Connectivity in Spanish metapopulation of Dupont's lark may be maintained by dispersal over medium-distance range and stepping stones

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Background: Dupont's lark is an endangered passerine with a fragmented distribution in Spain, the only European country where it is present. This species inhabits natural steppe lands linked to traditional anthropic uses, currently threatened by rural abandonment and land use changes, and shows a pronounced population decline and range contraction. In this scenario, increasing knowledge about the connectivity of the Spanish metapopulation and identifying the most important connectivity nodes is crucial for the species conservation. **Methods:** The study was carried out in peninsular Spain, using over 16,000 Dupont's lark georeferenced observations. We used distance buffers to define populations and subpopulations, based on the available scientific information. We identified potential stepping stones using a MaxEnt probability of presence model. Connectivity was assessed using Conefor software, using the centroid of each subpopulation and stepping stone as nodes. Each node was assigned a quantitative attribute according to total habitat area, within-node habitat quality and internal fragmentation. We evaluated different connectivity scenarios according to potential movement thresholds (5-20-100 km) and presence or absence of stepping stones in the network. **Results:** Dupont's lark Iberian metapopulation comprises 24 populations and 100 subpopulations, plus 294 potential stepping stones. Movement thresholds and stepping stones had a strong influence in the potential network connectivity. The most important nodes are located in the core of the metapopulation, which shows connectivity among subpopulations in the different indices and scenarios evaluated. Peripherical subpopulations show a higher isolation and need the presence of stepping stones and/or potential medium (20 km) or long (100 km) movement thresholds to join the network. **Discussion:** Metapopulation connectivity could be higher than previously expected, thanks to stepping stones and potential medium-distance movements. Connectivity is crucial for the species conservation and it can be strengthened by preserving or improving adequate habitat in the most important nodes.

Given the current species decline, steppe habitat should be urgently protected from intensification and land use changes, at least in the critical subpopulations and stepping stones. Long-term conservation of steppe lands and Dupont's lark in Spain requires the recovery of traditional grazing and more research on juvenile dispersion. Meanwhile, the conservation of potentially critical stepping stones should be incorporated to management plans.

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Abstract

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Results: Dupont's lark Iberian metapopulation comprises 24 populations and 100 subpopulations, plus 294 potential stepping stones. Movement thresholds and stepping stones had a strong influence in the potential network connectivity. The most important nodes are located in the core of the metapopulation, which shows connectivity among subpopulations in the different indices and scenarios evaluated. Peripherical subpopulations show a higher isolation and need the presence of stepping stones and/or potential medium (20 km) or long (100 km) movement thresholds to join the network.

Discussion: Metapopulation connectivity could be higher than previously expected, thanks to stepping stones and potential medium-distance movements. Connectivity is crucial for the species conservation and it can be strengthened by preserving or improving adequate habitat in the most important nodes. Given the current species decline, steppe habitat should be urgently protected from intensification and land use changes, at least in the critical subpopulations and stepping stones. Long-term conservation of steppe lands and Dupont's lark in Spain requires the recovery of traditional grazing and more research on juvenile dispersion. Meanwhile, the conservation of potentially critical stepping stones should be incorporated to management plans.

Introduction

Connectivity of animal populations is of major importance for biodiversity conservation and plays a special role when managing threatened species (*Crooks & Sanjayan, 2006*; *Pascual-Hortal & Saura, 2006*). Both ecosystem functionality and population persistence depend on the degree of connectivity among the habitat patches, which is associated to the movement capacity of the focal species and to the landscape configuration (*Pascual-Hortal & Saura, 2007*). Patch isolation relies on factors such as size, distance to neighbours or the degree of permeability of the matrix. In general, small and isolated patches have a lower probability of occupancy than large and connected ones (*Levins, 1970*; *Hanski, 1999a*), depending on the ecology of the studied species: minimum patch size required (*Vögeli et al., 2011*; *Shake et al., 2012*), dispersal capacity (*Rolstad, 2008*) or matrix composition (*Ricketts, 2002*; Vögeli *et al.*, 2010; *Watling et al., 2010*).

A population can occupy a group of isolated habitat patches if they are connected enough to permit movements and gene flow and thus form a metapopulation (*Levins, 1969*; *Hanski, 1998*, *1999a*; *Hanski & Gaggiotti, 2004*). In the traditional island biogeography theory, mainland areas constitute a source of individuals colonizing new areas (*MacArthur & Wilson, 2001*). Colonization probability depends mainly on size of the island and distance to the mainland (*MacArthur & Wilson, 2001*). In a metapopulation context, immigration may occur from different habitat patches and populations (*Hanski, 1998*). From the connectivity perspective, the loss of a part of the metapopulation can have consequences for the rest, being more or less severe depending on the importance of the lost patch in the whole network (*Hanski, 1999a*, *1999b*).

Graph models are a useful tool for the analysis of connectivity in fragmented populations (*Pascual-Hortal & Saura, 2006*; *Bodin & Saura, 2010*; *Saura & Rubio, 2010*), assessing the potential movements of individuals among scattered patches immersed in a matrix of unsuitable habitat (*Pascual-Hortal & Saura, 2006*; *Bodin & Saura, 2010*; *Saura & Rubio, 2010*). They offer quantitative information to identify critical patches for the maintenance of the functionality of the whole network (*Calabrese & Fagan, 2004*; *Visconti & Elkin, 2009*). These models rely on network structures based on two elements: nodes and links between them (*Saura & Torné, 2009*). Nodes represent habitat patches occupied by the species or those acting as stepping stones (*Loehle, 2007*). Links are the connections between nodes, frequently estimated as the distance between them. Each node is also given a numerical value that defines its quality within the network; usually, habitat area or other factor that describes focal species requirements (*Mazaris et al., 2013*; *Pereira et al., 2017*).

Dupont's lark (*Chersophilus duponti*; *Vieillot, 1824*) constitutes a paradigmatic case for the study of connectivity, given the high degree of both natural and human-induced fragmentation of its habitat in Spain (*García-Antón et al., 2019*), and its strong specialization (*Suárez, 2010*). It is a small (~17.5 cm, ~38.5 g) bird that is extremely elusive, rare and, in Europe, only found in Spain, though it also occurs in northern Africa (*de Juana & Suárez, 2020*). The Spanish population is isolated from the African one and they are genetically and morphologically different (*García et al., 2008, García-Antón et al., 2018*). It exclusively inhabits natural steppe lands that, in Spain, are linked to traditional anthropic uses (sheep extensive grazing). It selects slopes below 10-15%, low vegetation (20-40 cm) and a high proportion of bare ground (*Garza & Suárez, 1990*; *Martín-Vivaldi et al., 1999*; *Garza et al., 2005*; *Garza et al., 2006*; *Nogués-Bravo & Agirre, 2006*; *Seoane et al., 2006*). Adults are sedentary (*Cramp & Simons, 1980*; *Suárez et al., 2006*) but there are records of juvenile dispersion (*García-Antón et al., 2015*) and observations out of the breeding range (*Dies et al., 2010; García & Requena, 2015; Balfagón, 2021*).

Isolation is a major concern for the species in Spain (*Garza et al., 2004*; *Íñigo et al., 2008*; *Méndez et al., 2011*). Its fragmented distribution conforms a metapopulation (Gómez-Catasús *et al.,* 2018a; *García-Antón et al., 2019*; *Traba et al., 2019*) with different subpopulations with their own demographic parameters (*Pérez-Granados et al., 2017*), individual movements connecting them (*García-Antón et al., 2015*) and recolonization events of extinct patches (*Bota et al., 2016*). The sample bias toward adult males associated to the capture method (*Garza et al., 2003*; *Suárez, 2010*) provides scarce information regarding other age and sex classes, though the persistence of small and isolated subpopulations suggests medium to longer distance movements: 4.5 km (*Pérez-Granados & López-Iborra, 2015*); 8 km (*V. Garza*, unpublished data); 33 km (*García-Antón et al., 2015*). Some recent records reveal the existence of longer movements: 37 km (recolonization of Timoneda de Alfés, Lérida; *Bota et al., 2016*), 80.40 km (Salinas de Marchamalo, Murcia; *García & Requena, 2015*) and 98.77 km (Albufera de Valencia; *Dies et al., 2010*), these being the minimum distance to the nearest occupied locality. Historic observations reveal even longer distance events: 127 km (Barcelona), 241 km (Trebujena-Sanlúcar, Cádiz), and up to 324 km (Marismas del Odiel, Huelva), among others (see Supplemental Table S1).

Dupont's lark occupation is restricted to around 1,000 km^2 in Spain, with another 965 km^2 of potential habitat with no species presence (*García-Antón et al., 2019*), which suggests the metapopulation to be better connected than expected. A generalized and pronounced decline in most Spanish subpopulations (*Gómez-Catasús et al., 2018a*) and a contraction of the distribution range (*García-Antón et al., 2019*) have been recently reported. Fragmentation process of natural steppe habitats is considered a main threat for Dupont's lark (*Íñigo et al., 2008*). Thus, the identification of critical patches for the maintenance of the metapopulation connectivity is basic for the conservation of the species.

In this work we address a detailed analysis of Dupont's lark metapopulation connectivity in Spain, necessary for the management and conservation of this threatened species. We hypothesize that the metapopulation must be better connected than expected, as connectivity and gene flow would explain the maintenance of the smallest and most isolated subpopulations, More specifically, we i) update the cartography of populations and subpopulations of Dupont's lark in Spain; ii) identify both vulnerable and critical nodes from the connectivity point of view for the conservation of the metapopulation; iii) assess the role of unoccupied but adequate regions in the metapopulation, testing the effect of different dispersal distance thresholds; iv) evaluate the degree of isolation of each subpopulation; and v) propose adequate conservation measures for the maintenance of the metapopulation.

Materials & Methods

The ethics committee of Animal Experimentation of the Autonomous University of Madrid as an Organ Enabled by the Community of Madrid (Resolution 24th September 2013) for the evaluation of projects based on the provisions of Royal Decree 53/2013, 1st February, has provided full approval for this purely observational research (CEI 80-1468-A229).

Species observations

We used the database of georeferenced observations of Dupont's lark updated to 2017, including own unpublished data (TEG-UAM) and adding all available external records (*Traba et al., 2019*). We gathered a total of 17,755 Dupont's lark locations corresponding to the temporal series of 1985-2017, both years included. We considered as recent those observations belonging to the post-2000 period (n = 17,282; 97.34%), when the II National Census was carried out (2004-2006; *Suárez, 2010*). This work allowed to standardize the field work using the territory mapping census method, which corrects the bias detected in previous works (*Garza et al., 2003*; *Pérez-Granados & López-Iborra, 2013*). We considered that pre-2000 observations do not represent the current distribution of the species (see *García-Antón et al., 2019*), and were discarded for this analysis.

Among the post-2000 locations, 14,203 came from own data (TEG-UAM), while the rest (n = 3,079) was provided by administrations, other research entities and individual ornithologists. We only used breeding season (February - July) observations. We excluded anomalous observations, thus resulting in 16,676 independent locations to include in further analyses.

Species habitat

To build a map of Dupont's lark habitat at a national scale we used CORINE land cover (CLC) inventory from the Copernicus European program, following the same method as in the distribution model (*García-Antón et al., 2019*). First, we intersected the 16,676 georeferenced observations with CLC 2006 layer (maintaining temporal correspondence with the period in which the majority of the observations belonged to, i.e., II National Census, 2004-2006; *Suárez 2010*). We selected the land use categories that accumulated 95% of the observations (see a description in Supplemental Table S2), interpreting them as the habitat preferred by the species.

Then, we extracted those categories from the most updated CLC available (2012) to get the current habitat map in Spain. To obtain a more detailed result and avoid overestimation, we discarded the surface with a slope over 15% (rejected by the species; *Suárez, 2010*), and patches with a surface under 20 ha (suggested threshold for the species occupancy; *Suárez, 2010*). We used this map to estimate the habitat area within subpopulations and stepping stones (used as nodes in the connectivity model, see below). More details on the map building can be found in *García-Antón et al. (2019)*.

Criteria for the definition of locality, subpopulation and population

We defined three sequentially hierarchized levels of actual occupancy by the species based on the map of 16,676 observations and distance thresholds substantiated in the scientific knowledge available to date (*Laiolo, 2008*; *Suárez, 2010*; *Vögeli et al., 2010*; *Méndez et al., 2014*; *García-Antón et al., 2015*; *Bota et al., 2016*), as well as own unpublished data. Those were: locality, subpopulation and population.

We defined a locality as the area delimited by observations separated less than 1 km, distance that allows territorial males to be in close contact by singing or short flights (*Suárez, 2010*; *Vögeli et al., 2010*). Data from capture-recapture of territorial adults indicate they are strongly sedentary, with regular movements below 2-3 km (*Laiolo et al., 2007*; *Vögeli et al., 2008*; *Suárez, 2010*; *Vögeli et al., 2010*). Bioacoustic data suggest cultural similarity and adult males contact at a distance of 5 km (*Laiolo, 2008*), supported by the recovery of two marked adults at 5.4 and 5.8 km in Rincón de Ademuz, Valencia (*Pérez-Granados & López-Iborra, 2015*). There is only one record of an adult out of this range, recaptured at 13 km from its capture location (*V. Garza*, unpublished data). Thus, we established 5 km as the plausible threshold for resident movements. Therefore, a subpopulation was delimited by observations separated 5 km or less. Finally, a population was considered as the set of subpopulations separated by a maximum distance of 20 km, following a conservative criterion and accounting for the few available data on juvenile dispersal (up to 20 km in *Vögeli et al., 2010*, 33 km in *García-Antón et al., 2015*). This upper level represents those entities that, despite being connected sporadically would maintain a high genetic similarity due to individuals exchange (*Méndez et al., 2011*; *Méndez et al., 2014*). We used a GIS software (*QGIS.org, 2021*) to build the correspondent buffers of 0.5, 2.5 and 10 km over the observations layer (Fig. 1).

Definition of stepping stones

We also identified those areas that, despite being unoccupied by the species, could be potentially used and relevant in the connectivity process due to their high probability of presence, as shown in the distribution model (*García-Antón et al., 2019*). To do so, we used the 1x1 km cells considered to be of potential distribution (n=5,575; those that accounted for a probability value higher than the mean of the 1,370 ones with confirmed presence, see *García-Antón et al., 2019*). We discarded those cells intersecting with the observations buffer (included in the subpopulations layer), obtaining a total of 3,597 1x1 km cells of unoccupied potential habitat. Adjacent cells were grouped into clusters, resulting in 902 independent entities. Following a conservative criterion, we removed those formed by a single 1x1 km cell, reducing it to 294 polygons. More details on the stepping stones building can be found in *García-Antón et al. (2019)*.

Movement scenarios

The compilation of historic and recent Dupont's lark observations out of the known breeding range (Supplemental Table S1) reveals the existence of longer displacements than the thresholds defined previously, considered as rare events corresponding to sporadic long-distance movements. Taking into account all together, we defined three potential scenarios (see below): short (5 km); medium (20 km) and long (100 km) movements thresholds.

Nodes and habitat attribute

We built the connectivity model at the subpopulation level, to obtain a more detailed result and considering that subpopulations, better than populations, constitute the metapopulation functional units, each of them with its own extinction risk and probability of connection with the rest. This way, our network included one node located in the centroid of each subpopulation and stepping stone.

Each node was assigned a quantitative value that estimates its quality or importance in the network. We defined such attribute as Available Habitat Surface (AHS) and calculated it considering the surface of adequate habitat, its quality and its degree of fragmentation by intersecting the species habitat map (see above) with the subpopulation and stepping stone layer. Population size (number of territorial males) was not included in the AHS attribute as stepping stones account for no data on population size. Besides, we avoided bias in the result of our connectivity model toward historically occupied localities, regardless of their position in the actual metapopulation configuration Therefore, the AHS was defined as following:

$$AHS = HS * HQ * 1/NP$$

Where HS (habitat surface) is the total surface of adequate habitat within the subpopulation (or stepping stone), calculated as the sum of all habitat patches within each one; HQ is habitat quality, estimated as the mean value of probability of presence of the intersecting 1x1 km cells, as estimated in the MaxEnt model (*García-Antón et al., 2019*); and NP is the number of habitat patches within the subpopulation or stepping stone, as a measure of fragmentation. This way, each node obtained a value positively associated to its surface, quality and continuity of habitat.

To calculate the network links, we used the linear distance between borders of each pair of subpopulations and stepping stones. We discarded the use of distances to the centroid due to the large size of some subpopulations, which could artificially increase the distance among neighbour patches.

Connectivity model

We used software Conefor (*Saura & Torné, 2009*) to generate the connectivity model, which is widely used to analyse network structures (*Saura et al., 2011*; *Vergara et al., 2013*; *Grafius et al., 2017*). It builds the model in a two-step process: First, it calculates a connectivity index for the whole network (PC, probability of connection). It is based on nodes quality (AHS attribute), the distance between nodes and the species' dispersal capacity. Then, it removes each node independently and calculates the loss of PC according to that removal (dPC), obtaining an estimation of the contribution of each node to the global structure.

Conefor also allows the comparison between different general scenarios by means of the *equivalent connectivity index* (EC, see *Saura & Torné, 2009*), a modification of PC provided in the same units than the node attribute (see *Saura et al., 2011*; *Saura & Torné, 2009*). Prior to subsequent analyses, we compared scenarios resulting from the different movement thresholds considered (see above): short (5 km), medium (20 km) and long distance (100 km) and the presence or absence of stepping stones in the network (building the network with two different node maps, one including exclusively subpopulations and another one with the addition of all the stepping stones).

To evaluate the importance of each node for the network, dPC is fractioned into three more specific metrics: dPC_{intra}, dPC_{flux} and $dPC_{connector}$ (*Pascual-Hortal & Saura, 2006*). The fraction dPC_{intra} refers to the internal quality of the node (intra-patch connectivity), as it had been defined through the attribute considered (in this case, AHS). Thus, it is independent of the distance to others nodes and its spatial position in the network. dPC_{flux} is a value of inter-patch connectivity, giving information about the degree of flow that each node generates within the network; this index considers all the connections in which each node is either the origin or the destination point, as well as the quality of such connections (based on the AHS of the nodes involved). So, dPC_{flux} depends on the spatial position of each node within the network, but also on the quality of those nodes it is connected to. Finally, $dPC_{connector}$ adds a second value of inter-patch connectivity, indicating the contribution of each node to the connectivity among the rest. This index provides information about the importance of each node for the maintenance of other nodes or group of nodes connectivity, that is, if it acts as a stepping stone whose absence would implicate that others increase their isolation or remain connected through a worse route (with a longer distance or passing through lower quality nodes). The total value of dPC is just the sum of these three fractions, so it gives a general value to each of the nodes in the network.

Finally, we calculated the matrix of probability of connection for each pair of nodes (subpopulations and stepping stones), what allows building connectivity maps for all different scenarios considered.

Results

Populations, subpopulations and stepping stones

Based on the map of post-2000 observations and after the application of considered criteria we obtained 123 subpopulations, 23 of which are currently extinct, considering the most recent field data, updated to 2019. After removing them, we defined a present network of 100 subpopulations, 24 populations, plus the already mentioned 294 potential stepping stones (Fig. 2, Supplemental Table S3, Supplemental Data S1).

The metapopulation structure (Fig. 2) is formed by a core region comprising the largest population: Iberian Range - Ebro Valley (considered two independent populations to date, *Suárez, 2010*). Northwards, the metapopulation shows a myriad of small populations scattered through the Iberian Range (provinces of Soria, Zaragoza, Teruel, Navarra and Huesca), perhaps remnants of a historical more continued distribution. Further east and more isolated, the only Catalonian population: Alfés (Lérida province). Through the west (Zamora province) three small populations exist, with an apparent greater degree of isolation due to their distance with the core. Southwards, a group of 12 disperse populations and progressively more isolated from the core of the distribution are distributed along the provinces of Valencia, Cuenca, Toledo, Albacete, Murcia, Almería and Granada (Fig. 2, Supplemental Data S1).

Global connectivity under different scenarios

The EC index increased with the movement threshold and with the presence of stepping stones (Table 1). Due to the marked effect of both factors on the network connectivity, all subsequent analyses were carried out considering all the different scenarios.

Classification of nodes according to internal importance index (dPC_{intra})

The subpopulations of *Monegros* (Z) and *Blancas* (TE) stand out with the highest dPC_{intra} values (Table 2), meaning the best relation between habitat surface, quality and continuity (AHS attribute). The complete list (Supplemental Data S2) shows two stepping stones in the first 20 positions: *Castronuño* (in Valladolid province, with the same dPC_{intra} value than the 10^{th} ranked subpopulation) and *Bardenas 2* (Navarra province).

Classification of nodes according to importance for flow generation (dPC_{flux})

The subpopulations of *Monegros* (Z) and *Blancas* (TE) were again the most important ones for this fraction, together with *Torralba de los Frailes* (TE), *Paramera de Molina* (GU) and *Gelsa* (Z) (Table 3). According to dPC_{flux} values, these subpopulations were those generating a larger number of connections as starting or ending point. No stepping stones were important when considering medium and long movement thresholds (20 or 100 km), but they appeared to be relevant in the scenario of short movements (5 km): *Monegrillo 2* (Z), *Alfajarín 1* (Z) and *Torralba de los Sisones* (TE) (top 10 ranking in Table 3, complete dataset is available in Supplemental Data S2 and S3).

Classification of nodes according to importance for connectivity maintenance ($dPC_{connector}$)

Three subpopulations, all included in the Iberian Range - Ebro Valley population, were the most important according to their function as connectivity nodes between others: *Paramera de Molina* (GU), *Layna* (SO) and *Altos de Barahona* (SO) (Table 4), followed by *Gelsa* (Z) and *Altiplano de Teruel* (TE), which were also present in all the scenarios. Four stepping stones were in top positions in the list: *Alba*, *Rubielos de la Cérida*, *Ojos Negros 1* and *Hoz de la Vieja*, all of them in Teruel province and within the Iberian Range - Ebro Valley population: (top 10 ranking in Table 4, complete dataset is available in Supplemental Data S2 and S3).

Classification of nodes according to general importance index (dPC)

Taking into account the sum of all previous fractions, *Monegros* (Z) and *Blancas* (TE) were highlighted as the most important subpopulations, followed by *Torralba de los Frailes* (TE) and *Paramera de Molina* (GU), all of them within the Iberian Range - Ebro Valley population (Table 5). When considering the presence of stepping stones, three important areas for the network connectivity were detected, also belonging to the same population: *Alba* (TE), *Rubielos de la Cérida* (TE) and *Cuerlas 1* (Z), which appear within the 10 most important nodes (Table 5). See Fig. 3 for a graphical view in an intermediate situation (scenario 5: 20 km movements and presence of stepping stones); the complete dataset is available in Supplemental Data S2 and S3.

Connectivity network

The degree of connectivity showed a strong variability under the different scenarios, highlighting the influence of potential movement thresholds and presence/absence of stepping stones in the metapopulation dynamics (Supplemental Data S2 contains the complete matrix, with the probability of connection for each pair of nodes under each scenario).

The most conservative situation (scenario 1: 5 km movements and absence of stepping stones) showed an extreme isolation, with connections among nearby subpopulations only in the metapopulation core (Fig. 4). Moreover, these connections seemed to be weak (0.001-20% probability), and lacking inter-population connections. In this situation, all the subpopulations outside of the Iberian Range - Ebro Valley population would be completely isolated. For this movement threshold, the presence of stepping stones would not be enough to connect the outermost subpopulations (scenario 4, Fig. 4).

For potential movements up to 20 km (scenario 2, Fig. 4), the situation changed notably. Despite the connections among nearby subpopulations continued being of low-to-medium probability, inter-subpopulation connectivity occurred within the Iberian Range - Ebro Valley population and within the western populations. With the presence of stepping stones (scenario 5, Fig. 4), high probability connections (over 80%) were frequent in near all the subpopulations within and north to the Iberian Range - Ebro Valley population. The most western populations increased their inter-subpopulation connectivity but remained unconnected with the metapopulation core. The situation of the southern part of the distribution remained dramatically unconnected, even considering the presence of stepping stones (scenario 5, Fig. 4).

Only with potential movements up to 100 km (scenarios 3 and 6, Fig. 4), Dupont's lark Iberian metapopulation would be completely connected, although even for this distance threshold, the absence of stepping stones (scenario 3) would result in weak connections of the western and southern subpopulations with the metapopulation core.

Discussion

The criteria applied in this work for the definition of localities (habitat patches separated by less than 1 km), subpopulations (group of localities separated 5 km or less) and populations (set of subpopulations separated by a maximum distance of 20 km) led to a Dupont's lark metapopulation in Spain formed by 24 populations and 100 subpopulations currently occupied. This metapopulation is probably dynamic and therefore should be periodically updated with continuous monitoring. 23 additional subpopulations became extinct in the last 2 decades and should be regularly monitored to verify possible recolonizations. Population turnover is an extremely rare event and Dupont's lark seems not to fit a classic Levins model of colonization-extinction balance. On the contrary, extinctions seem to be permanent, in a source-sink pattern that reveals a contraction process from the peripheral subpopulations to the core of the distribution. A high number of adequate habitat patches (n = 294) are spread out along the distribution range, although they are heterogeneously distributed. The distant western populations might be better connected than expected due to stepping stones. The southern range, however, is critically isolated and accounts for the majority of recent subpopulation extinctions. This work has allowed to point those subpopulations and stepping stones critical for the connectivity network and should constitute a useful tool for management. Conservation measures should include steppe land habitat protection: avoiding infrastructures installation and land use changes, restoring habitat structure with active management and introducing traditional grazing to allow long-term conservation. Dispersal mechanisms remain poorly known but, according to our results, medium-distance movements (20-30 km) and the existence of stepping stones, would help to explain the current situation of the metapopulation, with the persistence of small and isolated populations that should be already extinct based in previous PVAs (*Traba et al.,* 2011; Suárez *and Carriles,* 2010; Laiolo *et al., 2008*). In this sense, a recent study in Rincón de Ademuz (Valencia, eastern Spain) obtained only 1 recovery out of 26 juvenile individuals marked, suggesting that juveniles either leave their natal site and disperse, or their survival rate is very low (*Pérez-Granados et al., 2021*).

Populations, subpopulations and stepping stones

According to our definition of populations and subpopulations, the two main populations considered to date (Iberian Range and Ebro Valley) turn into a large, single one. The map of subpopulations presents continuity in the core of the metapopulation and a strong degree of fragmentation and isolation southwards and in the western range, which is in accordance with previous consideration (*Suárez, 2010*). Our results support the high vulnerability of the peripheral subpopulations, as showed previously in the Ebro Valley (*Vögeli et al., 2010*) and in genetic analysis (*Méndez et al., 2011*), which are more prone to extinction (*Méndez et al., 2014*; *Gómez-Catasús et al., 2018a*).

Potential stepping stones (unoccupied adequate habitat patches) are numerous (n=294), though unevenly distributed, but their importance in metapopulation dynamics seems to be high. The majority of them are located in the easternmost distribution (Teruel and Zaragoza provinces). On the contrary, the southern range presents the highest degree of isolation of the metapopulation, which could help to explain the dramatic trends of the southernmost subpopulations (*Gómez-Catasús et al., 2018a*). The apparently strong isolation of the western range (Zamora province) might be better connected than expected thanks to the higher abundance of stepping stones (Fig. 2). Most of the areas along the metapopulation with apparent optimal habitat but absence of the species (*García-Antón et al., 2019*) are considered as stepping stones in this work, and they might play a role in the species movements. Whether these areas correspond to empty patches in a classic colonization-extinction balance (Levins 1969) remains unknown. However, population turnover in Dupont's lark seems to be extremely rare at both metapopulation (*García-Antón et al., 2021*, under review) and local scales (*Gómez-Catasús et al., 2018b*). To our knowledge, just one known subpopulation has been recolonized after being extinct (*Bota et al., 2016*). Intensive field work in the Iberian Range along the study period has recorded one single habitat patch (within a known locality) reoccupied (own data). Rather than a classical Levins model, Dupont's lark metapopulation could adopt a source-sink structure (*Hanski, 1998*, *1999a*). The smaller and more isolated subpopulations would be in a higher risk of extinction due to its lower connectivity with the core of the distribution, besides other risks associated to its lower size. More than 50% of the Iberian subpopulations have less than 5 individuals (*Traba et al., 2019*), which from a genetic and demographic point of view suggests low medium-term viability, if there is no connection with other subpopulations (*Méndez et al., 2011*, *2014*).

Those subpopulations extinct during the post-2000 period (n=23, which means 18.7% of the extant subpopulations at the beginning of the century) could correspond to stochastic factors or to changes in habitat quality (*Hanski, 1999a*). In the first case, such patches would be immediately available for recolonization, as the one recorded by *Bota et al.* (2016) in Alfés (Lérida) in 2015. In the latter, that subpopulation would be unavailable for recolonization until habitat was restored. There are two main factors promoting habitat loss in the case of Dupont's lark. First, the abandonment of extensive grazing leads to plant succession and transformation of the steppe land habitat (*Peco et al., 2012, Íñigo et al., 2008; Gómez-Catasús et al., 2019*), besides decreasing habitat quality due to food (arthropod) availability linked to sheep deposition (*Gómez-Catasús et al., 2019; Reverter et al., 2019*). Second, direct habitat destruction by land use changes, mainly wind farms (*Gómez-Catasús et al., 2018b*) and ploughing (*Garza et al., 2004*; *Íñigo et al., 2008*), together with new ones expected to appear in the near future (wind farms and solar photovoltaic installations; *Serrano et al., 2020*).

Therefore, two key elements are crucial for Dupont's lark conservation: the avoidance of land use changes in the areas inhabited by the species (or those considered important for the connectivity network) and the promotion of active management to guarantee long-term habitat persistence. Recent initiatives in this direction have shown positive results (LIFE Ricotí in Soria, local projects in Valencia region; see a revision in *Traba et al., 2019*), and could be a useful tool for key areas (such as critically isolated subpopulations or important stepping stones). Anyway, long-term effective measures for habitat and species conservation should include the promotion of traditional sheep grazing, in order to avoid dramatic plant structure changes and maintain habitat functionality. These measures should be considered, at least, in the most critical connectivity nodes.

Regarding the extinct subpopulations, only 7 out of 23 have become stepping stones following our habitat-suitability criteria (Supplemental Data S4). This result suggests that low habitat quality (i.e. low food availability, changes in vegetation structure) in those areas could have contributed to the local extinction of the species, apart from isolation. Indeed, 14 out of these 23 extinct subpopulations are located in the southern range (Fig. 2), where isolation is more accused, following a centripetal contraction process from the periphery to the metapopulation core (*García-Antón et al., 2021*, under review).

In Supplemental Data S1, S2, S3 and S4 we offer detailed data and updated cartography of the metapopulation that can constitute a useful guide for the different regional administrations, which have legal obligations for the conservation of Dupont's lark in Spain. Management coordination and common guidelines are of vital importance in the case of Dupont's lark, as several regional administrations are affected by its distribution and share populations or subpopulations.

Global connectivity under different scenarios

Despite the apparent strong fragmentation and high degree of isolation of Dupont's lark metapopulation, our results suggest two elements that seem to be relevant for the connectivity of the whole network. These factors may contribute to explain the prevalence of the smallest and most isolated subpopulations, which were expected to be extinct according to the population viability models (*Laiolo et al., 2008*; *Suárez, 2010*), genetic structure (*Méndez et al., 2011*, *2014*), and data on the general situation of the species (*Suárez, 2010*; *Traba et al., 2019*). First, the large area of vacant adequate habitat (*García-Antón et al., 2019*), that should be interpreted as a network of stepping stones unnoticed to date. The size of this stepping stone network approximately equals the size of the occupied range of Dupont's lark (around 1,000 km^2; *García-Antón et al., 2019*). The Equivalent Connectivity index (EC) comparison (Table 1) showed the lowest value of EC for scenario 1 (5 km movement threshold without stepping stones), while EC for scenario 6 (100 km movement threshold with stepping stones) had the highest value. For each scenario, EC was always higher when adding stepping stones than increasing potential movements to the next threshold. Therefore, the role of these unoccupied potential areas seems crucial for the functionality of the network and could have even a stronger influence than the movement capacity of the species (Table 1). In other words, even if we consider Dupont's lark as a strongly sedentary species with sporadic medium-distance movements, the metapopulation could be connected thanks to the presence of stepping stones. The relative low values of stepping stones in dPC_{intra} (Table 2) but higher ones in dPC_{flux} and $dPC_{connector}$ (Tables 3 and 4) suggest that these patches may have lower habitat quality than occupied subpopulations (according to the AHS attribute), thus being unsuitable for occupancy, but maintaining a high relevance for the metapopulation connectivity.

On the other hand, results of the simulation of different movement thresholds (Fig. 4) suggest that 2-5 km maximum dispersal distance assumed previously (*Laiolo et al., 2007*; *Vögeli et al., 2008*; *Vögeli et al., 2010*; *Suárez, 2010*) could have undervalued actual dispersal ability of the species. Recent records of longer movements, that could correspond to juvenile dispersal (*García-Antón, 2015*), recolonization (*Bota et al., 2016*) or sporadic long-distance movements (*García and Requena, 2015*, *Dies et al., 2010, Balfagón and Carrion Piquer, 2021*), as well as historical records summarized in Supplemental Table S1, point to medium to large distance events that could be contributing to slow down local extinction as fast as predicted by the viability models (*Laiolo et al., 2007*; *Suárez, 2010*).

Nodes importance and AHS attribute

Indices dPC_{intra}, dPC_{flux} and dPC all pointed to the same most important nodes: *Monegros* (Z), *Blancas* (TE), *Torralba de los Frailes* (TE) and *Paramera de Molina* (GU), all of them located in the Iberian Range – Ebro Valley population. The conservation of these top ranked subpopulations is imperative to ensure the conservation of the metapopulation, as it is also crucial to focus on the third fraction of dPC ($dPC_{connector}$). In the case of Dupont's lark, in which isolation may constitute a critical factor for the species conservation, the loss of those subpopulations with a higher value in $dPC_{connector}$ could implicate the subsequent extinction of other subpopulations or groups of subpopulations, so they should be considered of highest priority. Several nodes of the Iberian Range close to the geographical centroid of the metapopulation are included in this set, mainly *Layna* (SO), *Paramera de Molina* (GU) and *Altos de Barahona* (SO), as well several stepping stones that are also among the top ranked nodes: *Alba*, *Rubielos de la Cérida*, *Ojos Negros 1* and *Hoz de la Vieja*, among others (Table 4).

Finally, the particular case of the military National Training Centre of *San Gregorio*, a few km North of Zaragoza city, must be considered. This area holds around 34,000 ha of mostly continuous steppe habitat and due to its huge extension it might certainly constitute one of the most important nodes of the connectivity network. Our method of stepping stones determination identified several potential habitat areas in this region (stepping stones of *Zaragoza 1, 3, 4, 5, 6*, Supplemental Data S4), what suggests that this area should be considered of potential importance by the regional administration of Aragón.

Supplemental Data S2 includes the complete lists of nodes importance by province in all the scenarios considered and should constitute a useful management tool. Each regional administration should consider the most important nodes within its territory, either subpopulations or stepping stones, of high priority and concern. These areas should be included in national and/or regional species conservation plans, as their protection and management seem to be crucial for the maintenance of the species at a national scale, and coordinated measures between neighbour administrations are needed. Stepping stones require special attention, as they are relevant for their spatial and habitat features, but not for the presence of the species, which may difficult the application of conservation measures.

Connectivity network

In the most restrictive scenario (movements of 5 km and absence of stepping stones), the metapopulation showed practically total isolation among subpopulations, excepting low probability connections within the Iberian Range – Ebro Valley. Assuming a medium movement threshold of 20 km, a significant increase of connections appears within the central distribution, though their probability continued being low. Thus, the uttermost western populations seem to be isolated and their persistence depend on the presence of stepping stones. The most unfavourable situation is shown by the southern subpopulations, which remain completely isolated unless there are movements of 100 km.

The strong general population decline of the species described recently (*Gómez-Catasús et al., 2018a*), its current and future distribution (*García-Antón et al., 2019*) and the genetic analyses (*Méndez et al., 2011*; *Méndez et al., 2014*) point to a high degree of isolation. But, at the same time, small and isolated peripheral subpopulations persist. Therefore, we consider as the most probable situation the coexistence of several of the scenarios evaluated here. According to movements of the different age classes, and considering the little information on juvenile capture-recapture, we suggest that adult displacements below 1 km could be events of high probability, and intra and inter-sexual communication at this distance must be a common phenomenon. Adult movements between 1 and 5 km could be mid-to-low probability events; those between 5 and 20 km, of low probability; and those over 20 km must be considered highly improbable events. Juveniles are presumable the dispersive fraction of the population, as it is widespread in other bird species (*Weise & Meyer, 1979; Greenwood & Harvey, 1982; Ferrer 1993; Cooper et al., 2008; Whitfield et al., 2009)*. Juveniles are prone to leave their natal site (as recently suggested for Dupont's lark, *Pérez-Granados et al., 2021*), moving long distance across non-habitat areas and to settle new populations with few initial individuals (*Harrison et al., 1989)*. In the case of the Dupont's lark, we consider juvenile movements of 5 km of very high probability; those comprising 5-20 km, of high probability; 20-100 km movements, of low probability; and over 100 km, of very low probability. This last distance would represent rare events corresponding to sporadic long-distance movements (Supplemental Table S1).

The importance of stepping stones facilitating movements between habitat fragments has been reported in different ecosystems and species. *Uezu et al. (2008)* showed in the bird community of the Brazilian Atlantic forest that the efficiency of stepping stones is species-dependent and it seems to be related to the matrix resistance. *Baum et al. (2004)* also highlighted the importance of the surrounding matrix for the effectiveness of stepping stones in plants. *Saura et al. (2014)* found that the loss of stepping stones can cause a sharp decline in the potential movement distance in bird species, which can't be compensated by other factors (as, for example, source population size). Stepping stones could also have some negative effects, as *Kramer-Schadt et al. (2011)* found in a mammal species, with a trade-off related to stepping stone size and location, as small-size ones could cause a distraction in dispersers and avoid them to find suitable breeding patches.

The situation of Dupont's lark, with dramatic declines and ongoing habitat fragmentation and contraction (*Gómez-Catasús et al., 2018a*; *García-Antón et al., 2019*) urges to act on the species and habitat management. In the current context of land intensification and rural abandonment, Dupont's lark habitat has a finite lifetime. As smaller patches disappear, the larger ones, which presently hold the majority of the population, will become more vulnerable due to the loss of linked habitat and the decrease of connectivity. Besides, several aspects of this species remain partially unknown and are crucial for its conservation, as dispersal mechanisms, reproductive biology or genetics, which are needed for a detailed evaluation of the connectivity and population viability of Dupont's lark.

Conclusions

This work lists the most important areas for conservation and management of the Dupont's lark in Spain and an updated structure of populations and subpopulations (and potential stepping stones). Regional administrations with presence of Dupont's larks are urged to use this scientific basis for their management duties and to coordinate management among different regions.

Actions implying habitat loss and fragmentation (such as ploughing, windfarms or afforestations) must be avoided in Dupont's lark subpopulations or in those potentially important stepping stones. Additionally, the increase of habitat quality both in short (restoration measures) and long terms (extensive grazing) is desirable for the species conservation. Isolation of the southern range is extreme and, according to the recent subpopulation extinctions, we speculate a near-future distribution restricted to the current metapopulation core. Research on movements, specially on breeding dispersal, would help clarifying movement patterns in the metapopulation and establishing ecological corridors to increase connectivity.

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Figure 1

Definition of localities, subpopulations and populations.

Localities are demarcated by a 0,5 km buffer (red), so that observations separated by a distance > 1 km belong to different localities. Subpopulations are delimited by a buffer of 2,5 km (blue) and a distance of 5 km between observations. Finally, observations distanced > 20 km belong to different populations (buffer of 10 km, black). Red dots indicate Dupont's lark observations and green polygons, the adequate habitat within subpopulations.

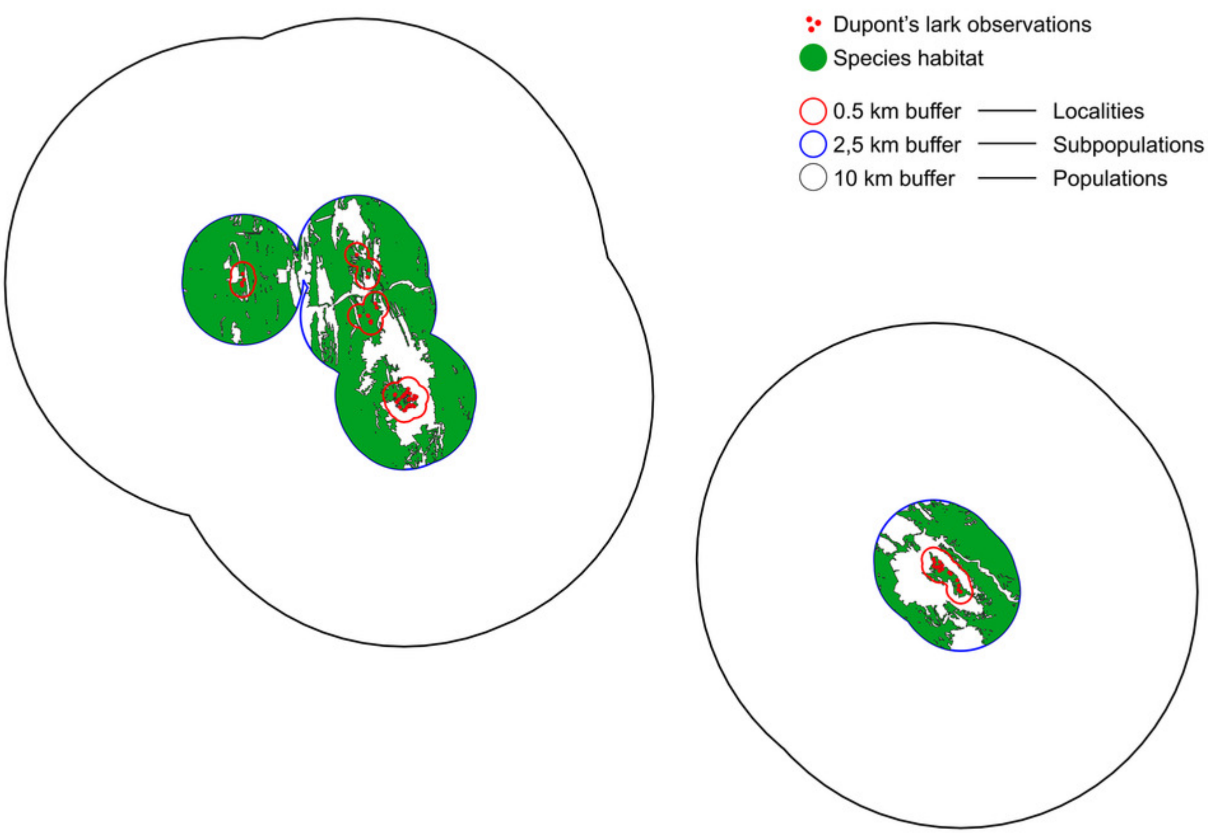

Figure 2

Map of current populations, subpopulations and stepping stones of the Iberian metapopulation of Dupont's lark.

Black contours represent populations (n=24), green polygons are subpopulations (n=100) and black dots indicate stepping stones (n=294). Red crosses represent the 23 subpopulations of recent extinction (post-2000). See detailed cartography in Supplemental Data S1.

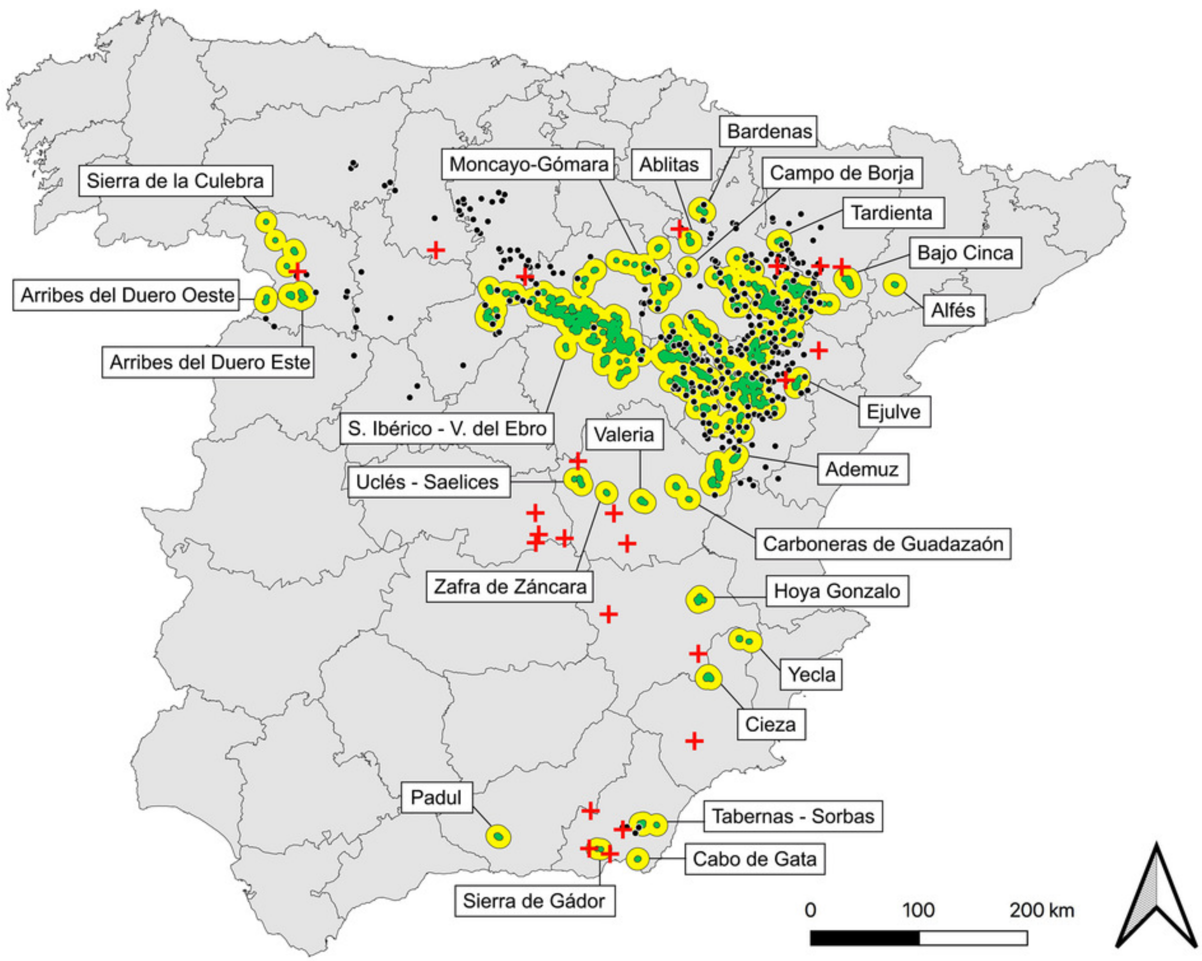

Figure 3

Map of nodes importance in the Iberian metapopulation of Dupont's lark.

Nodes classified according to general importance index (dPC). The core of the distribution, focused in the Iberian Range - Ebro Valley population, gathers the most important nodes. Here we show scenario 5 (movements of 20 km and presence of stepping stones). Maps for all possible scenarios are included in Supplemental Data S2.

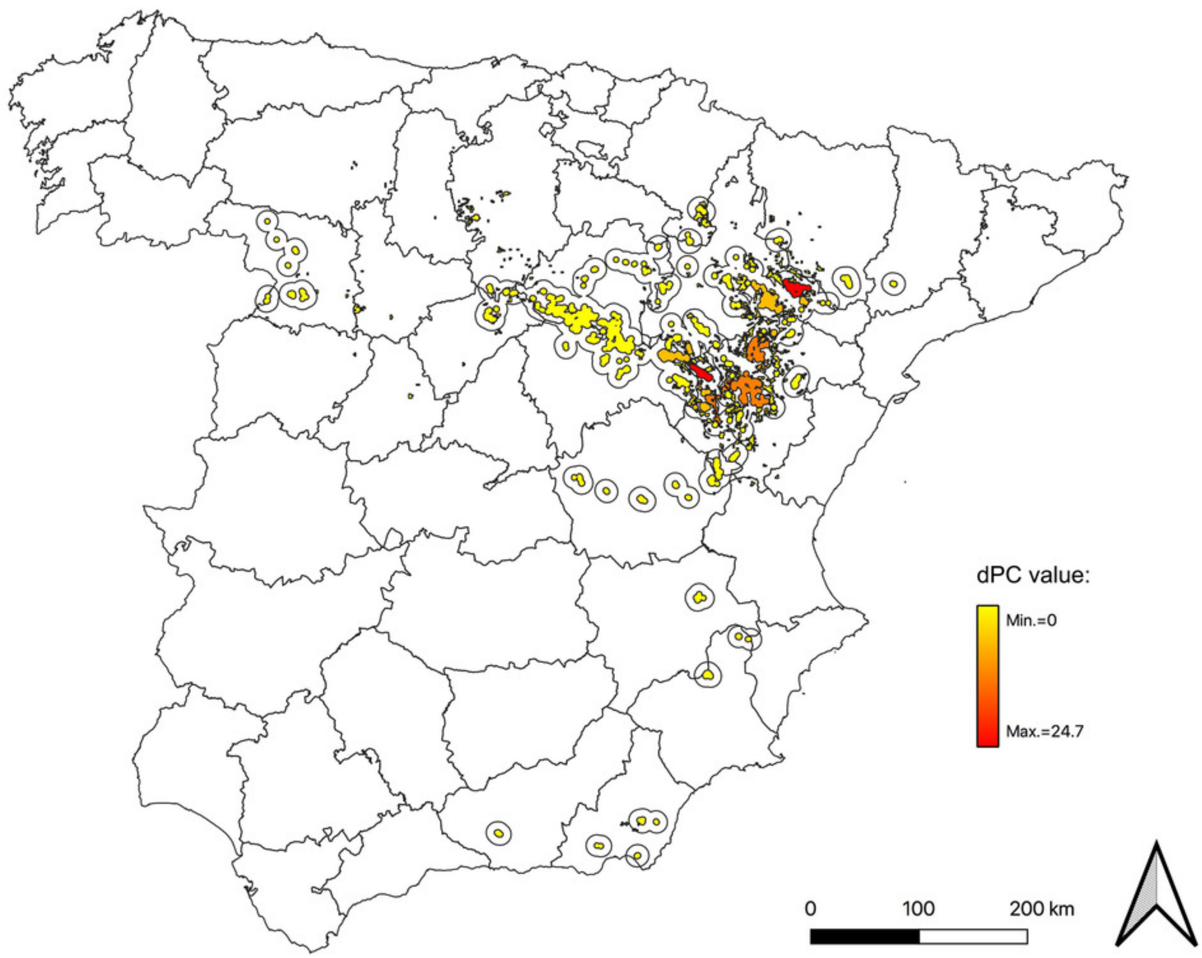

Figure 4

Probability of connection of Dupont’s lark metapopulation under the different scenarios evaluated.

Effect of the distance (movements of 5, 20 and 100 km) and the presence/absence of stepping stones in the probability of connection among Dupont’s lark subpopulations. See Supplemental Data S2 for the complete matrix of probability of connection for node pairs.

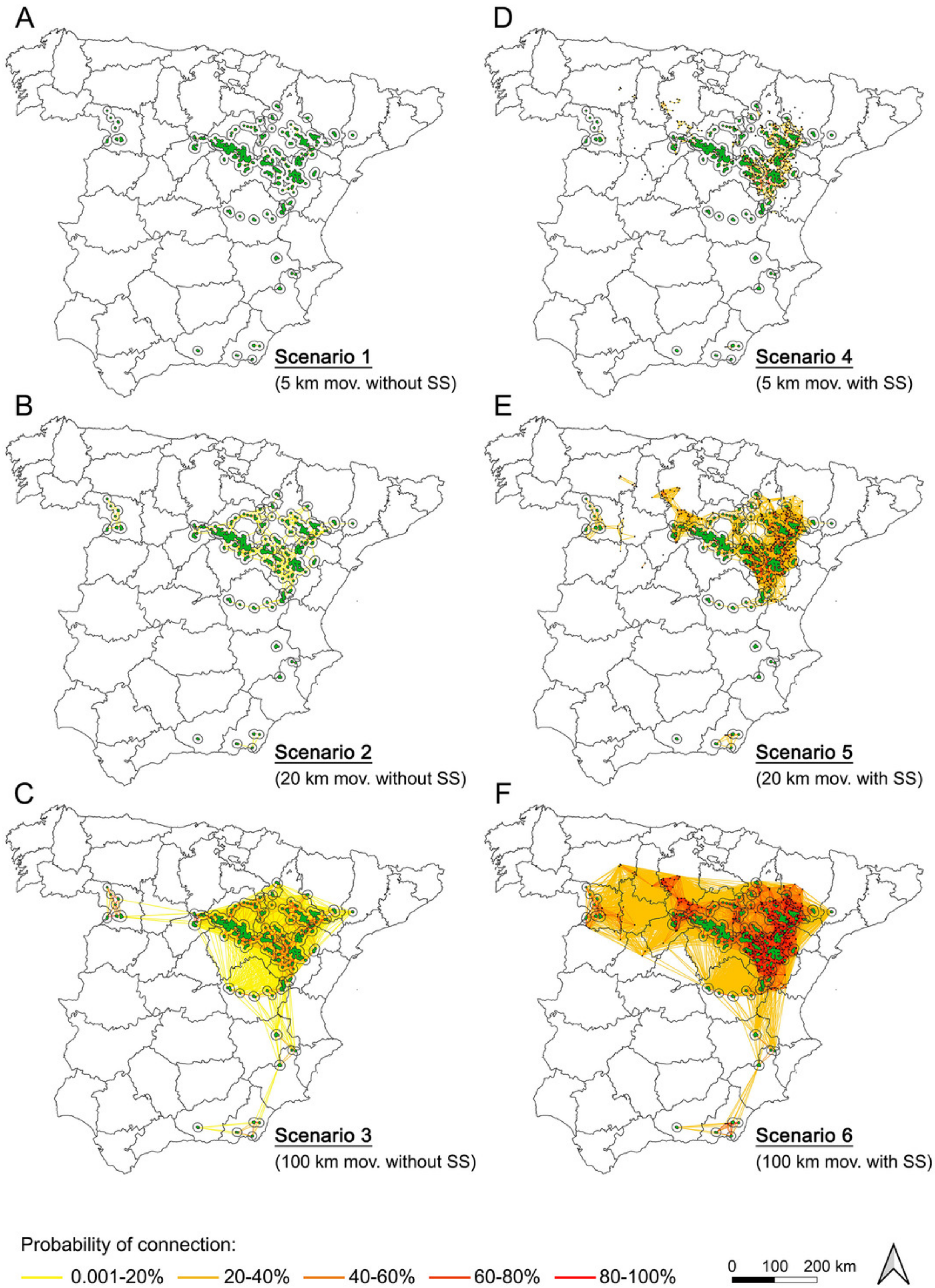
A
Scenario 1
(5 km mov. without SS)
B
Scenario 2
(20 km mov. without SS)
C
Scenario 3
(100 km mov. without SS)
D
Scenario 4
(5 km mov. with SS)
E
Scenario 5
(20 km mov. with SS)
F
Scenario 6
(100 km mov. with SS)
Probability of connection:
0.001-20%
20-40%
40-60%
60-80%
80-100%
0 100 200 km

Table 1(on next page)

Equivalent Connectivity Index (EC) comparison among different scenarios of movements and presence/absence of stepping stones.

The Equivalent Connectivity Index represents the global connectivity of the metapopulation. Both the movement threshold and the presence of stepping stones generate increments in connectivity, with a stronger effect of the latter.

Movements	EC without s. stones	EC with s. stones
Short distance movements (5 km)	8935.65 (scenario 1)	14560.55 (scenario 4)
Medium distance movements (20 km)	11529.18 (scenario 2)	24340.81 (scenario 5)
Long distance movements (100 km)	21956.86 (scenario 3)	46319.15 (scenario 6)

Table 2(on next page)

Summary of the 10 most important nodes for intra-patch connectivity (dPC_{intra}).

dPC_{intra} makes reference to the internal importance of each node and it is independent on spatial position. Thus, the ranking is the same for the different movement thresholds. See the complete list in Supplemental Data S2.

Without stepping stones (scenario 1, 2, 3)			**With stepping stones (scenario 4, 5, 6)**		
Name	Prov.	dPC_{intra}	Name	Prov.	dPC_{intra}
Monegros	Zaragoza	33.34	Monegros	Zaragoza	4.49
Blancas	Teruel	17.77	Blancas	Teruel	2.39
Torralba de los Frailes	Teruel	4.16	Torralba de los Frailes	Teruel	0.56
Bardenas	Navarra	2.64	Bardenas	Navarra	0.36
Lécera	Zaragoza	2.10	Lécera	Zaragoza	0.28
Pinilla del Campo	Soria	1.49	Pinilla del Campo	Soria	0.20
Campo Romanos	Zaragoza	1.47	Campo Romanos	Zaragoza	0.20
Paramera de Molina	Guadalajara	1.39	Paramera de Molina	Guadalajara	0.19
Orihuela del Tremedal	Teruel	1.25	Orihuela del Tremedal	Teruel	0.17
Gelsa	Zaragoza	1.16	Gelsa	Zaragoza	0.16

Table 3 (on next page)

Summary of the 10 most important nodes for flow generation in the network (dPC_{flux}).

Stepping stones are indicated as '*SS*'. See the complete list in Supplemental Data S2.

Scenario 1 (5 km mov. without SS)			**Scenario 2** (20 km mov. without SS)			**Scenario 3** (100 km mov. without SS)		
Name	Prov.	dPC_{flux}	Name	Prov.	dPC_{flux}	Name	Prov.	dPC_{flux}
Monegros	Zaragoza	7,64	Blancas	Teruel	15,14	Blancas	Teruel	20,86
Gelsa	Zaragoza	7,06	Monegros	Zaragoza	13,48	Monegros	Zaragoza	19,70
Torralba de los Frailes	Teruel	5,82	Torralba de los Frailes	Teruel	11,07	Torralba de los Frailes	Teruel	11,30
Paramera de Molina	Guadalajara	5,33	Paramera de Molina	Guadalajara	7,89	Lécera	Zaragoza	7,22
Blancas	Teruel	3,52	Gelsa	Zaragoza	7,81	Paramera de Molina	Guadalajara	6,94
Alforque	Zaragoza	1,05	Belchite	Zaragoza	3,34	Campo Romanos	Zaragoza	5,49
Pinilla del Campo	Soria	1,02	La Torresaviñán	Guadalajara	2,82	Gelsa	Zaragoza	5,35
Milmarcos-Llumes	Guadalajara	1,02	Lécera	Zaragoza	2,81	Orihuela del Tremedal	Teruel	5,21
Pozalmuro	Soria	0,89	Cenegro	Soria	2,61	Belchite	Zaragoza	5,09
Cenegro	Soria	0,82	Alforque	Zaragoza	2,54	La Torresaviñán	Guadalajara	4,85

Scenario 4 (5 km mov. with SS)			**Scenario 5** (20 km mov. with SS)			**Scenario 6** (100 km mov. with SS)		
Name	Prov.	dPC_{flux}	Name	Prov.	dPC_{flux}	Name	Prov.	dPC_{flux}
Blancas	Teruel	14,77	Blancas	Teruel	16,33	Monegros	Zaragoza	15,01
Monegros	Zaragoza	14,03	Monegros	Zaragoza	13,50	Blancas	Teruel	12,94
Torralba de los Frailes	Teruel	7,64	Torralba de los Frailes	Teruel	8,08	Torralba de los Frailes	Teruel	6,42
Paramera de Molina	Guadalajara	6,11	Paramera de Molina	Guadalajara	5,25	Lécera	Zaragoza	4,74
Gelsa	Zaragoza	4,79	Orihuela del Tremedal	Teruel	5,07	Paramera de Molina	Guadalajara	3,84
Orihuela del Tremedal	Teruel	4,23	Lécera	Zaragoza	5,00	Orihuela del Tremedal	Teruel	3,70
(SS) Monegrillo 2	Zaragoza	3,62	Gelsa	Zaragoza	3,74	Belchite	Zaragoza	3,44
Pozondón	Teruel	3,11	Belchite	Zaragoza	3,48	Campo Romanos	Zaragoza	3,43
(SS) Alfajarín 1	Zaragoza	2,69	Pozondón	Teruel	3,38	Gelsa	Zaragoza	3,19
(SS) Torralba de los Sisones	Teruel	2,58	Celadas Este	Teruel	2,51	La Torresaviñán	Guadalajara	2,48

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Table 4(on next page)

Summary of the 10 most important nodes for connectivity maintenance ($dPC_{connector}$).

Stepping stones are indicated as '*SS*'. See the complete list in Supplemental Data S2.

Scenario 1 (5 km mov. without SS)			**Scenario 2** (20 km mov. without SS)			**Scenario 3** (100 km mov. without SS)		
Name	Prov.	dPC_{conn}	Name	Prov.	dPC_{conn}	Name	Prov.	dPC_{conn}
Paramera de Molina	Guadalajara	2.38	Paramera de Molina	Guadalajara	6.65	Layna	Soria	8.28
Layna	Soria	0.87	Layna	Soria	4.58	Segura de los Baños	Teruel	8.22
Altos de Barahona	Soria	0.83	Altos de Barahona	Soria	3.57	Paramera de Molina	Guadalajara	7.89
Gelsa	Zaragoza	0.78	Gelsa	Zaragoza	2.60	Altos de Barahona	Soria	7.08
Pozalmuro	Soria	0.11	Maranchón	Guadalajara	1.55	Altiplano de Teruel	Teruel	3.78
Aldealpozo	Soria	0.06	Villar del Salz	Teruel	1.30	Blancas	Teruel	3.60
Cueva de la Hoz	Guadalajara	0.04	Azaila	Teruel	1.28	Maranchón	Guadalajara	2.86
Altiplano de Teruel	Teruel	0.02	Alforque	Zaragoza	1.25	Azaila	Teruel	2.52
Alforque	Zaragoza	0.02	Blancas	Teruel	1.03	Lécera	Zaragoza	2.50
Conquezuela	Soria	0.01	Altiplano de Teruel	Teruel	0.91	Gelsa	Zaragoza	2.16

Scenario 4 (5 km mov. with SS)			**Scenario 5** (20 km mov. with SS)			**Scenario 6** (100 km mov. with SS)		
Name	Prov.	dPC_{conn}	Name	Prov.	dPC_{conn}	Name	Prov.	dPC_{conn}
(SS) Alba	Teruel	9.30	(SS) Alba	Teruel	12.12	Segura de los Baños	Teruel	7.91
Villar del Salz	Teruel	6.89	Segura de los Baños	Teruel	10.24	Layna	Soria	4.90
(SS) Rubielos de la Cérida	Teruel	6.70	(SS) Rubielos de la Cérida	Teruel	10.20	(SS) Rubielos de la Cérida	Teruel	4.09
Paramera de Molina	Guadalajara	5.70	Villar del Salz	Teruel	8.32	(SS) Alba	Teruel	4.07
(SS) Ojos Negros 1	Teruel	4.85	Altiplano de Teruel	Teruel	8.26	Altiplano de Teruel	Teruel	4.03
(SS) Cuerlas 1	Zaragoza	4.68	Blancas	Teruel	5.97	Altos de Barahona	Soria	3.97
Blancas	Teruel	3.84	(SS) Ojos Negros 1	Teruel	5.25	Paramera de Molina	Guadalajara	3.80
Pozondón	Teruel	3.54	(SS) Hoz de la Vieja	Teruel	5.08	(SS) Pinilla Trasmonte	Burgos	3.48
(SS) Celadas	Teruel	2.98	(SS) Moneva	Zaragoza	4.75	(SS) Hoz de la Vieja	Teruel	3.06
Monegros	Zaragoza	2.37	Paramera de Molina	Guadalajara	4.41	Villar del Salz	Teruel	2.76

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Table 5(on next page)

Summary of the 10 most important nodes for the connectivity according to the global index dPC.

Stepping stones are indicated as '*SS*'. See the complete list in Supplemental Data S2.

Scenario 1 (5 km mov. without SS)			**Scenario 2** (20 km mov. without SS)			**Scenario 3** (100 km mov. without SS)		
Name	Prov.	dPC	Name	Prov.	dPC	Name	Prov.	dPC
Monegros	Zaragoza	40.99	Monegros	Zaragoza	33.79	Blancas	Teruel	27.40
Blancas	Teruel	21.29	Blancas	Teruel	26.85	Monegros	Zaragoza	25.50
Torralba de los Frailes	Teruel	9.98	Paramera de Molina	Guadalajara	15.37	Paramera de Molina	Guadalajara	15.06
Paramera de Molina	Guadalajara	9.10	Torralba de los Frailes	Teruel	13.62	Torralba de los Frailes	Teruel	12.05
Gelsa	Zaragoza	8.99	Gelsa	Zaragoza	11.10	Segura de los Baños	Teruel	10.18
Bardenas	Navarra	2.64	Layna	Soria	5.77	Lécera	Zaragoza	10.06
Pinilla del Campo	Soria	2.51	Altos de Barahona	Soria	4.89	Layna	Soria	9.67
Lécera	Zaragoza	2.27	Belchite	Zaragoza	4.73	Altos de Barahona	Soria	8.67
Orihuela del Tremedal	Teruel	1.90	Lécera	Zaragoza	4.42	Gelsa	Zaragoza	7.70
La Torresaviñán	Guadalajara	1.77	Alforque	Zaragoza	3.89	Belchite	Zaragoza	7.08

Scenario 4 (5 km mov. with SS)			**Scenario 5** (20 km mov. with SS)			**Scenario 6** (100 km mov. with SS)		
Name	Prov.	dPC	Name	Prov.	dPC	Name	Prov.	dPC
Monegros	Zaragoza	28.96	Blancas	Teruel	24.70	Monegros	Zaragoza	17.19
Blancas	Teruel	25.30	Monegros	Zaragoza	20.46	Blancas	Teruel	16.28
Paramera de Molina	Guadalajara	12.33	(SS) Alba	Teruel	14.04	Segura de los Baños	Teruel	9.14
(SS) Alba	Teruel	11.22	Segura de los Baños	Teruel	11.67	Paramera de Molina	Guadalajara	7.69
Torralba de los Frailes	Teruel	9.49	(SS) Rubielos de la Cérida	Teruel	10.93	Torralba de los Frailes	Teruel	6.60
Villar del Salz	Teruel	7.96	Altiplano de Teruel	Teruel	10.31	Belchite	Zaragoza	6.20
Gelsa	Zaragoza	7.37	Paramera de Molina	Guadalajara	9.84	Layna	Soria	5.59
(SS) Rubielos de la Cérida	Teruel	7.35	Villar del Salz	Teruel	9.40	Altiplano de Teruel	Teruel	5.46
Pozondón	Teruel	6.83	Torralba de los Frailes	Teruel	8.76	(SS) Alba	Teruel	5.36
(SS) Cuerlas 1	Zaragoza	6.43	Belchite	Zaragoza	6.74	Lécera	Zaragoza	5.17

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