

1 **Landscape traits can contribute to range limit equilibrium: habitat constraints refine**
2 **potential range of an edge population of Black-headed Bunting *Emberiza melanocephala***

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11 **Abstract**

12 The potential range of Black-headed Bunting *Emberiza melanocephala* in Lombardy, northern Italy,
13 is restricted to the small area actually occupied by a tiny and isolated population; distribution
14 modelling suggests that both climatic and habitat features contribute to the observed
15 correspondence between the potential and realized range.

16

17 **Keywords** climate; distribution; habitat; MaxEnt; range limit

18 **Running head** Range limit in Black-headed Bunting

19 Ecology of range limits has attracted ecologists' attention for a long time (Gaston 2003, Sexton *et*
20 *al.* 2009 and references therein). Researchers are fascinated by the mechanisms determining such
21 limits, and the ecological and evolutionary dynamics acting at range limits may be relevant also for
22 conservation.

23 General patterns of range limits of multiple species may occur together due to climatic
24 thresholds (Gaston 2003), but more often species-specific patterns can be detected (Sexton *et al.*
25 2009). Range limits can occur without hard boundaries, and also in the lack of environmental
26 gradients or biotic interactions, only a few general patterns can occur, almost invariably having
27 many exceptions (Gaston 2009). Whenever non-climatic factors constrain distribution and so shape
28 range limits, the potential effects of climate change on the species distribution are difficult to
29 predict (Engler *et al.* 2013); therefore, it may be particularly important to understand the role of
30 non-climatic factors on species distribution.

31 A particular case is represented by small, isolated populations located far from the main range
32 of a species. Such populations may be not particularly relevant for conservation at the global level,
33 because they often include a negligible percentage of the species population. At the same time, they
34 can be of high biogeographical interest, or they may be genetically distinct or adapted to particular
35 environmental conditions (Alba *et al.* 2013). Moreover, they can allow for testing intriguing
36 ecological hypotheses: do range limits and local rarity depend on habitat limitation, or are they
37 'simply' determined by the large distance from the main species' range, with consequent low
38 recruitment and lack of significant immigration, or by lower fitness towards the margins? All these
39 hypotheses have been formulated as possible scenarios at range limits, but have been only rarely
40 tested (Sexton *et al.* 2009). Such populations may also allow for testing whether a very specific part
41 of the range limit is at equilibrium, or if range boundary disequilibrium is occurring. Equilibrium
42 occurs when species are largely present in areas with suitable climate, while they are generally
43 absent from unsuitable ones; disequilibrium takes place when a species' actual distribution and
44 potential geographic distribution are different because of limitations due to dispersal, or to lags in

45 tracking appropriate conditions, which prevent some suitable areas from being colonised by the
46 species (Sexton *et al.* 2009). Because of their extraordinary dispersal abilities, flying birds are
47 usually believed to be able to largely occupy all potentially suitable areas. This leads to niche filling
48 and equilibrium between distribution and climatic areas, as shown for European breeding species
49 (Araújo & Pearson 2005). However, at a finer spatial scale, other scenopoetic (i.e. physical and
50 structural) factors, such as topography and land cover, may be very important for the distribution of
51 animal species (Thuiller *et al.* 2004, Hortal *et al.* 2010, Brambilla & Gobbi 2014). The effect of
52 those factors may prevent range to be at equilibrium with climate even in the case of high dispersal
53 abilities.

54 Here, I focus on a very small and geographically isolated population of Black-headed Bunting
55 *Emberiza melanocephala*, a declining species of conservation concern (SPEC2, which means
56 unfavourable status and populations concentrated in Europe; BirdLife International 2004). The
57 study population is located in southern Lombardy (northern Italy) and is separated by more than
58 300 km from the closest conspecific populations in the northern Adriatic and central-southern Italy
59 (the species occurs from central Mediterranean eastwards; Cramp & Perrins 1994, BirdLife
60 International 2004). First identified in the 1970's, this local population has never exceeded
61 approximately 10 breeding pairs per year. In recent years, this small population has been regularly
62 surveyed. Overall, 21-22 territories (16 in Lombardy, 5-6 in the neighbouring regions, within a few
63 kilometres from the regional boundaries; M. Brambilla, E. Vigo *et al.*, unpublished data) have been
64 occupied (i.e. with observations of individuals with territorial or breeding behaviour since early
65 June) at least once between 2002 and 2013, and population size has ranged between a very few and
66 a known maximum of nine territories occupied per year. In Lombardy, the species has never bred
67 outside this small belt in the Apennines foothills, even in the years with highest numbers of
68 occupied territories. This could suggest range equilibrium; however, explicit modelling of potential
69 distribution is lacking and thus it is impossible to confirm equilibrium and to define the factors
70 determining it.

71 Here, I test whether the restricted range of the species in this northern enclave is likely due to
72 environmental constraints (range equilibrium), rather than a consequence of other factors, e.g. the
73 low fitness or recruitment suffered by such a marginal population, located so far from the main
74 range of the species (range disequilibrium). I used distribution modelling techniques to assess the
75 potential effect of different environmental factors such as climate, topography, and land cover on
76 the distribution of the species.

77 I built a distribution model first by considering the species occurrence in the region as a
78 function of bioclimatic variables (scale 1 km x 1 km). Then, I looked at the effect of landscape
79 features on species occurrence and built a distribution model using land-cover variables (scale 1 km
80 x 1 km). I built a third distribution model to evaluate the effect of fine-scaled habitat availability,
81 based on detailed descriptors of habitat at a scale coinciding with the supposed territory size of the
82 species in the area (~3 ha). Finally, I compared the output of the three models, and overlaid them to
83 obtain a potential distribution according to the combined availability of suitable climate, landscape
84 and fine-scaled habitat.

85 I built distribution models using the 16 territories known to be occupied at least once since
86 2010. For each territory, the estimated centre was used for modelling.

87 All models were built with MaxEnt 3.3.3k (Phillips *et al.* 2006), one of the most commonly
88 employed and better performing presence-background methods (i.e., that do not require absence
89 sites) for building species distribution models (Elith *et al.* 2006, 2011), reported to perform well
90 even with very low sample size (e.g. Pearson *et al.* 2007, Wisz *et al.* 2008, Baldwin 2009), and thus
91 particularly appropriate in this study case. The background was created using 10 000 random points
92 generated by MaxEnt. All models were built using only linear and quadratic fitting functions to
93 reduce overfitting.

94 Bioclimatic variables were gathered from WorldClim (www.worldclim.org, Hijmans *et al.*
95 2005), at 30 arc-seconds resolution. I gave particular attention to the warmest period, according to
96 the phenology of the species (cf. Engler *et al.* 2014, Brambilla *et al.* in press): as the species is

97 strictly a summer visitor to the Western Palearctic including the study area (mostly the end of May-
98 August), I selected the following variables: BIO1 (Annual Mean Temperature), BIO5 (Max
99 Temperature of Warmest Month), BIO10 (Mean Temperature of Warmest Quarter), BIO12 (Annual
100 Precipitation), BIO18 (Precipitation of Warmest Quarter).

101 Land-cover variables were extracted from the regional database DUSAF 4.0 (resolution 20 m,
102 date: 2012; Regione Lombardia 2014). DUSAF includes detailed land-cover and length of
103 hedgerows as vector data. I pooled some categories to obtain a smaller sample of land-cover types
104 potentially relevant for the species at the two spatial scales (Table 1). At the landscape level, I used
105 the extent of different land-cover types within the 1 km x 1 km cells. At the territory level, I used
106 aspect and slope (derived from a 20-m resolution Digital Terrain Model), and the extent of the
107 different land-cover types and hedgerow length within 100-m from each pixel (20 m x 20 m cell).
108 Given that some territories occur within the same 1 km x 1 km cell used for the climatic and
109 landscape models and that I discarded replicates, the actual sample sizes for these models was
110 reduced to 9. I calculated the Area Under the Curve (AUC) and the relative standard deviation on
111 100 bootstrap replicates; I use AUC despite its limitation, given the lack of alternatives for this kind
112 of models (Baldwin 2009, Engler *et al.* 2014). Most important, given that the distribution of the
113 species is well known, a visual inspection of the predicted distribution against the realized
114 distribution may help evaluate the reliability of the distribution models (cf. Engler *et al.* 2014).

115 At all the three scales, some commonly used thresholds for binary reclassification coincided:
116 minimum training presence, equal training sensitivity and specificity, maximum training sensitivity
117 plus specificity coincided in each one of the three models. The value of the coinciding thresholds
118 was used to reclassify the continuous environmental suitability provided by MaxEnt into a binary
119 variable representing presence vs. absence.

120 Models are summarised in Table 1. Despite the very small sample sizes, models show
121 excellent discriminatory ability (although a high value of AUC is expected for rare species modelled
122 under MaxEnt), and the very low standard deviations confirm the models' stability. All models

123 represent quite accurately the current species distribution in the region (Fig. 1). Furthermore, the
124 climatic model was projected to the 30 x 30 degrees-area including central and southern Europe
125 (bioclimatic data obtained from www.worldclim.org, tile no. 16), and it correctly identified the
126 major areas of species occurrence despite the very low sample size and peripheral location (details
127 not shown), thus confirming that the occurrence area in Lombardy is actually similar in climate to
128 most of the species' European range.

129 Among the five tested bioclimatic variables, the ones most affecting the species' distribution
130 are BIO18 and BIO12 (related to precipitation; Table 1).

131 At the landscape level, buntings are associated with vineyards and intermediate cover of
132 arable land, and negatively affected by forest, urbanized areas, ricefields, waterbodies and bare
133 ground. The fine-scale distribution model (territory level) suggests that the species is associated to
134 gently sloping, south-facing areas, covered by a mosaic of vineyards and arable land, whereas it
135 avoids urban areas, ricefields, alpine grassland, forest and bare ground.

136 The three distribution models for Black-headed Bunting in Lombardy point out different
137 determinants of distribution at varying scales. All models perform well, but each one somewhat
138 overestimates the species range (Fig. 1). However, the combined output of the models depicts as
139 suitable a small area matching the known occurrence of sites for the species (Fig. 1) and shows how
140 the three models taken together provide an excellent range estimation for this rare species, which
141 occurs only in suitable territories within suitable landscapes in the suitable climatic area. These
142 results suggest that both climatic and habitat constraints limit the range of the species in this
143 northern enclave: although other effects are also possible (low fitness, reduced recruitment, etc.;
144 Sexton *et al.* 2009), the species actually occupies the only area in the region which is classified as
145 suitable by all the models.

146 In conclusion, the peculiar range limit of Black-headed Bunting in Northern Italy, as defined
147 by this small and isolated population, appears to be at equilibrium, as the actual and potential
148 distributions are largely coincident. Habitat features (both topographic and land-cover variables)

149 clearly contribute to refining the potential range of the species within the climatically suitable area.
150 Considering habitat factors affecting the species' occurrence, in particular the maintenance of the
151 crop mosaic on gently sloping and south-facing hillsides may strongly benefit the species.

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206 **Table 1.** Summary of distribution models at the three scales. All values are from the 100-bootstrap
 207 replicated models. The described effects are the ones derived from the single-variables models,
 208 which are easier to interpret (Phillips *et al.* 2006). All quadratic effects are in the form of a positive
 209 effect of intermediate values.
 210

Variable	effect	% contribution	Permutation importance
Climatic model (AUC±SD: 0.98±0.003)			
BIO18 (precipitation of warmest quarter)	negative	66.0	68.1
BIO12 (annual precipitation)	quadratic	25.1	27.0
BIO10 (mean temperature of warmest quarter)	positive	0.9	0.0
BIO1 (annual mean temperature)	positive	0.6	4.5
BIO5 (max temperature of warmest month)	positive	7.4	0.4
Landscape model (AUC±SD: 0.99±0.005)			
vineyard	positive	39.1	2.9
shrubland	slightly positive	0.6	0.0
arable land	quadratic	8.1	16.2
forest	negative	12.6	31.9
urban areas	negative	22.9	19.8
bare soil	negative	6.6	3.1
ricefield	negative	4.3	24.4
water	negative	5.2	1.4
mown grassland (all)	null	0.6	0.3
wetland	negative	0.0	0.0
Territory model (AUC±SD: 0.999±0.001)			
vineyard	quadratic	26.8	29.5
shrubland	null	1.5	0.0
arable land	quadratic	7.3	0.4
forest	negative	10.6	23.2
urban areas	negative	11.0	34.7
alpine grassland	negative	2.2	0.4
bare soil	negative	4.4	10.8
ricefield	negative	2.2	0.0
water	negative	1.3	0.1
mown grassland	negative	1.4	0.1
mown grassland with trees/shrubs	positive	0.7	0.1
slope (°)	quadratic	26.8	29.5
aspect (N, S, E, W)	S favoured, N avoided	6.9	0.0

continuous hedgerows (m)	positive	0.1	0.0
non-continuous hedgerows (m)	negative	1.2	0.7
wetland	negative	0.0	0.0

211 **Figure 1.** Predicted distribution (black areas) of *Emberiza melanocephala* in Lombardy according
212 to the three different distribution models: climate model (upper left; actual areas of species
213 occurrence are also shown in this map), landscape model (upper right), territory model (lower left),
214 and cells depicted as suitable by all the three models (lower right).

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