date, climate change and habitat change were identified as the most important. However, their relative importance remains unknown because few studies investigated their effects at the continental level and were limited to smaller sets of species, namely the common ones. For this purpose, we related population trends of 268 European breeding birds to their traits reflecting the climate and habitat changes using linear mixed-effects models accounting for their dietary niche, life history and migration strategies and phylogeny. Our results showed that the habitat related variables were more important than the variables that mirror climate change effects. Specifically, habitat niche breadth and species position along habitat humidity gradient were significant across all species indicating that recent environmental changes, such as agricultural intensification, were detrimental for habitat specialists, especially within the common species. On the other hand, we suggest that successful conservation effort may underpin population increase of species of humid habitats, especially the rare ones. We do not rule out the effect climate change completely because it can be included manifested in the significant decline of long-distance migrants when species migrating over long distances are constrained by their innate schedule and thus sensitive to the adverse effects of warming temperatures, but also to habitat degradation at wintering grounds. Taken together, our results highlight the need to focus on problems originating from human land use in the first step to secure populations of European bird species.

1. Introduction

Due to their large body size and popularity for citizens (Jiguet et al., 2012), birds are among the most important organisms for indicating state of environmental health (Gregory et al., 2005, Butchart et al., 2010). As indicators, populations of bird species mirror influences of factors acting at larger spatial scales (Gregory and Van Strien, 2010) and it is thus important to learn what are the factors driving changes in bird population sizes.

Population size is one of the key determinants of the probability of species' extinction (Lande, 1993) and the rate of its change, often expressed as population trend over a given time period, is important for assessment of species' conservation status (Mace et al., 2008). Finding patterns in long-term population trends is thus essential first step for defining targets of further detailed analysis of causes underlying the population changes (Greenwood, 2003).

Interspecific variability in population trends is determined by various factors (see Reif, 2013, for review), but two of them seem to be the most important according to recent studies: climate change and habitat change (e.g. Devictor et al., 2012; Møller, 2014; Jørgensen et al., 2015). Their influence on bird populations was reported at the local, national, as well as regional levels and examples include amelioration of spring temperatures resulting in population declines of species breeding in colder areas (Julliard et al., 2004; Jiguet et al., 2010), shifts in arrival dates with increases in species arriving earlier and declines in species with delayed arrivals (Møller et al., 2008; Salido et al., 2012), agricultural intensification causing declines in farmland birds (Fuller et al., 1995; Laaksonen and Lehikoinen, 2013; Hallmann et al., 2014), forest expansion and maturation underlying woodland birds increases (Sirami et al., 2008; Wilson et al., 2012) or deterioration of wetlands with negative consequences for waterbirds (van Turnhout et al., 2010).

However, only a handful of studies investigated simultaneously the effects of climate and habitat changes at the pan-European level (but see Møller et al., 2008; Jiguet et al., 2010; Jørgensen et al., 2015) and these studies focused solely on selected species, usually the common ones, due to the lack of data on long-term population trends for the rare species. This bias to the use of common species can provide incomplete and perhaps flawed inferences about the relative importance of particular drivers. To fill this knowledge gap, we used data from BirdLife International (2004) providing population trends of almost all bird species breeding in Europe including both common and rare ones.

1 Relating population trends to their possible drivers and testing their relative importance can be
2 performed by using species' traits. The traits mirror the influence of various environmental
3 filters thereby a group of species sharing a given trait should exhibit similar population trends
4 (Webb et al., 2010). For example, in the case of the effects of habitat changes species can be
5 sorted into the groups defined by their habitat use with the assumption that species breeding in
6 different habitats will differ in population trends if areas and/or quality of these habitats
7 showed divergent temporal trajectories (Jarošík, 2005). In this study, we used two traits
8 describing species' climatic niche and four describing habitat niche. We can assume that if
9 climate change is more important driver of changes in long-term bird populations, then the
10 traits describing climatic niche will be important to explain the variability in population trends
11 and vice versa.

12 To test the climate change effects, most researchers focus on species' climatic niche which
13 can be describe by geographic position of centre of species' range (e.g. Julliard et al., 2004;
14 Lemoine et al., 2007; Møller et al., 2008). In northern temperate zone, species breeding in
15 northern latitudes are associated with colder climate, while the species breeding in southern
16 latitudes with warmer climate (Huntley et al., 2007). As climate proceeds across the continent,
17 environment becomes less suitable for northern species resulting in decline of their
18 populations. In southern species, the same process should result in population increase.
19 However, we suggest that the relationship between the climate change and the trends is not so
20 straightforward indeed because the position of species' range centre does not fully reflect the
21 intensity of climate change pressure on species – clearly, tolerance to the climate change
22 effects can vary across species irrespective to their range position. For this reason, we
23 expressed the intensity of pressure of the climate change upon species using the potential
24 shifts of species' climatic ranges (Huntley et al., 2007). These shifts were calculated as a
25 difference between mean centres of current and projected climatic ranges (Koschová et al.,
26 2014). We can expect that the longer the potential range shift, the higher the pressure of
27 climate change on a given species (Koschová and Reif, 2014). As a result, population
28 consequences of climate change should depend on the interaction between latitudinal range
29 position and potential range shift: the species with long potential shifts should have more
30 positive trends when breeding southern latitudes than the species with long shifts breeding in
31 northern latitudes. This expectation was confirmed for the trends of common birds breeding in
32 central Europe but remains untested at the whole-European level and for a larger set of
33 species (Koschová and Reif, 2014).

1 The first aim of this study is to test relative importance of climate and habitat changes as
2 drivers of bird population trends, controlling for other potential factors, using the Pan-
3 European-level data unbiased to a specific species group. The second aim is to compare the
4 results between common and rare species. Common species are habitat generalists (Godet et
5 al., 2015; Reif et al., 2015) and, at the same time, climate largely accounts for spatial patterns
6 in their abundance (Howard et al., 2015). Therefore, we can assume that common species
7 should be tolerant to habitat changes, whereas climate change may be the principal driver of
8 their population trends. By contrast, rare species are typically highly specialized in terms of
9 habitat use (Godet et al., 2015; Reif et al., 2015) and it was already shown that the climate
10 change effects cannot override the adverse impacts of serious habitat deterioration in such
11 species (Reif et al., 2010). Therefore, we expect that habitat change will dominate over
12 climate change effects in the case rare species.
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25 **2. Materials and Methods**

26 **2.1 Population trends**

27 We focused on 268 bird species breeding in Europe that were previously analyzed for
28 potential range shifts by Koschová et al. (2014). We excerpted their population trends from
29 BirdLife International (2004). These trends were expressed for the time period 1990-2000
30 using categories large decline (n = 13 species), moderate decline (n = 55), small decline (n =
31 40), stable or fluctuating (n = 134), small increase (n = 23), moderate increase (n = 13) and
32 large increase (n = 7) (BirdLife International, 2004). We transformed these categories into
33 numbers following Møller et al. (2008) from -3 (large decline) to +3 (large increase).
34 Although these values were derived from discrete categories, Møller et al. (2008) showed they
35 are closely correlated to quantitative values of trends from 1980 to 2004 estimated from
36 annual monitoring data by Pan-European Common Bird Monitoring Scheme (PECBMS,
37 2006) in 58 common species. Therefore, we treated the numerical expression of the trend
38 categories as quantitative in further analysis, as did also Donald et al. (2007) and Koleček et
39 al. (2014).
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57 **2.2 Species' traits**

58 For each species, we collected information about following traits.
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1 Habitat use was expressed using four variables taken from Koschová et al. (2014). Each
2 species was assigned to one of more habitats along a gradient from forest interior (position of
3 1) to open treeless landscape (position of 7) assessed in Bohning-Gaese and Oberrath (2003).
4 From this assignment (i) habitat niche position was calculated a mean value of across habitats
5 used by a given species (Reif et al., 2011). As a complement to the habitat niche position, (ii)
6 habitat niche breadth was expressed as a difference between the values of habitats used by a
7 given species at the extremes of the gradient mentioned above (Reif et al., 2011).

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12 Classification of species' position along the (iii) humidity gradient discriminated species of
13 non-humid (1), wetland (2) and water habitats (3) assessed in Bohning-Gaese and Oberrath
14 (2003). Finally, we assessed (iv) species' relation to built-up areas discriminating species
15 breeding in such areas (1) and species not breeding in these areas (0) using information in
16 Cramp (1977-1994).

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22 The effects of climate change were expressed using two variables taken from Koschová et al.
23 (2014) based on characteristics of European breeding ranges of particular species: (i) latitude
24 of the mean range centre and (ii) magnitude of potential range shift. Koschová et al. (2014)
25 used maps from Huntley et al. (2007) for their inference. These maps were constructed using
26 bioclimatic modelling of the breeding bird distribution in Europe using the information from
27 Hagemeyer and Blair (1997) on current breeding ranges of particular species. Huntley et al.
28 (2007) first modelled the present climatic range of every species and the revealed relationship
29 between species' breeding distribution and climatic variables was applied in the next step to
30 predict the future climatic ranges of bird species under the climatic projection for the period
31 2070 – 2099 (IPCC 2001). Using these data from Huntley et al. (2007), Koschová et al.
32 (2014) calculated the mean centre (mean longitude and mean latitude), for both the current
33 and the predicted future climatic range of every species. The potential range shift of a given
34 species was the difference between these mean centres in kilometres (Koschová et al., 2014).

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46 Besides the variables describing the effects of habitat and climatic changes we took values of
47 several more ecological traits from Koschová et al. (2014) because their influence on bird
48 population trends were described in previous studies (e.g. Jiguet et al., 2010; Koleček and
49 Reif, 2011): (i) dietary niche breadth was based on a classification of species into three groups
50 obligatory herbivorous or obligatory insectivorous/carnivorous (1), herbivorous and
51 insectivorous/carnivorous (2) and omnivorous (3), (ii) migration strategy distinguished
52 between residents (1), short-distance migrants (2), and long-distance migrants (3) and (iii) life
53 history strategy. Life history strategy was expressed as a position of each species along a
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1 slow-fast life history axis revealed by principal component analysis of six life-history traits:
2 body mass, egg mass, number of broods per year, laying date (julian date of the beginning of
3 laying in the first breeding), clutch size and length of incubation .
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8 **2.3 Data analysis**

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10 We related the predictor variables to bird population trends using linear mixed-effects models
11 containing the main effects of particular species' traits and the interaction between the
12 potential range shift and the latitude of the mean range centre as fixed effects. If predictor
13 variables included into a statistical model are not independent, an issue of multicollinearity
14 may arise. For this reason, we calculated pairwise correlations between all species' traits. All
15 correlation coefficients were less than 0.7 which is treated a value above that the
16 multicollinearity affects statistical relationships (Dormann et al., 2013). Therefore, we can
17 conclude that multicollinearity among explanatory variables was not an issue in our analysis.
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25 We performed model selection based on information-theoretic approach to infer relative
26 importance of particular predictor variables (Burnham & Anderson, 2002). Using Akaike
27 Information Criterion corrected for small sample sizes (AIC_c) we assessed relative
28 performance of every combination of predictor variables within the R-package MuMIn
29 (Barton, 2015) and selected the models with ΔAIC_c less than two as the best performing
30 models (Burnham & Anderson, 2002). Parameters of these models were averaged using AIC_c
31 weights obtaining model-averaged estimates of each predictor variables with 95% confidence
32 intervals (Johnson & Omland, 2004). Those variables with confidence interval not
33 overlapping zero were treated as important predictors of bird population trends.
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42 To compare the predictors of trends for groups of species differing in abundance we followed
43 the approach recently applied by Inger et al. (2015). The species were sorted into four
44 quartiles according to the estimates of their European population sizes in BirdLife
45 International (2004). For each of the four species groups we run a separate analysis in the
46 same way as described above.
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52 As closely related species can share many ecological traits (Buckley and Kingsolver, 2012),
53 we accounted for potential effect of the common evolutionary history of the focal species on
54 the observed relations by including genus, family and order of each species as respective
55 random effects in each model.
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3. Results

For all species together, ten models had ΔAIC_c lower than 2 implying their superior performance over models containing other combinations of fixed effects (Table 1a). All these models contained following three predictor variables: habitat humidity gradient, habitat niche breadth and migration strategy (Table 1a). In majority of selected models were represented also habitat niche position and latitudinal range shift (Table 1a). Variables dietary niche and relation to built-up areas were included in only three of the ten best performing models (Table 1a). Only the variables included in all ten models were significantly related to bird population trends according to their confidence intervals (Table 1b). Specifically, bird species breeding in more humid habitats had more positive trends than species breeding in drier habitats and birds with broader habitat niches had more positive trends than birds with narrower niches (Table 1b). Finally, species' population trends became more negative with increasing migration distance (Table 1b). These results thus indicate that the variables describing species' habitat use were more important predictors of trends than the variables that mirror the climate change effects.

Higher importance of habitat-related variables was maintained also in the separate analyses for particular species groups defined by the abundance quartiles (Tables 2-5). These analyses thus partly uncovered which species were mostly responsible for the overall patterns described above. The significant effects of habitat humidity gradient and migration strategy were maintained only in the quartile of the least abundant species (Table 2). The least abundant species had also more positive trends when associated to built-up areas and being of more specialized dietary niche (Table 2). In contrast, in the quartile of the most abundant species the trends were significantly related to the habitat niche breadth and habitat niche position with more negative trends of habitat specialists and species breeding in more open habitats, respectively (Table 5). Finally, in the case of second and third abundance quartiles the model averaged estimates of all predictor variables had confidence intervals overlapping zero (Tables 3 and 4).

4. Discussion

1 Population trends of bird species breeding in Europe showed closer relationships to species'
2 traits related to habitat changes than to the traits that mirror the effects of climate change.
3 While the habitat-related variables, i.e. habitat niche position, habitat niche breadth, humidity
4 gradient, and relation to built-up areas, occurred in all models well-supported by data and
5 their confidence intervals often indicated their significance. Confidence intervals of the
6 variables reflecting climate change effects, namely latitudinal range position and latitudinal
7 range shift, always overlapped zero indicating they do not explain significant part of
8 variability in bird population trends.
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15 Based on these results, we suggest that the habitat change was more important driver of bird
16 populations than the climate change at least in 1990-2000 when the population trends were
17 collected (BirdLife International, 2004). These results contrast with findings of some previous
18 studies reporting important or even dominant effects of climate change on bird populations.
19 However, these differences can be attributed to the limited number of species used in these
20 studies (Møller et al., 2008; Gregory et al., 2009; Jiguet et al., 2010; Devictor et al., 2012),
21 limited spatial scope (Lemoine et al., 2007; Reif et al., 2008; Salido et al., 2012, Koschová
22 and Reif, 2014; Virkkala et al., 2014) or space-for-time substitution (Howard et al., 2015).
23 Moreover, several of these studies did not focus on both habitat and climatic niche of the focal
24 species simultaneously resulting in possible confusion of these drivers (see also Clavero et al.,
25 2011). On the other hand, our results broadly correspond to recent conclusions that the habitat
26 change is key driver of breeding bird population changes (e.g. Koleček et al., 2014; Møller et
27 al., 2014), which also result from findings of vast majority of studies reviewed by Reif (2013).
28 Although the climate change proceeded quickly over the time period when data on bird
29 population trends were collected (Devictor et al., 2012), deep habitat changes, including
30 agricultural intensification in Western Europe (Donald et al., 2006) or socioeconomic changes
31 with great implications for land use in Eastern Europe (Reif et al., 2011), took place at same
32 time. Therefore, although the dominance of habitat-related predictors over the climate-related
33 predictors observed in our data is somewhat surprising in the recent era of climate change,
34 closer examination of the environmental context of our study supports these findings.
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52 Our expectation about differences in relative importance of climate vs. habitat change
53 between rare and common species was not supported. Indeed, population trends of both
54 common and rare species showed closer relationships to habitat than to climate change
55 effects, although we expected dominance of climate change in the case of common species
56 based on their presumed higher tolerance to habitat changes due to their wider habitat niches
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1 (Godet et al., 2015; Reif et al., 2015). However, it seems possible that the habitat changes
2 were so extensive that they limit populations even in the common species. Indeed, the effect
3 of habitat niche breadth on population trends was significantly positive across all species
4 together and strongest in the fourth quartile, i.e. in the most abundant species. Therefore,
5 although the common species with broad habitat niches are probably resilient to
6 environmental changes, common specialists are not and their populations decline. This pattern
7 corresponds well to widespread declines of common specialists reported across Europe (e.g.
8 Julliard et al., 2004; Jiguet et al., 2007; Davey et al., 2012; Le Viol et al., 2012; Reif et al.,
9 2013). By contrast, our results do not show significantly negative effects of habitat
10 specialization in rare species. We can speculate that this result may indicate success of the
11 effort to conserve rare habitat specialists. It was already found that the that conservation
12 measures are effective, if specifically designed and targeted to reverse negative population
13 trajectories of specialized rare and threatened species (Brooke et al., 2008) such as *Emberiza*
14 *cirlus* in the United Kingdom (Peach et al., 2001) or species protected by national legislation
15 (Koleček et al., 2014), but they are largely insufficient to benefit common birds, as is the case
16 of broad and shallow agri-environmental schemes (Kleijn and Sutherland, 2003; Davey et al.,
17 2010; but see Pellissier et al., 2013).

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31 Habitat humidity gradient showed significant relationship to trends across all species, as well
32 as within the species of the first abundance quartile (i.e. the least abundant ones), with more
33 positive trends observed in species preferring more humid water habitats. Similar pattern of
34 water bird increase was observed over last 50 years in Finland (Fraixedas et al., 2015). We
35 suggest that the increase of water birds within the rare species can be explained both, by the
36 habitat protection and species protection. Conservation effort including prosecution of hunting
37 in many European countries lead to recovery of many predator species such as eagles, herons
38 and cormorants (Donald et al., 2007; Koleček et al., 2014; Sanderson et al., 2015) together
39 with better management of wetlands (Kleijn et al., 2014).

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48 Our results showing more negative trends of species breeding in more open habitats within
49 the most abundant species (fourth quartile) confirmed declines of farmland birds already
50 reported by many previous studies on common species (Donald et al., 2001; 2006; Gregory et
51 al., 2005; Reif, 2013). These declines can be generally attributed to agricultural intensification
52 (Fuller et al., 1995; Chamberlain et al., 2000), although the exact causes vary regionally and
53 include also abandonment of arable land in some areas (Reif, 2013). Since a recent study
54 discovered further declines of farmland birds coinciding with the spread of neonicotinoid
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1 pesticide use in Netherlands (Hallmann et al., 2014), we can conclude that management of
2 farmland bird populations towards recovery remains one of the crucial challenges for current
3 bird conservation.
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6 An interesting result is dominance of positive population trends within rare species breeding
7 in built-up areas. We are not aware of any previous studies reporting such a pattern, although
8 it is not unexpected given long-term expansion of human settlements in European landscape
9 (Fuchs et al., 2015). Moreover, more positive trends should be observed in species recently
10 colonizing European cities because positive population trend is among factors contributing to
11 species' urbanization success (Evans et al., 2010). At the same time, human settlements
12 became less suitable for some abundant species which colonized cities very long time ago
13 such as *Passer domesticus*, *Delichon urbicum* or *Apus apus* (e.g. Hole et al., 2002).
14 Population decline of such common urban dwellers may be an explanation why the positive
15 trends of species breeding in built-up areas were largely confined to rare species.
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19 An analysis confined to the least abundant species also uncovered an important negative
20 effect of dietary niche breadth indicating more positive trends towards more specialized
21 species. This somewhat contra intuitive result, when one would expect broader diet niche
22 being a buffer against adverse environmental changes as observed in the case of habitat niche
23 breadth, was driven by serious declines of many wetland bird species, especially ducks (e.g.
24 *Anas acuta*, *Aythya nyroca*), feeding both on animals and plants. Because the overall positive
25 trends of wetland dwelling species were factored out, it seems that the increase of this species
26 group is mostly driven by species feeding in fish such as *Ardea cinerea* or *Pandion haliaetus*,
27 while the species filtering water such as ducks decline. This pattern may reflect an adverse
28 impact of eutrophication on food supply in wetland habitats (van Turnhout et al. 2010) which
29 impacts by trophic cascades on filtering species (Møller and Laursen, 2015).
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33 Migration strategy was significant across all species as well as within the least abundant
34 species, but it was indeed included among the best performing models in all but one species
35 group. This suggests a great importance of the effects of this trait on bird population trends.
36 Many studies have already proved declines in long-distant migrants (Sanz et al., 2003;
37 Sanderson et al., 2006; Both et al., 2010; Vickery et al., 2014), but it remains unclear what is
38 the principal driver because both climatic and habitat changes may have similar population
39 consequences. According to the phenological mismatch hypothesis (Both and Visser, 2001),
40 long-distance migrants suffer from climatically-induced shift in timing of the food supply
41 peak because they are not able to adjust their breeding accordingly due to their innate
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1 migration schedule (Visser et al., 1998; Both et al., 2006). However, a recent study suggesting
2 tuning of departure dates from southern African wintering grounds in respect to climatic
3 conditions in Europe (Bussiere et al., 2015) questions this line of argumentation.

4 Alternatively, long-distance migrants may suffer from habitat deterioration in African
5 wintering grounds and/or at stopover sites, which are important during their migration (Zwarts
6 et al., 2009; Morrison et al., 2013; Cresswell, 2014). Such deterioration often results from a
7 high level of human disturbance (Stevens et al., 2010; Miede et al., 2010) which can be
8 strengthened by adverse climatic conditions such as drought (Mantyka-Pringle et al., 2012).

9 In conclusion, our study shows that besides some previously well documented patterns such
10 as population declines of farmland birds or long-distance migrants there are also surprising
11 increases in some species groups suggesting conservation success, such as in species
12 associated with wetlands. Interestingly, our results do not support strong climate change
13 impacts on populations of European birds suggesting that the habitat changes, mirrored by
14 significant effects of traits related to species' habitat niche, were more important. Even within
15 the most abundant species where we expected higher resilience to habitat change due to their
16 generally broader habitat niches we observed declines related to species' both habitat niche
17 position and breadth. These results suggest that while there is some evidence for successful
18 conservation in rare bird species in Europe, delivering conservation benefits to common birds
19 remains challenging.

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Table 1: (a) Linear mixed-effects models relating ecological traits to population trends of 268 species of European breeding birds from 1990 to 2000 selected according to Akaike information criterion (AIC_c) as the best fitting to data ($\Delta AIC_c < 2$). (b) Abbreviations, coefficients and confidence limits (CL) of ecological traits included in the models from (a) as revealed by model averaging (for details see the Section 2.3). Variables with confidence intervals not overlapping zero are printed in bold.

(a)

model	AICc	No. Parametres	$\Delta AICc$	weight	pseudo R ²
Hab_hum + Hab_niche_breadth + Mig_strat + Shift	899.5	4	0.00	0.047	0.057
Hab_hum + Hab_niche_breadth + Hab_niche_position + Mig_strat + Shift	900.2	5	0.76	0.032	0.067
Hab_hum + Hab_niche_breadth + Hab_niche_position + Mig_strat	900.4	4	0.98	0.029	0.064
Hab_hum + Hab_niche_breadth + Mig_strat + Relat_built.up + Shift	900.5	5	1.1	0.028	0.063
Dietary_n + Hab_hum + Hab_niche_breadth + Mig_strat + Shift	900.5	5	1.8	0.027	0.058
Hab_hum + Hab_niche_breadth + Hab_niche_position + Mig_strat + Relat_built.up + Shift	900.7	6	1.24	0.025	0.076
Hab_hum + Hab_niche_breadth + Mig_strat	900.8	3	1.31	0.024	0.052
Hab_hum + Hab_niche_breadth + Hab_niche_position + Mig_strat + Relat_built.up	901.2	5	1.76	0.019	0.072
Dietary_n + Hab_hum + Hab_niche_breadth + Hab_niche_position + Mig_strat + Shift	901.4	6	1.90	0.018	0.067
Dietary_n + Hab_hum + Hab_niche_breadth + Hab_niche_position + Mig_strat	901.4	5	1.97	0.017	0.064

(b)

trait variable	coefficient	lower CL	upper CL
position along a humidity gradient (Hab_hum)	0.3096	0.0429	0.5763
habitat niche breadth (Hab_niche_breadth)	0.1359	0.0316	0.2402
migratory strategy (Mig_strat)	-0.2855	-0.5006	-0.0704
range shift (Shift)	0.0004	-0.0001	0.0014
habitat niche position (Hab_niche_position)	-0.0396	-0.1825	0.032
relation to built-up areas (Relat_built.up)	0.0976	-0.2504	0.9685
dietary niche position (Dietary_n)	-0.1860	-0.5414	0.1694

Table 2: (a) Linear mixed-effects models relating ecological traits to population trends of the European breeding birds (first abundance quartile of 268 species used in this study) from 1990 to 2000 selected according to Akaike information criterion (AIC_c) as the best fitting to data ($\Delta AIC_c < 2$). (b) Abbreviations, coefficients and confidence limits (CL) of ecological traits included in the models from (a) as revealed by model averaging (for details see the Section 2.3). Variables with confidence intervals not overlapping zero are printed in bold.

(a)

model	AIC_c	No. Parametres	ΔAIC_c	weight	pseudo R^2
Dietary_n + Hab_hum + Hab_niche_breadth + Mig_strat + Relat_built.up	266.8	4	0.00	0.055	0.230
Dietary_n + Hab_hum + Mig_strat + Relat_built.up	268.1	5	1.25	0.029	0.202

(b)

trait variable	coefficient	lower CL	upper CL
dietary niche position (Dietary_n)	-1.4443	-2.7485	-0.1401
position along a humidity gradient (Hab_hum)	0.5290	0.0484	1.0095
migratory strategy (Mig_strat)	-0.5808	-1.1367	-0.0249
relation to built-up areas (Relat_built.up)	2.5757	0.0279	5.1236
habitat niche breadth (Hab_niche_breadth)	0.0488	-0.1179	0.3981

Table 3: (a) Linear mixed-effects models relating ecological traits to population trends of the least abundant European breeding birds (second abundance quartile of 268 species used in this study) from 1990 to 2000 selected according to Akaike information criterion (AIC_c) as the best fitting to data ($\Delta AIC_c < 2$). (b) Abbreviations, coefficients and confidence limits (CL) of ecological traits included in the models from (a) as revealed by model averaging (for details see the Section 2.3).

(a)

Model	AIC_c	No. Parametres	ΔAIC_c	weight	pseudo R^2
Hab_hum + Hab_niche_position + Latitude +Life_hist	229.7	4	0.00	0.028	0.163
Life_hist	229.7	1	0.02	0.028	0.056
Hab_niche_breadth + Life_hist	230.3	2	0.63	0.021	0.065
Hab_hum + Hab_niche_position + Life_hist	230.3	3	0.66	0.020	0.105
Hab_niche_position + Life_hist	230.6	2	0.97	0.017	0.088
Latitude + Life_hist	231.0	2	1.32	0.015	0.084
Hab_hum + Hab_niche_breadth + Hab_niche_position + Latitude +Life_hist	231.1	5	1.46	0.014	0.165
Hab_hum + Hab_niche_position	231.3	2	1.61	0.013	0.070
Hab_niche_breadth + Latitude +Life_hist	231.4	3	1.67	0.012	0.099
Hab_niche_position + Latitude +Life_hist	231.4	3	1.67	0.012	0.125
Dietary_n + Life_hist	231.4	2	1.75	0.012	0.057
Life_hist + Mig_strat	231.5	2	1.77	0.012	0.079
Hab_hum + Hab_niche_breadth + Life_hist	231.5	3	1.83	0.011	0.065

(b)

trait variable	coefficient	lower CL	upper CL
position along a humidity gradient (Hab_hum)	0.2024	-0.0805	1.0899
habitat niche position (Hab_niche_position)	-0.1002	-0.4686	0.0566
latitude of mean centre (Latitude)	-0.0139	-0.0928	0.0194
life history (Life_hist)	-0.2541	-0.5411	0.0011
habitat niche breadth (Hab_niche_breadth)	0.0341	-0.0681	0.3208
dietary niche position (Dietary_n)	-0.0175	-1.0925	0.4517
migratory strategy (Mig_strat)	-0.0110	-0.6878	0.2830

Table 4: (a) Linear mixed-effects models relating ecological traits to population trends of the least abundant European breeding birds (third abundance quartile of 268 species used in this study) from 1990 to 2000 selected according to Akaike information criterion (AIC_c) as the best fitting to data (Δ AIC_c < 2). (b) Abbreviations, coefficients and confidence limits (CL) of ecological traits included in the models from (a) as revealed by model averaging (for details see the Section 2.3).

(a)

model	AICc	No. Parametres	Δ AICc	weight	pseudo R ²
Hab_niche_position	216.7	1	0.00	0.035	0.188
Hab_hum	217.1	1	0.39	0.029	0.036
Mig_strat	217.4	1	0.71	0.025	0.006
Latitude	217.6	1	0.90	0.022	0.009
Hab_niche_breadth	217.8	1	1.6	0.021	0.011
Dietary_n	217.9	1	1.23	0.019	0.010
Life_hist	218.3	1	1.61	0.016	0.074
Hab_niche_position + Latitude	218.3	2	1.62	0.016	0.043
Relat_built.up	218.3	1	1.65	0.015	0.0003
Shift	218.4	1	1.67	0.015	0.002
Hab_niche_position + Mig_strat	218.5	2	1.77	0.014	0.038
Hab_hum + Hab_niche_position	218.6	2	1.93	0.013	0.049
Dietary_n + Hab_niche_position	218.6	2	1.95	0.013	0.048
Hab_hum + Latitude	218.6	2	1.95	0.013	0.046

(b)

trait variable	coefficient	lower CL	upper CL
habitat niche position (Hab_niche_position)	-0.0296	-0.2457	0.0734
position along a humidity gradient (Hab_hum)	-0.0469	-0.7057	0.2540
migratory strategy (Mig_strat)	-0.0225	-0.4953	0.1882
latitude of mean centre (Latitude)	-0.0008	-0.0143	0.0061
habitat niche breadth (Hab_niche_breadth)	0.0054	-0.1183	0.2572
dietary niche position (Dietary_n)	0.0206	-0.4103	0.7521
life history (Life_hist)	0.0043	-0.2475	0.3936
relation to built-up areas (Relat_built.up)	-0.0069	-1.7657	1.5248
range shift (Shift)	<0.0001	-0.0015	0.0016

Table 5: (a) Linear mixed-effects models relating ecological traits to population trends of the least abundant European breeding birds (fourth abundance quartile of 268 species used in this study) from 1990 to 2000 selected according to Akaike information criterion (AIC_c) as the best fitting to data ($\Delta AIC_c < 2$). (b) Abbreviations, coefficients and confidence limits (CL) of ecological traits included in the models from (a) as revealed by model averaging (for details see the Section 2.3). Variables with confidence intervals not overlapping zero are printed in bold.

(a)

model	AICc	No. Parametres	$\Delta AICc$	weight	pseudo R ²
Hab_hum + Hab_niche_breadth + Hab_niche_position	176.4	3	0.00	0.093	0.521
Hab_niche_breadth + Hab_niche_position	177.8	2	1.42	0.046	0.229
Dietary_n + Hab_hum + Hab_niche_breadth + Hab_niche_position	177.8	4	1.44	0.045	0.290
Hab_hum + Hab_niche_breadth + Hab_niche_position + Latitude	177.9	4	1.52	0.043	0.281

(b)

trait variable	coefficient	lower CL	upper CL
position along a humidity gradient (Hab_hum)	0.3736	-0.0154	0.9503
habitat niche breadth (Hab_niche_breadth)	0.2560	0.0896	0.4224
habitat niche position (Hab_niche_position)	-0.1692	-0.3117	-0.0267
dietary niche position (Dietary_n)	0.0464	-0.2189	0.6840
latitude of mean centre (Latitude)	-0.0053	-0.084	0.0282

Závěr:

Práce se zabývá vyhodnocováním dopadu změn klimatu a habitatu jakožto faktorů, které mají na distribuci a rozšíření ptačích druhů v Evropě největší vliv.

Populační trendy českých ptáků zkoumané mezi lety 1982 a 2006 v kontextu s klimatickou změnou odhalily, že populace druhů s jižním typem rozšíření v průměru narostly, zatímco populace druhů se severním typem rozšíření zaznamenaly pokles. Jde zjevně o reakci na měnící se klima, což se v podmínkách České republiky projevuje zejména vzestupem teplot v jarním období, tj. v době, kdy zde ptáci hnízdí. Vyšší teplota v hnízdí době je potom dosud ne zcela objasněným mechanismem, který bude zřejmě souviset s množstvím a načasováním potravní nabídky pro ptáky, má vliv na hnízdní produktivitu a potažmo na početnost u nás hnízdících ptáků. Je zajímavé, že opačné populační trajektorie druhů s rozdílným typem rozšíření reagují na měnící se klima i v poměrně malé oblasti, jakou je Česká republika, a v časovém horizontu několika dekád.

V budoucnu se má klimatická změna podepsat na dosti radikální reorganizaci evropské avifauny, přičemž podle klimatických modelů rozšíření se mají areály většiny druhů posunout do jiných oblastí, než se nachází teď. Bez ohledu na to, do jaké míry se tato predikce jednou ukáže reálná, lze ony predikované posuny použít jako proměnnou kvantifikující citlivost jednotlivých ptačích druhů vůči klimatické změně. Lze jednoduše postulovat, že více se posunující druhy jsou citlivější. My jsme zjistili, jaké vlastnosti druhů vysvětlují variabilitu zjištěnou v míře posunu areálů (tedy citlivosti k následkům klimatické změny). Ukázalo se, že predikovaný posun je nejlépe vysvětlován typem hnízdního habitatu a že největší míru posunu vykazují druhy lesní a vodní. Měla by se jim proto věnovat zvýšená pozornost ze strany ochrany přírody.

Míra posunu je tedy považována jako měřítko intenzity tlaku klimatu na konkrétní druhy. Jelikož ale není jisté, zda k posunu areálu v budoucnu skutečně dojde, je zajímavé vědět, jak takto vyjádřená citlivost souvisí se současnými populačními trendy. Při zjišťování vztahu mezi posunem areálu a dlouhodobými populačními trendy českých ptáků jsme zjistili, že se tento vztah liší v závislosti na typu rozšíření, a sice že druhy s největší mírou posunu klesají, pokud mají severský typ rozšíření, a na druhou stranu přibývají, pokud jde o druhy s jižním typem rozšíření. Klimatická změna patří tedy mezi hlavní faktory působící na právě probíhající populační změny. Toto zjištění je důležité proto, že daleko razantnější proměna klimatu, než jakou zažíváme dnes, celý svět v průběhu 21. století ještě čeká.

Na druhou stranu řada studií ukazuje, že klimatická změna sice na ptáky působí velmi silně, ale nejde o ten úplně primární faktor řídící změny ptačích populací. Lze si např. představit, že i když bude druh měnícím se klimatem „tlačen“ ze svého původního areálu jinam, posun

areálu neproběhne, pakliže tam nebude k dispozici příznivé prostředí, do něhož by se daný druh mohl šířit. Habitat tedy zásadně limituje rozšíření ptáků v prostoru a výrazně ovlivňuje i dlouhodobé změny jejich početnosti. Proto jsme chtěli otestovat na robustním datovém materiálu zahrnujícím údaje o populačních trendech na celém evropském kontinentu pro většinu v Evropě hnízdících druhů, jestli variabilita v těchto trendech je vysvětlena spíše změnou klimatu, anebo habitatu. Potvrdilo se, že na celoevropském měřítku je pravděpodobně významnější vliv změn habitatu podmíněný lidskou činností, nežli účinek klimatu. Zdá se, že změny v krajině působí jako hlavní iniciátor změn početnosti a distribuce a klimatická změna už pak jen zesiluje, nebo naopak zmírňuje tlak vyvolávaný lidmi způsobenou změnou prostředí.