Mimicry as a novel pathway linking biodiversity functions and individual behavioural performances

Paola Laiolo^{1,*}, José Ramón Obeso¹ and Yari Roggia²

¹ICAB, CSIC and Oviedo University, 33071 Oviedo, Spain

²Department of Animal Biology, Turin University, 10123 Turin, Italy

The feedback of biodiversity on individual trait variation is a poorly explored mechanistic pathway in ecological research. We analysed the relationship between biodiversity and individual performance by focusing on vocal mimicry, a widespread interaction that may serve in intra- and interspecific communication. We studied the songs of two lark species (genus *Galerida*) that increase the complexity of their song displays by mimicking other birds, and analysed the influence of bird species richness on individual song performance. The diversity of mimicked species and the prevalence of mimicry increased in areas characterized by great α and γ diversity (i.e. where larks experience more diverse encounters with community members, many of them being highly vocal owing to breeding). Conversely, the variability in species-specific song components peaked where larks were abundant, probably matching the complexity of conspecific social milieu. Some trade-offs existed between homo- and heterospecific complexity, suggesting that larks could change from population- to community-driven song variation by tracking the composition of the auditory environment. Mimicry, which serves communication with conspecifics or predators, may mediate interactions, ultimately cascading to aspects of ecological diversity other than those promoting its complexity.

Keywords: acoustic mimicry; biodiversity functions; birdsong; community ecology; sexual selection; social facilitation

1. INTRODUCTION

The functional significance of biodiversity is a major ecological issue [1]. Evidence published over the last 50 years led to the identification of a broad array of diversity functions at all levels of biological organization, from ecosystem process rates and state downscaling to community regulation and population performance [2–4]. Even at a lower level, the question of how diversity changes aspects of genotypic diversity or individual phenotypes, and how the latter may feedback to processes observed at the levels above, has been the focus of recent mechanistic approaches in community and ecosystem ecology [5,6]. It has been shown, for instance, that components of biodiversity may be associated with intraspecific genotypic richness [7], as with the empirical evidence of the ‘niche-variation hypothesis’ proposed by Dobzhansky [8]. Plant genotypic diversity may correlate with arthropod diversity [9], and feed back to components of the herbivorous and predator communities [10].

A link with individual behaviour has been suggested for those traits involved in trophic interactions (for instance, when prey diversity conditions consumer foraging strategies [11]). In the opposite direction, individual foraging decisions can feed back to biodiversity, in turn becoming important drivers of trophic cascades

[12]. Evidence of the effects on other, non-trophic behaviours is lacking, regardless of the potential of behavioural traits to be moulded by heterospecific stimuli when compared with other phenotypic features [13]. The plasticity of these traits may be enhanced by learning, a condition-sensitive regulatory mechanism that increases environment–phenotype matching and the correlation between behavioural responses and aspects of environmental complexity [14,15]. The link between behavioural traits and the complexity of higher-level systems may assume great evolutionary and ecological relevance when behaviours influence aspects of individual performance, or feed back to the levels above by generating new interactions.

Mimicry is a component of species communication in its broader meaning, which also includes deceitful exchanges and interspecific interactions [16]. The best-known examples involve visual sensory modalities [17], but it is also widely documented for sounds, which many vertebrate species acquire through learning processes. Acoustic mimicry is adopted by at least one-fifth of songbird species through this modality [18]. Bird mimic behaviour may have evolved in a sexual context, because of female preference for complex male songs including several imitations; alternatively, it may serve as a defence to confound predators, or as an aggressive strategy against heterospecific attacks when competing species are selectively copied (see table 1 and electronic supplementary material, S1, for a complete overview of mimicry evolutionary and ecological implications).

* Author for correspondence (paola.laiolo@gmail.com).

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Table 1. Main hypotheses explaining interspecific vocal imitation in birds and predicted links with diversity components.

driving process	predicted behavioural pattern	receiver	link with diversity components
heterospecific territoriality [26–29]: by mimicking competing species, birds maintain mutually exclusive territories	selective copying of competing species; context-dependent mimicry	other species	no relationship with taxonomic diversity is expected; consequences on interspecific interactions
avoidance of threats [23,30,31]: the mobbing or alarms calls of species forming heterospecific flocks converge to achieve group defence	selective copying of species sharing communal defence or predators; context-dependent mimicry	other species	no relationship with taxonomic diversity is expected; consequences on interspecific interactions
individual/nest defence and predator confusion [32,33]: mimicry serves to confuse predators	mimicry enhances song complexity; the most abundant species are copied; mimicked sounds are used out of context	other species	a relationship between model diversity (bird species richness) and mimicry diversity is expected; consequences on interspecific interactions
sexual selection [21,22,34,35]: mimicry increases male song performance in a sexual context	mimicry enhances song complexity; the most abundant species are copied; models with more complex songs are copied; mimicked sounds are used out of context	same species	a relationship between model diversity (bird species richness) and mimicry diversity is expected; consequences on intraspecific interactions
no function, mimicry depends on learning mistakes [36–40]: failure in recognizing conspecific tutors	mimicry enhances song continuity; the most abundant species are copied; models with simpler songs are copied; mimicked sounds are used out of context	same species	a relationship between model diversity (bird species richness) and mimicry diversity is expected; each singing individual causes an associated rise in song diversity within the population and community
prematuring isolation (for brood parasites; [41,42])	females breed preferentially with males raised by the same host species	same species	no relationship with taxonomic diversity is expected; consequences on intraspecific interactions

Diverse repertoires are supposed to require greater mnemonic capability and more complex cognitive skills than poor songs [19], and may be achieved through the imitation of other species' vocalizations as an alternative to improvisation and invention of new song elements. It has been shown that song complexity may honestly indicate individual quality and, as such, elicit female response more than monotonous repetitions of simple tunes [20]. By comparing mimicry performances, females may evaluate male learning capabilities, an indicator of cognitive skills [21]. Mimicry may also correlate with other ecological aspects that benefit females and their offspring, such as the male's previous experience with local habitat conditions [22], or capability to deter or confound ground predators [23].

Although there is no consensus on the function of acoustic mimicry in songbirds, all the hypotheses listed in table 1 attribute a functional significance to this trait, with the notable exception of the hypothesis suggesting that it may result from learning mistakes in species with long songs. All things considered, acoustic signalling in species with mimicking capabilities could be a proper individual trait to test for the relationship between diversity and individual characteristics, given that mimicry may directly link song performance to the complexity of the surrounding auditory environment

and, in turn, mediate intra- and interspecific interactions, in this way feeding back to components of ecological diversity (table 1).

In this study, we looked for evidence of diversity feedback on individual song performance by analysing the learned songs of the crested and the Thekla lark (*Galerida cristata* and *Galerida theklae*), two Old World songbirds well known for their ability to mimic other bird vocalizations [24]. First, to demonstrate the functional significance of mimicry we explored its proximate functions, testing whether mimicry improved song performance and complexity (as predicted for a character undergoing sexual selection) rather than song continuity. Second, with the same objective, we analysed the factors that determine the choice of model species: morphological or historical constraints, model species abundance or the complexity of their vocalizations. Finally, we analysed the pattern of mimicry diversity and other traits related to song performance in a gradient of α and γ bird species richness (diversity at different spatial scales [25]), population characteristics and environmental conditions. With the latter purpose in mind, we scaled down from the community and ecosystem levels to individual functions, exploring the effects of diversity on a widespread behaviour among songbirds.

2. MATERIAL AND METHODS

(a) *Study species and area*

The crested and Thekla larks constitute two independent non-hybridizing lineages that diverged approximately 3.7 Myr ago in the Sahara range [43]. They live in sympatry in most of the western Palaearctic, sharing similar food items and habits, with some habitat divergence: crested lark densities peak in dry agropastoral or semi-desert habitats, and Thekla lark in bushy sclerophyllous vegetation [24]. They may show interspecific territoriality and utter converging territorial calls in conditions of close syntopy. Matching of competing congener calls represents a special case of hetero-specific mimicry for territorial defence [44].

This study was carried out in spring 2007 in Ebro Valley, northeastern Spain, in an area encompassing 10 700 km². Here, traditional agropastoral activities have created complex habitat mosaics of cereal fields, stubbles, fallows and grazed steppes that have favoured the strict coexistence of the two *Galerida* larks and the presence of one of the richest steppeland bird communities of western Europe [45].

(b) *Data collection and environmental predictors*

Across the entire Ebro Valley, we selected 20 sites, at which we walked 3–7 (4.3 ± 0.4 s.e.) 2-km-long transects. The length of the transect was established, taking into account the low densities and wide territories of crested and Thekla larks (on average 4 ha [24]), whose maximum abundances in the most favourable habitats of the Iberian Peninsula do not exceed 4.7 and 7.4 birds per 10 ha, respectively (www.vertebradosibericos.org). Study sites were separated on average by 10.1 ± 2.2 km, the nearest transects within sites by 0.95 ± 0.21 km. During transects, we recorded all singing *Galerida* larks within 50 m of either side of the transect with TC-D8 DAT and Marantz PMD670 recorders, and Sennheiser ME67 microphones (frequency response 50–20 000 Hz). Most of the sampled individuals were not marked, but they were recorded in their territories during a single visit only, thus avoiding the problems of individual identification (*Galerida* larks are sedentary, territorial and show high site fidelity [46]). The position of all crested and Thekla larks (including non-vocal ones) we spotted was recorded by means of Garmin GPS eTrex Navigator, and the species visually identified with Leica Trinovid 7 × 42 binoculars. Coordinates were used to estimate species densities in 20 ha plots (2 km × 100 m). Overall 85 transects were walked: at least one *Galerida* species was recorded in 82 transects, and the two species were found to coexist in 38. We also noted the occurrence of other bird species within 50 m of either side of the transect, to obtain a measure of bird species richness at the scale of transects (α species richness) and use this measure as a proxy of the complexity of the auditory environment. The overall number of species detected was 77.

Land-use cover (steppe vegetation, ploughed fields, cereal fields, fallows, etc.) was estimated visually and then checked by inspecting the aerial photographs of the study area (<http://sigpac.mapa.es/feqa/visor/>). The Shannon–Wiener diversity index of the relative proportions of land uses at the transect scale was then calculated ($H' = -\sum p_i \times \ln(p_i)$, where p_i is the relative frequency of habitat i), to obtain a measure of habitat complexity. Information at the local scale was completed by collecting data at a larger spatial scale: that of sites. We took into account the total number of bird species spotted within each site transect to obtain a measure of

overall species richness at the site scale (γ species richness [47]) and the composition of the habitat within sites by clipping the CORINE land-use/land-cover digital map ([48]; map resolution 100 m) with 20 site polygons of 3000 ha each. The relative proportions of land-use cover at this scale (non-irrigated agricultural lands, irrigated agricultural lands, steppelands, complex mosaics, etc.) were used to calculate an index of landscape diversity (Shannon–Wiener index).

(c) *Sound analysis and song performance predictors*

Galerida song is given in flight, and is mostly audible during spring. Singing activities concentrate in the pre-laying phase, a finding that suggests that the function of song is primarily concerned with mate attraction; territorial defence is attained by emitting typical territorial calls from the ground [44]. Songs of these larks share the same structural organization: noticeable time intervals separate song strophes; the latter contain species-specific (hereafter homospecific) or heterospecific (i.e. copied from other species) syllables.

Model species were identified by two of us—P.L. (passerines and non-passerines excluding waders) and J.R.O. (waders). We combined acoustic and visual information, identifying species by ear and comparing spectrograms of model and mimic songs. Bird identification by ear is routinely used to monitor bird species in the wild, as human ear is able to detect interspecific differences in birdsong; the methodology is referred as ‘*station d’écoute*’ [49] or point counts [50,51]. While visually inspecting spectrograms, we listened to each strophe to obtain a first tentative identification of each syllable as homospecific or belonging to another species we had experience with. After this first identification by ear, we matched the spectrograms of lark mimic syllables with those of the hypothesized model, as obtained from an archive of spectrograms of almost 100 species, obtained from recordings of the study bird community or from published guides [52]. When aural and visual identification coincided (i.e. syllables had similar tempo, temporal and frequency range; see electronic supplementary material, S2), we considered the classification process as concluded. When aural and visual classification did not match, we inspected spectrograms of model species with similar songs, until the full identification was achieved; we were able to identify model syllables in 97.6 per cent of *Galerida* strophes.

Heterospecific syllables averaged 33 per cent of the crested lark song syllables and 42 per cent of the Thekla lark syllables in Ebro Valley. Fifty bird species were recognized to be mimicked in the recorded songs of 117 crested lark males (554 strophes inspected) and 87 Thekla lark males (495 strophes; electronic supplementary material, S2 and S3), with a maximum of 18 species mimicked per individual in the study populations. Overall, approximately 700 h were spent inspecting spectrograms and listening to recorded songs, five times our effort in taking measurements from homospecific songs (see below).

Strophes could contain either complete songs of single model species or a rotation of imitations of several species embedded in a matrix of homospecific syllables (figure 1 and electronic supplementary material, S2). In general, most model species are neither competitors nor predators of *Galerida* larks (electronic supplementary material, S3), making unlikely mimicry to be directed to all the copied community members. Context-dependent mimicry (for

Figure 1. Spectrogram of a Thekla lark song strophe including imitations of the lesser short-toed lark (the first three syllables), the skylark (syllables 4–9), the crested lark (syllables 10–14), homospecific syllables (syllables 15–16) and the house sparrow (syllable 17).

communication between the crested and Thekla lark) has been recorded for another vocalization, the territorial call [44].

We took into consideration several acoustic parameters to describe song structure: (i) song complexity of the whole song, (ii) song complexity of the homospecific component of the song, (iii) song continuity and (iv) song complexity of the heterospecific elements of the song (mimicry performance). Twenty-one temporal and frequency parameters were measured in those song strophes that included at least six homospecific syllables (electronic supplementary material, S4a,b). The number of unique (not repeated) syllables per strophe was used as a measure of overall song complexity (or repertoire size). This parameter was established by inspecting the whole song database with the following procedure: a collection of individual strophe spectrograms was compiled, and each syllable was visually compared and assigned to a given type that had already been detected, or labelled as a new type. Complete sample inspection was separately carried out by two of us (Y.R. and P.L.), and categorization proved to be highly consistent between observers ($R_s = 0.99$, $n = 105$ individuals, $p < 0.001$; the average inter-observer difference in syllable number was 0.050 ± 1.03). The number of unique homospecific syllables (overall song complexity minus the number of heterospecific syllables), the coefficients of variation of the duration, minimum frequency and frequency range of the first, middle and last two homospecific syllables were measured to represent song complexity of the homospecific component of songs (electronic supplementary material, S4b). Strophe and inter-strophe duration were considered as proxies of song continuity, assuming that the longer the strophes and the shorter the pauses, the more continuous the song [36].

Mimicry prevalence (the proportion of syllables that were imitated) and mimicry diversity (the number of mimicked species) were used to express mimicry performance (electronic supplementary material, S4b). Individual mimicry diversity increased steeply when less than four successive strophes were recorded, then kept increasing but at a slow rate (logarithmic trend: $\text{mimicry diversity} = 3.5 + 1.5 \times \ln(\text{strophe sample size})$; $R = 0.40$, $F_{1,256} = 50.9$, $p < 0.001$; electronic supplementary material, S5a). We therefore considered in the analyses only those individuals for which sample size attained greater than or equal to four strophes (54 crested larks and 51 Thekla larks), and entered the number of strophes recorded per bird in the statistical tests involving mimicry performance. In the case of the other acoustic variables characterizing strophes, we considered mean values per individual bird.

(d) Data analysis

(i) *The proximate function of mimicry*

We first analysed the relationships among the different vectors of song performance (i.e. among overall song complexity, complexity of the homospecific elements of strophes, mimicry prevalence, mimicry diversity and song continuity) by means of generalized linear models (GLMs). We tested whether mimicry served to increase song complexity (as predicted if vocal mimicry is favoured to increase repertoire size via female preference for complexity) or song continuity (if it increases song duration in species with large repertoires [36]). We used a Poisson distribution of errors for mimicry diversity and a Gaussian distribution for the other song variables (homospecific song complexity and mimicry prevalence were log-transformed and arcsine-transformed, respectively).

(ii) *Factors affecting the choice of models*

Models were classified on the basis of the complexity of their repertoires (e.g. species with complex repertoires or simple vocalizations) in order to test whether models with the simplest signals could be more frequently imitated, as predicted by the learning mistake hypothesis [37]. Categorization was based on published evidence on song type, repertoire size and syllable repertoire size [36,52,53], and is detailed in electronic supplementary material, S3. We performed GLMs with a Gaussian distribution of errors, with arcsine-transformed values of the frequency of imitation of each model entered as dependent variable. We controlled for model size (wing length [52]), as body size is an indicator of the size of the sound-producing apparatus [54], and as such may determine selective copying of model species of similar sizes. We also considered the effect of the frequency of encounters on the probability of a model being imitated, entering in GLMs overall model abundance (number of transects in which the species was spotted/total number of transects) and the family within the birds' order (to control for the effect of model taxonomic status).

(iii) *Ecological correlates of song performance*

We tested for the effects of α (transect) and γ (site) species richness, habitat (transect) and landscape (site) diversity, percentage cover of the most common land uses at the two scales, and crested and Thekla lark densities, on the indicators of song complexity considered in this study (overall song complexity, mimicry performance and complexity of the homospecific elements), by means of generalized linear mixed models (GLMMs [55]). GLMMs permitted to

Figure 2. Relationship among components of song performance. (a) Mimicry diversity is significantly associated with the repertoire of syllables (overall song complexity). (b) Mimicry prevalence increases when the homospecific repertoire is poor. The residuals of syllable complexity were used instead of raw values, controlling for syllable number. Each point represents an individual bird (54 crested larks and 51 Thekla larks). Open circles, Thekla lark; filled circles, crested lark.

control for the non-independence of recordings obtained from individuals sharing similar social and ecological settings within transects and sites. The latter were entered as nested random factors (transects nested within sites).

In all statistical tests, sample size corresponds to the number of individuals recorded (105 birds: 54 crested larks and 51 Thekla larks). Model selection was based on Akaike's Information Criterion (AIC); all statistical analyses were performed with R [56].

3. RESULTS

(a) Association among song features

In both the crested and Thekla larks, the more complex songs (e.g. including more diverse syllables) were those presenting the longest strophes, many diverse homospecific syllables, the greatest mimicry diversity and prevalence ($R_S = 0.32\text{--}0.89$, $p < 0.05$; $n = 54$ crested larks and 51 Thekla larks; figure 2a). An apparent triangle size effect emerges in the correlation between song complexity and mimicry diversity (figure 2a), suggesting that many species cannot be mimicked when strophes include few syllables. However, as mimicry diversity refers to the whole song repertoire of the individual (i.e. considering several strophes), the bias inherent to the correlation is reduced when controlling for strophe number (see GLMs and GLMMs below). A significant negative relationship resulted between mimicry prevalence and the number of diverse homospecific syllables in strophes when controlling for syllable number ($R_S = -0.80$ and -0.68 in the crested and Thekla lark, respectively, $p < 0.05$; figure 2b). In the crested lark, a significant positive association also resulted between inter-strophe duration, mimicry diversity and prevalence (all $R_S > 0.4$, $n = 54$; $p < 0.05$).

Mimicry prevalence and diversity were significantly associated with the number of diverse syllables, thus mimicry increased song complexity in both species (the most probable GLMs are quoted in electronic supplementary material, S5b). The two descriptors of mimicry performance were positively and significantly related to inter-strophe duration (in the crested lark)

and negatively related to song duration (in both species; electronic supplementary material, S5b). This implies that longer strophes and shorter pauses were associated with songs in which homospecific elements prevailed, an opposite pattern to that expected if mimicry serves to enhance song continuity. Those crested lark individuals that showed greater song diversity also sang songs with greater switches in the minimum frequencies of their homospecific syllables (electronic supplementary material, S5b).

(b) Model choice

Only 26.6 per cent and 25.1 per cent of the species mimicked by crested and Thekla larks occurred in the immediate surroundings (same transects) of the recorded birds. Many species were imitated more than expected by their occurrence at this small scale (see electronic supplementary material, S5c); the kestrel is the bird that is most disproportionately mimicked with respect to its abundance, which is scarce when compared with other raptors in the study area. GLMs testing for the relationship between the frequency of imitation of each model and model abundance, body size, taxonomic status and song complexity showed that there was a significant tendency in both larks to mimic the most common bird species ($t = 4.1$ and 4.2 , in the crested and Thekla lark, respectively, $p < 0.001$; $n = 45$ model species), with a slight propensity to copy species uttering the most complex songs (crested lark: $t = 1.8$, $p = 0.07$; Thekla lark: $t = 2.2$, $p = 0.03$; $n = 45$ model species; electronic supplementary material, S5d). Model taxonomic status or body size had no significant effect on the probability of being copied.

(c) Environmental correlates of song complexity

GLMs testing for the relationship between mimicry performance and geographical location showed that 64 per cent (crested lark) and 73 per cent (Thekla lark) of the inter-individual variability in mimicry diversity, and 59 per cent (crested lark) and 53 per cent (Thekla lark) of the variability in mimicry prevalence were explained by site and transect grouping factors. When controlling for

Figure 3. Summary of the main effects of bird community and conspecific abundance on descriptors of song performance of the crested and Thekla lark. Plus (+) indicates positive association, minus (–) indicates negative association, as highlighted by GLMMs listed in electronic supplementary material, S6a.

their identity in GLMMs and testing for the effects of social, habitat and landscape determinants, we found that mimicry diversity increased with α and β species richness in both species, and crested lark's overall song complexity also increased in the most diverse communities (figures 3 and 4a; electronic supplementary material, S6a). In general, matching of mimicry diversity and α species richness was greater when γ species richness was low, as shown by the negative sign in the $\alpha \times \gamma$ species richness interaction (electronic supplementary material, S6a). In the crested lark, greater mimicry prevalence and diversity were recorded in the most heterogeneous habitats, not only in those with the richest communities (electronic supplementary material, S6a).

When considering variation of the homospecific elements of songs, it was conspecific density that had a positive association with many coefficients of acoustic variation (figure 3). The number of diverse homospecific syllables in Thekla lark songs increased at those sites where conspecific density was high, especially where γ species richness was low (figure 4b). A diverse array of land uses was significantly associated with indices of song complexity; a common pattern is represented by greatest mimicry performance or homospecific song complexity in the most diverse transects (electronic supplementary material, S6a). The greatest densities of *Galerida* species were found in plots characterized by great α species richness and embedded in diverse landscape matrices. The crested lark was more abundant in diverse habitats as well, whereas the congener favoured more homogeneous transects (electronic supplementary material, S6b).

4. DISCUSSION

Our results demonstrate that a component of biodiversity (taxonomic species richness) and a characteristic of populations (conspecific abundance) are positively associated with individual song performance, the former enhancing

mimicry and the latter mainly affecting the variability of homospecific song components (figure 4). Heterospecific acoustic mimicry may be especially effective in increasing song complexity in temperate latitudes, where bird vocal activity explodes during breeding, providing mimic birds with a variety of templates. Although *Galerida* mimicry performance improves in localities characterized by high species richness, the process of heterospecific song acquisition does not appear to be entirely unselective (copying of the most common sounds in the environment), as only one-fourth of the species mimicked are found in the immediate surroundings of individual territories. Larks are, however, matching diversity at a larger spatial scale (γ species richness), probably storing experience of inter-specific encounters throughout their life. An alternative consideration is that heterospecific vocalizations may be predominantly transmitted among conspecifics rather than learned directly from the model [40]. The latter phenomenon may explain why some rare or distant species are frequently copied [44], although in these conditions we would expect enhanced mimicry diversity at sites with great conspecific density. Conversely, we found stronger evidence for density-driving homospecific variation than mimicry complexity (figure 3).

If we assume that bird density is one of the dimensions of bird habitat quality along with survival and reproduction [57,58], results support the idea that where the better conditions for species abundance are found (heterogeneous landscape, great α diversity), so are the most varied *Galerida* songs. The effect of conspecific density on mimicry performance does not appear to be direct, because density poorly affected mimicry when compared with species richness, although the two measures tended to increase in diverse landscapes. Density appears, however, to be an important agent of social facilitation when considering homospecific song variation (figure 4b). Increased conspecific densities may be associated with greater opportunities to learn songs from different tutors and with higher innovation rates, two

Figure 4. (a) Relationship between crested lark mimicry diversity and α species richness. Residuals of mimicry diversity were used, controlling for strophe number. Each diamond represents an individual crested lark (54 individuals). (b) Relationship between Thekla lark homospecific song complexity and conspecific density in sites characterized by high (dark grey) and low (light grey) γ species richness. The classes of species richness were established according to the residuals of the number of species detected per site, controlling for the number of transects walked (high = positive residuals; low = negative residuals). The dashed line represents the positive relationship between homospecific song complexity and density where a poor species pool was present. Each diamond represents an individual Thekla lark (51 individuals).

cultural phenomena that together may increase homospecific song complexity [59]. In addition, strong intra- and intersexual selection in high-density areas may drive the evolution of complex individual performances in their homospecific component [60]. Our results are in line with findings of recent sexual signal research, which is increasingly shifting from the study of a few individuals in isolation to the multi-level ecological context, where diffuse interactions among local population members, density-dependent phenomena and the environment also play a role under natural conditions [59,61–63].

In this study, we do not address the ultimate functions of song mimicry, but available data permit the analysis of various predictions of its significance (table 1). Mimicry

in *Galerida* species enhances overall song complexity but not song continuity, contrary to what is predicted by the learning mistake hypothesis. It may represent an alternative to the improvisation of novel themes or the imitation of conspecifics, given that it improves when homospecific syllables are monotonous (figure 2b). Species uttering complex vocalizations are copied irrespective of their abundance, and most model species are not competitors. These findings dismiss the heterospecific territoriality and the learning mistake hypotheses (brood parasitism is not described either; table 1). Although non-adaptive arguments are difficult to refute, the considerable amount of information from the environment stored in *Galerida* songs, as well as the mnemonic and vocal skills required to match the motor patterns of models of different sizes and taxonomic origins, may instead suggest that mimicry is a functional trait that has evolved as an honest signal, in a context of mate choice or predatory confusion.

When dealing with mate choice, song differentiation among geographical locations (such as site and transect in this study) may be viewed as an irrelevant source of variation for sexual selection, which in theory operates on inter-individual variability at small scales. In *Galerida* system, however, transect and site differences only account for a proportion of inter-individual differences, leaving room for sexual selection to act within local areas. On the other hand, it should be stressed that bird local populations are rarely isolated, and natal and breeding dispersal permits females to move and come into contact with different social environments [64]. Lark females dispersing in winter or early spring [65,66], for instance, may experience the songs of males from different local neighbourhoods and eventually choose their breeding territories on the basis of song cues at the transect or site scale [67,68].

Predation selection may also contribute to the maintenance of song mimicry and complex song patterns, if acoustic switching distracts or threatens chasing predators, or predators overlook variable songs they are not familiar with. In this sense, acoustic aposematism (i.e. the conspicuous transition of song types that indicates prey's ability to escape [69]) may be particularly effective with naive lark predators [70,71]. On the other hand, complex or switching prey sounds may be advantageous when predators develop skills to hunt typical or familiar preys and overlook variable prey cues (the acoustic equivalent of predators' 'search image' [72]). 'Aspect diversity' (phenotypic variability within prey populations [73,74]) has been proposed to explain the variable morphological adaptations of invertebrate species preyed upon by visually hunting predators, but the phenomenon may also involve other communication channels, such as the acoustic one.

5. CONCLUSIONS

Although local adaptations of populations to the community context have been widely described in nature, evidence is limited for behavioural traits when compared, for instance, with morphological or molecular traits [75]. There is evidence of components of animal signals responding to selection pressure exerted by other species, such as competitors [76], parasites [77] or predators [78]. These interactions, however, involve two species and rarely spread to several parties or entire communities, as

documented by this study on songbird vocal mimicry. Mimic species are indeed providing an example of how complex individual traits can depend on the larger, more complicated systems in which individuals are embedded, and how community- and population-driven variation can occur in the same type of vocal display. This complex variation can ultimately generate a mosaic of spatially and temporally varying individual phenotypes, whose evolutionary potential can remain largely unexplained if tackled using traditional signal evolution theory and cannot be predicted from the individual characteristics of target species.

Although we did not focus on the effects of song variation on higher-level components, a pathway can be envisaged and could be examined in future studies. Individual variation can in fact affect community functioning through the effects of extended phenotypes. Mimicry may mediate competitive interactions among conspecifics or competing heterospecifics, favouring coexistence [79]. By minimizing spatial overlap, it may generate density-dependent phenomena within populations and between competing species, ultimately affecting community dynamics. Scaling up, the impact of mimicry can cascade through the food chain when this behaviour is used as a strategy to avoid being attacked or eaten, as in the case of vocal aposematism, aspect diversity or other forms of context-dependent mimicry [23,80]. In this sense, mimicry increases the diversity of interactions at community level and might condition its dynamics.

We stress that more integrative efforts and research in natural conditions are needed to improve the generality of the results discussed above, which still lack detailed mechanistic understanding. Nonetheless, this study may represent the first attempt to tackle the 'diversity begets diversity' hypothesis [81] targeting non-genetic behaviours inherited across generations (via cultural processes), in a field in which most evidence is provided by studies of genetic diversity in plants [6].

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