

Stepping stones are crucial for species' long-distance dispersal and range expansion through habitat networks

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Summary

1. Climate and land-use changes will require species to move large distances following shifts in their suitable habitats, which will frequently involve traversing intensively human-modified landscapes. Practitioners will therefore need to evaluate and act to enhance the degree to which habitat patches scattered throughout the landscape may function as stepping stones facilitating dispersal among otherwise isolated habitat areas.
2. We formulate a new generalized network model of habitat connectivity that accounts for the number of dispersing individuals and for long-distance dispersal processes across generations. By doing so, we bridge the gap between complex dynamic population models, which are generally too data demanding and hence difficult to apply in practical wide-scale decision-making, and simpler static connectivity models that only consider the amount of habitat that can be reached by a single average disperser during its life span.
3. We find that the loss of intermediate and sufficiently large stepping-stone habitat patches can cause a sharp decline in the distance that can be traversed by species (critical spatial thresholds) that cannot be effectively compensated by other factors previously regarded as crucial for long-distance dispersal (fat-tailed dispersal kernels, source population size).
4. We corroborate our findings by showing that our model largely outperforms previous connectivity models in explaining the large-scale range expansion of a forest bird species, the Black Woodpecker *Dryocopus martius*, over a 20-year period.
5. The capacity of species to exploit the opportunities created by networks of stepping-stone patches largely depends on species-specific life-history traits, suggesting that species assemblages traversing fragmented landscapes may be exposed to a spatial filtering process driving long-term changes in community composition.
6. *Synthesis and applications.* Previous static connectivity models seriously underestimate the importance of stepping-stone patches in sustaining rare but crucial dispersal events. We provide a conceptually broader model that shows that stepping stones (i) must be of sufficient size to be of conservation value, (ii) are particularly crucial for the spread of species (either native or invasive) or genotypes over long distances and (iii) can effectively reduce the isolation of the largest habitat blocks in reserves, therefore largely contributing to species persistence across wide spatial and temporal scales.

Key-words: connectivity metrics, conservation biology, dispersal kernels, ecological networks, graph theory, habitat connectivity, habitat fragmentation, landscape configuration, population spread, species dispersal

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Introduction

Climate and land-use changes will inevitably make large habitat areas inhospitable for many species, whereas new habitats matching species' environmental requirements may become available at higher latitudes or altitudes (Parmesan & Yohe 2003). Long-term persistence of species will therefore rely upon their capacity to respond to these changes by moving large distances across human-modified landscapes (Loarie *et al.* 2009; Schloss, Nuñez & Lawler 2012). Depending on the land-use patterns and on the conservation measures implemented in these human-modified landscapes, they may be entirely inhospitable for the species or, on the contrary, retain a scattered mosaic of habitat fragments that might facilitate species dispersal and range expansion through a series of successive stepping-stone movement steps (Baum *et al.* 2004; Uezu, Beyer & Metzger 2008; Kramer-Schadt *et al.* 2011; Leidner & Haddad 2011).

Disentangling the actual role of networks of stepping-stone patches as habitat connectivity providers and their implications for species movement is, therefore, of paramount importance for developing effective conservation strategies that help to mitigate the impacts of global change on biodiversity (Heller & Zavaleta 2009; Crosby *et al.* 2010), including the control of invasions by exotic species and their spread rates. Achieving this objective requires methods that are able to assess the connectivity between habitat units and to quantify the impacts of landscape change and fragmentation on the capacity of species to disperse among suitable habitat patches.

Dynamic and spatially explicit population models can be used to account for the effects of habitat spatial configuration and connectivity on species distribution patterns and expansion rates (e.g. Tilman & Kareiva 1997; Cantrell & Cosner 2003; Gardner & Gustafson 2004; Hanski & Gaggiotti 2004; Hastings & Botsford 2006). However, these dynamic population models are generally difficult to apply in practice (Hanski 1994; Calabrese & Fagan 2004; Saura & Pascual-Hortal 2007) due to (i) their high data requirements, which generally cannot be met in real-world studies at wide spatial scales; (ii) their analytical complexity, which frequently involves repeated numerical simulations over different combinations of the input parameters, which can be tedious and time-consuming; (iii) the difficulty of interpreting the results as they depend on a large number of interacting parameters, some of them being non-intuitive or hard to relate to actual characteristics of the landscapes or populations that can be measured or managed; and (iv) the fact that some are based on assumptions that are difficult to verify or do not hold in the currently changing environmental conditions (e.g. the equilibrium assumption). As stated by Hanski (1994), 'spatially explicit metapopulation models seem hard to construct using any other approach than numerical simulation. But simulation models, though having the potential to answer quantitative questions, are typically tedious

to construct, are pestered by many assumptions which are difficult to verify, and include many parameters that are hard to estimate'.

For these reasons, considerable research efforts have been devoted to the development of simpler – but sound and empirically supported – connectivity models that are more tractable and amenable for practical use and do not explicitly account for time; that is, they provide a single time-invariant (static) outcome on the assessment of connectivity and related ecological implications, rather than results that vary with the temporal frame considered. A large number of static connectivity models (hereafter referred to simply as 'connectivity models') are available, ranging from some derived from or used within metapopulation theory (Hanski & Ovaskainen 2000; Moilanen & Nieminen 2002) to others based on network analysis (graph theory) (Urban & Keitt 2001; Urban *et al.* 2009; Saura & Rubio 2010). These connectivity models are being widely and increasingly applied for ecological research and conservation planning in a variety of management contexts and ecosystem types (e.g. Hanski & Ovaskainen 2000; Moilanen & Nieminen 2002; Bodin *et al.* 2006; Saura & Pascual-Hortal 2007; Neel 2008; Urban *et al.* 2009; Gurrutxaga, Rubio & Saura 2011; Morzillo, Ferrari & Liu 2011; Awade, Boscolo & Metzger 2012).

Despite the conceptual and analytical differences among these connectivity models, they all share a fundamental characteristic: they consider a spatially explicit setting of habitat patches connected to each other through dispersal, and they rely on a dispersal kernel that provides the estimated probability of an individual moving a certain distance from its source location. Dispersal kernels decay rapidly with distance, which translates to a very low probability of dispersal far beyond the observed average species dispersal distance (Clark *et al.* 1998; Nathan 2006). However, dispersal kernels with fatter tails make long-distance dispersal events comparatively more likely and have been shown to play a major role in explaining large-scale processes such as population spread, genetic transmission or range shifts following climate changes (Clark *et al.* 1998; Nathan 2006). It is also possible to simply define whether the connections between patches exist or not based on a given distance threshold. This threshold approach can be useful for several purposes (e.g. Estrada & Bodin 2008; Bodin & Saura 2010), but often more detailed and ecologically realistic estimates of the dispersal likelihood are desired and advocated (Moilanen & Nieminen 2002; Saura & Pascual-Hortal 2007; Moilanen 2011; Awade, Boscolo & Metzger 2012). The simpler threshold approach will therefore not be considered in this study.

Habitat connectivity models can be broadly classified into two categories based on how they quantify the probability of dispersal between habitat patches i and j (p_{ij}); these categories are referred to here as Sdirect and Sstep (S standing for standard models) and are illustrated in Fig. 1. Sdirect models only consider direct dispersal

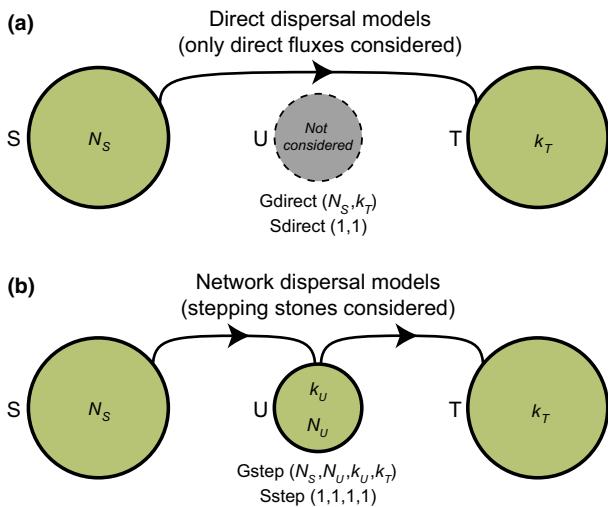


Fig. 1. Illustration of the assumptions and implications of the different connectivity models in a three-patch system. The system consists of a source patch S, a destination (target) patch T and a patch U that may act as a stepping stone facilitating dispersal from S to T. Patch S is fully occupied up to its carrying capacity by the focal species (with N_S individuals dispersing from S), whereas U and T are initially vacant. The species may get established in U or T if at least k_U or k_T individuals are able to colonize the patch, respectively. Many connectivity models (Sdirect, Gdirect) do not consider the potential role of U in facilitating the colonization of T (a), which is accounted for in models Sstep and Gstep through network analysis (b).

between patches (with p_{ij} given directly by the species dispersal kernel), such as those used in the incidence function models and their extension as described by Moilanen & Nieminen (2002) and some flux or area-weighted flux metrics (Urban & Keitt 2001; Morzillo, Ferrari & Liu 2011). Sdirect models will consider the two landscapes in each of the comparisons in Fig. 2 as equally connected and/or estimate that the amount of dispersal arriving to any of the patches in landscape a1 is the same as for any of the patches in landscape a2 (Fig. 2). Sstep consists of network-based models that, in addition to direct dispersal, also account for the potential contribution to connectivity of intermediate stepping-stone patches, which might result in a more realistic connectivity assessment (Urban *et al.* 2009; Bodin & Saura 2010; Saura & Rubio 2010). A stepping stone is here defined as a habitat patch q that facilitates movement between at least two other patches i and j ($i \neq q$, $j \neq q$) (Fig. 1), resulting in a higher p_{ij} value (as assessed by these Sstep models) than that directly derived from the dispersal kernel (Saura & Rubio 2010; Morzillo, Ferrari & Liu 2011). Sstep models will indicate a different connectivity in the landscapes compared in Fig. 2 and higher p_{ij} values for the patches in landscape a2 than for those in landscape a1 (Fig. 2). Recent studies using a Sstep network modelling approach have concluded, however, that stepping stones usually have a relatively modest or non-dominant importance for determining the amount of habitat that can be reached by species (Bodin & Saura 2010; Morzillo, Ferrari & Liu 2011; Rubio & Saura

2012). The widely used metapopulation capacity metric (Hanski & Ovaskainen 2000) is based on the equilibrium assumption (with species extinction and colonization being in balance in the entire landscape) and does not account for the role of patches as stepping stones upholding the capacity of species to expand their ranges and reach a larger amount of habitat resources, as illustrated in Fig. 2.

Despite recent advances in habitat connectivity models in general and in network-based approaches in particular, the current static connectivity models do not explicitly account for the processes of dispersal, colonization of intermediate habitat patches and further dispersal that could, over several generations, expand the species invasion front at large spatial and temporal scales. Thus, the effect that a stepping-stone patch can have in providing a refuge for species reproduction and further long-distance dispersal and range shift is, despite its potentially strong ecological implications, not accounted for by current static habitat network connectivity models. This limitation is a consequence of the large gap existing among different disciplines and particularly between network-based models of connectivity and spatially explicit population models. We here contribute to bridge this gap in connectivity analysis by focusing on novel and improved ways to assess through network models the movement component behind species distributions and their changes in fragmented landscapes.

For this purpose, we formulate a generalized habitat network connectivity model, Gstep (Fig. 1) (G standing for generalized model), that accounts for (i) N_i : the number of individuals or propagules of a species that are available for dispersal in a fully occupied patch i (with \bar{N} being the average N_i value for all of the patches in a network); (ii) k_j : the number of immigrants that need to reach a vacant patch j to allow for species establishment and subsequent population growth up to the carrying capacity of j (referred to as k if assumed constant for all of the patches); (iii) the relative likelihood of long-distance dispersal events, as controlled by a parameter β that decreases for fatter-tailed dispersal kernels; and (iv) the potential role of stepping stones to enhance species dispersal across generations. Species establishment in a stepping-stone patch q would allow for the generation of N_q dispersing offspring that might further expand the species' range by subsequently colonizing other vacant patches. We also formulate Gdirect as a variant of the generalized model that is identical to Gstep except in that Gdirect does not account for the effects of stepping stones, considering only direct fluxes between i and j (no other intermediate patches are used along the dispersal process) (Fig. 1). We compare the Gstep and Gdirect generalized models with the equivalent Sstep and Sdirect standard models currently used in research and conservation, which are particular cases of the generalized models in which $N_i = 1$ and $k_j = 1$ (Fig. 1). We compare these four models by (i) applying them in a simple but illustrative three-patch system and in two real fragmented landscapes in Madagascar and SW

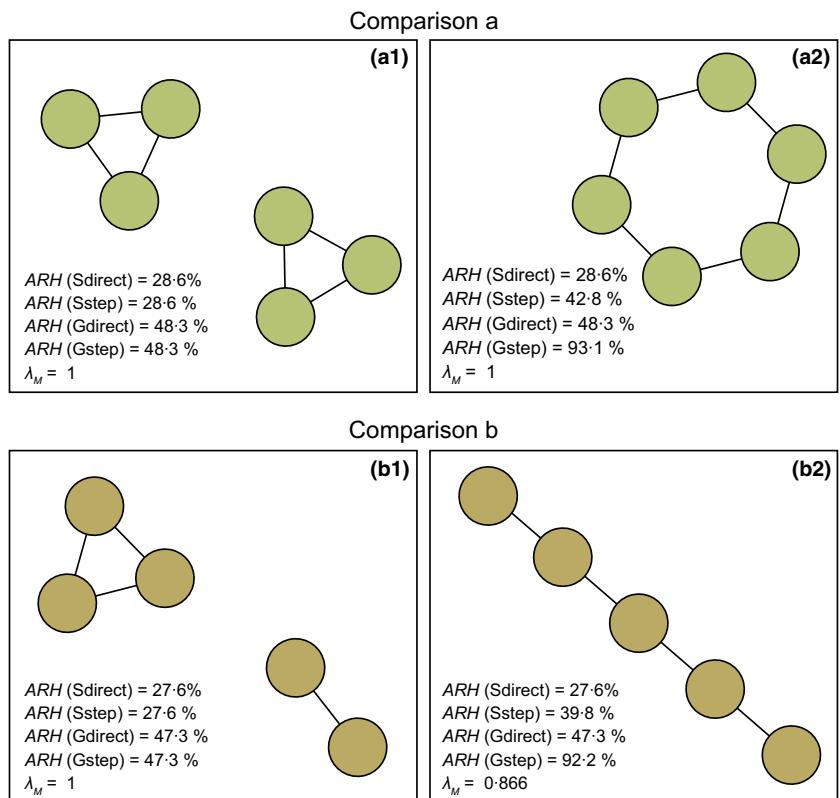


Fig. 2. Two examples of landscape networks with the same number of habitat patches (circles) and number of direct connections (lines) between patches but different spatial arrangement (a1 to be compared with a2, and b1 with b2). Species will be able to reach a larger amount of habitat in landscape a2 than in a1 and in landscape b2 than in b1 due to intermediate stepping stones that provide indirect paths connecting all patches; all patches belong to the same component in a2 and b2, whereas the network is broken in two isolated components in a1 and b1. Direct connectivity models (Sdirect, Gdirect) will, however, indicate that connectivity is the same in each of the two landscapes being compared, whereas Sstep and Gstep models will recognize landscapes a2 and b2 as more connected than a1 and b1, respectively. The metapopulation capacity (λ_M) is the same in landscapes a1 and a2 and smaller in landscape b2 than in b1. The particular values shown for λ_M and for the amount of reachable habitat (ARH) in Sdirect and Sstep correspond to landscapes with $a_i = 1$ for all patches and with all connections (lines) having a probability of direct dispersal of $p_{Sdirect,ij} = 0.5$ and, additionally for the case of Gdirect and Gstep, to $N_i = 10$ and $k_i = 3$ for all patches, but the same above-mentioned conclusions hold for other values of these parameters. $p_{Sdirect,ij} = 0$ for all pairs of patches not directly connected. λ_M was calculated as the leading eigenvalue of a matrix with values $a_i a_j p_{Sdirect,ij}$ as in Hanski & Ovaskainen (2000).

Europe and by (ii) evaluating their performance in explaining the range expansion of the Black Woodpecker in northeast Spain over two decades. We found that current connectivity models largely underestimate the potential of species to move between habitat patches and show that our generalized model Gstep provides novel insights and improved predictions on the role and importance of stepping stones in fragmented landscapes that should be valuable for guiding conservation planning over wide spatial or temporal scales.

Materials and methods

CONNECTIVITY MODELS: INTERPATCH DISPERSAL PROBABILITIES AND NETWORK ANALYSIS

Dispersal kernels

We used the exponential power distribution (Clark *et al.* 1998) to generate kernels with any tail fatness as controlled by β . $\beta = 1$ gives

a negative exponential; fatter tails are obtained by decreasing $\beta < 1$. Details and equations are provided in Appendix S1, Supporting information. Dispersal probabilities as a function of the distance between patches i and j (d_{ij}) were given in Sdirect ($p_{ij} = p_{Sdirect,ij}$) directly by the dispersal kernel, whereas dispersal probabilities were modified by accounting for N_i and k_j in the generalized models and for stepping stones in Sstep and Gstep, as explained below.

Accounting for N_i and k_j in the generalized models

In Gdirect, we assessed the probability that at least k_j of the N_i dispersing individuals in a source patch i were able to directly reach destination patch j ($p_{ij} = p_{Gdirect,ij}$) using a binomial distribution with the probability of a single individual dispersal success given by $p_{Sdirect,ij}$:

$$P_{Gdirect,ij} = 1 - \sum_{m=0}^{m=k_j-1} \binom{N_i}{m} p_{Sdirect,ij}^m (1 - p_{Sdirect,ij})^{N_i-m}$$

when $N_i = 1$ and $k_j = 1$, then $p_{Gdirect,ij} = p_{Sdirect,ij}$. If $d_{ij} = d_{ji}$, then $p_{Sdirect,ij} = p_{Sdirect,ji}$, but even in this case, $p_{Gdirect,ij} \neq p_{Gdirect,ji}$ as

long as $N_i \neq N_j$ and/or $k_i \neq k_j$, leading to asymmetric or directed flows in the generalized model.

Accounting for stepping stones in the standard and generalized models

We built a network in which the nodes corresponded to habitat patches weighted by an attribute a_i representing the amount of habitat resources in patch i (typically accounting for habitat area and/or quality). Links (edges) were weighted by $p_{Sdirect,ij}$ in the standard model and by $p_{Gdirect,ij}$ in the generalized model. We used network analysis to calculate p_{ij} as the maximum product probability of all the possible paths between source and destination patches (Saura & Pascual-Hortal 2007; Saura & Rubio 2010). This term included the possibility of using intermediate habitat patches and gave $p_{ij} = p_{Sstep,ij}$ for Sstep and $p_{ij} = p_{Gstep,ij}$ for Gstep, with $p_{Sstep,ij} \geq p_{Sdirect,ij}$ and $p_{Gstep,ij} \geq p_{Gdirect,ij}$. In the standard model, $p_{Sstep,ij} > p_{Sdirect,ij}$ when intermediate patches reduce the distance that needs to be traversed through non-habitat areas (Bodin & Saura 2010). In the generalized model, $p_{Gstep,ij}$ could also be increased compared to $p_{Gdirect,ij}$ as a result of the presence of intermediate patches in which $N_i \geq k_i$. The paths with the maximum product probability will be in general different in Sstep and Gstep, as the latter model accounts not only for the distance between each pair of patches but also for the N_i and k_i values in each of the intermediate patches along the path.

BLACK WOODPECKER RANGE EXPANSION DATA AND ANALYSES

Black Woodpecker range expansion data

We analysed data on Black Woodpecker range expansion in response to afforestation and forest maturation between 1980 and 2000 in the region of Catalonia (northeast Spain) as derived from field surveys in the Catalan Breeding Bird Atlases (Estrada *et al.* 2004) and further analysed by Gil-Tena, Brotons & Saura (2009, 2010). These data were available at a resolution of 10×10 km cells, which were considered as the patches (nodes) for the analysis, and showed that the species had more than doubled its range during that period (Fig. 3a). To ensure that real distribution changes were not masked by a different intensity of the field surveys on the two dates, we only analysed the 309 cells in which the variation in sampling effort between the atlases was available (Fig. 3a).

Connectivity model parameters for the Black Woodpecker

We considered the species' mean natal dispersal distance (average of unpaired males and females) of 16.25 km (Christensen 2002) and calculated the Euclidean distance between cell centroids. The species' population size in Catalonia was estimated at 867 individuals in 2000 from atlas field surveys, which concurs with the estimates derived by considering the species' home range, as further described in Appendix S2 (Supporting information). A surrogate for species habitat suitability in each cell was derived from niche-based modelling (Estrada *et al.* 2004) and was used to account for the possibility that colonization occurred in the cells

with the best habitat quality regardless of connectivity and to distribute population size in each cell proportional to the cell's habitat suitability (a_i). The number of dispersing individuals (N_i) in the analysed period was made proportional to the population size in each cell. Available estimates on juvenile and adult survival rates, nest success rate and fledgling success for this species, yielded $\bar{N} = 116.3$ (Appendix S2, Supporting information). Survival rates made $k = 6$ necessary in order to allow for the establishment of at least one pair of immigrants in the colonized areas after accounting for mortality in their first year as juveniles and during their whole first year as adults raising their offspring. In the absence of information on the dispersal kernel tail fatness for this species, we used the standard negative exponential function ($\beta = 1$). However, a range of other plausible values for β and the other model parameters were considered to evaluate the robustness of the results (Appendix S3, Supporting information). In Gdirect, the dispersal fluxes to initially vacant sites (where the species was absent in 1980) could only have come from the cells where the species was present in 1980, whereas Gstep additionally accounted for the possibility that initially vacant sites could act as stepping stones producing new immigrants as the sites were colonized along the twenty-year period.

Statistical models of Black Woodpecker colonizations

We built generalized linear models with a binomial error distribution in which the response variable was species colonization or absence in 2000 in those cells where the species was not already present in 1980 ($n = 276$). Three predictors of species colonization patterns were standardized to zero means and unit variances and considered in generalized linear models: variation in sampling effort [log transformed as in related studies by Gil-Tena, Brotons & Saura (2009, 2010)], species habitat suitability and the amount of incoming dispersal flux as estimated by each connectivity model. The estimated amount of incoming dispersal flux in a given focal (initially vacant) cell j was calculated as the sum of all of the p_{ij} values in which i corresponded to the source (initially occupied) cells. To avoid potential multicollinearity problems, we checked that there were not strong correlations (Spearman's rho < 0.8) among the predictors and that variance inflation factors were always below 2.5. Spatial autocorrelation in model residuals was checked using Moran's I coefficients at 17 distance classes with a spatial lag of 15 km (encompassing up to eight immediate neighbour cells). The significance of the autocorrelation coefficients was assessed through 999 randomizations.

LANDSCAPE-LEVEL CONNECTIVITY ANALYSIS: HABITAT NETWORKS AND THE AMOUNT OF REACHABLE HABITAT

In order to compare the overall landscape-level connectivity as assessed by the different connectivity models for different species traits, rather than focusing on the dispersal probabilities between predefined pairs of patches (as above), we analysed the expected amount of reachable habitat (hereafter *ARH*) in two real-world habitat networks. These networks were the subject of recent connectivity studies and correspond to different spatial configurations and ways of measuring the distance between habitat patches, as described in the following section.

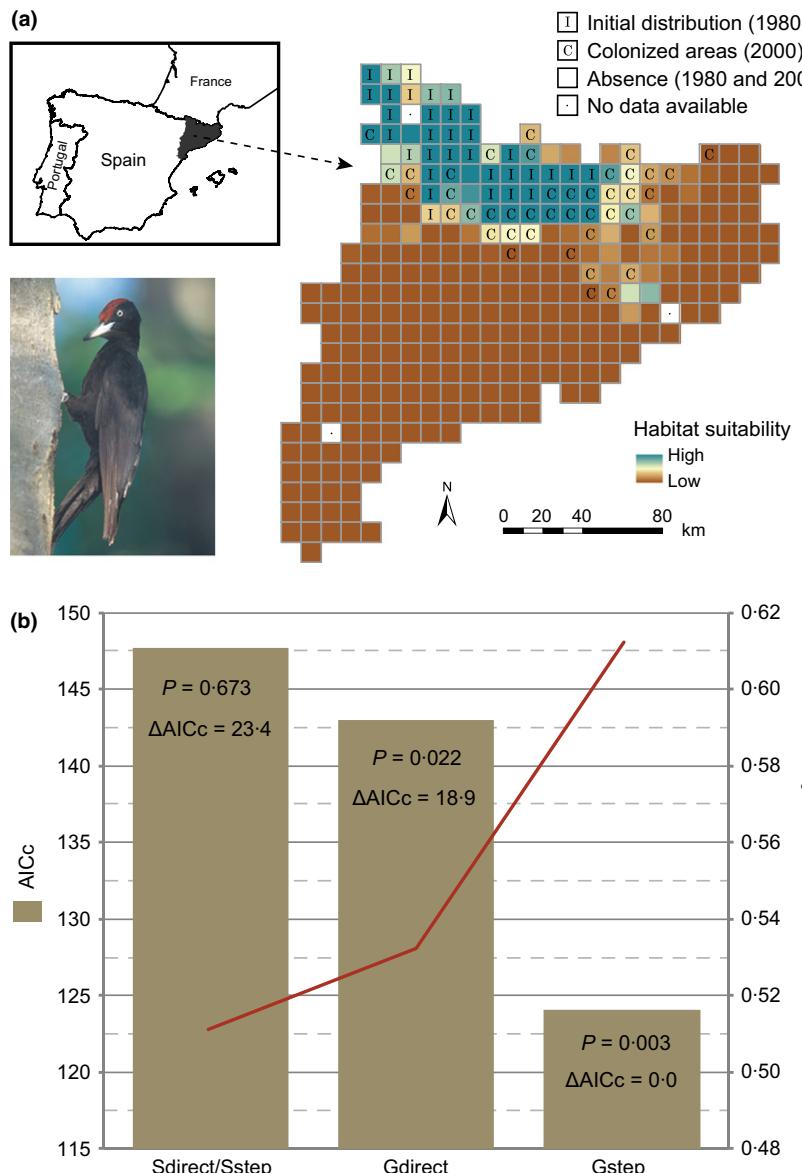


Fig. 3. Black Woodpecker range expansion and the performance of the different connectivity models: (a) species distribution data (10 x 10 km cells) in 1980 and 2000 in the region of Catalonia and (b) results of the generalized linear models that evaluated the capacity of each connectivity model to explain observed colonization patterns, as given by Akaike Information Criterion corrected for small samples (ΔAIC_c), the difference in AIC_c with respect to the most supported model (ΔAIC_c), Nagelkerke R^2 and the statistical significance of the amount of dispersal flux estimated by each connectivity model (P). $\Delta\text{AIC}_c < 2$ suggests substantial evidence for the competing models, while $\Delta\text{AIC}_c > 10$ indicates no statistical support. Sdirect and Sstep provide here the same results due to habitat cell adjacency. Woodpecker photograph: Jordi Bas.

Analysed habitat networks

We considered a network of 203 forest patches (nodes) in the region of Androy in southern Madagascar (Bodin *et al.* 2006; Bodin & Saura 2010) (Fig. 5a) and a transnational network of 176 protected forest areas (hereafter patches) in SW Europe ranging from the Cantabrian Range to the Western Alps (Gurrutxaga, Rubio & Saura 2011) (Fig. S1, Supporting information). In both networks, we used forest habitat area in the patch as the node weight a_i , assumed N_i in each patch to be proportional to a_i and calculated the distance between patch edges to derive the p_{ij} values in each connectivity model. The distance between patches was calculated in the Madagascar network as a Euclidean distance and in the transnational network as an effective distance corresponding to the accumulated cost in the least cost path through a friction surface parameterized to represent the resistance of the landscape matrix to the movement of forest mammal species (Fig. S1, Supporting information).

Amount of reachable habitat (ARH)

In all of the connectivity models, we calculated ARH as the expected percentage of the total habitat area in the network that could be reached by a source population located randomly in a single patch within the habitat distribution (Appendix S4, Supporting information). ARH was given by an adapted version of the probability of connectivity metric (Saura & Pascual-Hortal 2007) scaled as the related equivalent connectivity metric (Saura *et al.* 2011), as further described in Appendix S4 (Supporting information). ARH ranges from 0 ($p_{ij} = 0$ for every pair of patches when $i \neq j$) to 100% ($p_{ij} = 1$ for every pair of patches; that is, all habitat patches in the network are fully accessible for the species) and accounts for the amount of habitat resources (a_i) in each of the patches that the species could reach through dispersal. We also calculated the percentage of the total habitat resources in the landscape that could be reached exclusively due to the role of stepping stones (ARH_{ss}), rather than to the amount of habitat available within the source patches (intrapatch

connectivity) or to that reachable via the direct connections to other patches (without accounting for stepping stones), as further described in Appendix S5 (Supporting information). ARH_{ss} quantifies the impact that the loss of stepping-stone patches would have for connectivity, calculated as the difference in ARH between Gstep and Gdirect for the generalized models and between Sstep and Sdirect for the standard models (Appendix S5, Supporting information).

Results

LONG-DISTANCE DISPERSAL AND HABITAT NETWORK CONNECTIVITY

Long-distance dispersal events that were rare in the standard models ($p_{ij} < 0.01$) were predicted to be very likely ($p_{ij} \approx 1$) in the generalized models, particularly in Gstep (Fig. 4a). Increasing N_i (i.e. larger population size) or decreasing k_j (i.e. assuming that a relatively small proportion of the species population in the source patch has to reach another patch in order to establish a new foothold for further range expansion) translated into higher p_{ij} and

ARH in Gdirect and particularly in Gstep (Figs 4a,b, 5b,c and S2, Supporting information). When k_j was high compared to N_i , p_{ij} could be even lower in the generalized than in the standard models (Fig. 4b). Kernels with fatter tails (lower β) had a very modest effect on the results of the standard models, but largely increased connectivity in the generalized models; even using fat-tailed kernels, Gstep provided much higher chances of dispersal than Gdirect (Figs 4c, 5c and S2b, Supporting information). Interestingly, we found critical spatial thresholds in the generalized models, that is, sharp decreases in p_{ij} as a function of the distance between the source and destination patches, particularly for higher k (Fig. 4).

The benefits of stepping stones for increasing dispersal probabilities (p_{ij}) and ARH were drastically more prominent in the generalized than in the standard network models (Figs 4–6 and S2–S3, Supporting information). Unlike in Sstep, in Gstep, stepping stones had a crucial and dominant role in determining the total amount of habitat that species could reach; if stepping-stone patches were removed from the landscape, most of the ability of species

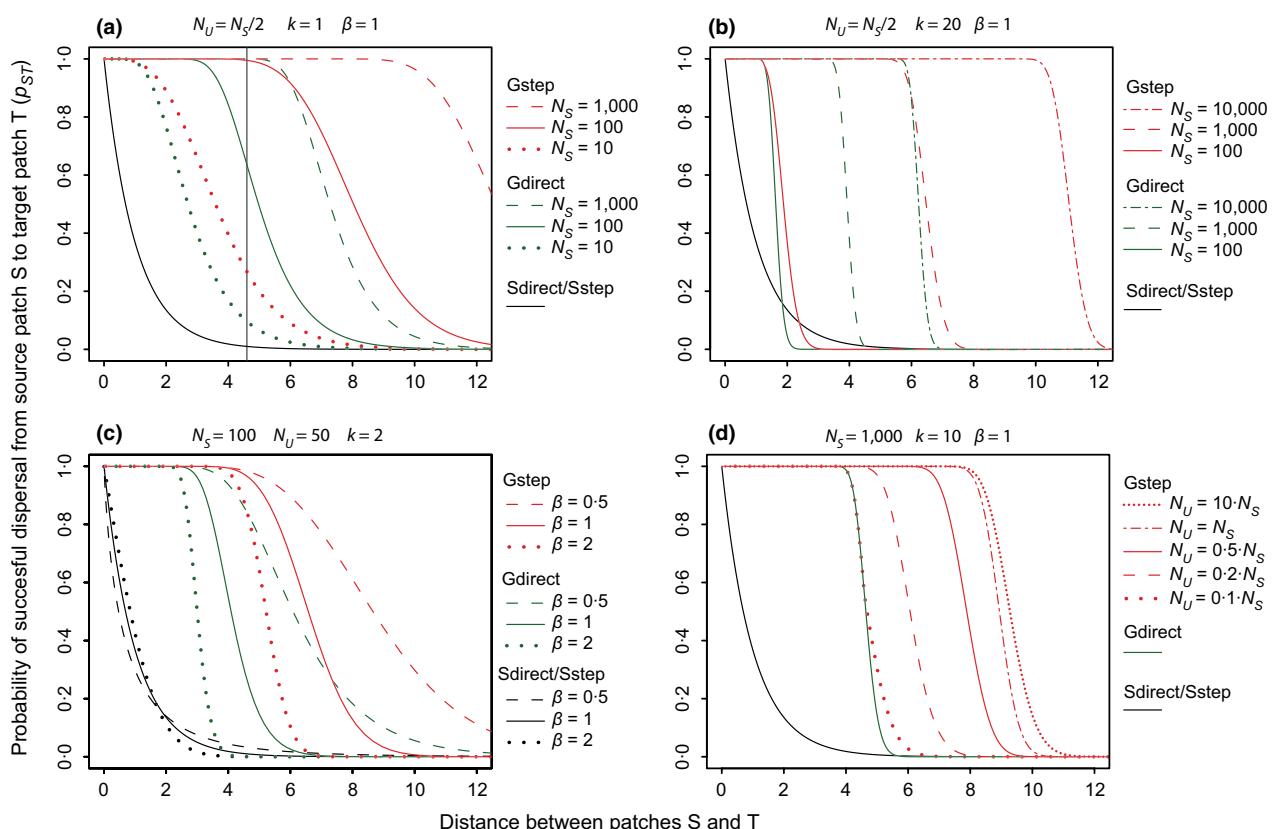


Fig. 4. Probability of successful dispersal in the three-patch system (Fig. 1) as assessed by the different connectivity models for different combinations of the model parameters (a–d). The y-axes give the probability of successful dispersal and establishment from source patch S to destination patch T (p_{ST}). The x-axes give the number of times that the distance between patches S and T (d_{ST}) exceeds the species' mean dispersal distance. The impact of losing stepping stone U corresponds to the difference in p_{ST} between Gstep (red lines) and Gdirect (green lines) for the same values of the model parameters. Here we assume that $k = k_U = k_T$. We also assume that $d_{SU} = d_{UT}$ and $d_{ST} = d_{SU} + d_{UT}$. This means that the size of U is considered negligible compared to d_{ST} , which implies that Sdirect and Sstep give the same results (the differences between Sdirect and Sstep in real-world habitat networks are shown in Figs 5 and S2, Supporting information). The vertical grey line in (a) indicates the distance beyond which only rare long-distance dispersal would occur according to the standard model ($p_{ij} < 0.01$ for $\beta = 1$ in Sdirect).

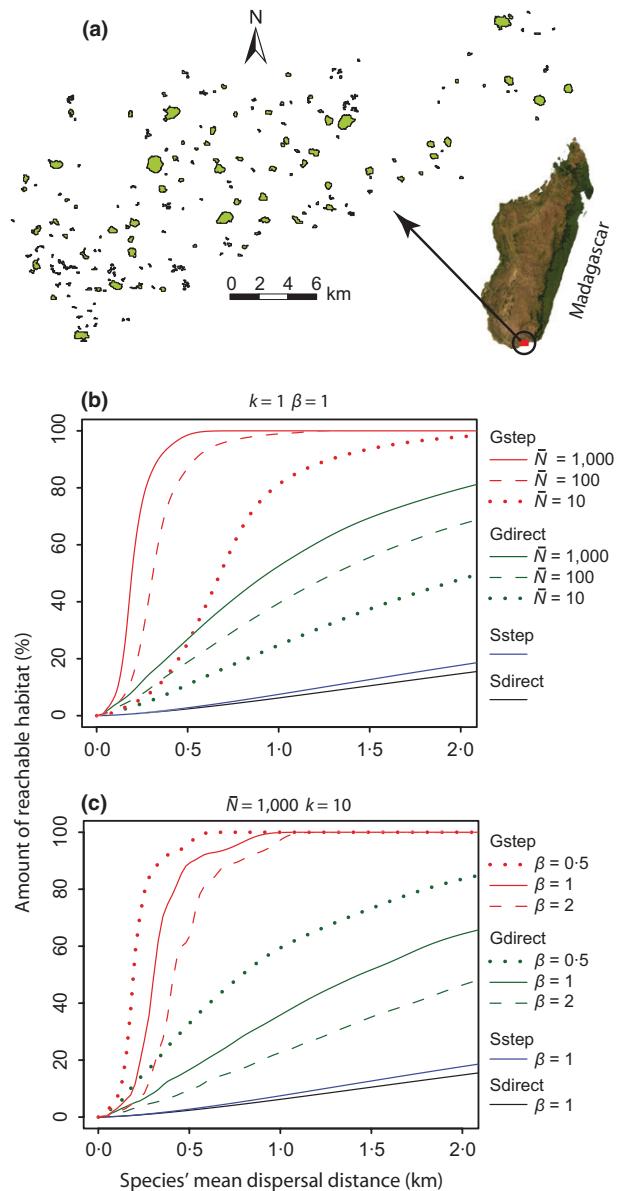


Fig. 5. Amount of reachable habitat (ARH) in the Madagascar network: (a) set of forest habitat patches in the region of Androy, southern Madagascar, (b–c) ARH (y-axis) as a function of species' mean dispersal distance (x-axis) for different connectivity models and parameter values. In (c), the curves for the standard models and $\beta \neq 1$ are indistinguishable from those for $\beta = 1$ at the plot scale; only the curves for $\beta = 1$ are shown.

to reach habitat resources further apart would be lost (for large N_i), as quantified by ARH_{ss} . For smaller \bar{N} or larger k , the maximum ARH_{ss} value decreased mildly and was found at larger dispersal distances (Figs 6 and S3, Supporting information). Results were similar in the Madagascar and transnational networks (see Appendix S6, Supporting information, for a description of small differences).

Stepping stones with scarce or poor habitat resources (low N_i) were, however, basically useless in promoting long-distance dispersal, with Gstep converging with Gdirect (Fig. 4d). A larger amount of habitat resources (N_i

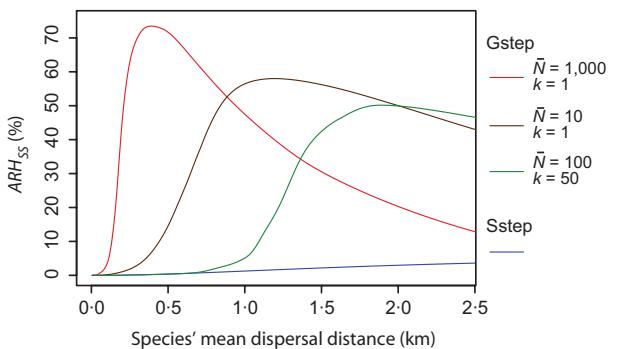


Fig. 6. Percentage of the total amount of habitat in the Madagascar network that species can reach using stepping stones (ARH_{ss}) as a function of species' mean dispersal distance in the generalized connectivity model Gstep (for different \bar{N} and k values) and the standard model Sstep. $\beta = 1$ in all cases.

in the stepping stones increased p_{ij} and the distances that could be traversed in the network, but such benefits diminished as N_i in the stepping stones became equal or higher than that in the source patches (Fig. 4d).

In the generalized models, the presence of stepping stones could be much more beneficial for species with modest average dispersal abilities, but large population sizes (\bar{N} , number of dispersing individuals) than for more mobile species with smaller population sizes, allowing the former species to reach much larger distances and amount of habitat resources than the latter, particularly for fat-tailed kernels (Figs 7 and S4, Supporting information). Compensation between species' mean dispersal distance and population size was much more prominent in Gstep than in Gdirect (Figs 7 and S4, Supporting information). Such compensation was not possible in the standard models as, by definition, they do not account for \bar{N} ; the differences in ARH for the two species in Fig. 7 were small, negative (i.e. higher ARH for the species with larger mean dispersal distance) and very similar in Sdirect (-0.734%) and Sstep (-0.892%).

WOODPECKER RANGE EXPANSION

Gstep was the only statistically supported model in explaining the observed colonization patterns (Fig. 3b; Table S1, Supporting information). The dispersal flux estimated by the standard connectivity models was a non-significant factor. The direct flux between the source and colonized areas accounting for the number of dispersers (Gdirect) was significant, but only slightly improved the standard models, whereas Gdirect performed drastically worse than Gstep for all considered parameter values, including fat-tailed kernels (Fig. 3b; Tables S1–S5, Supporting information). Sstep/Sdirect and Gdirect models presented significant spatial autocorrelation in the model residuals in almost half of the distance classes (Table S1, Supporting information). Autocorrelation in the model residuals was, however, non-significant ($P > 0.05$) in all of

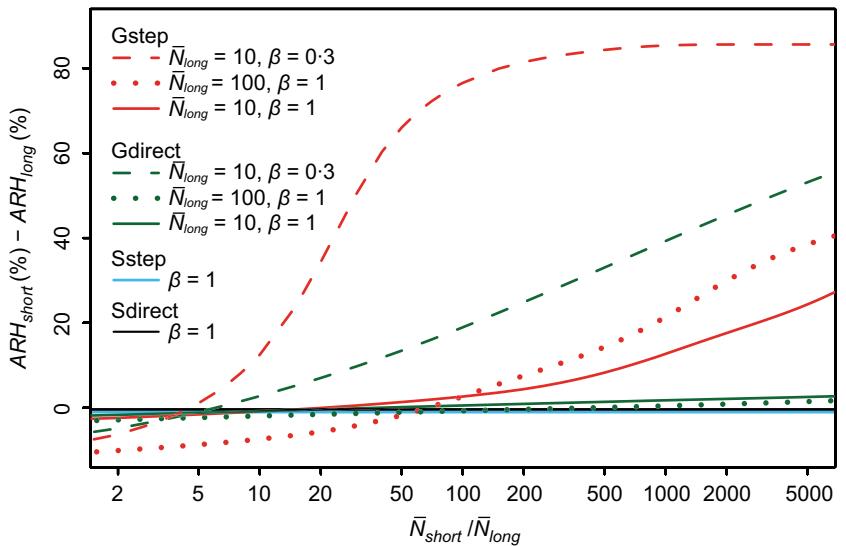


Fig. 7. Difference in the amount of reachable habitat (ARH) for two species (*short* and *long*) with different mean dispersal distance and population size in the Madagascar network. Both species have $k = 1$, but differ in their mean dispersal distance (100 m for species *short*, 200 m for species *long*) and number of dispersing individuals ($\bar{N}_{short} > \bar{N}_{long}$). The plot gives the difference in ARH for these two species ($ARH_{short} - ARH_{long}$) as a function of the ratio between their number of dispersing individuals ($(\bar{N}_{short}/\bar{N}_{long})$) for the different connectivity models and two β values (kernel tail fatness). At the plot scale, the lines for the standard models Sdirect and Sstep when $\beta = 1$ almost overlap and are hardly distinguishable from those for the standard models when $\beta = 0.3$; only the lines for $\beta = 1$ are shown. Note that the x -axis is in logarithmic scale.

the distance classes when the flux was estimated using the Gstep model (Table S1, Supporting information).

Discussion

TEMPORAL SCALES AND APPLICABILITY OF THE CONNECTIVITY MODELS

Standard connectivity models (Sdirect, Sstep) are built such that they focus on the fate of a single average disperser during its life span. Therefore, these models are suited to identifying those pathways that carry a large number of dispersers in the short term and the related patterns of species occurrence and abundance (Bodin & Saura 2010; Awade, Boscolo & Metzger 2012). However, the standard models seriously underestimate the likelihood and importance of long-distance fluxes and the key role of intermediate patches in sustaining rare but crucial dispersal events that allow expanding the species ranges across generations. In the Sstep model, the importance of stepping-stone patches is only given by the degree to which they shorten the distance that species need to traverse through the matrix (non-habitat areas) when moving between source and destination patches. If, however, the distances to be traversed are much larger than the size of stepping-stone patches, as it is likely to be the case when dealing with wide spatial and temporal scales, these patches will be inevitably considered as of little importance by Sstep, which completely disregards the possibilities for population spread that encompass multiple generations and reproduction in intermediate habitat patches.

This analytical finding was corroborated by empirical data on Black Woodpecker range expansion during a 20-year period in northeast Spain (Fig. 3). The Gstep model largely outperformed all the other analysed connectivity models according to all the statistics considered. In addition, the significant spatial autocorrelation in model residuals found for Sstep/Sdirect and Gdirect indicates that these models are unreliable because a relevant spatially dependent predictor has not been accounted for or because the species spatial distribution pattern has remaining and unaccounted for autocorrelation due to biotic processes (Melles *et al.* 2011), which was not the case for Gstep. This result provides additional support for the improved performance and credibility of the Gstep model. Hence, a progressive population spread facilitated by stepping stones, and implicitly accounted for by species reproduction in the intermediate patches in the network, was the most realistic and best supported process.

STEPPING STONES UPHELD LONG-DISTANCE DISPERSAL AND RANGE EXPANSION

Previously reported key factors behind long-distance dispersal, that is, the fatness of the dispersal kernel tail and the number of dispersers (Clark *et al.* 1998; Nathan 2006), only showed up fully or were much amplified in the presence of a network of patches efficiently acting as connectivity providers due to their size and spatial arrangement. Increasing population size (increasing N_i) or the tail fatness of the dispersal kernel could by themselves (Gdirect model) considerably increase the maximum distances at which species were likely to disperse, but only at

shorter ranges than those made possible by stepping stones (Gstep model), which upheld habitat reachability further beyond (Figs 4a–c, 5b,c and S2, Supporting information). The impacts of the loss of stepping stones could hardly be compensated by simply increasing the habitat resources (habitat amount and/or quality) and population sizes in the source patches or the fatness of the dispersal kernel tail, the latter not being able to explain Black Woodpecker range expansion without explicitly accounting for stepping stones (Table S5, Supporting information). These results illustrate the importance of integrating concepts and analytical approaches from different disciplines (e.g. network theory and long-distance dispersal models) to develop a more holistic view and improved understanding of all the factors determining functional connectivity in heterogeneous landscapes.

THE FULL VALUE OF STEPPING STONES COMES WITH TIME

The outcomes of the analysed connectivity models imply that the conservation value of stepping stones comes with time, across generations, as colonizers reproduce in newly accessed distant patches and enable their offspring to reach other available habitat resources that are further apart. There will be a lag or delayed response (the so-called immigration credits) (Jackson & Sax 2010) in the benefits provided by conserving or restoring a scattered mosaic of habitat fragments over large areas, the implementation cost of which will only be paid off over long temporal scales. Conversely, the currently observed species declines may be the result of past landscape intensification and homogenization that seriously impacted the connectivity of habitat networks. Despite these temporal lags, the signal of stepping stones in determining key ecological processes is already detectable over the time-scale of a few decades, as shown here in the case of the Black Woodpecker or, more broadly, as suggested by recent studies concluding that biodiversity losses in tropical protected areas during the last 20–30 years have been strongly determined by changes outside reserves such as deforestation (Laurance *et al.* 2012), which may include the loss of stepping-stone patches that uphold connectivity with other habitat areas.

SMALL OR LOW-QUALITY STEPPING STONES ARE OF LITTLE VALUE

Our results stress that stepping stones must be of sufficient size and/or quality to be of conservation value, which is further supported by Kramer-Schadt *et al.* (2011), who concluded that stepping stones that are too small can even distract dispersers from colonizing more suitable habitat patches. Our findings, and the Gstep model from which they derive, reduce the reported discrepancy between population models and previous network models when assessing the conservation value of individual habitat patches as noted by Moilanen (2011).

The Gstep model corrects the tendency of some of these previous network models of spuriously overstating the actual importance for connectivity of arbitrarily small stepping-stone patches (Moilanen 2011), while explicitly accounts for the role of these connecting elements to uphold dispersal fluxes and related species range shifts.

HABITAT NETWORKS AS SPATIAL FILTERS

Our findings imply that stepping stones are particularly crucial and beneficial for those processes that depend on the capacity of just a small portion of a large population to disperse over long distances and establish a new local population in the colonized patches ($k_j \ll N_i$), such as the spread of species (either native or invasive) or genotypes that are able to efficiently out-compete other taxa or conspecifics and of *r*-selected species with the capacity to produce more offspring. This means that stepping stones can allow modest movement abilities (species mean dispersal distance) to be compensated by high competitive abilities and establishment success rates (low k_j) and by large population sizes (high N_i) (Figs 7 and S4, Supporting information). Habitat network connectivity (or the lack of it) can therefore impose a spatial filter on dispersal by comparatively favouring the range shifts of species with certain life-history traits and can modulate potential long-term changes in community composition. When considering only one individual of different species (as in the standard models), there will be only one possible filtering factor: the species with the largest mean dispersal distance will always reach a larger amount of habitat resources. However, when considering populations of different species (as in the generalized models), other species-specific factors such as N_i or k_j may have a large effect in the actual (realized) connectivity between habitat areas.

LANDSCAPE INTENSIFICATION AND CRITICAL SPATIAL THRESHOLDS

Critical spatial thresholds emerged even when continuously decreasing dispersal kernels were used in the generalized analysis (both in Gstep and Gdirect). These thresholds will impose abrupt declines in the likelihood of dispersal success beyond a certain distance, which will be considerably shortened in the lack of stepping stones (Fig. 4) as may result from increased landscape intensification and homogenization. This finding may be related with the conclusion that the characteristics of intermediate areas between patches have a strong effect on species' occupancy patterns across many taxonomic groups and ecosystems world-wide (Prugh *et al.* 2008). In addition, it provides some justification for the use of a sharp distance threshold to define connections between patches, as long as the focus is on long-distance and long-term processes such as species range shifts and/or genetic transmission across generations. This could explain why Neel (2008) found a higher correlation of connectivity metrics with

genetic diversity when using a distance threshold than when using a standard negative exponential dispersal kernel to define connections between patches.

CONCLUSIONS

Insights about the pivotal role of stepping stones in species movement through inhospitable landscapes were made possible by a generalized but still tractable and static network connectivity model (Gstep) that focuses on the potential, long-term implications of a given habitat network connectivity and its modifications. Even though one of our aims was to develop a relatively simple model that would lower the barrier for deployment in practice, further complexity could be easily incorporated into the model (e.g. by accounting for random walk processes using multiple pathways or for demographic stochasticity and extinction events). However, its present formulation already provides substantial novel insights and improved predictions in comparison with previous connectivity models. The analytical approach of Gstep and the estimated dispersal probabilities that it provides can benefit and be readily incorporated within broader models such as those accounting for the future distributions of suitable habitats resulting from climate warming scenarios (e.g. Maiorano *et al.* 2011).

Our results highlight the need to (i) reassess the capacity of species to adapt to climate and landscape change through rare but crucial long-distance movements facilitated by habitat networks, which may have been largely underestimated by current connectivity models, to (ii) acknowledge the key role of sufficiently large stepping stones on the ability of species to successfully colonize newly available habitats and transmit better-adapted traits to subsequent generations and to (iii) ensure a durable protection for the mosaics of suitable patches scattered in the intermediate landscapes to allow for species movements between reserves. Stepping-stone networks can play a crucial role for species persistence at wide spatial and temporal scales by alleviating the isolation of large habitat blocks embedded in increasingly modified landscapes, which is a major concern in modern conservation biology.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Appendix S1. Details on the dispersal kernels.

Appendix S2. Details on Black Woodpecker population size and N_i values in the generalized connectivity models.

Appendix S3. Results for other plausible connectivity model parameters for the Black Woodpecker.

Appendix S4. Details on the calculation of the amount of reachable habitat.

Appendix S5. Partitioning the amount of reachable habitat in the landscape.

Appendix S6. Results for the transnational network of protected areas.

Fig. S1. Transnational network of protected areas in SW Europe.

Fig. S2. Amount of reachable habitat in the transnational protected area network.

Fig. S3. Percentage of the total amount of habitat in the transnational protected area network that species can reach by using stepping stones.

Fig. S4. Difference in the amount of reachable habitat for two species with different mean dispersal distance and population size in the transnational protected area network.

Table S1. Fitted generalized linear models explaining the Black Woodpecker colonization patterns.

Table S2. Results of the generalized linear models explaining the Black Woodpecker range expansion for other plausible values of the species' mean natal dispersal distance.

Table S3. Results of the generalized linear models explaining the Black Woodpecker range expansion for other plausible values of \bar{N} .

Table S4. Results of the generalized linear models explaining the Black Woodpecker range expansion for other plausible values of k .

Table S5. Results of the generalized linear models explaining the Black Woodpecker range expansion for other plausible values of β .