

# Divergence in the ecological niches of the white wagtail (*Motacilla alba* Linnaeus, 1758) complex using the ecological niche modeling approach

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The mtDNA data presently being used for estimating biodiversity is not sufficient for evaluating the *Motacilla alba* complex species status. Because there is a lack of congruence between morphological and mtDNA data, there are debates about the best approach to use. In this study, we utilize niche modelling to study nine taxa of *M. alba* complex. Using eight bioclimatic- environmental layers, altitude, and slope MaxEnt modeling was applied to predict distributions. A total of 9087 input points for presence of species were also used. Results showed nine distinct ecological boundaries based on MaxEnt and ecological niche modeling (ENM) tools. The results provide some ecological variables for determining the ecological requirements and distribution patterns of the white wagtail species complex in the Palearctic region.

**Key words:** niche modeling, *Motacilla alba*, complex species, ecological boundaries

## INTRODUCTION

The area of distribution of a species shows its ecological and evolutionary history (Brown et al., 1996; Gaston, 2003). Limits of the species' tolerances, its needs for particular abiotic situations, its compatibility with other interacting species, and the potential for dispersal and colonization within a given period of time are the most important parameters that determine a species distribution area. (Grinnell, 1917; Pulliam, 2000; Soberón and Peterson, 2005). These factors must be emphasized across a dynamic geographic boundary. In such a matrix, the species faces variable climatic conditions, coastlines, river banks, mountain ranges, and other variables over the course of time (Jackson & Overpeck, 2000; Zachos et al., 2001). A species response to its physical and biotic environment varies differently and can cause geographic isolation and eventual speciation (Wiens, 2004; Byrne et al., 2008; Stigall, 2008).

Basic debates about the niche concept date back to at least Grinnell (1917) and form a core element of ecological and evolutionary arguments. Some researchers subjectively define species as groups of individuals live in the same niche or adaptive zone (Andersson, 1990; Van Valen, 1976). In the process of species recognition, niche conservatism and niche evolution are also very critical for species delimitation (Sites & Marshall, 2003).

A variety of experts have tried to compare a variety of approaches to understand species complexes. Along with other parameters, ecological factors may be also regarded as useful tools for delimiting species boundaries, presuming that each species has its own specific niche. Nevertheless, scientists

often face many critical problems for collecting life history details even for sister-species pairs with distinct niches.

Using a wide range of approachable environmental data and universally georeferenced points as agents for species ecology, Ecological Niche Modelling (ENM) has been introduced as a solution to this problem (Hawlitshchek et al., 2011). In addition to data showing species locality, raster maps which represent various environmental status, at the top of them climatic variables form the principals of applicable explicit models (Guisan & Zimmermann, 2000). Though limited to restricted environmental parameters, these models proved to be potentially capable of forecasting species distribution styles as well as appraising the effects of the ecological variables (Elith & Leathwick, 2009). In this regard, Modelling approaches are helpful for species delimitation only if the respond differently to the environmental variables (Rödder & Lötters, 2010).

The white wagtail (*Motacilla alba*) complex consists of common passerine birds that are distributed in most regions of Eurasia (Badyaev et al., 1996; Cramp, 1988; Dementev & Gladkov, 1954). White wagtails in different geographical regions have different colors such as black, white, and gray on the body (Stepanyan, 2003). Some authors consider the white wagtail as a single species (*Motacilla alba*) with fourteen (Cramp, 1988) and or eleven subspecies (Dickinson et al., 2004). Nevertheless, others divide them into two (Sibley & Monroe, 1993), three (Stepanyan, 2003), or nine distinct species (Sangster et al., 1999).

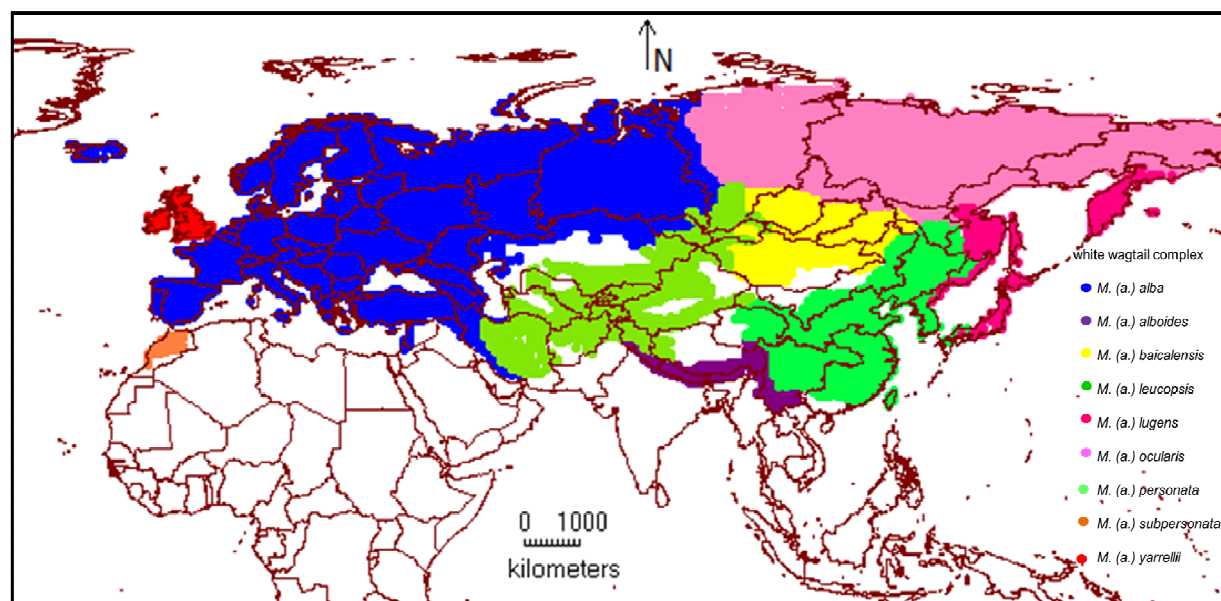
The taxonomy based on some particular morphological characteristics does not provide adequate scientific requirements for delimiting living species (subspecies) phylogenetically (Avice, 1989; Steinberg et al., 2009). We have used ENM based on the maximum entropy (MaxEnt) algorithm and ENMtools to determine the distinct ecological niches of various taxa of white wagtail (*Motacilla alba*) complex and comparing niche modeling results with morphological and molecular data in previous studies. Also, we have tried to understand potential distributional ranges and ecological requirements of white wagtail (*M. alba*) complex.

## MATERIAL AND METHODS

### Occurrence records and environmental variables

This study is based on 9087 occurrence records of nine white wagtail taxa including *M. (a.) alba*, *M. (a.) alboides*, *M. (a.) baicalensis*, *M. (a.) leucopsis*, *M. (a.) lugens*, *M. (a.) ocularis*, *M. (a.) personata*, *M. (a.) subpersonata*, and *M. (a.) yarrellii* (see Table 1) distributed all over the Palearctic region (see Fig. 1). These occurrence data were used with 21 environmental variables (19 bioclimatic, plus altitude and slope) for modeling ecological niches of white wagtail. Here, we follow Sangster's classification scheme to assign species names (Sangster et al., 1999). We also used distribution data records gathered from museum skin labels as well as the published literature (Aliabadian et al., 2005) and all of this points have been plotted one degree grid (grid cell area: 4062 km<sup>2</sup>) with an equal area. The occurrence data are available from the corresponding author and will be sent upon request.

Bioclimatic variables were derived from monthly temperature and rainfall values in order to generate more biologically meaningful information. All of the layers (2.5 min or 225 km of resolution, each cell) were downloaded from the Worldclim database (available at [www.worldclim.org](http://www.worldclim.org)). Layers were tested for Pearson's correlation coefficient ( $r \leq \pm 0.85$ ) (Elith et al., 2010) with ENMtools (Warren et al., 2010) and 2000 random points extracted from <http://www.geomidpoint.com/random/>. Highly correlated variables were removed until no pairwise correlation coefficient was greater than 0.85. This process resulted in nine layers of seven bioclimatic variables (including bio3= isothermally, bio4= temperature seasonality, bio5= max temperature of warmest month, bio7= temperature annual range, bio8= mean temperature of wettest quarter, bio13= precipitation of wettest month, bio14= precipitation of driest month, bio15= precipitation seasonality) plus altitude and slope layers.



**FIGURE 1.** Occurrence points of nine taxa of *M. alba* complex.

### Ecological niche modeling (ENM)

In this study, we mainly focused on the ENM analyses available in MaxEnt (Phillips et al., 2006; Phillips et al., 2004) because the recent literature has indicated a better performance for MaxEnt compared with other ENM methods (Araujo & Guisan, 2006; Elith J. et al., 2006; Elith et al., 2006; Merow et al., 2013) for delimiting species boundaries and ecological niches (Dupin et al., 2011; Reeves & Richards, 2011; Ross et al., 2010; Smith & Donoghue, 2010). Furthermore, MaxEnt is basically programmed for predicting species occurrence points based on generally incomplete available data from the study area.

This paper focuses on ENM constructed via maximum entropy using MaxEnt software package (Phillips et al., 2006). To test the model, we performed MaxEnt with the input georeferenced points and 25% random test percentage. To display suitability degrees ranging from 0 (unsuitable) to 1 (optimal), the logistic output format was selected.

We also applied the Jackknifing method in order to rank the significance degree of the variables. Model affirmation was done based on computation of Area under curve (AUC) ranging from 0.5 for models without any predictive accuracy to 1.0 for models with perfect predictive accuracy. This index reflects model's accuracy for making a distinction between the present georeferenced points and random background points (Phillips et al., 2006). AUC >0.9, >0.8 and >0.7 are considered as 'very good', 'good' and 'useful' differentiation abilities, respectively (Swets, 1988).

For further statistical analysis, the ENMtools software package was applied (Warren et al., 2010). Using Schoener's *D* (Schoener, 1968) and *I* statistic (Warren et al., 2008), niche overlap of nine taxa (pairwise comparisons) were calculated.

In addition, two hypothesis tests in ENMtools were analyzed (identity and background tests). Firstly, the identity test was used to assess whether ENMs generated from data available for two or more species appear different than expected ENMs when drawn from the same underlying distribution. Under the presumption that (1) the populations act interchangeably with use of ecological niche region, (2) each identity is randomly selected, and (3) original samples two new samples with the same point are extracted from earliest samples, this test mixes the two populations occurrence points into a common pool. Secondly, the background test was performed in order to evaluate

whether all divergences seen in the ecological niches of nine given taxa, based on the niches being shown by nine regions, can be illustrated by the variations in their niches. Based on the environmental layer, we applied background test for parapatric or allopatric species including 13 pairs of taxa for comparisons in their absolutely disjunctive ranges. In many occasions, different geographic locations have different environmental conditions. The background test is based on random points of one of the two populations. Furthermore, niche overlap between these points is calculated in two directions. Two populations are considered as distinct if, based on the background test, the overlap is significantly different. Two- way of identity and background tests, each of 500 iterations, were also applied in this research.

## RESULTS

### Species distribution modeling

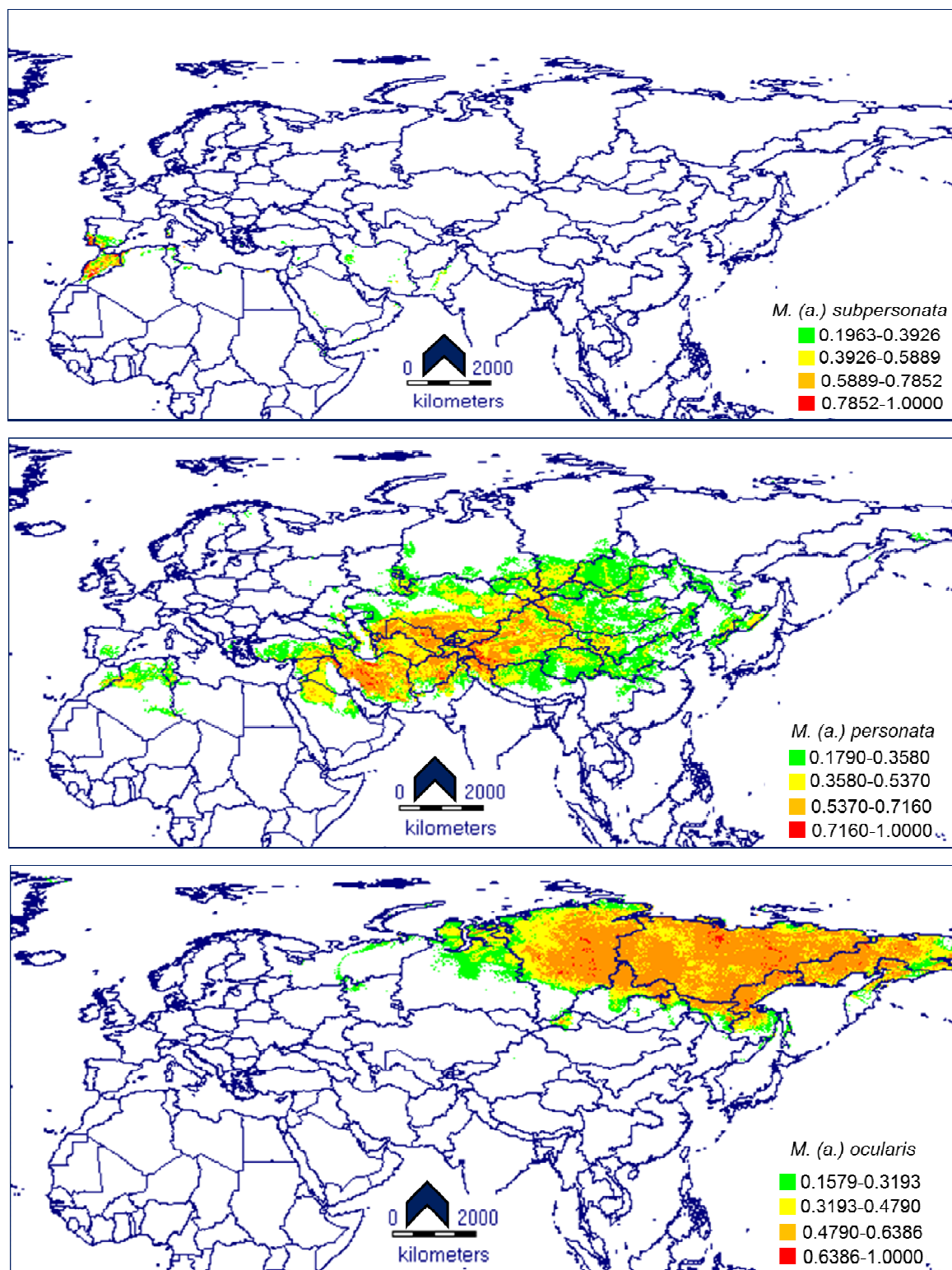
Nine different distribution maps were prepared using nine environmental parameters in addition to maximum entropy algorithm for each taxa (*M. (a.) alba*, *M. (a.) alboides*, *M. (a.) baicalensis*, *M. (a.) leucopsis*, *M. (a.) lugens*, *M. (a.) ocularis*, *M. (a.) personata*, *M. (a.) subpersonata*, and *M. (a.) yarrellii*). The warmer color (yellow and red colors) of each pixel in each map, the more suitable habitat for the species is (Fig. 2). Also, the species distribution modeling does not contradict the known range of these species.

The created model showed high AUC values for every training and test data (Table 1). AUC ranging from 0.878 to 0.997 exhibited 'very good' discrimination abilities for all taxa except for *M. (a.) alba* showing 'good'.

Isothermality for *M. (a.) alba* (59.5%), *M. (a.) baicalensis* (33.4%), *M. (a.) leucopsis* (47.9%), *M. (a.) lugens* (41.9%), *M. (a.) ocularis* (51.9%), *M. (a.) personata* (54.3%), (Table 2) was highly significant in predicting distribution patterns for every taxa. Annual temperature, precipitation of driest month, and seasonal temperature acted as the most important variables for *M. (a.) alboides* (33.4%), *M. (a.) subpersonata* (24.7%), and *M. (a.) yarrellii* (31.1%), respectively. A list of less important predictors for the *M. alba* complex is prepared in Table 2 as well.

**TABLE 1.** The occurrence data points used in the present study and AUC values in the *M. alba* complex.

Taxa	Data points	Training data	Test data
<i>M. (a.) alba</i>	3529	0.879	0.878
<i>M. (a.) alboides</i>	416	0.985	0.979
<i>M. (a.) baicalensis</i>	701	0.973	0.970
<i>M. (a.) leucopsis</i>	1317	0.952	0.950
<i>M. (a.) lugens</i>	251	0.990	0.986
<i>M. (a.) ocularis</i>	1640	0.939	0.931
<i>M. (a.) personata</i>	1120	0.955	0.950
<i>M. (a.) subpersonata</i>	39	0.998	0.997
<i>M. (a.) yarrellii</i>	74	0.997	0.995
<b>Total occurrence points</b>	<b>9087</b>		



**FIGURE 2.** MaxEnt distribution modeling logistic output of the white wagtail complex for *M. (a.) alba*, *M. (a.) alboides*, *M. (a.) baicalensis*, *M. (a.) leucopsis*, *M. (a.) lugens*, *M. (a.) ocularis*, *M. (a.) personata*, *M. (a.) subpersonata*, and *M. (a.) yarrellii*. More suitable and less suitable habitat for the taxa is shown in yellow-red colors and green-white colors, respectively.



FIGURE 2. continued.

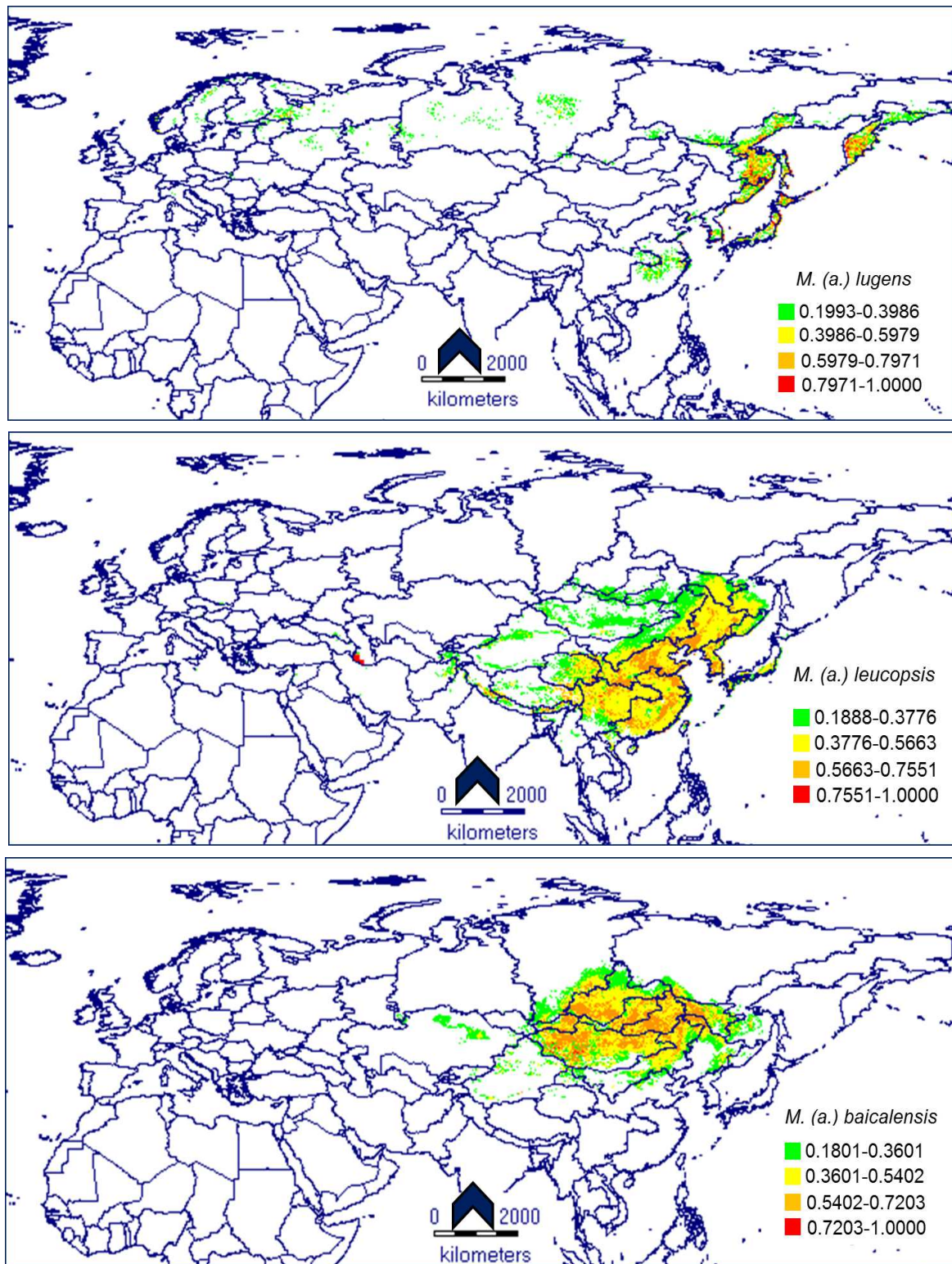
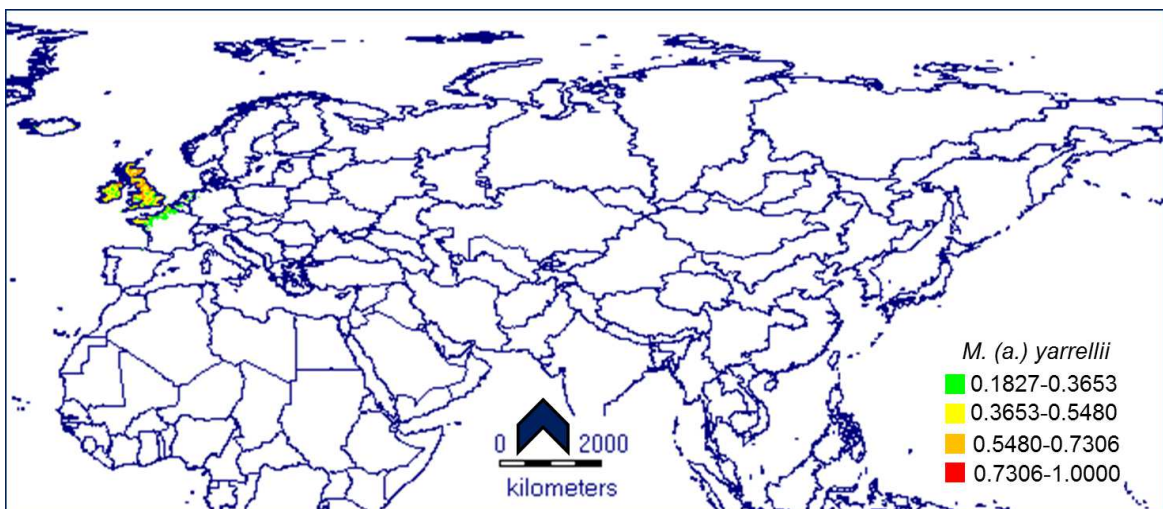
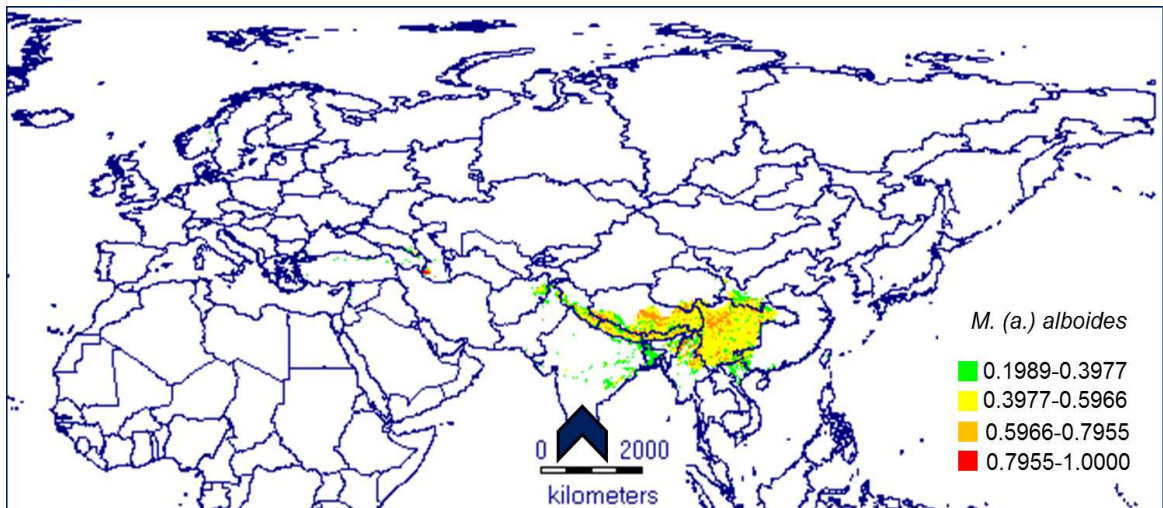
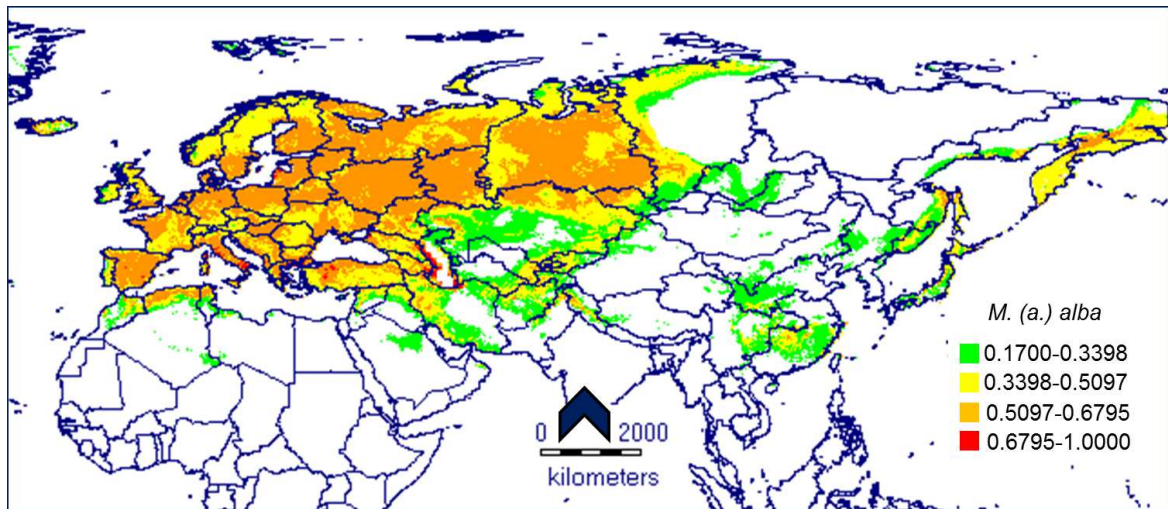


FIGURE 2. continued.



**TABLE 2.** MaxEnt output of the environmental variable contribution of the white wagtail complex for *M. (a.) alba*, *M. (a.) alboides*, *M. (a.) baicalensis*, *M. (a.) leucopsis*, *M. (a.) lugens*, *M. (a.) ocularis*, *M. (a.) personata*, *M. (a.) subpersonata*, and *M. (a.) yarrellii*.

Taxa	Variable based on importance	Percent contribution
<i>M. (a.) alba</i>	bio3	59.5
	bio15	9.6
	bio14	8.3
<i>M. (a.) alboides</i>	bio7	23.6
	bio3	19.7
	bio4	11.6
<i>M. (a.) baicalensis</i>	bio3	33.4
	bio14	23.9
	bio7	20
<i>M. (a.) leucopsis</i>	bio3	47.9
	bio13	16.2
	bio15	13.9
<i>M. (a.) lugens</i>	bio3	41.9
	bio13	18.6
	bio15	7.6
<i>M. (a.) ocularis</i>	bio3	51.9
	bio8	23.4
	bio4	9.9
<i>M. (a.) personata</i>	bio3	54.3
	bio14	18.6
	bio7	6.4
<i>M. (a.) subpersonata</i>	bio14	24.7
	bio4	22.9
	bio3	12.7
<i>M. (a.) yarrellii</i>	bio4	31.1
	bio8	21.1
	bio14	21.1

### Niche similarity tests

The niche overlaps between all nine taxa were calculated based on *D* and *I*. Overlap values vary in the range of 0-1. Therefore, the closer the value to 1, the higher the similarity in niches. Results showed zero between *M. (a.) subpersonata*-*M. (a.) lugens* and *M. (a.) subpersonata*- *M. (a.) ocularis*, suggesting no overlap in niches. The most niche overlap was 0.58 between *M. (a.) personata* and *M. (a.) leucopsis* (Table 3).

The identity tests ranged from 0.45 to 0.92 (*D* and *I*). Results obtained for the identity tests rejected the null hypothesis, meaning that climate envelopes, as modeled here, for every taxon are recognized as significantly distinct (Table 4). Table 5 and 6, provides background test (*D* and *I*) between species pairs. The background test ranged from 0.11 to 0.86. The niches (*I* and *D*) are significantly different than expected based on the location of 13 pairs of allopatric and parapatric taxa. The null hypothesis of the background test results suggests that mere environmental differences in their areas of occupancy may explain divergences in ecological niches, is rejected.



**TABLE 3.** Niche overlap estimates between taxon pairs (*D* statistic in upper right and *I* statistic in lower left).

Taxa	<i>M. (a.) alba</i>	<i>M. (a.) alboides</i>	<i>M. (a.) baicalensis</i>	<i>M. (a.) leucopsis</i>	<i>M. (a.) lugens</i>	<i>M. (a.) ocularis</i>	<i>M. (a.) personata</i>	<i>M. (a.)subpersonata</i>	<i>M. (a.) yarrellii</i>
<i>M. (a.) alba</i>	N/A	0.11	0.16	0.25	0.33	0.26	0.37	0.08	0.08
<i>M. (a.) alboides</i>	0.41	N/A	0.03	0.23	0.05	0.02	0.09	0.05	0.01
<i>M. (a.) baicalensis</i>	0.45	0.35	N/A	0.32	0.11	0.21	0.36	0.01	0.01
<i>M. (a.) leucopsis</i>	0.53	0.39	0.55	N/A	0.20	0.11	0.37	0.04	0.02
<i>M. (a.) lugens</i>	0.55	0.35	0.40	0.46	N/A	0.27	0.13	0.00	0.02
<i>M. (a.) ocularis</i>	0.51	0.33	0.47	0.41	0.52	N/A	0.14	0.00	0.01
<i>M. (a.) personata</i>	0.59	0.40	0.47	0.58	0.41	0.43	N/A	0.11	0.01
<i>M. (a.)subpersonata</i>	0.38	0.36	0.31	0.34	0.30	0.43	0.39	N/A	0.01
<i>M. (a.) yarrellii</i>	0.39	0.31	0.30	0.32	0.32	0.31	0.31	0.31	N/A

**TABLE 4.** Identity test estimates between taxon pairs (*D* statistic in upper right and *I* statistic in lower left).

Taxa	<i>M. (a.) alba</i>	<i>M. (a.) alboides</i>	<i>M. (a.) baicalensis</i>	<i>M. (a.) leucopsis</i>	<i>M. (a.) lugens</i>	<i>M. (a.) ocularis</i>	<i>M. (a.) personata</i>	<i>M. (a.)subpersonata</i>	<i>M. (a.) yarrellii</i>
<i>M. (a.) alba</i>	N/A	0.862±0.028 **	0.879±0.028 **	0.894±0.031 **	0.847±0.022 **	0.916±0.013 **	0.889±0.020 **	0.754±0.028 **	0.770±0.014 **
<i>M. (a.) alboides</i>	0.833±0.019 **	N/A	0.899±0.006 **	0.885±0.016 **	0.880±0.017 **	0.891±0.010 **	0.893±0.006 **	0.739±0.008 **	0.874±0.011 **
<i>M. (a.) baicalensis</i>	0.833±0.019 **	0.866±0.011 **	N/A	0.906±0.007 **	0.875±0.016 **	0.921±0.006 **	0.909±0.010 **	0.773±0.011 **	0.801±0.009 **
<i>M. (a.) leucopsis</i>	0.881±0.019 **	0.850±0.015 **	0.881±0.010 **	N/A	0.846±0.013 **	0.920±0.008 **	0.922±0.005 **	0.756±0.013 **	0.765±0.009 **
<i>M. (a.) lugens</i>	0.812±0.015 **	0.837±0.020 **	0.834±0.019 **	0.803±0.013 **	N/A	0.876±0.011 **	0.868±0.013 **	0.765±0.016 **	0.814±0.019 **
<i>M. (a.) ocularis</i>	0.900±0.009 **	0.857±0.012 **	0.899±0.008 **	0.905±0.009 **	0.836±0.012 **	N/A	0.926±0.004 **	0.813±0.019 **	0.835±0.012 **
<i>M. (a.) personata</i>	0.876±0.012 **	0.853±0.009 **	0.880±0.010 **	0.900±0.007 **	0.824±0.019 **	0.908±0.006 **	N/A	0.794±0.014 **	0.729±0.037 **
<i>M. (a.)subpersonata</i>	0.670±0.045 **	0.594±0.014 **	0.657±0.026 **	0.647±0.027 **	0.682±0.026 **	0.748±0.035 **	0.696±0.024 **	N/A	0.833±0.076 **
<i>M. (a.) yarrellii</i>	0.709±0.018 **	0.678±0.018 **	0.703±0.014 **	0.659±0.015 **	0.45±0.030 **	0.775±0.024 **	0.774±0.046 **	0.876±0.072 **	N/A

\*\*The true calculated overlap values (*D*, *I*) are far outside the 99.9% confidence intervals of the identity test results and thus highly significant.

**TABLE 5.** Background test estimates (*I* statistic) between taxon pairs.

Taxa	<i>M. (a.) alboides</i>	<i>M. (a.) baicalensis</i>	<i>M. (a.) leucopsis</i>	<i>M. (a.) lugens</i>	<i>M. (a.) ocularis</i>	<i>M. (a.) personata</i>	<i>M. (a.)subpersonata</i>	<i>M. (a.) yarrellii</i>
<i>M. (a.) alboides</i>	N/C	0.589±0.003 **	N/C	0.642±0.006 **	0.494±0.002 **	N/C	N/C	0.692±0.011 **
<i>M. (a.) baicalensis</i>	0.694±0.014 **	N/C	N/C	N/C	N/C	N/C	0.740±0.036 **	0.513±0.017 **
<i>M. (a.) leucopsis</i>	N/C	N/C	N/C	N/C	N/C	N/C	N/C	0.732±0.024 **
<i>M. (a.) lugens</i>	0.661±0.006 **	N/C	N/C	N/C	N/C	N/C	0.671±0.039 **	0.751±0.014 **
<i>M. (a.) ocularis</i>	0.752±0.006 **	N/C	N/C	N/C	N/C	N/C	0.788±0.025 **	0.803±0.024 **
<i>M. (a.) personata</i>	N/C	N/C	N/C	N/C	N/C	N/C	N/C	0.752±0.021 **
<i>M. (a.)subpersonata</i>	N/C	0.418±0.002 **	N/C	0.862±0.003 **	0.363±0.001 **	N/C	N/C	0.708±0.007 **
<i>M. (a.) yarrellii</i>	0.557±0.004 **	0.502±0.006 **	0.492±0.004 **	0.543±0.004 **	0.432±0.002 **	0.477±0.004 **	0.674±0.043 **	N/C

\*\*The true calculated overlap values (*I*) are far outside the 99.9% confidence intervals of the background test results and thus highly significant.

**TABLE 6.** Background test estimates (*D* statistic) between taxon pairs.

Taxa	<i>M. (a.) alboides</i>	<i>M. (a.) baicalensis</i>	<i>M. (a.) leucopsis</i>	<i>M. (a.) lugens</i>	<i>M. (a.) ocularis</i>	<i>M. (a.) personata</i>	<i>M. (a.)subpersonata</i>	<i>M. (a.) yarrellii</i>
<i>M. (a.) alboides</i>	N/C	0.348±0.004 **	N/C	0.427±0.012 **	0.204±0.003 **	N/C	N/C	N/C
<i>M. (a.) baicalensis</i>	0.751±0.017 **	N/C	N/C	N/C	N/C	N/C	0.594±0.063 **	0.558±0.023 **
<i>M. (a.) leucopsis</i>	N/C	N/C	N/C	N/C	N/C	N/C	N/C	0.598±0.041 **
<i>M. (a.) lugens</i>	0.513±0.009 **	N/C	N/C	N/C	N/C	N/C	0.551±0.060 **	0.660±0.020 **
<i>M. (a.) ocularis</i>	0.682±0.012 **	N/C	N/C	N/C	N/C	N/C	0.696±0.037 **	0.727±0.036 **
<i>M. (a.) personata</i>	N/C	N/C	N/C	N/C	N/C	N/C	N/C	0.643±0.028 **
<i>M. (a.)subpersonata</i>	N/C	0.117±0.003 **	N/C	0.161±0.005 **	0.037±0.009 **	N/C	N/C	0.560±0.013 **
<i>M. (a.) yarrellii</i>	0.337±0.005 **	0.227±0.009 **	0.214±0.004 **	0.284±0.005 **	0.112±0.004 **	0.182±0.003 **	0.557±0.065 **	N/C

\*\*The true calculated overlap values (*D*) are far outside the 99.9% confidence intervals of the background test results and thus highly significant.

## DISCUSSION

In this research, ecological niche modelling (mainly based on maximum entropy algorithm available in MaxEnt) and ENMtools were performed to determine the niche divergence of various taxa of the white wagtail (*Motacilla alba*) complex. Results obtained from the executed distribution models clearly showed the ability of ENM to delimiting ecological niches of every taxon with a significant AUC.

Based on DNA-DNA hybridization, Sibley and Monroe (1993) suggested *M. alba* consisting of *M. (a.) alba*, *M. (a.) yarrelli*, *M. (a.) subpersonata*, *M. (a.) personata* and *M. lugens*. Whereas, Cramp (1988) used some morphological characteristics to categorize *M. alba* as a single species including four subspecies group which are identified by the males' head colorful pattern; these were named as (1) *M. a. personata*, *M. a. alboides* (2) *M. a. ocellaris*, *M. a. lugens* (3) *M. a. alba*, *M. a. dukhunensis*, *M. a. yarrelli* (4) *M. a. baicalensis*, *M. a. leucopsis* (Pavlova et al., 2005). Sangster et al. (1999) elevated all the subspecies into nine distinct morphological species including: *M. alba*, *M. yarrelli*, *M. alboides*, *M. baicalensis*, *M. leucopsis*, *M. ocellaris*, *M. personata*, *M. lugens*, *M. subpersonata*. However, we doubt the distinction of western Asia (*dukhunensis*) populations from *M. alba*. Moreover, *M. a. persica*, which is presumably derived from varying hybrid populations of *alba* and *personata*, is not recognized either (Cramp, 1988). Based on his evidences on infertility properties and reproductive isolation of *M. alba*, Stepanyan (2003) introduced three new species including: *M. personata*, *M. lugens* and *M. alba*.

Using mitochondrial DNA sequence data consisting of Control Region (CR), NADH dehydrogenase subunit 2 (ND2), ATPase 8 and ATPase 6 (ATP8+6), and nuclear chromo-helicase-DNA binding protein gene (CHD-Z), Ödeen and Alström (2001) introduced two subspecies groups for *M. alba* complex *alba* (including *M. a. alba*, *M. a. yarrelli*, *M. a. ocellaris*, *M. a. lugens*, *M. a. baicalensis* and *M. a. subpersonata*), and *alboides* (including *M. a. alboides*, *M. a. leucopsis* and *M. a. personata*).

In another study, Voelker (2002) analyzed 960 base pairs (bp) of cytochrome *b*, and 1006 bp of NADH dehydrogenase subunit 2 (ND2) gene from 33 individuals of *Motacilla*. The results showed that *M. alba* is a paraphyletic species and very close to *M. lugens*.

Pavlova et al. (2005) suggested that all the above mentioned taxa might be recognized as one species, *M. alba*. Pavlova's claim is mainly based on eleven morphological and molecular (ND2 and CR) data. However, there is an apparent incongruence between the morphological and molecular records though the Maximum Parsimony tree reconstructed from morphological characters showing the highest compatibility with Cramp's proposed classification. In a more recent study, Li et al. (2015) reconstructed the evolutionary history of *M. alba* on the basis of molecular analysis of two mitochondrial genes (ND2, CR) and MaxEnt models. According to the results of their study, the divergence time for all taxa date back to Pleistocene. They concluded that, due to incongruence between the genetic and morphological divergences, it could be assumed that independent evolution occurred in distinct geographical regions.

Ecological niche modeling in MaxEnt, for *M. (a.) alba*, in our study, suggests a wide potential distribution for the species from western to eastern Palearctic region, which is predominantly observed in warmest and coldest months of the year depending on seasonal precipitation. The resulted models showed a potential distribution pattern from northern and south central part of China to Tibet, Eastern and western Himalaya, North of Myanmar, Nepal, and Bangladesh for *M. (a.) alboides*. Therefore, it is evidently seen that temperature during the warmest and the coldest months of the year play as deterministic parameters which define the species niche.

Based on ENMs, *M. (a.) baicalensis* occupy Mongolia, Tuva, China, North of Manchuria, Amur, Buryatia and Irkutsk while *M. (a.) personata* is almost dominated in southeastern Palearctic regions and some parts of northern Africa in Algeria. Temperature during the warmest and coldest month as well as precipitation of driest month are the most important bioclimatic factors in determining the distribution of *M. (a.) baicalensis* and *M. (a.) personata*.

The ENMs of *M. (a.) leucopsis* and *M. (a.) lugens* are determined mainly by the warmest month temperature and wettest month precipitation. The potential distribution of *M. (a.) leucopsis* is southeastern, northern and south-central China, Japan, Korea, Manchuria, China, and Amur, whereas the potential distribution of *M. (a.) lugens* is Japan, Sakhalin, Primorye, Kuril Island, Kamchatka, Khabarovsk and Aleutian Island.

Moreover, the geographic distribution of *M. (a.) ocularis*, which is mainly distributed in Magadan, North of Kamchatka, Khabarovsk, Yakutskiya, Irkutsk, and Krasnoyarsk, is strongly influenced by the temperature of warmest-coldest months and the wettest quarter of year. In contrast, *M. (a.) subpersonata* is widely distributed in Morocco and in the southern parts of Spain and Portugal, influenced by seasonal temperature and precipitation values during driest month. Finally, *M. (a.) yarrellii* was observed in Great Britain and Ireland. Also, seasonal temperature and the amount of precipitation during the wettest quarter of the year determine the species distribution pattern.

The white wagtail complex is distributed in a wide variety of non-forest wet and dry habitats including: seashores, rocky or sandy upland rivers, lake banks, farmlands, gardens, parks and short grasslands. Additionally, many of them are observed around human habitats in towns and villages (Del Hoyo et al., 2010). Largely restricted to the vicinity of running water, *M. (a.) subpersonata* is usually found in NW Africa. This reveals that all nine taxa except for *M. (a.) subpersonata* are influenced by temperature, with the latter strongly influenced by amount of precipitation.

Based on MaxEnt analyses, temperature plays the most important role in the *M. alba* species complex distribution pattern except for *M. (a.) subpersonata*, for which precipitation takes that role. Therefore, based on MaxEnt analyses and ecologically speaking, temperature is a limitation factor in distributional behavior of *M. alba* species complex just in comparison with precipitation.

Results obtained from the identity test showed a significant niche divergence among the above mentioned taxa because of completely diverse climate envelopes for each taxon. Moreover, results obtained from the background test indicated that all of the parapatric and allopatric taxa are separated by their niches, not by geographic features of the sites which they live in. Therefore, we suggest that each taxon occupies a particular ecological niche. This supports the morphological character distinction of white wagtail complex that classified by Sangster et al. (1999).

## Conclusion

According to the ecological species concept proposed by Van Valen (1976) and Andersson (1990), individuals that occupy the identical niche or adaptive zone form a single species. The results of MaxEnt models and ENMtools suggest that the white wagtail complex includes nine distinct ecological niches: *M. (a.) alba*, *M. (a.) alboides*, *M. (a.) baicalensis*, *M. (a.) leucopsis*, *M. (a.) lugens*, *M. (a.) ocularis*, *M. (a.) personata*, *M. (a.) subpersonata*, and *M. (a.) yarrellii*. As stated by Rokas et al., (2002), if the rate of speciation is high for a particular period, interlineage discrimination is expected to be low and would result in poorly resolved molecular topologies. This could be the main reason for the observed incongruence between the molecular and morphological/ecological data.

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