# QUANTIFYING DISPERSAL PATHS IN PROBABILISTIC HABITAT NETWORKS: A REPLY TO HOCK AND MUMBY (2015) AND AN OVERVIEW OF RECENT DEVELOPMENTS AND APPLICATIONS

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## 1. Network reliability, maximum product probability paths and the probability of connectivity metric

Hock and Mumby (2015) describe an approach to quantify dispersal probabilities along paths in networks of habitat patches. This approach basically consists in determining the most probable (most reliable) path for movement between habitat patches by calculating the product of the dispersal probabilities in each link (step) along the paths in the network. Although the paper by Hock and Mumby (2015) has value and includes interesting analyses (see comments in section 7 below), the approach they describe is not new. Jordán (2000) presented explorations of reliability methods for assessing probabilities of species migrations and corridor designs in some illustrative habitat networks. Saura and Pascual-Hortal (2007) described an approach for analysing connectivity in probabilistic habitat networks through the probability of connectivity (PC) metric that was widely applied and developed after (see sections below). PC combines the attributes of the patches (e.g. habitat area or quality) with the maximum product probability paths for movement between patches. The approach of using the most reliable paths described by Hock and Mumby (2015) is the same as the maximum product probability paths in Saura and Pascual-Hortal (2007). The product probability along a path (product of the dispersal probabilities in each link in the path) as defined by Saura and Pascual-Hortal (2007) is the same as the reliability of the path, rel(p), in Hock and Mumby (2015). The maximum product probability in Saura and Pascual-Hortal (2007) is the same as rel(MRP) in Hock and Mumby (2015). Bode et al. (2008) also used the maximum product probability paths or most reliable paths, which were called the strongest connections (paths) in that paper.

## 2. A widely used approach implemented in a free software package

The maximum product probability paths (most reliable paths) and the PC metric were implemented in the Conefor software package (Saura and Torné 2009), a free and open source software available at www.conefor.org. The first version of Conefor was released in 2007, already including the maximum product probabilities and the PC metric (Saura and Pascual-Hortal 2007b), and has been regularly updated since then. The last version was published at www.conefor.org in September 2014. This version includes both a graphical user interface (easier to apply for most users) and a more powerful command line interface that allows for automation via scripting and batch processing of multiple probabilistic (stochastic) networks.

The maximum product probability paths and the PC metric have been widely used since 2007 in a large variety of studies on the connectivity of habitat networks (see section 3 below). A list of published studies using the maximum product probability paths and PC through Conefor can be found amongst those listed at http://www.conefor.org/applications.html

The implementation of the maximum product probability paths (most reliable paths) in Conefor (in 2007 and in subsequent versions) applies the Dijkstra's algorithm to a negative logarithmic transformation of the link probabilities. This is the same as the calculation procedure described in Hock and Mumby (2015); i.e. finding the maximum product probability paths (and calculating PC) is equivalent to using the classical additive network search algorithms to find the path with the minimum sum of the weights in the log-transformed network. The source codes of Conefor in C++, with this implementation included, are freely available since 2009 under a GNU license (GPLv2) at www.conefor.org or directly at http://sourceforge.net/projects/conefor/

**3. Using the probability of connectivity and the maximum product probability paths to support management and conservation**

The maximum product probability paths (most reliable paths) in the probability of connectivity (PC) metric have been used in a large number and variety of applications, such as the following:

- Identifying the habitat patches or links that are critical for connectivity, generally based on path or link removal procedures followed by an evaluation of the disruption of the dispersal pathways (Saura and Pascual-Hortal 2007, Bodin and Saura 2010, Laita et al. 2011, Saura et al. 2011b, Carranza et al. 2012, Rubio et al. 2012, Szabó et al. 2012, Ziólkowska et al. 2012, Blázquez-Cabrera et al. 2014, Zhao et al. 2014, Merken et al. 2015, Giannini et al. 2015, Rubio et al. 2015).
- Quantifying the connectivity of protected area networks (Gurrutxaga et al. 2011, Estreguil et al. 2013, Fajardo et al. 2014, Mazaris et al. 2013, Maiorano et al. 2015).
- Evaluating the barrier effect of transport infrastructure and identifying priority locations for fauna passages (Fu et al. 2010, Gurrutxaga et al. 2011, Gurrutxaga and Saura 2014, Loro et al. 2015).
- Assessing the impacts of habitat types and landscape matrix on species distributions, movements, space use or population dynamics (Cheveau et al. 2013, Harris et al. 2014, Saura et al. 2014, Pérez-Hernández et al. 2015).
- Evaluating the effects of connectivity on gene flow and population genetic structure (Neel 2008, Aavik et al. 2014).
- Assessing the impacts of landscape changes on connectivity and monitoring landscape dynamics (Mitsova et al. 2011, Rippa et al. 2011, Saura et al. 2011, Rubio et al. 2012, Khalyani and Mayer 2013, Martín-Martín et al. 2013, Vergara et al. 2013, Liu et al. 2014, Nogués and Cabarga-Varona 2014).
- Planning for restoration of habitats and landscapes (Tambosi et al. 2014, Tambosi and Metzger 2014, Giannini et al. 2015, Rappaport et al. 2015).
- Evaluating the role of landscape connectivity on species distribution, community composition and colonization patterns (Pereira et al. 2011, Awade et al. 2012, Zozaya et al. 2012, Zozaya et al. 2012b, Gil-Tena et al. 2013, Gil-Tena et al. 2013b, Saura et al. 2014, Rodríguez-Pérez et al. 2014, Fernandes et al. 2015).
- Quantifying habitat connectivity and availability (amount of reachable habitat) as a function of dispersal abilities, scale and/or habitat configuration parameters (Pascual-Hortal and Saura 2007, Laita et al. 2011, Perotto-Baldivieso et al. 2011, Rubio and Saura 2012, Crouzeilles et al. 2014, Ernst 2014, Ernst 2014b).
- Quantifying the impacts of sea-level rise and drought scenarios on network connectivity and species conservation status (O'Farrill et al. 2014, Zhang and Gorelick 2014).
- Forest harvesting and zoning (Neto et al. 2013).
- Urban planning (Tannier et al. 2012, Xun et al. 2014, Frazier and Bagchi-Sen 2015).
- Evaluating the effectiveness of conservation strategies (Trainor et al. 2013).

These applications of the maximum product probability paths (MPP) and of the PC metric include a variety of network types and management contexts, showing the versatility of MPP and PC for network analysis. Different types of nodes have been used, such as habitat patches (e.g. Neel 2008, Pereira et al. 2011, Awade et al. 2012), protected areas (e.g. Gurrutxaga et al. 2011, Mazaris et al. 2013, Maiorano et al. 2015), sets of nearby patches (e.g. Rubio et al. 2012, Blázquez-Cabrera et al. 2014), individual cells as resulting from raster-based habitat suitability models (e.g. Saura and Pascual-Hortal 2007), landscape units (e.g. Khalyani and Mayer 2013, Tambosi and Metzger 2014), animal territories (Trainor et al. 2013), forest stands (Neto et al. 2013) or individual trees (e.g. Rodríguez-Pérez et al. 2014). Different attributes

of the nodes (node weights) have been considered, such as habitat area (the most frequent option), species occurrence or occupancy probabilities (Saura and Pascual-Hortal 2007, Vergara et al. 2013), habitat quality or suitability (e.g. Mazaris et al. 2013, Trainor et al. 2013), area weighted by habitat quality (e.g. Loro et al. 2015), water depth (Fernandes et al. 2015) or tree fruit production (Rodríguez-Pérez et al. 2014, Pérez-Hernández et al. 2015). The links in the network (and the probabilities in these links) have been characterized through different options, such as Euclidean (straight-line) distances (the most frequent option), effective least-cost path distances through a resistance surface (e.g. Gurrutxaga et al. 2011, Carranza et al. 2012, Estreguil et al. 2013, Trainor et al. 2013, Fajardo et al. 2014), structural corridors (Saura et al. 2011b), or dispersal kernels derived from stochastic simulations of a spatially explicit and mechanistic dispersal model (Pérez-Hernández et al. 2015). Several studies (Saura et al. 2014, Merken et al. 2015) have also used the maximum product probabilities and the PC metric in directed probabilistic networks (asymmetric exchanges between habitat patches), i.e. those in which the probability of movement from patch A to B is different than from patch B to A. The management applications and ecological implications of the maximum product probability paths (most reliable paths) and the PC metric have focused on a variety of species and habitat types. Further details on these and other related studies and applications are available at http://www.conefor.org/applications.html

## 4. Empirical support to the use of the maximum product probability paths and the probability of connectivity metric

Apart from the analytical developments and the applications of the maximum product probability paths (most reliable paths) in habitat connectivity assessments (see previous sections and section 6 below), several studies have evaluated the ability of the PC metric, and of the maximum product probability paths (MPP) in this metric, to explain or predict ecological processes related to habitat connectivity. These studies have supported the use of PC and MPP after confronting them with empirical data on species distributions or seed deposition patterns, as described next.

Pereira et al. (2011) analysed a pond system used by an endangered species, the European pond turtle (*Emys orbicularis*), at a coastal region under strong agriculture intensification in south-western Portugal. Their study took into account different types of species-specific behavioural and ecological information: a surface of resistance to movement through the landscape matrix, the maximum travelled distance, observed pond presence/absence data, and an empirical habitat suitability model based on field sampling. Pereira et al. (2011) evaluated a set of network metrics in their ability to explain the actual species pond occupancy patterns in the study area. They found that, among the analysed network metrics, PC was the one that allowed a better discrimination of the occupied and unoccupied sites by adult and juvenile turtles; see the results for the three metrics in figure 6 in that article, plus the lack of relationship with turtle presence that is reported for betweenness centrality in page 74 of that article. Note that the betweenness centrality metric does not consider probabilities of dispersal nor MPP paths. PC also outperformed the results obtained when considering only the information provided by the habitat suitability model. In words of the authors, "*the difference in dPC values* [patch-level PC values] *between occupied and unoccupied ponds was slightly more pronounced than habitat suitability values alone. This was especially true for the presence-absence of hatchlings and juvenile individuals*". They concluded that "*among the different estimated parameters, this* [PC] *is possibly the most relevant for management purposes*".

Awade et al. (2012) used playback techniques to empirically determine the inter-patch movements and occurrence patterns of a rainforest insectivorous bird (*Pyriglena leucoptera*) in three fragmented Atlantic forest landscapes in Brazil. They considered several models as candidates for predicting the observed presence/absence patterns of the species in the study area, including variables at the patch and landscape levels and different ways to characterize the links between patches. Awade et al. (2012) found that (i) the Equivalent Connected Area index, ECA(PC), which is a square root transformation of

the PC index that was proposed by Saura et al. (2011), was the best predictor of the bird occurrence patterns, and that (ii) the probabilistic connection model in ECA(PC) outperformed in this case the results provided by a similar metric that only accounted for the number of links in the paths between patches (and not for the product probabilities along the paths). In their words, "*the single landscape-level model including ECA(PC) was found to be the best*", "*all three best-supported models included ECA(PC)*", and "*we advise the use of probabilistic metrics, such as ECA(PC), when inferring the effects of habitat availability on the occurrence of a certain species*". They stated that "*models should include at least one landscape-level habitat availability predictor and that a probabilistic measure of connectivity is mandatory to obtain good predictions*". They concluded that "*habitat availability is an essential factor determining species occurrence in fragmented landscapes*" and that "*evaluation of the abovementioned habitat availability aspects is strongly recommended to properly guide management decisions*".

Rodríguez-Pérez et al. (2014) analysed avian seed dispersal of fleshy-fruited trees in a secondary forest of the northern Iberian Peninsula. In this forest they set up an 18 hectare plot where they recorded the standing fruit crop of all trees and the abundance of seeds deposited by birds below the canopy of each tree. They aimed to infer the effects of connectivity between trees on the seed deposition patterns in each tree resulting from seed dispersal by frugivorous birds. They calculated the contribution of each tree to network connectivity for frugivorous birds through different connectivity metrics, which included PC but also two other metrics: the total number of links in the study area (NL) and IIC (Pascual-Hortal and Saura 2006), a similar metric to PC but that only considers the number of links in the paths between patches (and not the product probabilities along the paths). Rodríguez-Pérez et al. (2014) found that from the three connectivity metrics in the univariate models of fruit crop PC was the one that best predicted (lowest AIC) seed abundance (see table 1 in that paper). They concluded that trees with higher PC had higher seed abundance below them (see figure 3 in that paper), and that PC was the most important factor explaining seed abundance (see table S5 in the supporting information in that paper). PC was therefore able to capture factors driving seed dispersal and the abundance of seed deposition by frugivorous birds. Trees with the highest PC values accumulated larger seed clumps under their canopies, demonstrating agreement between the network connectivity as characterized by MPP and PC and the actual process of seed dispersal by birds.

Zozaya et al. (2012) evaluated the role of forest fires that occurred in recent decades in Catalonia (NE Spain) as drivers of the pattern of expansion of early-successional, open-habitat bird species. 44 large forest fires occurring between 2000 and 2005 (with sizes ranging from 50 to more than 6000 hectares) were analysed and surveyed in the field for the presence of six bird species with preference for open habitats in Mediterranean landscapes. Several scenarios of potential colonizer sources were assessed: open habitats created by previous recent fires, shrublands and farmlands. They used the flux fraction of the PC index (see a brief description of this fraction in section 6.1 below) to estimate potential species colonization dynamics on the selected fires. They differentiated the nodes comprising the sources of colonisers and the nodes corresponding to the new suitable habitat patches originated by the wildfires. They evaluated the capacity of that PC flux metric to explain the empirically observed species occurrences in the studied sites by using generalized linear mixed models. They found that the occurrence and colonization patterns of the focal species on the newly burnt sites were significantly related to the potential flux as estimated by PC. This occurred for five of the six surveyed open-habitat bird species and for all the scenarios of potential colonizer sources (although with a stronger signal for the scenario that considered previous wildfires). The authors concluded that "*fires occurring in the last decades are acting as sources of immigrants to the new suitable habitats appearing in the landscape. Overall, the probability of colonisation of a recently burnt area was greatest in those sites well connected by dispersal to other previously burnt areas*".

Finally, it is interesting to mention the study by Visconti and Elkin (2009), who assessed five connectivity metrics for their ability to predict the contribution of each patch to metapopulation viability. The probability of connectivity (PC) was one of the five evaluated metrics. The study was based in simulating the dynamics and viability of species occupying the landscapes using a metapopulation model linked to continuous time logistic population growth models. The authors compared the results from that model with the patch importance ranking derived from each connectivity metric. They concluded that from all the five evaluated metrics "*only the metapopulation capacity and the PC index were reasonably successful in predicting patch value in over-dispersed, heterogeneous landscapes*". They also concluded that "*to assess the persistence of a species in a landscape,* [interpatch] *connectivity is a necessary but by itself insufficient factor to consider. It is also necessary to consider the other components of metapopulation dynamics, which are taken into account in metapopulation capacity and PC index*". This is not an empirical validation study since it is based in landscape simulations and modelling, but provides a different kind of support to the PC metric by comparing it with a much more complex, biologically detailed and data hungry spatially explicit population model. A related study is that by Bode et al. (2008), who showed that the simulated probability of metapopulation extinction was negatively related to the average of the maximum product probabilities between all pairs of patches (called average path strength in that paper) in a set of small networks.

**5. Cases in which the maximum product probability paths (most reliable paths) may not be the best option for analysing habitat network connectivity**

Despite of the advantages and the improved approach for connectivity analysis provided by the probability of connectivity (PC) metric and the maximum product probability (MPP) paths, as outlined above and noted by Hock and Mumby (2015), PC and MPP are not necessarily always the most appropriate way to analyse the connectivity of habitat networks.

Bodin and Saura (2010) compared the behaviour of the PC metric (MPP) with IIC, a similar metric that only accounts for the number of links (and not for the probabilities) in the paths connecting each pair of patches (Pascual-Hortal and Saura 2006). Bodin and Saura (2010) noted that the MPP paths in the probabilistic PC metric resulted in the intermediate stepping-stone patches being highlighted as less important for network connectivity than when an unweighted network with binary links (IIC) was used. They also noted that since PC uses the product of the individual dispersal probabilities between pairs of patches (MPP) to assess the flows throughout the network, it follows that if these individual pair-wise probabilities are considerably lower than 1, the product (MPP) decreases very rapidly, and essentially vanishes for network distances (i.e. number of intermediate links) higher than just a few number of steps (links). Thus, in this case, the patches that are highlighted as those most important for connectivity (stepping stones) by PC and MPP are generally confined within relatively dense clusters where the patches are situated fairly close to each other.

PC and MPP give more weight to patches and links that potentially carry large flows of organisms, and much less weight to patches and links that carry fewer organisms (lower MPP) (Bodin and Saura 2010). Therefore, in those studies intending to explain the abundance of individuals, or to explain species presence in those cases in which species detection likelihood increases with population size, PC (MPP) may be the best way to characterize habitat connectivity (see some of the empirical validation studies mentioned in section 4). However, in other cases the focus may not be so much on how much flow there is or on how many individuals may move, but just on whether the movement of some individuals (even if not many) is possible. In this latter case, it may be more appropriate to use other metrics like IIC, which focus on whether movement is possible or not between two patches (unweighted network that does not differentiate the strength or probability of dispersal along the different links in the network). If focus is, for example, on genetic transmission, is does not matter that much if the flow of organisms is very high or low, as long as it is high enough to provide at least one or few immigrating individuals per

generation (Mills and Allendorf 1996, Wang 2004). Similarly, for an invasive species to spread it is generally not required that a large number of individuals can colonize a vacant habitat patch, but just that very few individuals are able to do so. Since the MPP paths in PC give much less weight to the less frequently used paths than to those with a high product probability, it follows that the actual importance of the long-distance (low-frequency) movements will be underestimated in the connectivity analysis, which will be dominated by a potentially small subset of very strong and frequently used paths (those with high MPP). In using IIC (or more broadly a network with unweighted links), more focus is laid on the likelihood of a successful movement happening throughout the network, and less focus is laid on assessing the actual quantities of organisms that flow throughout the landscape, which would be better captured by PC and MPP paths. This implies that IIC (unweighted network with no link probabilities) may be better suited to study long-term mixing of populations. As long as the movement probability for an individual situated in a certain patch to reach a neighbouring patch is not too low, it is reasonable to assume that at least one individual can mix with the local population in the neighbouring patch and thus create a new foothold from where further genetic transmission can take place. This means that all patches that are genetically connected would, over time, make up a single metapopulation. This suggesting discussion is supported by the findings from a study where more significant correlations were found between genetic diversity statistics and IIC compared to PC (Neel 2008). Related to this discussion, more recently Saura et al. (2014) noted that the maximum product probability paths (most reliable paths) and the PC metric may be need to be generalized to better account for the number of dispersing individuals, both those that are available for dispersal in a source patch and those that need to reach a vacant patch for a certain species spread or population mixing process to occur. This generalized network approach by Saura et al. (2014) seems to better account for the actual patterns of species range expansion through habitat networks and is summarized below in section 6.3.

## 6. Further analytical developments beyond the definition of the maximum product probability paths

The approach for assessing connectivity in probabilistic networks based on maximum product probability paths (most reliable paths) has been considerably developed in the last five years. These further developments have provided further insights or enriched analyses on the PC metric and on the maximum product probability paths in this metric, as summarized next in sections 6.1, 6.2 and 6.3.

### 6.1. Partitioning network connectivity in commeasurable fractions

Saura and Rubio (2010) showed how the PC metric can be partitioned in three fractions quantifying the different ways in which a habitat patch can contribute to connectivity. Two of these fractions directly deal with interpatch connectivity as quantified by the maximum product probability paths (most reliable paths). These two fractions are the flux fraction and the connector fraction. These fractions are measured in the same units (a common currency for connectivity) and can be directly compared to each other.

The flux fraction of PC quantifies how well a given habitat patch is connected to the rest of the habitat patches in the network. The flux fraction for a given patch is quantified as the attribute-weighted (usually area-weighted) dispersal flux along the maximum product probability paths of that patch with all the other habitat patches in the network.

The connector fraction quantifies how important a given patch is for maintaining connectivity between the rest of the patches, as a connecting element or stepping stone between them. The connector fraction for a given patch quantifies how much the maximum product probability paths (most reliable paths) between other pairs of patches would be affected by the removal of that patch (Saura and Rubio 2010). A given patch can only contribute through the connector fraction if it is part of the maximum

product probability path between other patches different from itself. The connector fraction of PC can also be calculated in the same way for links in the network (and not just for nodes or patches).

An example of the values of these fractions for patches and links is shown in figure 1 and in tables 1 and 2 in Saura and Rubio (2010). Saura and Rubio (2010) showed how the relative importance of these fractions varies for different network and species traits, and how each of the fractions highlights different critical patches for connectivity. Related analyses of interest can also be found in Baranyi et al. (2011). The calculation of these fractions is also implemented in the Conefor software package (version 2.6 or newer). Further details on conservation management applications resulting from these fractions can be found in some of the studies mentioned above in section 3 (e.g. Gurrutxaga et al. 2011, Rippa et al. 2011, Carranza et al. 2012, Trainor et al. 2013, Rodríguez-Pérez et al. 2014).

More recently, Saura et al. (2014) presented and applied a conceptually similar partitioning but focusing on the network-level (landscape-level) connectivity values rather than on the importance of individual nodes (patches) or links (the latter already addressed in Saura and Rubio (2010)). Two of these three network-level fractions in Saura et al. (2014) are the direct and step fractions, accounting respectively for how much of the overall connectivity is due to direct and indirect movements between patches (as given by the maximum product probability paths in the network).

### 6.2. Network centrality and maximum product probability paths

Bodin and Saura (2010) combined patch removal techniques and network analytical approaches into one integrated modelling framework for assessing the role of individual patches as connectivity providers. They showed that (i) the connector fraction of PC and the maximum product probability paths can be linked with classical network centrality metrics (betweenness centrality, BC), and that (ii) the classical betweenness centrality (BC), which is based on identifying the shortest paths (as given by the number of links along the path), can be generalized to incorporate the maximum product probability paths and then be measured in the same units as PC.

Bodin and Saura (2010) described the different connectivity aspects captured by the connector fraction of PC and by the generalized BC. The generalized BC captures how much a given patch is part of the maximum product probability paths between other patches, i.e. how much that patch sits between (or is involved in) movements between other pairs of patches by serving as an intermediate stepping stone patch in the network (as captured by the maximum product probability paths). The connector fraction of PC quantifies which proportion of that connector role (given by the generalized BC) would be actually lost if the patch was removed from the network, i.e. how much the connectivity between other habitat areas actually depends on the presence of that patch in the network.

If the removal of a patch X breaks the only path that was available for movement between the other patches, then the connector fraction for X will be high, as high as the generalized BC; this is the case of an irreplaceable patch (or path). If, on the contrary, there are many other alternative paths and patches that can compensate for the network disruption, then the impact on the network connectivity will be low; and the connector fraction of PC will be low for X even if the generalized BC was high (because the alternative paths for movement not affected by the removal of X have a product probability that is almost as high as that of the maximum product probability path in the intact network). Therefore, how high the connector fraction of PC is compared to the generalized BC may be linked to the difference between the maximum product probability path (most reliable path) and the product probability in the nearest alternative path as identified in the dispersal simulations and related discussion by Hock and Mumby (2015).

The generalized BC, measured in the same units as the connector fraction of PC, is also implemented in the Conefor software package (version 2.6 or newer). The same concepts and metrics can be extended

to links in the network. Further details and analytical expressions are provided in Bodin and Saura (2010).

*6.3. Accounting for the number of dispersers in probabilistic networks*

Saura et al. (2014) presented a generalized network model that accounts for the number of dispersing individuals and for long-distance dispersal processes across generations. In this model, the dispersal probabilities and maximum product probability paths are modified to account for the number of dispersing individuals, the number of immigrants that need to reach a vacant patch to allow for species establishment and reproduction, and the potential long-term role of stepping stones to promote species range shift and expansion across generations. In this way, Saura et al. (2014) provide a conceptually broader model to assess connectivity in probabilistic habitat networks. When confronted with empirical data on the large-scale range expansion of a forest bird species, the Black Woodpecker *Dryocopus martius*, over a 20-year period, this generalized model was shown to outperform previous standard network connectivity models (Saura et al. 2014). The developments in this generalized network model may be in line with some of the possibilities suggested by Hock and Mumby (2015) of modifying link probability values and maximum product probability paths by considering parameters such as population size or patch quality.

## 7. Concluding remarks

The analytical approach of the maximum product probability paths (most reliable paths) and the probability of connectivity metric has been widely used and developed for assessing the connectivity of habitat networks. This analytical approach has supported a better understanding of ecological processes, has contributed to assessments of the impacts of habitat network changes, and has provided guidance for decision making in conservation planning, as outlined in previous sections. The applications of the maximum product probability paths (most reliable paths) in previous studies include the prediction of patterns of species distribution, spread or colonization and planning for spatially-explicit measures focusing on the key patches or links along the dispersal paths in probabilistic networks (see section 3 and the references therein for further details).

Hock and Mumby (2015) add several valuable results on this previously presented approach through the demonstrative dispersal simulations they performed in a set of random graphs. These simulations show that the maximum product probability path is the path most likely (most frequently used) to conduct dispersal through the analysed habitat networks. The maximum product probability path (most reliable path) was used nearly twice as often as the next more frequently used path in these dispersal simulations, and it was also used more often than the path with the fewest number of links or the path determined by classical additive network search algorithms (Hock and Mumby 2015). It is also of interest that Hock and Mumby (2015) explicitly linked the path probabilities with the speed of the expected traversal time in terms of the number of necessary dispersal events, and that they explored the effect of targeted disruptions on patch occupation delay in the dispersal simulations. These findings by Hock and Mumby (2015) provide valuable insights that add to the considerable body of research on the maximum product probability paths (most reliable paths) outlined in previous sections. These insights by Hock and Mumby (2015) contribute to understand why the maximum product probability paths and the probability of connectivity metric may provide better predictions of different ecological processes than other classical network metrics, as reported in some previous studies (see section 4). It may be noted, however, that in some cases there might be reasons that may make other approaches different from the maximum product probability paths more appropriate in certain management or ecological applications (see section 5).

The intention of this document was to provide an overview of the wider context and considerable body of published research that has previously presented and developed this analytical framework for assessing probabilistic dispersal in habitat networks based on the maximum product probability paths. Hopefully, this overview will help researches and conservationists to make further use and have a better understanding of this analytical framework and of the software tools in which it has been implemented, which may be in the benefit of improved insights on ecological processes and better informed decisions for managing connectivity in habitat networks.

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