Large changes in the avifauna in an extant hotspot of farmland biodiversity in the Alps

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Summary

Large declines of farmland bird species have been observed in the lowlands of Western Europe, whereas important populations of some of these species have survived in parts of Eastern and Southern Europe and in small areas within Western Europe, e.g. in parts of the Alps. However, such extant hotspots of farmland biodiversity are at risk: The economic and technical developments threaten to erode biodiversity in existing hotspots, potentially repeating the collapse previously observed in Western Europe. We here present changes in the abundance of farmland birds in the Engadin in the Swiss Alps. Farmland birds such as Whinchat Saxicola rubetra and Skylark Alauda arvensis were still numerous in 1987/1988 when we first censused the area. During our second census period in 2009/2010, we noticed strong declines of such open country species, while several hedge and tree breeders as well as some species preferring warmer climate increased. We observed a good correlation between the change in the vegetation and in the birds. Both these changes were especially pronounced in areas with a recent agricultural improvement project. Thus, we believe that the change in farmland practices, which affected our mountainous study area much later than the lowlands, and possibly climate change, have led to a profound change in the regional avifauna. Using our data as a case study, we argue that similar, and similarly fast, changes may be on-going or imminent in many other areas with extant important populations of farmland species such as Whinchat and Skylark. Thus, our data add to the repeatedly declared urgency to adjust the advancement of agricultural subsidy systems to better accommodate biodiversity considerations, both in depauperated areas as well as in extant hotspots.

Introduction

Populations of wild birds depending on farmland habitats have undergone a great decline in the 20th century in parts of Europe and elsewhere (Schifferli 2000, Donald *et al.* 2001a, 2006, Vorisek *et al.* 2010); and the birds' fate illustrates the large loss of farmland biodiversity as a whole (Gregory *et al.* 2004, Tryjanowski *et al.* 2011). This erosion of biodiversity is caused by a plurality of alterations to the traditional farming techniques (Stoate *et al.* 2001, Vickery *et al.* 2001, Robinson and Sutherland 2002, Newton 2004): Marginal areas are abandoned or afforested. Traditional mixed farming is often given up in favour of more uniform farming systems, a transition encouraged, for example, by land consolidation. Wet areas are drained and dry areas irrigated. Harvest timing has changed, speed increased and waste reduced. The general nutrient levels greatly increased (through the use of inorganic fertilizers and the import of animal fodder that yields large amounts of farm manure) as well as the control of organisms competing with agricultural plants (through the application of pesticides).

Since a few decades, agri-environment schemes (AES) have been installed in many countries to counteract the negative trends observed in species depending on farmland (Kleijn *et al.* 2006). The promotion of farmland biodiversity has become a declared function within the framework of a

sustainable agriculture, in parallel with the production of goods (and other functions; European Commission 2014). Nowadays, a lot of money is invested in AES, and monitoring programmes have yielded some positive responses (Aviron *et al.* 2009), but the great turn-around is still not secured and the magnitude of the overall response is often disappointingly small (Kleijn *et al.* 2006, Birrer *et al.* 2007, Vorisek *et al.* 2010). To increase biodiversity on farmland, the investments need to be better focused towards environmental goals, and the efforts have to be continued for a long time period.

However, it is crucial to note that this presentation of the situation mainly pertains to most of Western Europe. While the bulk of farmland biodiversity has vanished in Western Europe, a much richer farmland biodiversity persists mainly in Central and Eastern Europe (Verhulst *et al.* 2004; Baldi and Batary 2011, Polakova *et al.* 2011, Tryjanowski *et al.* 2011, Sanderson *et al.* 2013), parts of Southern Europe (Suarez *et al.* 1997, Stoate *et al.* 2001) and, on much smaller areas, on marginal land in Western Europe.

The richness of farmland biodiversity in these hotspot regions is mostly due to limitations in economic and/or technical development, and not to conservation considerations. In the recent past, political changes, mainly the accession of the Eastern European countries to the EU and the concomitant extension of the Common Agricultural Policy (CAP) to these countries, as well as developmental incentives (Stoate et al. 2001, van Rensburg 2001) and technical innovations (e.g. machines operating on steep slopes, or the increase of biofuel production; Liu et al. 2014) tend to increase farming intensity in extant hotspot regions. On the other side, and again driven by socio-economic changes, much marginal farmland is in danger of abandonment (MacDonald et al. 2000, Strijker 2005). Both processes, intensification and abandonment, will potentially lead to the loss of semi-natural farmland habitat greatly exceeding the recreation of such habitat in Western Europe under the AES (Suarez et al. 1997, Donald et al. 2001b, Polakova et al. 2011, Sanderson et al. 2013). From both an economic and an ecological standpoint, it should be desirable to promote a development of the extant hotspots of farmland biodiversity directly towards a multifunctional agriculture, wherein farmland biodiversity is protected and promoted effectively, rather than making a detour loop through a period of severe depletion of farmland biodiversity as experienced in Western Europe (Vorisek et al. 2010).

Extant hotspots, large or small, of farmland biodiversity deserve special attention as they can provide guidance for the intended turn-around in impoverished landscapes (Baldi and Batary 2011). Also, the species pool from such hotspots may contribute to the recolonisation of depauperate regions.

Here, we present data on the development of a hotspot of farmland biodiversity within Western Europe, namely in the Engadin, a long valley in the Swiss Alps. Our focus is on the development of farmland bird species. A previous publication presented the vegetation changes in the same study area (Graf *et al.* 2014b). There, we showed that about 20% of the area covered with nutrient-poor grassland vegetation types during a first census in 1987/1988 was lost due to intensification or, to a smaller degree, due to abandonment by the second census in 2009/2010. Furthermore, among five measured landscape parameters, agricultural improvement projects were shown to have the greatest influence on the change of the vegetation (the other parameters were elevation, slope, impediments to cultivation, and distance to farm). Irrigation projects, which often are an important part of the agricultural improvement projects, were especially effective in intensifying meadows (Graf *et al.* 2014a,b).

One problem for the assessment of the long-term trends of farmland bird populations in lowland Western Europe is that the large decline of these species (and of biodiversity in general) preceded systematic monitoring programmes (Fuller *et al.* 2005) which were implemented also in response to the declines of farmland biodiversity. The situation in the Engadin is different in that our first census was conducted when (at least some of the) farmland bird species were still numerous, e.g. whinchat *Saxicola rubetra* (Müller *et al.* 2005). The mechanisation of the agricultural processes in the Alps only set in during the 1960s (Stöcklin *et al.* 2007). Species-rich traditional hay meadows still dominated above 800 m asl in the Valais in the Swiss Alps by the end of the

1980s (Sierro *et al.* 2009). According to Stöcklin *et al.* (2007) such meadows decreased by about 30% between 1955 and 1990 in the Swiss Alps, while the same habitat essentially disappeared over the same time span in lowland Switzerland (Bosshard 2015). Therefore, our data from the Engadin may mirror, to some extent, the changes in the grassland avifauna in the lowlands of Western Europe a few decades earlier, changes which were mainly observed ex post, only.

In the present study, we first describe the observed changes of the bird populations and look at the correlation in the raw data between the vegetation and the bird change. Then, we use five landscape parameters, and the vegetation change, to investigate their influences on the bird changes using a path analysis.

Methods

Study site and study plots

The study was conducted in the Engadin, a valley in the Swiss Alps that stretches 80 km in a SW–NE direction. The valley can be subdivided into the "Lower Engadin" and the "Upper Engadin" with the valley floor at 1,000–1,600 m and 1,600–1,800 m, respectively. Surrounded by mountains reaching more than 3,000 m, the Engadin receives comparably little precipitation of around 700–1,000 mm per year. The landscape is characterised by wooded north-facing slopes; the valley floor is used for agriculture (mainly meadows) and, with increasing intensity during the last decades, for various infrastructures such as roads, railway, settlements for local people and tourists, golf courses, etc. Moderately steep south-facing slopes are used for agriculture (mainly meadows and pastures), steeper slopes are wooded. Above the tree line at about 2,200–2,300 m, alpine meadows, screes and rocks prevail.

We recorded the vegetation and bird community in 58 study plots spread along the entire length of the Engadin. Average plot size was 22 ha (SD 8.5 ha, range 4.5–43.3 ha; 1,253 ha in total) and up to five plots were adjacent to each other. The plots were selected to be topographically homogeneous and with the intention to represent the agricultural landscape of the Engadin below the tree line. Hence, all plots were mainly open agricultural areas.

We used five topographic or landscape parameters (hereafter landscape parameters) as predictors in the models: Elevation (mean \pm SD: 1,618 \pm 200 m, range: 1,159–2,136 m), slope (17° \pm 6.3°, 2–29°), distance to the next farm (air-line distance; 484 \pm 325m, 31–1,521 m), impediments to cultivation (on three levels: none, few, and much; e.g. stones, rocks or uneven ground), and whether and when an agricultural improvement project was conducted in the study plot (on three levels: none, before our 1st census in 1987/1988, between the 1st and 2nd census, i.e. between 1987/1988 and 2009/2010). Agricultural improvement projects (called "ameliorations" in Switzerland) usually include land consolidation and a number of infrastructure measures such as new or improved roads to access fields, new farms outside the traditional villages, and irrigation systems. Older projects also eradicated many marginal structures (which often have a large value for biodiversity, such as hedgerows), while newer projects claim to better take biodiversity issues into account. Numeric landscape parameters (elevation, slope, and distance to the next farm) were averaged across the study plot. Hence, each study plot had one value for each of the five landscape parameters.

Vegetation and bird census

On-site vegetation and bird census covered the entire area of all study plots. Censuses took place in 1987/1988 (1st census period) and in 2009/2010 (2nd census period). During both census periods, most plots were visited only in one of the two years (either 1987 or 1988, and either 2009 or 2010); some bird censuses were done in two consecutive years (36 of 116 plot-census period combinations). For the vegetation census, study plots were subdivided into parcels, i.e. areas covered with the same vegetation type. Such parcels often were one "field", a management unit of the

farmer; most parcels were between 100 m² and 1 ha in size. Twelve to 158 parcels were distinguished per study plot. Each parcel was assigned one vegetation type out of a list of 15 types as well as an intensity of utilisation on three levels: abandoned, low to medium intensity, high intensity. Many combinations of vegetation type and intensity were absent or found in small quantities only, therefore, the vegetation was aggregated into six combinations of vegetation type and intensity for the present analysis: low-intensity pastures (including xerothermic grassland, semi-dry and nutrient-poor pastures, and fertile pastures farmed at low or medium intensity), high-intensity pastures (fertile pastures farmed at high intensity), low-intensity meadows (semi-dry and nutrient-poor meadows and fertile meadows farmed at low or medium intensity), high-intensity meadows (fertile meadows farmed at high intensity and artificial meadows which are in rotation with crops), other open areas (tall herbaceous vegetation, wet meadows, crop fields, fallow land, boulder fields), and non-open areas (tree groups, forest, settlement areas). Further details of the vegetation census are described in Graf *et al.* (2014b; including keys for the vegetation types and the intensities in the online supplement).

A breeding bird census comprised three surveys conducted between 15 May and 25 June. The surveys were at least one week apart. Each survey covered one entire study plot and lasted 3–6 hours on a morning with suitable weather conditions (no rain, fog, or strong wind). On each survey, all contacts with birds of the agricultural landscape (see Table 1) were registered on a map, with specific focus on song and other behaviour indicative of reproduction. After the surveys, territories were established based on at least one observation (except for observations of likely migrants; details of the method are available on www.vogelwarte.ch/monitoring-bruetvoegel.html, "Anleitung TerriMap online"). The number of territories in each plot was used for analysis.

Vegetation and bird censuses were carried out by experienced field workers. Bird censuses were conducted by nine different field workers during the first census period and by four others during the second period. The vegetation was monitored by three and four people, respectively (RG was involved in both vegetation censuses). At the beginning of the season, some areas were visited together to align the vegetation categorisation among field workers. While we did not attempt to statistically correct for observer effects, the large number of ornithologists involved precludes a systematic bias due to a strong observer effect by a single field worker.

Analyses

The proportion of each of the six aggregated vegetation types is described using a normal linear model predicting the arcsine-square root-transformed proportions depending on the vegetation type and the census period, including the interaction. For the bird data, we built a Poisson model with an offset (log of the study plot area) to estimate the density for each census period. For both models, the study plot was included as a random term to account for repeated measurements. A random term identifying groups of study plots that were adjacent to each other was included as a second random term. In the bird model, each census (each plot-year combination) was used as a data point, even when two censuses were conducted in a single census period. Year was included as an additional random term. In this way, the fixed effect of census period is estimated accounting for the within-census period variation. Because only about one third of the plots were censused twice in both study periods, we also compared our trends with trends from a number of plots from other monitoring schemes in the vicinity (see online supplementary material). From these comparisons, we conclude that the trends we observed are representative of the general development of the species in the area and not substantially biased by (potentially) untypical conditions affecting the populations of the study area in one of our study years.

To investigate the influence of the five landscape parameters on the vegetation and on the bird populations (direct or indirect effects), we conducted a path analysis (see Figure 5; Clough 2012). For that, the change in vegetation was measured by the Bray-Curtis dissimilarity of the untransformed proportion values. Similarly, the bird change was measured by the Bray-Curtis dissimilarity of bird densities (mean values when two censuses were conducted in a census period; using

Table 1. Densities and changes in the abundance of bird species in the Engadin, together with ecological characteristics. Species ordered according to change. Horizontal lines separate species with an apparent decrease, with no clear trend, and with an apparent increase according to our data. Ecological characteristics are predominant diet (B = berries, I = invertebrates, S = seeds), nest site (B = bushes and trees, C = cavities, G-g = ground grassland, G-f = ground fallow-like areas), climate (latitude of the northernmost edge of global distribution), migration (L = long-distance, R = resident, S = short-distance and partial), body weight (g), trend for Switzerland (CH), and European trend (EBCC).

Species ^a		Density ^b		Change ^c [95%	Diet ^d	Nest	Cli-mate ^e	Migra-tion ^d	Body	Trend	Trend
		1987/88	88 2009/10	credible interval]		site ^d			weight ^f	CHg	EBCC ^h
Eurasian Skylark	Alauda arvensis	0.86	0.38	44% [31%; 63%]	S	G-g	71.16	S	40.6	66%	77%
Whinchat	Saxicola rubetra	2.54	1.48	58% [50%; 68%]	I	G-g	70.00	L	15.2	54%	81%
Linnet	Carduelis cannabina	0.46	0.27	58% [34%, 101%]	S	В	66.00	S	20.5	72%	34%
Tree Pipit	Anthus trivialis	1.76	1.07	61% [50%; 74%]	I	G-f	70.50	L	21.5	32%	52%
Red-backed Shrike	Lanius collurio	0.95	0.64	67% [49%; 92%]	I	В	66.33	L	28.6	91%	109%
Wryneck	Jynx torquilla	0.33	0.33	99% [41%, 245%]	I	С	69.50	L	38.0	83%	36%
Yellowhammer	Emberiza citrinella	0.94	1.07	113% [83%; 154%]	S, I	G-f, B	71.18	S	29.8	141%	77%
Common Redstart	Phoenicurus phoenicurus	0.32	0.43	(133%) from 9 to 12 pairs	I	C	70.50	L	16.0	41%	130%
Garden Warbler	Sylvia borin	0.44	0.60	138% [90%; 212%]	I, B	В	70.31	L	17.9	90%	80%
Common Quail	Coturnix coturnix	0.33	0.58	(163%) from 4 to 6-7 pairs	S, I	G-g	61.00	L	105.0	131%	no data
Green Woodpecker	Picus viridis	0.21	0.35	167% [90%, 309%]	I	C	66.00	R	185.0	194%	195%
European Goldfinch	Carduelis carduelis	0.21	0.56	264% [135%; 506%]	S	В	66.00	S	15.6	53%	129%
Eurasian Blackcap	Sylvia atricapilla	0.16	0.94	572% [260%; 1228%]	I, B	В	70.10	S	17.7	130%	176%
Rock Bunting	Emberiza cia	0.08	0.76	(1,000%) from 1 to 10 pairs	S, I	B, G-f	51.00	S		174%	(+)i)
European Serin	Serinus serinus	0.00	0.59	(inf) from 0 to 9 pairs	S	В	60.00	S	11.5	117%	53%

a)Other species on the target list that were absent or observed in small numbers only: Corncrake Crex crex (2 breeding pairs in 1987/88; o breeding pairs in 2009/10), Hoopoe Upupa epops (0; 1), Grey-headed Woodpecker Picus canus (3; 2), Common Stonechat Saxicola rubicola (0; 0), Northern Wheatear Oenanthe oenanthe (3; 2), Barred Warbler Sylvia nisoria (0; 0), Common Whitethroat Sylvia communis (2; 2), Cirl Bunting Emberiza cirlus (0; 0).

b)Breeding pairs per 10ha, including only study plots with at least one breeding pair during either census.

c)Poisson mixed model (log-link) with the number of breeding pairs per plot and year as the outcome variable, and the census as the fixed factor; plot, groups of plots (= adjacent plots) and year were random factors, the log of the plot area was used as an offset. Thereby, we estimate the change between the two census periods accounting, as much as possible, for the variability of the counts within a census period. No model for rare species, where the raw percentage change is given in parentheses and used for species ordering, only.

^{d)}According to Bauer *et al.* (2005) and own judgment.

e)According to Møller (2008) and, if missing there, Cramp (1978).

f) Average between mean male and mean female body weight in grams as given in Bauer et al. (2005).

g)Trend in Switzerland. Data are from the common bird monitoring scheme of the Swiss Ornithological Institute. Change calculated for predicted values for 1987 and 2009 from a linear regression through the available index points from 1990–2009 (ie 3-year extrapolation to 1987).

h)Trend in Europe according to www.ebcc.info (accessed 24/2/2015); change of fitted values for 1987 and 2009 of a linear regression through the index points 1987–2009. i)Data available only since 1998; 1998–2009: trend slightly positive.

absolute numbers of the bird populations, i.e. not correcting for plot size, yielded nearly identical results). We then built two models, one for the vegetation change with the landscape parameters as predictors ("vegetation model"), and one for the bird change with the landscape parameters and the vegetation change as predictors ("bird model"). Study plots adjacent to each other were again identified by a random factor. Uncertainties for parameter estimates were based on 5,000 samples from the posterior distribution. At first, more complex models included a quadratic term of elevation as well as an interaction between elevation and slope, but none of these were judged to be important based on their Bayesian 95% credible intervals and were, therefore, omitted from the final model.

The estimates from the two models are the direct effects of the predictors on the corresponding outcome variable. The indirect effect of the landscape parameters on the bird change was estimated by multiplying each value from the posterior distribution of the parameter in the vegetation model with one value from the posterior distribution of the vegetation parameter in the bird model (path landscape parameter -> vegetation change -> bird change). The sum of the direct and indirect effects yields the total effect.

All analyses were conducted using the software R 3.1.2 (R Core Team 2014). Bayesian analyses were done using the function 'sim' from the package 'arm' (Gelman and Hill 2007), which assumes flat priors. Model assumptions were checked graphically, including bubble plots and semi-variograms to check for undue spatial autocorrelation in the residuals.

Results

Vegetation change

From 1987/1988 until 2009/2010, the proportion covered by meadows used at low intensity decreased from about 32.0% to 26.6% on average while the proportion covered by meadows used at high intensity increased from 23.6% to 28.1% (Figure 1). The other vegetation aggregations used for the present analyses showed little absolute changes. Pastures of high intensity were uncommon during the first census, their increase, however, was ninefold (from 0.3% to 2.7%). Abandonment was not a major problem for most vegetation types; within the study perimeter, 7.3% of the area was scored as abandoned during the first census in 1987/1988 and 9.1% in 2009/2010 (Graf *et al.* 2014b). However, low-intensity vegetation was more prone to abandonment, while very little of the more intensively used land dropped out of the production.

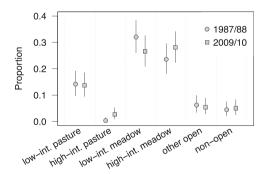


Figure 1. Mean proportion of the aggregated vegetation types during the first census in 1987/88 and during the second census 2009/10 (means of arcsin-square root transformed proportions, back transformed). Segments are Bayesian 95% credible intervals (using flat priors). "int." = intensity, "other open" includes tall herbaceous vegetation, wet meadows, crop fields, fallow land, and boulder, "non-open" corresponds to trees, woods, and settlements. N = 58 study plots.

Bird population change

We observed strong changes in the abundance of many bird species of the open landscape (Figure 2, Table 1). Skylark *Alauda arvensis* and Whinchat, ground breeders of the open grassland, and Tree Pipit *Anthus trivialis*, also a ground breeder but in grassland areas mixed with trees, all had strong populations at the end of the 1980s and all suffered severe declines up to 2009/2010; their populations dropped to 44–61% of the former counts (Table 1, Figure 3). Red-backed Shrike *Lanius collurio* showed a similar decline (down to 67%). The Linnet *Carduelis cannabina* population was reduced to 58%, though the decline is marginally non-significant and the species is difficult to census. On the other hand, strong population increases were observed in the Blackcap *Sylvia atricapilla* and Goldfinch *Carduelis carduelis*, species breeding in hedges and trees (Table 1, Figure 3). With the exception of the Red- backed Shrike, the other species of this habitat (Yellowhammer *Emberiza citronella*, Garden Warbler *Sylvia borin*, Green Woodpecker *Pica viridis*) also showed a (non-significant) positive trend. European Serin *Serinus serinus* and Rock Bunting *Emberiza cia* both increased from very small numbers during our first census. Overall, the number of breeding pairs of all species taken together declined (Figure 2). Furthermore, we observed that species with strong changes showed the same direction of change in almost all study plots (Figure 3).

Our species pool is too small to perform strong analyses regarding the correlations of ecological characteristics with the observed trends, as has been done by Møller (2008), van Turnhout *et al.* (2010), Salido *et al.* (2012), and Szep *et al.* (2012). Nevertheless, we added some of the variables often discussed with regard to population trends in Table 1. Insectivorous species were found about equally among both the increasing and decreasing species, the same holds for seed-eaters. Two of the three species characterised as grassland ground-nesters have strongly declined; the count of Quails *Coturnix coturnix* slightly increased but at very low numbers (and Quails are difficult to census and erratic in appearance). Long- and short-distance migrants were again found

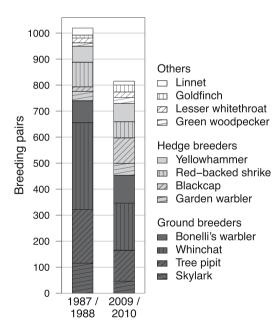


Figure 2. Total number of breeding pairs in the study plots (1,253 ha) during the two study periods. For better readability, only species with at least 20 breeding pairs in either of the two censuses are depicted. See Table 1 for the complete list of species with scientific names and their corresponding densities.

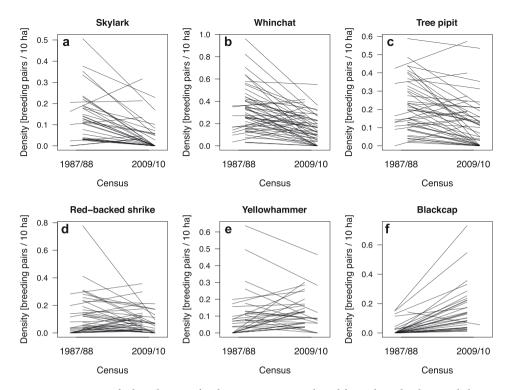


Figure 3. Densities of selected species for the two census periods and for each study plot (single lines). Increasing and decreasing cases are notched sideways for better readability; cases with no change were mostly plots with no presence during both censuses and are omitted (number of plots omitted, from the total of 58, from skylark to blackcap: 22, 6, 11, 17, 25, 20).

among increasing and decreasing species, though a tendency for better trends among short-distance migrants appears to be indicated. Body weight showed no obvious correlation with population trend in our data. Birds have been characterised according to their northernmost breeding limits as a surrogate for their susceptibility to climate change. We observed, overall, better trends in more southern species (Pearson's correlation coefficient r between the climate values and the log of the proportion change values in Table 1 = -0.67). Correlations with the trend during the same time period for Switzerland and for Europe were quite strong (correlations among log values of the proportion changes given in Table 1: r = 0.54, and r = 0.33, respectively). The Serin was the strongest outlier, with a strong decreasing trend in Europe while it appeared as a new breeding bird species in the Engadin.

Correlations between landscape parameters, vegetation change and bird population change

The vegetation change observed in our study plots correlated well with the bird change (Figure 4; regression line: 0.39 + 0.42 x vegetation change, Bayesian 95% credible interval for the slope parameter: 0.13–0.71). The explained variance was 11.7% (adjusted R²).

We used a path analysis to describe the effects of five landscape parameters (elevation, slope, impediments to cultivation, distance to the next farm, and agricultural improvement project) on the vegetation change, the direct effect of the landscape parameters on the bird change and their indirect effect on the birds via the vegetation change, and the direct effect of vegetation change on bird change. Study plots where a new agricultural improvement project was conducted between our $\mathbf{1}^{\text{st}}$ and $\mathbf{2}^{\text{nd}}$ census showed more vegetation change compared to plots where no such project

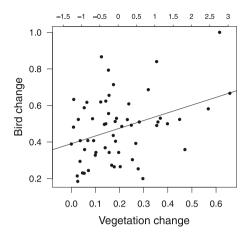


Figure 4. Bird change between 1987/88 and 2009/10 was larger in study plots with a larger vegetation change (dots = study plots, n = 58). Vegetation change was measured as the Bray-Curtis dissimilarity of the proportions of six aggregated vegetation types between the first and the second census, and, similarly, bird change was the Bray-Curtis dissimilarity of the number of breeding pairs of fifteen species of the open landscape (see Table 1). The line is the regression line. The upper axis indicates the centered and scaled values of the vegetation change to allow better interpretation of the effect sizes of the models that used these values (e.g., Figure 5).

ever was conducted (baseline level "none"; plots with a project before the 1st census showed no significant difference with the baseline level; Figure 5 and Appendix S1 in the online supplementary material). Such recent agricultural improvement projects also had an indirect effect, via the vegetation change, on the bird change. Furthermore, bird change was greater in plots with a greater vegetation change *per se*, i.e. after correcting for the effects of the five landscape parameters (direct effect of vegetation change on bird change). Finally, there was a significant negative total effect of slope on bird change. Elevation, impediments to cultivation and distance to farm did not significantly affect vegetation and bird change. Note that the parameter estimates given in Figure 5 and Appendix S1 can be compared with the raw data indicated in Figure 4 (y-axis and upper x-axis) to gauge the importance of the indicated relationships.

Discussion

We observed marked changes in the avifauna over 22 years in a hotspot of farmland biodiversity, the Engadin in the Swiss Alps. Skylark and Whinchat, ground-nesters of the open farmland habitat, both suffered severe reductions. Bush-breeders such as Blackcap and Goldfinch increased strongly, while the Red-backed Shrike, preferring smaller hedges in a matrix of low-intensive grassland that provide enough large-sized insect prey, declined. The establishment of small populations of Serin and Rock Bunting may be an effect of climate change since these two species prefer warmer conditions. Hence, the marked changes we observed cannot be explained by a single factor; in our opinion, the two most likely drivers are a changing landscape on the breeding grounds and climate change. Negative effects during long-distance migration may be the main or an additional problem for a few of the species we observed, especially for the Red-backed Shrike (Pasinelli *et al.* 2010).

Before we discuss these drivers in more detail, we focus on the degree of change in the avifauna and on the observed correlation between the change of the vegetation and the bird community. The change in the avifauna in the Engadin appears to be large. A numeric comparison with the change from all of Switzerland or all of Europe may not be entirely adequate (corresponding numbers in Table 1 for comparison) because of the very different sizes of these areas; in a smaller

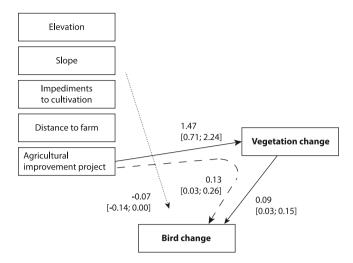


Figure 5. Main results of a path analysis showing a direct effect of agricultural improvement project on the magnitude of the vegetation change and an indirect effect on the magnitude of the bird change (only significant paths shown; see Appendix for the complete results). Solid lines: direct effects, dashed line: indirect effect (i.e., the product of the corresponding direct effects), dotted line: total effect. Vegetation and bird change are Bray-Curtis dissimilarities, values along arrows are effect sizes with Bayesian 95% credible intervals. Elevation, slope, distance to farm and vegetation change were scaled. Levels of agricultural improvement project: "none" (baseline), "before 1st census", and "between 1st and 2nd census" to which the indicated effects pertain.

area, a larger change may be expected *a priori*. A more important point to us seems to be the fact that some of the farmland species, especially Whinchat, Skylark, Tree Pipit and Red-backed Shrike, still had very high densities during our first census in many of the study plots, hence the habitat seemed to be (near-) optimal for them at that time. From Figure 3 we see that these species disappeared completely from a substantial number of study plots.

Hence a major decline of the farmland specialists among the birds has probably only happened after the 1980s in the Engadin, while the analogous decline in the lowlands of Western Europe started decades before (Donald *et al.* 2001a, Robinson and Sutherland 2002). The decline of farmland bird species within the Alps has also been observed by Archaux (2007) between 1980 and 2002 in a French valley, with the greatest declines at elevations below 1,000 m (farmland specialists declined by 70% below 1,000 m and by 20% above 1,000 m). Sierro *et al.* (2009) describe strong declines of farmland species in three low-elevation study sites in an Alpine valley between 1988 and 2006. In our experience, the erosion of farmland specialists reached the Alps probably during the 1960s, affecting e.g. large areas at the northern fringes of the Alps in Switzerland (Knaus *et al.* 2011). But later, even hotspots within the central Alpine valleys were affected. Economically stronger areas (due to tourism and/or substantial subsidy payments, such as in the Engadin) were mainly affected by intensification, while abandonment was strong in areas where human emigration promised better economical perspectives (e.g. large areas along the southern fringe of the Alps).

The correlation between the bird change and the vegetation change in the Engadin is clearly recognisable in our data (Figure 4). The variance in the bird change that can be explained by the variance in the vegetation change, though, is only about 10%. Nevertheless, given the rather crude vegetation types, this correlation is noteworthy. Data on potentially important changes in the structures, e.g. if hedges have grown denser and higher between our two censuses, as well as many other influencing factors are not available; hence, while the change in the vegetation may

be more directly linked to changes of true meadow birds, the measured vegetation change may rather be a surrogate for the general change in the landscape which, as a whole influences the composition of the avifauna.

There are several likely driving forces that contributed (and still contribute) to the change of the vegetation and the biodiversity in the Engadin during the recent past. For example, silage usage was introduced during the 1990s (M. Müller pers. comm.). Meadows are now mown earlier and faster, with direct (mortality of incubating females or nestlings) and indirect (reduction of prey and of suitable habitat for hunting and nesting) negative effects on the meadow birds (Müller et al. 2005, Grüebler et al. 2008, Strebel et al. 2015). Modern irrigation systems were built, especially during the 1980s; direct effects of irrigation on birds in the Engadin or similar areas are not well documented, but irrigation has led to the intensification of meadow use (Graf et al. 2014a), which is likely to have reduced habitat suitability especially for meadow breeders (due to earlier mowing and, possibly, denser vegetation structure). Former low hedgerows appear to have grown denser and larger. The general nutrient levels are likely to have increased, mainly through the import of animal fodder (which then yields more farm manure), and, to a smaller degree but affecting all habitats, by atmospheric nitrogen deposition (Peter et al. 2009, Roth et al. 2015). Landscape changes themselves are mostly a consequence of a more intensive, more mechanised usage by fewer farmers (527 farms used 7,445 ha agricultural area in 1980, 268 farms used 6,727 ha in 2010; stat-tab, www.pxweb.bfs.admin.ch).

Regarding biodiversity, agricultural improvement projects appear to be of special significance. According to our data, they mainly affected the vegetation composition, which in turn affected the bird compositions (Figure 5). While such projects likely help to prevent abandonment of hardto-reach marginal areas (though our data do not provide direct evidence for this; Graf et al. 2014b), they also strongly promoted the intensification of grassland usage, which led to significant changes in the avifauna and, most likely, in other taxa. Hence, our data suggest that biodiversity considerations have not sufficiently been taken into account in the agricultural improvement projects that were implemented during our study period. There is concern that even after our fieldwork in 2010, additional habitat rich in biodiversity has been lost, as new irrigation systems have been installed also on low- to medium-intensively used grassland (Graf et al. 2014a). On the other hand, considerable quantities of grassland, mostly of high biodiversity value, have recently been incorporated into a contracting scheme that prescribes late mowing and, in many cases, restricted nutrient inputs: Within our study plots, 36% of the farmland is now included in this scheme (data from Amt für Natur und Umwelt, canton of Graubünden), which should prevent intensification as well as abandonment, and which should improve the breeding success of ground-nesters, such as the Whinchat and Skylark. However, this expectation needs to be confirmed in the field in the future.

Except for agricultural improvement projects, the other landscape parameters we measured had only little influence on the change of the vegetation or the birds, according to our data. Only slope showed an effect, with less change of the avifauna on steeper slopes. This corroborates the notion that intensification pertains strongest to flatter areas suitable for larger agricultural machinery (e.g. silage balers).

Apart from habitat usage (mainly concerning farmland), migration strategy has been another focus of studies that tried to find relevant correlations between ecological factors and population trends of different bird species in Europe. Several studies linked long-distance migration with a higher chance of a negative population trend. Heldbjerg and Fox (2008) observed that trans-Sahara migrants breeding in Denmark declined especially since 1990, while farmland bird populations, on average, remained constant over this time. Van Turnhout *et al.* (2010) and Salido *et al.* (2012) also found many negative trends among long-distance migrants, but negative trends were also often observed in farmland species in the Netherlands and the UK. In our study, farmland specialists suffered more declines compared to most hedge species. Long-distance migrants also showed, overall, somewhat more negative trends compared to short-distance migrants. However, the fact that the farmland specialists such as Whinchat still had very good population numbers in the

Engadin when the populations in the lowlands had already collapsed suggests that habitat change must be a key driver of the decline.

The increase of a number of species in our study area may be due to a combination of climate change and, possibly, denser hedges (which we mainly attribute to a land use change, rather than climate change). This could explain the increase in Blackcap and Garden Warbler, Serin and Rock Bunting. Again, our species pool is too small to generalise this observation, but our data can add, together with other studies, to a better understanding of the correlations between ecological characteristics and population trends.

The future of the farmland bird populations in the Engadin – which still is a hotspot for farmland biodiversity – is hard to predict. On the one hand, encouraging developments in single study plots with a late-cut regime exist, e.g. regarding the Whinchat population development (own data). Thanks to the implementation of such late-cut regulations on a substantial part of the meadows in the region there is hope that the Whinchat and Skylark populations (and, with them, the typical biodiversity of low-intensive meadows) may recover, or, at least, may not decline further. On the other hand, the structural changes in the agronomy will continue, with even less farmers managing more land more efficiently. In addition, many farmers work part-time in other sectors, too. This increases the pressure to optimise farmland processes (MacDonald *et al.* 2000), which favours larger fields, a more homogeneous landscape, the abandonment of marginal land, and the increase of farming types that are less labour intensive such as suckler cow husbandry.

Conclusion

We propose that our study area and the changes we observed may be illustrative for other extant hotspots of farmland biodiversity. Much greater quantities of farmland birds are still present in Central, Eastern and Southern European countries (Kolecek *et al.* 2010, Baldi and Batary 2011, Tryjanowski *et al.* 2011, Szep *et al.* 2012, Reif 2013). However, changes appear to be imminent, especially since the EU enlargement and the adoption of the CAP by the new member countries (Donald *et al.* 2001b, Robinson and Sutherland 2002, Polakova *et al.* 2011, Sanderson *et al.* 2013). The situation in the Engadin is not directly transferable to other extant hotspots of farmland biodiversity, e.g. in Eastern Europe. Economic, topographic and many other characteristics are different in each region. However, the Engadin example demonstrates how quickly healthy populations of farmland specialists may decline.

We do not propose that the situation in extant regions of rich farmland biodiversity must be saved by conserving outdated farming practices. Biodiversity should not merely be a by-product of a lack of development and rural poverty. But there clearly must be types of modernisation that do not lead to the loss of most biodiversity without substitution and the erosion of a rich cultural landscape as seen in many parts of lowland Western Europe (Donald *et al.* 2001a, Ewald and Klaus 2009). Hence, the existing agri-environmental schemes should be further developed (as has been done to some degree; Sanderson *et al.* 2013) such that the modernisation in extant hotspots of farmland biodiversity directly and efficiently aims for a landscape that integrates the production of farmland goods with the presence of a rich farmland biodiversity. An efficient monitoring scheme must be an integral part of the modernisation efforts, and the results of such monitoring efforts must feed back promptly into the continuous advancement of agricultural subsidy systems and agricultural politics in general.

Finally, our observations put the spotlight on an area that still appears to be intact regarding farmland biodiversity from the point of view of the broad public, including tourists, but that has undergone important changes. Thus, the magnitude even of fast transformations (on a landscape time scale) may not be immediately visible to the non-specialist without specific monitoring programmes.

Supplementary Material

To view supplementary material for this article, please visit https://doi.org/10.1017/S0959270916000502

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