

Dear Dr. Ana S. L. Rodrigues,

Thank you very much for this second round of review. As you suggested, we have now clarified our results and we present more explicitly what this study brings to the habitat compensation hypothesis and what are its main limits. We have highlighted modifications associated with these responses in gray within the manuscript.

We hope that our revised manuscript is now suitable for recommendation by PCI Ecology.

We look forward to hearing from you.

Kinds regards,

On behalf of the authors,

Pierre Mallet

Recommender's comments – Ana S. L. Rodrigues:

General comment: *The main one is that I think there is a margin for improvement in the discussion. As context to my comments: the study design is one where for three bird guilds (9 forest edge species; 3 grassland species; 2 reedbed species), the authors investigate how the abundance of species is affected by the area of a type of semi-natural habitat considered to be their primary habitat (respectively: woodlands; grasslands; wetlands) and by the area of a type of field margin that may correspond to a substitute habitat (respectively: hedgerows; grass strips; reed strips) as a way of testing whether field margins can act as suitable substitute habitats. The expectation was thus that the results should confirm the value of the semi-natural areas as primary habitat for each of the species; and then the relative value of the respective type of field margin in relation to the semi-natural areas would let us know if it is or not an adequate substitute habitat, thus allowing for a test of the habitat compensation hypothesis.*

*The results are (inevitably) not as simple. Regarding the forest edge species, only 1/9 responds positively to woodland area (great tit), and only 1/9 (greenfinch) responds positively to the area of hedgerows. Regarding grassland species, only 1/3 (corn bunting) responds positively to grassland area, and it responds even more strongly to grass strips. Regarding wetland species, only 1/2 (reed warbler) responds positively to wetland area, and it responds even more strongly to reedbed strips. What these results are telling me is that this turned out not to be such a good model system for testing the habitat compensation hypothesis after all, because for most of the species analyzed (11/14) there is no evidence that the areas of semi-natural habitat studied correspond indeed to areas of "primary habitat". For the 3/14 species for which there is such evidence: for one (the great tit) there is positive but weak evidence that field margins are a substitute habitat (positive but no significant effect; for two of them, the substitute habitat turns out to be even better than the primary, so arguably it is not so much a "substitute" but a preferred habitat in its own right.*

*This is the beauty of studies based on real data, and the fact the results did not go always in the expected direction does not detract from the quality of the study. Nonetheless, the discussion needs to acknowledge it more explicitly. Currently the discussion focuses strongly on the specifics of the three individual species for which the result shows that they prefer field margins, and on the adverse effects of some types of field margins to some of the species. This is all very interesting, but what is missing at the beginning of the discussion is a broad level analysis of*

*what the results tell us (or cannot tell us) specifically regarding the habitat compensation hypothesis, which was the main question of the study (as reflected in the title), including perhaps a discussion of how the hypothesis could be better tested (with a different study design?)*

*I also find that currently the conclusions and the abstract are not well supported by the results (abstract lines 41-48: “Our study confirms that bird guilds are favored by the area of their primary habitat but are also influenced by the area of field margins. Reedbed birds are favored by the area of wetlands and reed strips and are negatively impacted by grassland cover. Grassland birds are favored by grassland and wetland areas and negatively impacted by woodland and hedgerow areas. Finally, forest edge birds are favored by hedgerows and negatively impacted by reed strips. These results suggest that field margins may represent substitute habitats for some bird species and highlight their importance for biodiversity conservation in wetland agricultural landscapes”; discussion lines 375-376: “In conclusion, our results highlight that field margins are valuable landscape components to improve biodiversity conservation while keeping a sufficient area dedicated to food production in rice paddy landscapes”). Indeed, in my interpretation the study does not add strong evidence to the importance of field margins as either a substitute habitat (the main question of the study; only weakly supported for 1/14 species tested – great tit) or as a habitat (valuable landscapes) in its own right (only for 2/14 species tested – corn bunting and reed bunting).*

Response: Thank you for these comments. We agreed that only a few species validate the habitat compensation hypothesis in our study. The discussion section now highlights this point and propose ways to better test this hypothesis lines 300-324:

“We found that (i) grass strips represent a substitute habitat to grasslands for corn bunting and (ii) reed strips represent a substitute habitat to wetlands for the Eurasian reed warbler, in line with the habitat compensation hypothesis. For these two species, the positive effect of field margins on the abundance of species was even stronger than the effect of the corresponding semi-natural habitat patch. This result suggests that field margins are currently valuable habitat rather than substitute ones for these two species. It is consistent with the meta-analysis conducted by Riva and Fahrig (2022), which highlighted the higher value of small habitat patches for biodiversity conservation. In contrast, we could not confirm the compensation hypothesis for 12 out of 14 species. Such a lack of support to the compensation hypothesis could be explained by different methodological and ecological reasons. First, we observed a general lack of species responses to their primary habitat with only 3 species responding positively to the primary habitat surface area. This may result from the use of broad categories of habitat preferences, while species abundance may vary along ecological continuums. Also, semi-natural habitats have been grouped into three primary habitat categories, which may not be detailed enough to match species habitats preferences. For example, wetlands include reedbeds but also ponds without emergent vegetation which are likely not very attractive for reedbeds birds. A more detailed mapping of primary habitats or functional description of habitats, such as habitat quality, nesting opportunities or food resources would therefore be necessary to further test the habitat compensation hypothesis for several of the species

considered. In addition, the observed species might potentially accommodate a diversity of habitats. Indeed, in the Camargue, some forest edge species like Carrion crow, Eurasian magpie or Common nightingale are known to be able to nest in very open landscape e.g. in isolated trees within a matrix of cultivated fields. Further studies aiming to test the habitat compensation hypothesis should therefore focus on species that are more strongly associated with their primary habitat.”

The abstract has also been modified to reflect the points raised in the discussion lines 41-51: “Results show partial support of the compensation hypothesis with species-dependent responses to primary and substitute habitat area. Some species within the reedbed and grassland bird guilds are favored by the area of their primary habitat as well as by the area of field margins, in line with the compensation hypothesis. Eurasian reed warbler is favored by the area of both wetlands and reed strips. Corn bunting is favored by grassland and grass strip areas. We could not confirm the compensation hypothesis for other species. However, this may be due to the fact that most of these species did not respond to their primary habitat. These results therefore suggest that field margins may represent substitute habitats for some species but further studies, in contexts where species are strongly associated with their primary habitat, would be needed to confirm the generality of this hypothesis.”

The conclusion has been modified to highlight the need to promote all components of landscape heterogeneity, not only field margins, lines 401-408:

“In conclusion, our results highlight that field margins are valuable landscape components to improve biodiversity conservation but cannot be the only components to be promoted in rice paddy landscapes. In Camargue, current conservation priorities concern the disappearance of wetlands and grasslands as well as the degraded conservation status of species associated with these habitats, whereas there is less concern for forest edge birds, which can be found in other agricultural landscapes. Our study therefore suggests that conserving and restoring wetlands and grasslands and the associated field margins, reed strips and grass strips, represent a promising avenue to increase biodiversity in the agricultural landscapes of Camargue.”

*Line 64: I recommend to add “focus on maintaining and increasing the capacity”*

Response: Corrected lines 66-68 “Rather, conservation efforts should also focus on maintaining and increasing the capacity of agricultural landscapes to support biodiversity”

*Lines 80-81: recommend being more precise as “the habitat compensation hypothesis has been investigated in the context of farmland abandonment and in dry agricultural areas”*

Response: Corrected lines 84-86 “The habitat compensation hypothesis has been investigated in the context of farmland abandonment and in dry agricultural areas”

*Lines 106-108: this sentence is ambiguous; clarify what the “the greatest rate of decline” means (in relation to what?)*

Response: Corrected lines 111-114 “Within this region, bird species associated with agricultural areas have experienced the greatest rate of decline over the past 50 years compared to waterbirds (Fraixedas et al., 2019; Galewski and Devictor, 2016).”

*Line 128: A reference from 1994 is not sufficient to support the statement that “the area... is now stable”*

Response: Corrected lines 133-135 “In Camargue, the area of semi-natural habitats decreased from 67 % to 39 % between 1942 and 1984 and since remained stable at around 58,000 ha (Mallet, 2022; Tamisier and Grillas, 1994).”

*Line 135: “fields” rather than “field”*

Response: Corrected line 142 “We selected 86 crop fields belonging to 17 farms across the Camargue (Fig. 1)”.

*Lines 154-155: when you say that the area of each type of field margin and semi-natural habitat was measured “within a 500 meter buffer around the centroid of each crop field”, it would be useful to clarify that the fields are much smaller than this (so that the field margins, where the bird counts were made are well within this buffer). You currently provide the size of the fields in the results (line 237), but it may make more sense to give earlier (in line 135, or in the legend of Figure 1). Also, in the abstract (line 37), saying “a 500 m buffer around each sampled crop” gives the impression it is a 500 m buffer around the boundaries of each field; please clarify it is around the centroid of the field.*

Response: We agreed and we now specified the maximum size of the selected crop fields, to illustrate that crop fields are smaller than the 500 m buffer: lines 162-163 “The maximum size of the sampled crop fields was 14 ha, hence much smaller than this buffer”. We also clarified the abstract lines 37-38 “within a 500 meter buffer around the centroid of each crop fields”.

*Line 190: recommend “birds that use urban areas” rather than “birds using” (the latter is a bit ambiguous in that it could suggest you assessed if birds were using urban areas as part of your study; the former makes it clearer that it is an information obtained from other sources)*

Response: Corrected lines 197-198 “birds that use urban areas for breeding”.

Reviewer's comments – Scott Wilson:

General comment: *I thought the authors did a nice job of addressing the reviewer comments. I enjoyed reading the revision and have only a few relatively minor suggestions for the text. Again, this is a nice contribution.*

Response:

We thank you for your positive assessment. Below, we have responded to each comment. Within the manuscript, we have highlighted modifications associated with these responses in green.

*Line 60: Suggest “European terrestrial area”*

Response: Corrected lines 63 “Agricultural areas represent 37 % of the European terrestrial area and host a large proportion of terrestrial biodiversity (DataBank, 2018; Herzog et al., 2013).”

*Line 135: Should be “crop fields” and then “variation” on line 136*

Response: Corrected lines 142-144 “We selected 86 crop fields belonging to 17 farms across the Camargue (Fig. 1). All fields were organic to limit confounding effects associated with variation in the intensity of agricultural practices.”

*Line 209-210: This sentence is repeated here and lines 206-207, otherwise a good description of this issue.*

Response: The repetition is now deleted.

*Results: I like the addition of the species-level effects, these help us understand within guild variation in responses and that's important for management. However, I think the new Results text could be streamlined to improve readability. As an example, in 3.3, I would combine 274-275 and 279-280 to a single line “There were no significant effects of woodland area, hedgerow area, crop diversity or crop mean field size on the abundance of the reedbed bird guild”. I would also reduce text in the other sections, for example 271-273 could be “The abundance of Eurasian reed warbler was positively related to both wetland area ( $\beta = 0.04 \pm 0.01$ ) and the area of reed margins ( $\beta = 0.26 \pm 0.09$ , Table 2, Fig. 2).” Readers can see Figure 2 for further comparisons of the magnitude of the effects. A similar integration of the text could be done for this guild on lines 276-278 and for the other two guilds in 3.2 and 3.1.*

Response: We agreed with this simplification. Therefore, in sections 3.1, 3.2, and 3.3, all non-significant effects are now grouped together and comparisons of the magnitude of the effects removed.

3.1 Forest edge bird guild

Lines 260-261 “There was no significant effect of wetland area or grass strip area on the abundance of species of this guild (Table 2, Fig. 2).”

3.2 Grassland bird guild

Lines 264-265 “The abundance of corn bunting was positively related to both grassland area ( $\beta = 0.12 \pm 0.03$ , Table 2, Fig. 2) and the area of grass strips ( $\beta = 0.46 \pm 0.18$ , Table 2, Fig. 2).”

3.3 Reedbed bird guild

Lines 277-283 “The abundance of Eurasian reed warbler was positively related to both wetland area ( $\beta = 0.04 \pm 0.01$ , Table 2, Fig. 2) and the area of reed margins ( $\beta = 0.26 \pm 0.09$ , Table 2, Fig. 2).

The abundance of great reed warbler was negatively related to both grassland area ( $\beta = -0.07 \pm 0.02$ , Table 2, Fig. 2) and the area of grass strips ( $\beta = -0.45 \pm 0.14$ , Table 2, Fig. 2).

There was no significant effect of woodland area, hedgerow area, crop diversity or crop mean field size on the abundance of species of this guild (Table 2, Fig. 2).”

*Lines 295-298: Based on the new results, one of the main highlights for me is that different types of field margins can provide substitute habitat but the responses vary even within guilds that we consider to have similar habitat requirements. I'd suggest an opening sentence presenting this idea and then that could be followed by the current line 295-298 on the cases where field margins were substitute habitats. The next two paragraphs then do a good job of developing this idea further. The point on lines 299-302 is very interesting and perhaps unexpected (at least to me) and is a second main highlight from this work.*

Response: Indeed, this point is interesting to underline lines 298-299 “Our study shows that different types of field margins can provide alternative habitats to terrestrial birds in a rice paddy landscape, but species responses vary even within species guilds.” We also add a sentence to highlight this idea in the abstract lines 51-52 “Our results also suggest that species response to increasing the area of a field margin type may vary among guilds and even within guilds”.

*Line 348: Should be “sample size”*

Response: Corrected line 375 “a sample size large enough to provide robust estimates of all parameters within associated statistical models.”

*Line 362: Suggest “within a single landscape”*

Response: Corrected line 389 “Our study therefore confirms that it may not be possible to favor all bird species within a single landscape”

*Line 363-364: Suggest “...type of field margins that most favour species in need of conservation attention”.*

Response: Corrected lines 389-390 “it may be necessary to focus on the type of field margins that most favor species in need of conservation attention.”

Reviewer's comments – Elena D. Concepción

General comment: *Thank you very much for the revised version of the article. I consider that the authors have responded adequately to the comments and suggestions I made on the initial version. I also consider that they have responded adequately to those of the other reviewers. In fact, I believe that the results of the new analysis are clearer than the previous ones and allow to draw more direct conclusions and implications for the management of the study area. I have no additional points to this new version of the article.*

Response:

Thank you for your comments.