

1 **Long Title:** Missing interactions: the current state of multispecies connectivity analysis

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3 **Short title:** A review of multispecies connectivity methods

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21 Landscape

22

23 **Abstract:**

24

25 Designing effective habitat and protected area networks, which sustain species-rich communities  
26 is a critical conservation challenge. Recent decades have witnessed the emergence of new  
27 computational methods for analyzing and prioritizing the connectivity needs of multiple species.  
28 We argue that the goal of multispecies connectivity prioritizations be the *long-term persistence of*  
29 *a set of species* in a landscape and suggest the index of metapopulation capacity as one metric  
30 by which to assess and compare the effectiveness of proposed network designs. Here we present  
31 a review of the literature based on 77 papers published between 2010 and 2020, in which we  
32 assess the current state and recent advances in multispecies connectivity analysis in terrestrial  
33 ecosystems. We summarize the four most employed analytical methods, compare their data  
34 requirements, and provide an overview of studies comparing results from multiple methods. We  
35 explicitly look at approaches for integrating multiple species considerations into reserve design  
36 and identify novel approaches being developed to overcome computational and theoretical  
37 challenges posed by multispecies connectivity analyses. We conclude that, while advances have  
38 been made over the past decade, the field remains nascent in its ability to integrate multiple  
39 species interactions into analytical approaches to connectivity. Furthermore, the field is hampered  
40 in its ability to provide robust connectivity assessments for lack of a clear definition and goal for  
41 multispecies connectivity, as well as a lack of common metrics for their comparison.

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## 45 **1. Introduction**

46 Designing effective conservation networks, which sustain species-rich communities across  
47 increasingly fragmented landscapes, is a critical challenge for this century as countries commit to  
48 the post-2020 Global Biodiversity Framework (Hilty et al. 2020). Central to the success of these  
49 networks will be their capacity to meet the connectivity and dispersal requirements of multiple  
50 species across remaining habitat areas (Crooks and Sanjayan 2006).

51  
52 Ecological connectivity measures the extent to which a landscape facilitates or impedes species  
53 movement (Crooks and Sanjayan 2006). It is fundamental to species persistence, allowing  
54 individuals to seek out food and habitat resources, avoid predation or anthropogenic threats, and  
55 promote gene flow (Chetkiewicz et al. 2006; Cushman et al. 2013). A network of connected  
56 habitats helps to sustain populations through time (Gonzalez et al. 2011) and to accommodate  
57 species undergoing climate or land-use driven range shifts (Pearson and Dawson 2003; Opdam  
58 and Wascher 2004; Keeley et al. 2018). Given accelerating rates of habitat loss and climate  
59 change, and their negative impacts on animal movement (Tucker et al. 2018), identifying key  
60 wildlife corridors that are robust to future environmental conditions is a pressing concern for  
61 conservation planners (Crooks and Sanjayan 2006).

62  
63 Connectivity models are regularly employed to assess habitat networks for individual species  
64 (reviewed in Baldwin et al. 2010; Correa Ayram et al. 2016; Arkilanian et al. 2020). However, there  
65 is wide consensus amongst scientists and conservation planners for the need to conduct  
66 connectivity analyses for multiple species within landscapes. Studies singularly focused on iconic  
67 or highly vulnerable species often fail to adequately address the habitat needs of the wider species  
68 pool in the landscape (Beier et al. 2009; Cushman and Landguth 2012; DeMatteo et al. 2017;  
69 Meurant et al. 2018). Thus, multispecies connectivity (MSC) approaches, which directly or

70 indirectly assess the needs of multiple co-occurring species in a landscape, offer an important  
71 avenue to improve spatial conservation planning.

72

73 We define an MSC analysis as “*a methodology for identifying a network of habitats and movement*  
74 *pathways that supports the long-term persistence of multiple species in a landscape*”. At a  
75 minimum, these analyses must take into consideration connectivity needs of more than one  
76 species in a landscape. The ultimate aim of such efforts, however, is to incorporate multiple  
77 species interactions into connectivity models and more accurately represent how they mediate  
78 habitat use, movement, and the long-term persistence of entire metacommunities (Gonzalez et  
79 al. 2011; Chase et al. 2020). This requires moving beyond thinking about connectivity  
80 conservation as a “stacking” of habitat networks or metapopulations, towards consideration of  
81 multiplex ecological networks in landscapes (Kéfi et al. 2016; Pilosof et al. 2017).

82

83 Over the past two decades, various methods have been developed to incorporate the  
84 requirements of multiple species into connectivity modelling approaches. Four broad families of  
85 approaches have emerged in MSC analyses. The first two integrate multiple species needs at the  
86 outset of analysis (hereafter ‘*upstream*’ approaches), while the final two integrate them at the end  
87 of the analysis (hereafter ‘*downstream*’ approaches):

88

89 – *Species agnostic* approaches, such as geodiversity or naturalness methods, which aim to  
90 prioritize habitat conservation for multiple species based on the connectivity of bio-  
91 geoclimatic features and/or the degree to which habitats have been modified by humans  
92 (e.g., Koen et al. 2014; Marrec et al. 2020)

93 – *Generic species* approaches, which combine the traits of multiple species into a single set  
94 of values representing the habitat needs and mobility of species groups (e.g. Opdam et al.  
95 2008; Albert et al. 2017);

96 – *Single surrogate species* approaches, which assess the connectivity requirements of an  
97 individual species, selected based on broad habitat needs or sensitivity to disturbance (e.g.  
98 umbrella species), to capture the ecological needs of the broader species community (e.g.  
99 Brennan et al. 2020); and  
100 – *Multiple focal species* approaches, which separately model connectivity for a set of species  
101 representing diverse ecological needs and combine them *post hoc* to identify shared  
102 connectivity priorities (e.g., Albert et al. 2017; Meurant et al. 2018; Jennings, Zeller, and  
103 Lewison 2020; Williamson et al. 2019).

104  
105 Currently, there is no general consensus on which of these approaches is most effective for  
106 multispecies planning (Marrec et al. 2020). Without a formalized model for implementing  
107 multispecies connectivity planning, disparities across methods may have divergent and  
108 unintended consequences for conservation design (Reed et al. 2017; Albert et al. 2017; Jennings  
109 et al. 2020). MSC assessments can also prove computationally challenging when considering  
110 many species in vast landscapes. Identifying faster and less data-intensive approaches with  
111 comparable outcomes may be preferred when resources are limited (Santini et al. 2016a) to make  
112 MSC assessments more accessible. Given the global push to achieve post-2020 biodiversity  
113 goals (IUCN WCPA 2019; Williams et al. 2020), now is a critical time to review progress on  
114 multispecies connectivity modelling and operationalize a framework with which countries can  
115 achieve their 2050 conservation objectives.

116  
117 The goal of this study was to evaluate the current state of MSC science in conservation planning.  
118 As such, we conducted a literature review to i) assess the frequency of different methods and  
119 workflows used to plan for multiple species in connectivity assessments, and ii) evaluate trade-  
120 offs across methods in terms of the data and time requirements needed to apply methods and  
121 evaluate outputs. We close with a discussion of future directions for this field of research.

## 122 **2. Methods**

### 123 **2.1. Literature review criteria**

124 On October 19th, 2020, we used a keyword search in ISI Web of Knowledge scholarly archive to  
125 identify scientific articles undertaking multispecies connectivity analyses. We restricted our search  
126 to articles published between 2010 and 2020 to focus on the most recent advances in this field.  
127 We used the following search terms: 'Multispecies' OR 'Multi-species' OR 'Multiple species' AND  
128 'Connectivity' OR 'Corridor' OR 'Surrogate' OR 'Geodiversity' OR 'Naturalness' OR 'Generic  
129 species' OR 'Focal species'. We also executed a search using the following terms: 'Connectivity'  
130 AND 'Focal species' OR 'Generic species' OR 'Geodiveristy' OR 'Naturalness'. Finally, we used  
131 'Metapopulation capacity' as a separate search term as it pertains to a new field of research that  
132 is related to multispecies connectivity.

133  
134 From these keywords we identified 503 unique records, which were downloaded along with their  
135 abstracts and corresponding publication information. We reviewed abstracts and source journals  
136 and restricted the list of articles to i) empirical studies ii) of terrestrial ecosystems, which iii)  
137 evaluated connectivity of multiple species, iv) at a landscape-scale or greater. We did however  
138 discriminate between single species studies and those that focused on a single umbrella species  
139 that was intended to represent the habitat needs and movement requirements of a much larger  
140 community of species. After applying these criteria to the abstract of articles,  $n = 172$  papers were  
141 retained for in-depth analysis. Articles that met these initial criteria were downloaded and  
142 reviewed by the author team. In-depth reading of articles led to the exclusion of an additional  $n =$   
143 95 studies based on the same criteria as mentioned above, leaving  $n = 77$  articles included in the  
144 review. Given that some of the reviewed papers explicitly reported on MSC analyses using  
145 contrasting methods, we catalogued each of these analyses separately (e.g., Meurant et al.  
146 2018), resulting in 110 case studies (hereafter 'studies') of multispecies connectivity modelling for  
147 consideration.

## 148 **2.2 Classification and summary of MSC methods**

149 We classified methods reported in the reviewed papers using Arkilanian's et al. (2020)  
150 classification system for connectivity analyses (see Box 1). In this system, connectivity analyses  
151 are classified according to a common set of methodological steps in their workflow: 1) species  
152 selection, 2) identification of species traits, 3) identification of habitat patches, 4) identification of  
153 potential movement pathways between habitat patches, and 5) modelling the degree of  
154 connectivity between patches (Arkilanian et al. 2020). Multiple methods exist at each step in the  
155 workflow with their own data requirements and capacity to integrate multiple species  
156 considerations into connectivity modelling. For methods that did not correspond to a predefined  
157 approach, we classified them as 'Other' and appended a short description to each record. Some  
158 MSC studies carry out connectivity analysis for each focal species separately, and only identify  
159 common connectivity priorities *post hoc*. We added a final sixth step to Arkilanian's classification  
160 system to classify different methods used to combine connectivity results at the end of the  
161 workflow.

162

163 For each study, we collected data on the study location, spatial extent, dominant ecosystem type,  
164 study taxa, any software mentioned in connection with the approach used and whether the study  
165 contrasted multiple connectivity modelling approaches. We tabulated the number of papers using  
166 specific methods at each step in the workflow and identified novel methods that could not be  
167 easily categorized in our classification system. We ranked methods in terms of their resource  
168 requirements and assessed tradeoffs between computational throughput and precision.

169 *Box 1. Common methodological steps in a multispecies connectivity analysis. Modified from*  
170 *(Arkilanian et al. 2020)*

### Multispecies connectivity analysis workflow

Multispecies connectivity assessments typically follow a six-step workflow to identify priority areas to conserve connectivity across a landscape. At any point along this workflow methods can be adopted to incorporate consideration of multiple species into the assessment process.

*Step 1. Select species.* Which species are included in a connectivity analysis influences subsequent data and modelling requirements. Four broad approaches exist for species selection: i) species agnostic methods which ignore species-specific data to model landscape characteristics, ii) generic species methods which create a virtual species embodying the characteristics of multiple species, iii) single surrogate species methods which select one species to represent the needs of the wider community, or iv) multiple focal species methods which selected a subset species from the larger pool based on important traits (e.g. phylogeny, taxonomy, functionality, inclusivity).

*Step 2. Identify species traits.* How species are represented in the analysis is based on trait data related to habitat needs, life history and dispersal patterns. These can be derived from direct measures in the field or reported in the literature, the creation of ecoprofiles (sensu Opdam 2008), or by using multivariate approaches that reduce multiple species traits into a singular value (e.g., Laitila and Moilanen 2013). In species agnostic studies this step is skipped.

*Step 3. Define habitat.* What size and types of ecosystems species use to carry out critical portions of their life cycle define which parts of the landscape are considered habitat. Ranking of habitat quality and the classification of what constitutes species' habitat depends on multiple environmental and ecological factors. Habitat definitions can be informed by GPS or telemetry studies, direct observation (e.g., camera traps, bird counts), distribution or mechanical models, expert opinion, and remote sensing/pattern analysis. The determination of discreet habitat patches is skipped in some methods which instead only rely on a relative ranking of habitat quality.

*Step 4. Define movement capacity.* How far a species can travel and how likely it is to cross less hospitable land covers define a species movement in a landscape. This information is used to determine if a species can travel from patch A to patch B of habitat in a particular landscape. This is commonly achieved by taking information on species habitat preferences and transforming it into a resistance layer by taking the inverse of habitat quality (step 3) and the links between patches established based on species' dispersal capacity. Studies can use statistical methods, rule-based methods, least-cost paths, circuit theory or through linear programming and optimization to determine and weigh these linkages.

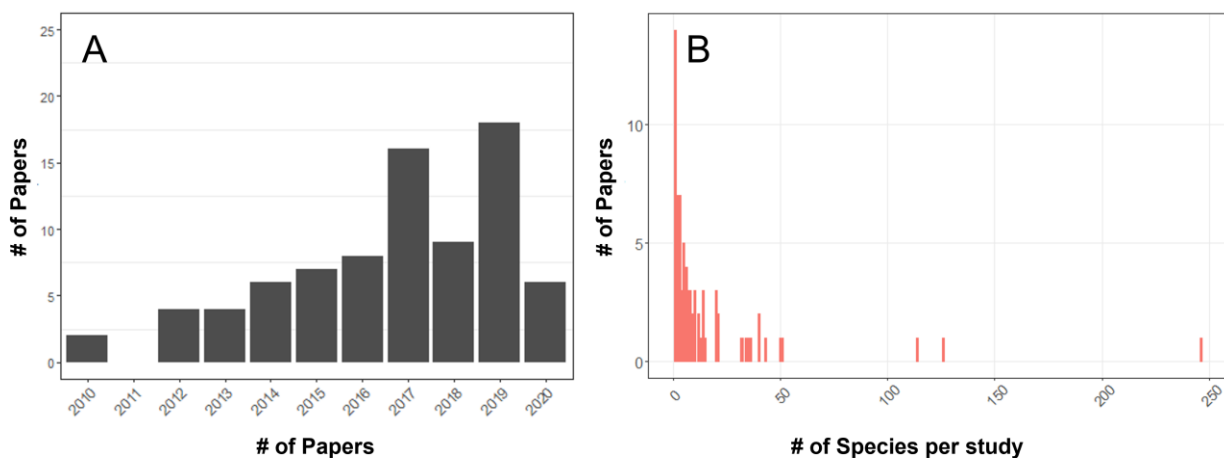
*Step 5. Assess connectivity.* Between which habitat patches and along which routes species are most likely to move define the connectivity of the habitat network. A number of metrics are commonly used to estimate connectivity (i.e. likely movement of individuals). These include benefit maps, conductance/current-density maps, cost maps, graph-theory indices, the metapopulation capacity and/or permeability and area-weighted permeability indices from graph theory. Studies often examine multiple metrics of connectivity to identify key habitat and corridors.

*Step 6. Prioritize multispecies networks.* Which parts of the landscape are most important to conserve species connectivity is based on their ability to maintain movement of species and connect important habitat areas. Prioritization can take place both on a single connectivity map or across multiple connectivity maps for different species/groups. Results from multiple connectivity analyses can be combined by assessing areas of spatial overlap amongst connectivity maps, tabulating the number of overlapping species networks across different parts of the landscape, normalizing and summing connectivity values across species, combining the top ranking percentile of connectivity values for each species or through a process of optimization.

### 172 3. Results

#### 173 3.1. Characterizing MSC studies

174 Many of the studies initially retained for review based on keywords in the title and abstract did not  
175 analyze MSC directly. After applying our selection criteria, 77 papers were retained detailing 110  
176 studies of multispecies connectivity assessments published between 2010 and 2020 (Fig.1A). In  
177 most cases, excluded studies alluded to the importance of multiple species considerations in  
178 conservation planning and in their selection of a single focal species but provided no further  
179 analysis on the relevance of the selected species to the wider community. A second set of studies  
180 that were excluded looked at the connectivity needs of multiple species but did not include  
181 methods to identify a common connectivity prioritization across species. A third group of studies  
182 aimed to predict species' use of the landscape based on predictors of habitat quality for multiple  
183 species and discussed connectivity amongst habitats but did not directly model the movement  
184 pathways through the landscape. Over the considered timeframe the annual number of published  
185 studies increased gradually with a spike in publications occurring in 2017 and 2019. As the  
186 literature search was conducted in October of 2020, it is possible that a number of additional  
187 papers were also published at the end of this year that were not considered.

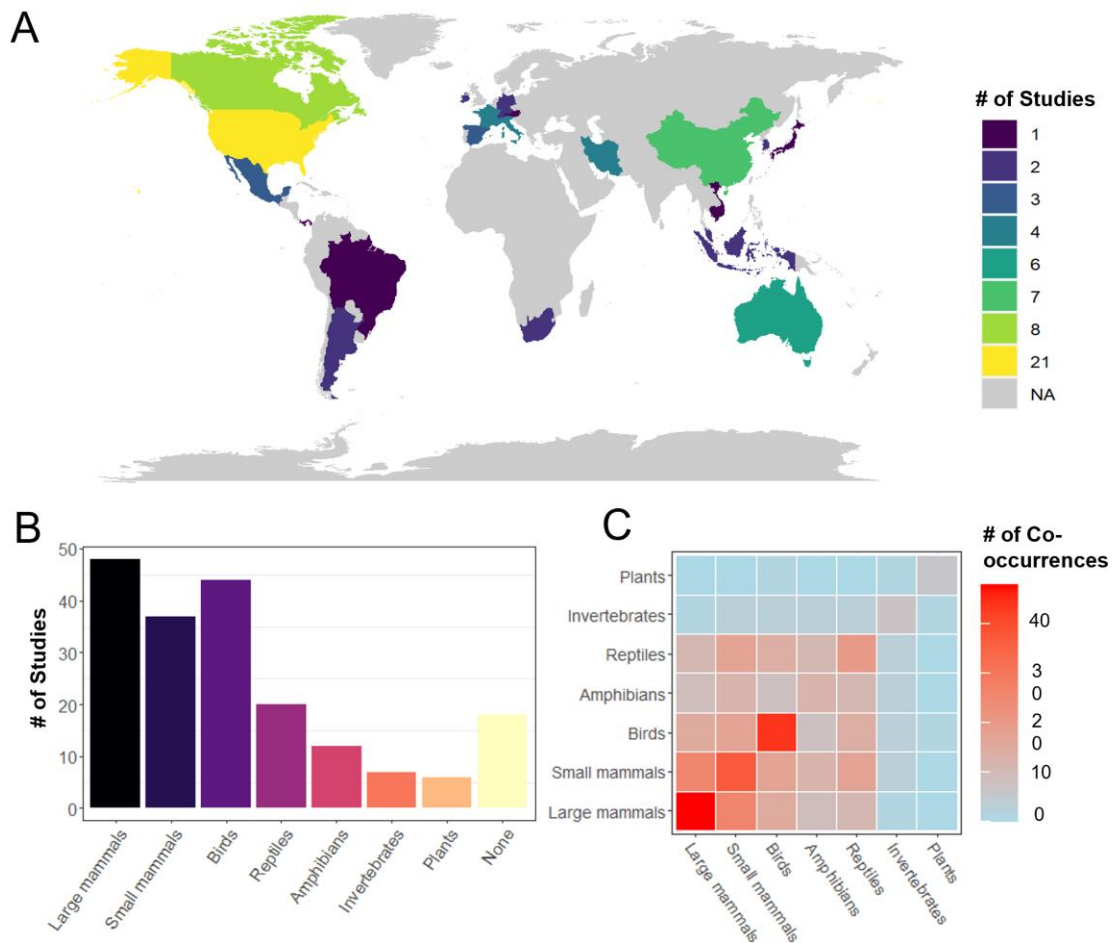


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189 Figure 1. (A) The number of papers meeting the criteria of an inclusion in the literature review  
190 between 2010 and 2020 (total n = 77), and (B) the distribution of the number of species assessed  
191 per study across reviewed papers (one study excluded with >2000 species)



192 Most retained studies were located in North America, Western Europe, China, and Australia with  
193 a smaller number of studies from Southeast Asia and South America (Fig. 2A). A few supra-  
194 national studies were also included in the review which looked at connectivity in regional Austral-  
195 Asian flyways (Iwamura et al. 2014), the European Alps (Hanson et al. 2019), as well as global  
196 patterns of connectivity amongst protected area networks (Santini et al. 2016b), forests in global  
197 biodiversity hotspots (Larrey-Lassalle et al. 2018), and tropical mangrove ecosystems (Huang et  
198 al. 2020).



199

200 Figure 2. A) Global distribution of reviewed multispecies connectivity studies (total n=110), B) the  
201 number of reviewed studies evaluating the connectivity of each considered taxonomic group  
202 included or no species (None) as in species agnostic approaches, (C) a heatmap of the number  
203 of times species of a taxonomic group were co-assessed with species from the same or other

204 taxonomic groups within studies. Warm colours indicate higher frequencies and cooler colours  
205 indicate lower frequencies  
206  
207 In the reviewed papers, the average number of species considered was  $16.6 \pm 34.5$  (min = 0, max  
208 = 246, one studied excluded with > 2000 plant species, Fig 1B). Of the 110 studies reviewed,  
209 52% focused on connectivity patterns of multiple species within a single taxonomic group (n = 57,  
210 small and large mammals were combined), while 47% (n = 53) looked at species across  
211 taxonomic groups (Fig 2C). The most frequently considered taxonomic groups were large  
212 mammals (44%) followed by birds (40%), small mammals (34%) and then reptiles (18%) and  
213 amphibians (11%), with few studies focused on invertebrates (7%) or plants (5%) (Fig. 1b). Of  
214 studies satisfying our criteria, 18% applied a species agnostic approach, 17% took a generic  
215 species approach, 9% used a single surrogate species to assess the wider community  
216 connectivity, and the remaining 55% took a multiple focal species approach (Table 1). Overall,  
217 most reviewed studies assessed connectivity in large landscapes (1,000-10,000 km<sup>2</sup>) up to the  
218 scale of subcontinents (>100,000km<sup>2</sup>) (Table 1) and were predominantly focused on temperate  
219 forests, agro-ecosystems, or landscapes that encompassed multiple large ecosystem types.

220

221 **Table 1. Frequency of studies employing each of the four broad approaches for species**  
222 **selection per spatial scales of consideration.**

Scale	Extent (km <sup>2</sup> )	Species agnostic	Generic species	Surrogate species	Multiple focal species	Total
Small landscape	10-100	1	1	0	3	5
Medium landscape	100-1,000	2	2	0	8	12
Large landscape	1,000-10,000	7	6	4	12	29
Ecoregion	10,000-100,000	4	6	4	20	34
Sub-continental	>100,000	5	4	2	16	27
Continental	NA	1	0	0	2	3
<b>Total</b>	-	<b>20</b>	<b>19</b>	<b>10</b>	<b>61</b>	<b>110</b>

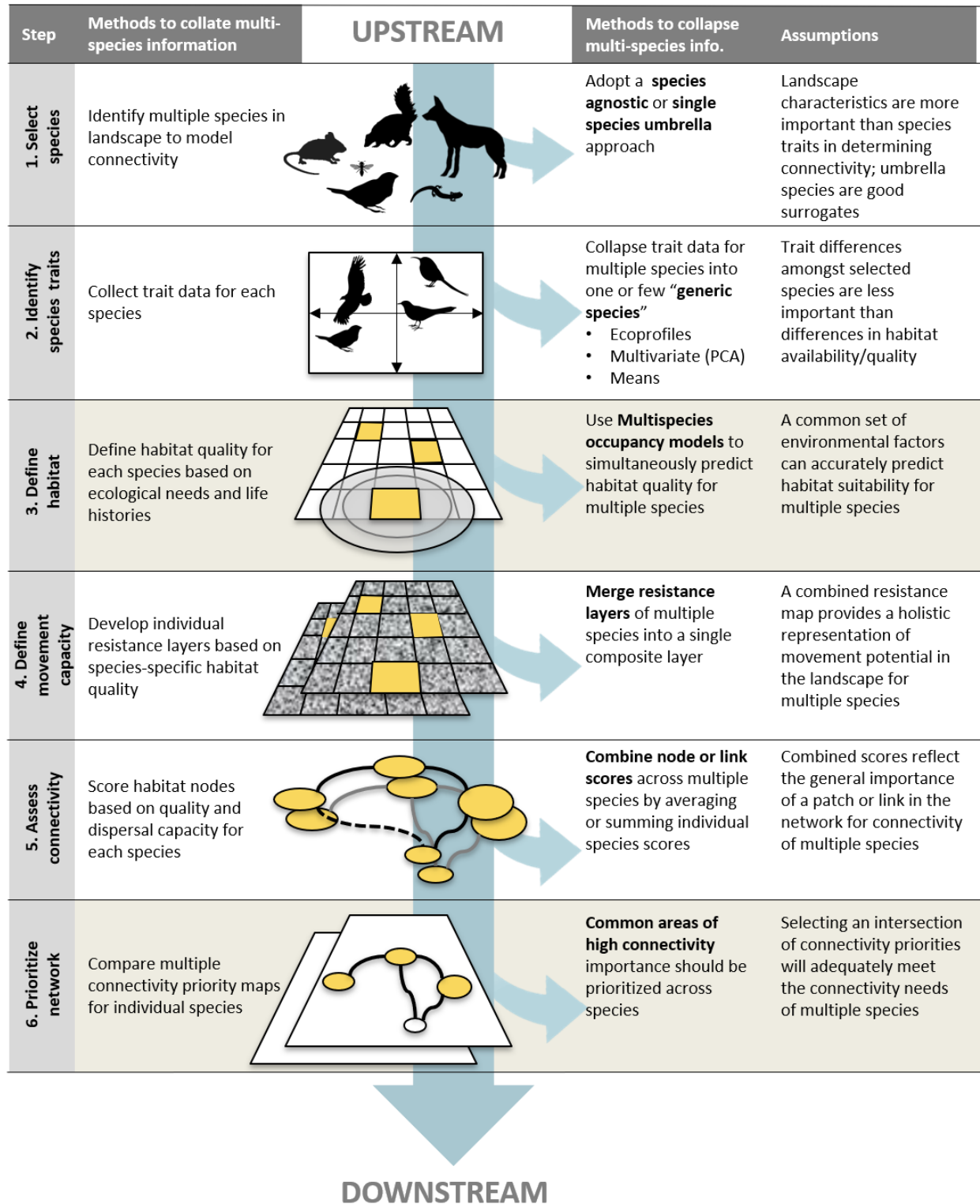
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### 224 **3.2. Upstream and downstream approaches**

225 Multispecies connectivity approaches invariably require collapsing information on multiple  
226 species' habitat or movement needs at some point in their analytical workflow. This can occur  
227 prior to calculating connectivity metrics, what we term *upstream* approaches, resulting in a  
228 composite connectivity map from a single connectivity analysis. In contrast, *downstream*  
229 approaches build connectivity maps for each individual species and then collapse them to arrive  
230 at a composite prioritization map. Some studies can adopt both upstream and downstream  
231 approaches in their workflow by collapsing species information into multiple generic species at  
232 the outset of analysis and afterwards combining connectivity results from their analysis (e.g.,  
233 Ecoprofiles, Opdam et al. 2008). One exception to our dichotomization of upstream and  
234 downstream approaches is the use of optimization algorithms during the connectivity analysis  
235 (step 5) to incorporate multiple species considerations simultaneously (e.g. Wang and Önal  
236 2016).

237

238 Upstream and downstream approaches vary in the computational resources required to  
239 parameterize connectivity models, and approaches that collapse multiple species information  
240 earlier in the workflow are less data-intensive. Upstream methods, such as species agnostic or  
241 generic species approaches, require substantially less species-specific data and computational  
242 resources than studies that collapse species information in steps 3-5. Upstream approaches are  
243 also much less data-intensive than multiple focal species connectivity analyses that requires  
244 carrying species-specific data through each step of the workflow. This tradeoff can become  
245 increasingly important as the resource requirements increase exponentially as the number of  
246 species and landscape extent increase (Santini et al. 2016a).



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Figure 3. A conceptual diagram of the six-step workflow in multispecies connectivity assessments characterizing upstream vs. downstream approaches to incorporate multiple species information. The column on the left indicates the general analysis followed in a multiple individual species connectivity assessment for each step. The columns on the right identify potential methods for

252 collapsing multiple species information at each step and the associated assumptions. Steps 2  
253 and 6 are shaded to indicate that they are not necessarily included in all multispecies connectivity  
254 assessments.

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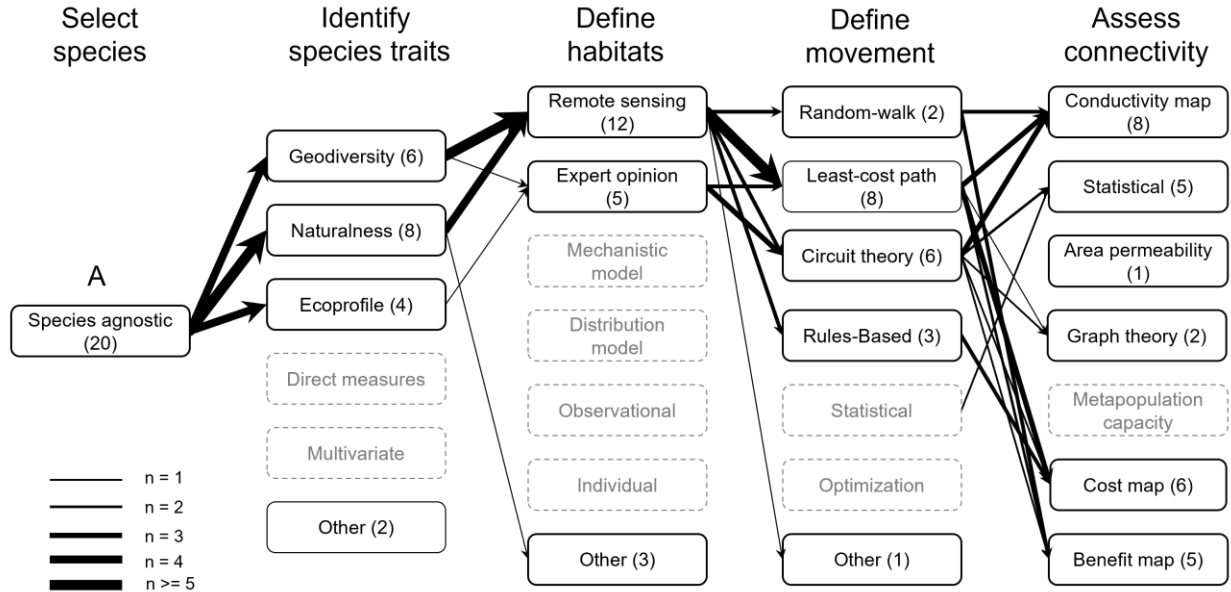
### 256 **3.3. Common approaches in MSC analyses**

257 We found the majority of reviewed studies applied downstream approaches when analyzing MSC  
258 by adopting a multiple focal species approach (Fig. 4). These studies selected a subset of species  
259 in their landscape (Fig. 3, step 1) using an array of criteria (e.g., representativeness, functional  
260 roles, vulnerability) and proceeded to carry out individual connectivity analysis for each species  
261 separately (steps 2-5). They then combined connectivity maps to identify common priority areas  
262 for connectivity (step 6), principally through overlap analysis or by summing multiple connectivity  
263 layers (Fig. 3, left hand column). A smaller number of studies adopted upstream approaches by  
264 adopting a species agnostic or generic species approach for their MSC analysis or combining  
265 multiple species data prior to running the connectivity analysis. These approaches are generally  
266 less data-intensive and are growing in frequency in more recent years.

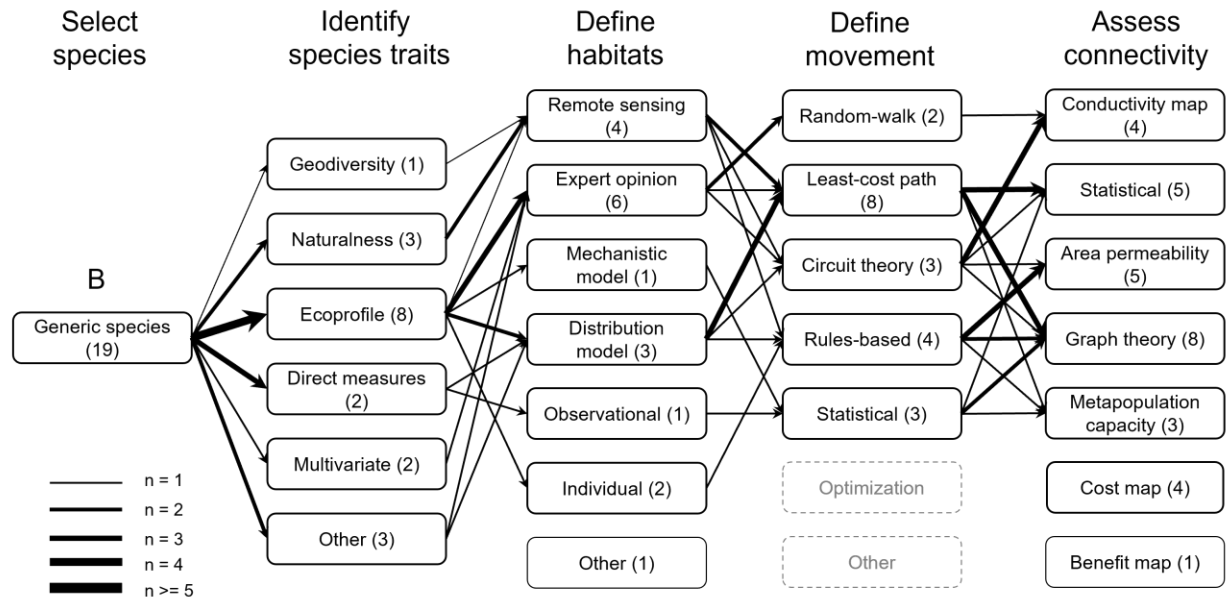
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268 Across all reviewed studies, the most common methods used to assess potential movement  
269 across a landscape (step 4), whether for an individual or generic species, was through least-cost  
270 path analysis and/or circuit theory analysis. Most studies also combined multiple methods for their  
271 connectivity assessment (step 5), the most common being graph theory metrics with either least-  
272 cost or current density maps. A handful of studies also calculated the metapopulation capacity,  
273 which is a measure of the capacity of a given landscape configuration to support the persistence  
274 of a specific species (Ovaskainen and Hanski 2001). Very few studies used optimization  
275 approaches to identify common connectivity priorities amongst multiple species and none  
276 explicitly incorporated species interactions into their methods.

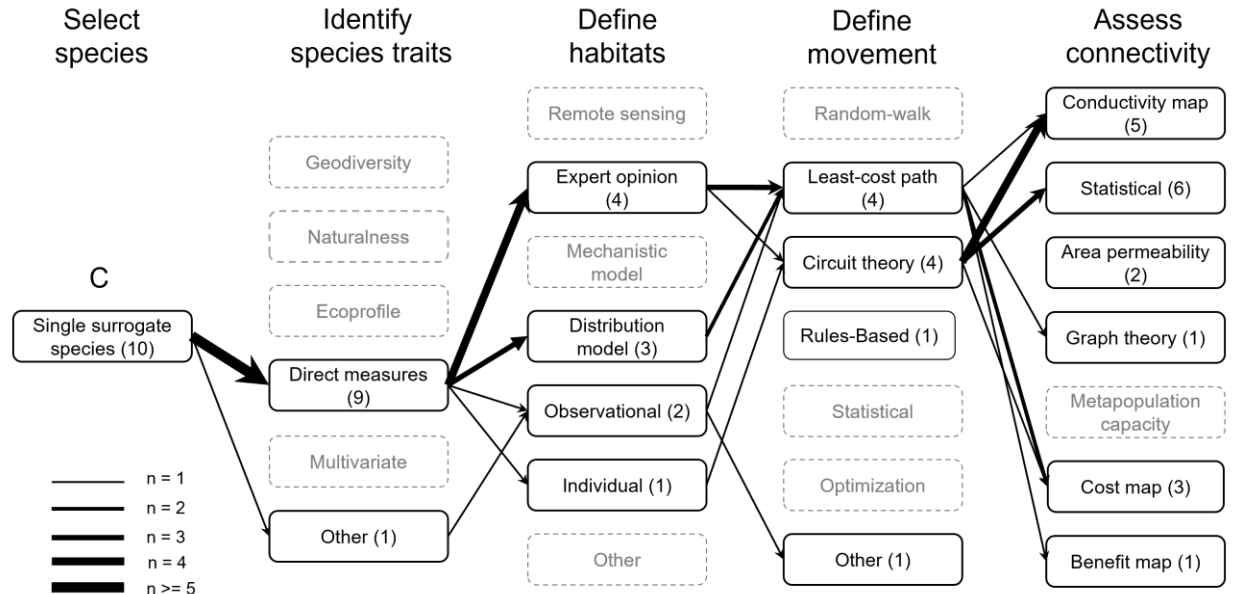
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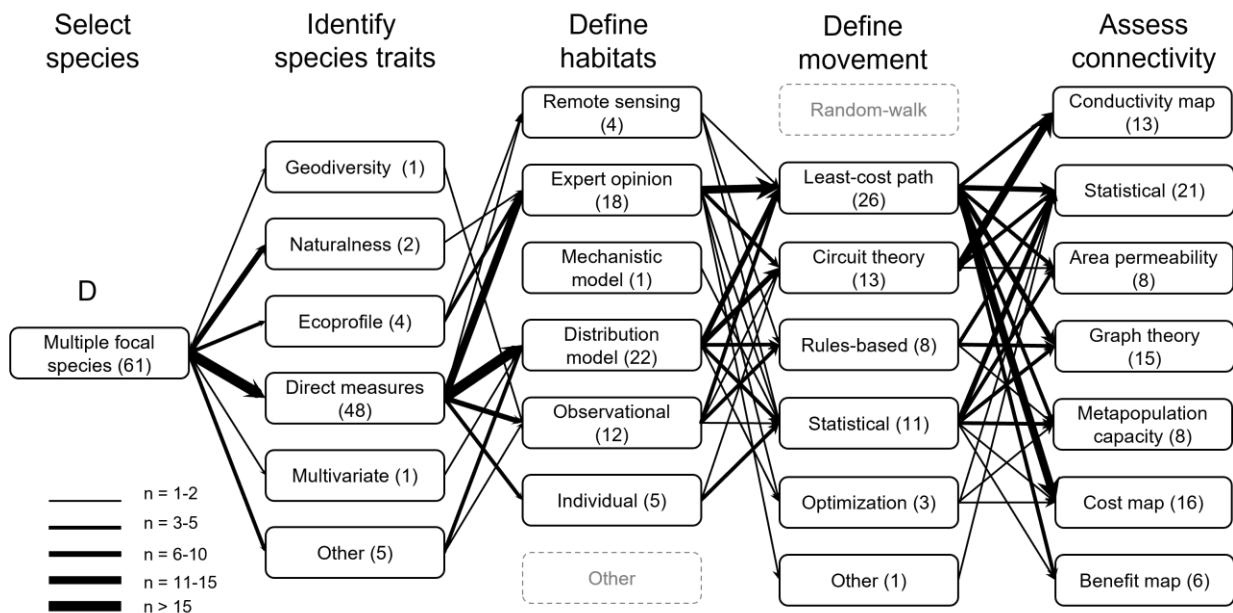
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Figure 4. Connectivity workflows for four common multispecies selection approaches: (A) species agnostic, (B) generic species, (C) single surrogate species and (D) multiple focal species. Boxes represent different available methods to employ for each step along the workflow. The number of studies employing each method is indicated in parentheses; the thickness of arrows linking methods across steps shows the frequency of method combinations (see legends). Greyed out boxes indicate methods that were not used by any workflow reviewed.

### 300 **3.4. Comparing effectiveness of MSC approaches**

301 Opting for simplified upstream approaches may be desirable or necessary in situations of limited  
302 data and/or computational capacity. However, given that connectivity maps are sensitive to the  
303 way in which connectivity is formalized and implemented in models (Reed et al. 2017; Albert et  
304 al. 2017), it is important to understand the potential trade-offs of the different MSC approaches  
305 when modelling the connectivity needs of diverse species. In our review we came across eight  
306 papers that explicitly compared the results from two or more of the broad classes of MSC  
307 approaches, each using a multiple focal species approach as the basis for comparison.

308

309 The most frequent comparison was between a single surrogate species and a multiple focal  
310 species approach. Across these studies, single surrogate species approaches were found to  
311 poorly capture the connectivity and habitat needs of the wider species community (Brodie et al.  
312 2015; DeMatteo et al. 2017; Meurant et al. 2018; Brennan et al. 2020).

313

314 Studies comparing generic species and multiple focal species approaches found significant  
315 differences in the priority rank-maps of the generic species to the composite maps, but overall  
316 connectivity maps of generic species performed better than single surrogate species (Brodie et  
317 al. 2015; Meurant et al. 2018). Importantly, however, Brodie et al. (2015) found in Borneo that  
318 their generic species approach became increasingly effective as the degree of ecological  
319 similarity and/or sensitivity to disturbances increased amongst the represented species in their  
320 tropical forest community.

321

322 Finally, studies comparing species agnostic approaches, which do not rely on any species-  
323 specific data, to multiple focal species approaches have been more varied in performance (Brost  
324 and Beier 2010, Koen et al 2014, Jennings et al 2020). The inconsistency of findings both within  
325 and amongst species agnostic studies suggest that more work is needed to refine and validate



326 these approaches before they can be used with confidence to capture the needs of diverse  
327 communities of species in landscapes.

328

329 To date, the few papers comparing methods seem to suggest that single surrogate species  
330 models may poorly represent the habitat and connectivity needs of the wider community of  
331 species. In contrast, carefully constructed generic or virtual species, where represented species  
332 share similar ecological traits, may provide a more promising approach to model multiple species  
333 connectivity when data and processing capacity is limited.

334

335 Finally, Williamson et al. (2020) compared the impact of different *post hoc* methods to combine  
336 connectivity analyses outputs in a multiple focal species approach. Their results underscore the  
337 challenge of consolidating multiple aspects of species biology into a single map (Williamson et al.  
338 2020). Each of the methods to combine species connectivity maps had limitations either in their  
339 ability to fairly represent the habitat needs and movement capacities of different species  
340 (normalized sum), may overlook moderate-to-high value habitats that could support multiple  
341 species (top percentile), and/or were sensitive to the selected threshold delimiting habitat from  
342 non-habitat (model count). Being aware of the limitations of each with regard to the type of species  
343 under consideration will be important to selecting the most appropriate metric to combine multiple  
344 connectivity analyses.

345

### 346 **3.5. Novel methods in MSC**

347 In addition to approaches that incorporate multispecies considerations either at the outset of the  
348 analysis (*upstream*) or as a final step in the connectivity analysis (*downstream*), our literature  
349 review uncovered several studies that employed novel methods for calculating MSC (see Fig. 3).  
350 Starting with a subset of species from the landscape, these studies combined individual species

351 information at different points along the workflow to produce a single connectivity assessment or  
352 prioritization.

353

354 *i) Multispecies occupancy models*

355 Multispecies occupancy models can be used to predict species locations and connectivity across  
356 landscapes when individual species presence-absence data are scarce (Meyer et al. 2020). This  
357 allows for a single model to predict the occupancy of habitat patches for multiple species, some  
358 of which may be rare and difficult to detect. In their study, Meyer et al. (2020) used camera-trap  
359 data for nine medium to large mammals and a hierarchical multispecies occupancy model to  
360 estimate species occupancy in the Mesoamerican Biological Corridor. They estimated species-  
361 specific model parameters as random effects of a community-level distribution, which permits  
362 more precise parameter estimates for rare species than traditional species-level analyses (Zipkin  
363 et al. 2010; Kéry and Royle 2015). From this, the authors developed an occupancy-weighted  
364 connectivity metric to evaluate species-specific functional connectivity. While Meyer et al. (2020)  
365 stop short of a full multispecies connectivity assessment by not identifying common priority areas  
366 of connectivity, their methodology could be used to great effect to improve multispecies habitat  
367 identification in data limited contexts.

368

369 *ii) Combining habitat suitability and resistance layers*

370 In their study in central-western Mexico, Correa Ayram et al. (2019) developed common habitat  
371 suitability and resistance layers for three multispecies groups to identify composite multispecies  
372 corridors. Starting with 40 focal species with contrasting habitat needs, Correa Ayram and  
373 colleagues (2019) grouped species based on shared inter-patch dispersal distances and  
374 minimum habitat requirements. Within each multispecies group, a common habitat layer was  
375 developed by retaining only habitat patches which were common to all species. Additionally,  
376 individual species resistance layers were summed and normalized to build a common resistance

377 layer for each multispecies group. These layers were then used as inputs into least-cost path  
378 and circuit theory analyses to prioritize common areas of connectivity importance. This approach  
379 could be considered a variant of Opdam et al.'s (2008) ecoprofile approach, however, by  
380 collapsing individual species information after developing and employing species-specific habitat  
381 models, Correa Ayram and colleagues carry forward a greater amount of species-specific habitat  
382 information along the workflow.

383

384 *iii) Combining node and link metrics*

385 In their study of all non-volant terrestrial mammals in Italy, Santini et al. (2016a) aimed to reduce  
386 the computational effort associated with large MSC assessments by combining probabilistic  
387 species graphs prior to conducting the network analysis. In their study, the authors tested multiple  
388 methods for aggregating node attributes (summing values of the probability of connectivity and of  
389 intra-patch connectivity) and link attributes (mean, weighted-means) for all species to increase  
390 computational efficiency. Based on a comparison with the summed results from having run the  
391 analysis separately for each of the 20 species, the best performing composite network showed  
392 very similar prioritization of habitats (Spearman's  $r = 0.976$ ). This composite network was  
393 calculated based on the sum of the intra-patch connectivity for nodes and the average of the link  
394 probabilities weighted by the average suitable habitat area, requiring a quarter of the computing  
395 resources as the full species analysis representing an important gain in efficiency.

396

397 *iv) Multi-node connectivity metrics*

398 Connectivity analyses typically rank the importance of individual habitat patches in the network  
399 using single-node metrics from graph theory, e.g., probability of connectivity (PC) or integrated  
400 index of connectivity (IIC). Pereira et al. (2017) argue that, depending on their spatial  
401 arrangement, complementarity or redundancy, some groups of patches may better contribute to  
402 connectivity than the top individual patches. Through a study of 20 bird species in the Natura 2000

403 conservation network in Catalonia, Pereira and colleagues illustrate how two multi-node centrality  
404 metrics, 'm-reach-closeness' and 'm-fragmentation', drawn from social network theory (An and  
405 Liu 2016) are complementary and can be differentially employed depending on the movement  
406 capacity of each species. The m-reach-closeness metric identifies the set of nodes that is  
407 maximally connected to all other nodes, thereby prioritizing access across the entire network for  
408 high mobility species. In contrast, the m-fragmentation metric seeks to identify key patches that  
409 bridge core habitats, important for reducing species fragmentation in isolated populations with low  
410 mobility.<sup>6</sup>

411

#### 412 *v) Metapopulation capacity*

413 Increasingly, connectivity analyses report the metapopulation capacity metric *lambda* of their final  
414 network prioritization. From metapopulation theory, the metapopulation capacity predicts the  
415 persistence of a population for a given landscape configuration based on rates of colonization  
416 and extinction (Ovaskainen and Hanski 2001). Based on an adjacency matrix, *lambda* is  
417 calculated as the leading eigenvalue of this matrix, where values above 1 indicate species  
418 persistence. In connectivity analyses it can be interpreted as the viability of a species population  
419 for a given habitat network configuration. In their study of 30 terrestrial mammals in Borneo, Brodie  
420 et al. (2016) apply *lambda* to identify network typologies that best support the community of  
421 species considered, i.e., the persistence of all species in the regional pool. Brodie et al. (2016)  
422 argue that an advantage of this approach is that it ranks links in the network according to their  
423 strength rather than their presence- absence as with graph theory metrics. Furthermore, their final  
424 response variable (metacommunity stability) ranks these linkages based on the ultimate measure  
425 of interest, species persistence, rather than the proximate goal of network connectivity (Brodie et  
426 al. 2016).

427

#### 428 *vi) Multispecies connectivity optimization*

429 Linear programming can identify an optimal network configuration that simultaneously meets  
430 habitat and connectivity requirements for two or more species. Due to their computation  
431 complexity, linear mixed integer programs traditionally include a single spatial attribute  
432 (connectivity) in their model resulting in long thin reserve designs that are likely suboptimal for  
433 species (Conrad et al. 2012). Wang and Önal (2016) design a linear integer programming model  
434 for multiple species that incorporates compactness in addition to the connectivity of landscape  
435 reserves. They apply their method to 10 bird species in Illinois to identify optimal reserves based  
436 on a minimum probability threshold. Their method also identifies multiple sub-reserves when a  
437 single reserve is inadequate for the overall species conservation goal. The authors explain that  
438 this is important when designing reserves for multiple species where habitats are scattered  
439 throughout the potential conservation area. In such cases, the spatial coherence of selected sites  
440 must be species-specific.

441

#### 442 **4. Discussion and Future Directions**

443 The field of multispecies connectivity analysis has grown steadily over the past decade. This has  
444 led to a flourishing of approaches as scientists and conservation planners seek more ecologically  
445 effective and efficient methods to model multiple species habitat and movement needs. However,  
446 work is needed to better define the goals of multispecies connectivity analyses, to agree on  
447 metrics that evaluate and compare the performance of conservation designs, and most crucially  
448 to incorporate species interactions into network selection.

449

##### 450 ***4.1 Setting a common definition and goals for MSC analyses***

451 In this review we propose multispecies connectivity analysis is a 'methodology for identifying a  
452 network of habitats and movement pathways that supports *the long-term persistence of multiple*  
453 *species in a landscape*'. Most papers we reviewed did not explicitly state species persistence as  
454 the goal of the analysis, but rather the identification of common habitat networks and movement

455 corridors. While a laudable goal, corridors alone will not ensure species survival in landscapes if  
456 a minimum area of habitat is not also protected. Habitat area and connectivity must be assessed  
457 together. A small number of studies estimated the metapopulation capacity of prioritized networks  
458 *post hoc* to assess whether they support the persistence of species, with a smaller number using  
459 the metric to inform network design (e.g. Drielsma and Ferrier 2009; Brodie et al. 2015). The  
460 metapopulation capacity metric can be used to test the resilience of different network  
461 configurations under future land use and climate change scenarios (e.g. Shen et al. 2015). We  
462 believe this is an important innovation to advance the field by both providing a metric to rank  
463 potential network configurations across species and a robust means of comparing the  
464 effectiveness of alternative conservation network plans (Grantham et al. 2010).

465

466 Connectivity maps are sensitive to the way in which connectivity is formalized and implemented  
467 in models (Reed et al. 2017; Albert et al. 2017) and there is little consensus as to the effectiveness  
468 of different approaches (Marrec et al. 2020). As new techniques are devised to reduce data and  
469 processing requirements, more studies are needed to understand the trade-offs in time, data,  
470 accuracy and effectiveness that these approaches engender (e.g., Meurant et al. 2018; Jennings  
471 et al. 2020). With an increase in MSC approaches, developing common criteria and metrics will  
472 be vital to selecting from competing network designs and establishing best practices as the field  
473 of MSC modelling continues to grow. Some studies are already tackling this challenge by using  
474 scenario-based simulation and common metrics to compare the effectiveness of different MSC  
475 approaches under climate change (Rayfield et al. *in prep*).

476

#### 477 **4.2 Need for greater network validation**

478 Across studies there was a striking lack of empirical validation of multiple species connectivity  
479 models. Only a handful of reviewed papers used independent datasets to validate the accuracy  
480 of their networks or select amongst them (see Koen et al. 2014; Marrotte et al. 2017; Brennan et

481 al. 2020). Of these, most relied on genetic data to assess how habitat fragmentation and corridors  
482 influence functional connectivity. Without validation, it is not possible to determine how effective  
483 different MSC methods are for predicting and conserving species connectivity. For instance,  
484 Marrotte et al. (2017) compared node-based estimates of genetic connectivity using neutral  
485 microsatellites for a set of mammals across Ontario with modelled estimates of current density.  
486 They found that current density was proportional to the probability of movement in fragmented  
487 parts of the landscape, but not where habitat was abundant. Furthermore, in their model high  
488 current density did not reflect high gene flow, rather, it identified pinch points restricting species  
489 movements. Using a naturalness-based approach, Koen et al. (2014) found that modelled current  
490 density was strongly correlated with between empirical roadkill and fisher movement patterns. As  
491 movement and occupancy data become more readily available through less expensive genetic  
492 sequencing and open data repositories, the validation of connectivity results should become a  
493 standard part of robust MSC analyses.

494

### 495 ***4.3 Integrating species interactions***

496 Despite the novel methods noted in this review, we find that the field is largely in a nascent stage  
497 with respect to its ability to meaningfully incorporate multiple species interactions into connectivity  
498 modelling. None of the studies reviewed incorporated behavioral or population dynamics between  
499 co-occurring species (but see Shahnasari et al. 2019 who included prey abundance in their habitat  
500 distribution model for focal predators). Studies continue to “stack” independent species networks  
501 to prioritize corridors rather than building “multilayer networks” that include ecological  
502 dependencies and interactions across layers (Kéfi et al. 2016; Pilosof et al. 2017). This omission  
503 in MSC analyses is critical as functional connectivity is not only shaped by landscape structure,  
504 but species interactions as well (Gonzalez, Rayfield, and Lindo 2011; Courbin et al. 2014). For  
505 example, in a study of a wolf-moose-caribou predator-prey system in a fragmented landscape of  
506 Quebec, Courbin et al. (2014) found that wolves use indicators of prey habitat quality and

507 preference, rather than the distribution of prey *per se*, to orient their movement in landscapes  
508 where prey are highly mobile. Such studies illustrate that to accurately predict movement in  
509 landscapes, MSC analyses must integrate metacommunity approaches that consider food-webs  
510 and the spatial dynamics of interacting species into modelling approaches (e.g., Yeakel et al.  
511 2020).

512  
513 One MSC analysis that did incorporate spatial species dynamics is Rayfield et al. (2009), a study  
514 published prior our review horizon. In it, Rayfield and colleagues develop a general framework to  
515 incorporate consumer-resources dynamics into spatial conservation networks. Their approach  
516 protects areas that maintain the connectivity between the distribution of consumers by using an  
517 interaction kernel that defines the probability distribution of foraging distances based on the  
518 movement abilities of the consumers and resources. When applied to the case of the American  
519 marten (*Martes americana*) and its prey (the red-backed vole, *Myodes rutilus*, and the deer  
520 mouse, *Peromyscus maniculatus*), their method prioritized spatially aggregated reserves that  
521 maintain local habitat quality for all species. Similarly, using a theoretical framework, Baggio et  
522 al. (2011) developed an agent-based model to explore connectivity designs while considering  
523 spatial predator-prey interactions in fragmented landscapes. Their model also concluded that both  
524 predator and prey benefit most from globally well-connected habitat patches. Results from both  
525 studies aligned with empirical findings of Courbin et al. (2014) on the wolf-moose-caribou system  
526 in which prey selected habitat patches that were connected by multiple links instead of isolated  
527 ones. The authors suggest that predators are cued into these connectivity preferences.

528  
529 Advancements emerging from food-web modelling to prioritize habitat conservation may provide  
530 new tools to better incorporate multispecies interactions into connectivity assessments (Yeakel et  
531 al. 2020). Promising studies on metawebs suggest that interacting species can be meaningfully  
532 grouped into trophic guilds based on species interactions and functional traits to understand



533 spatial variation of food webs (O'Connor et al. 2020). Such studies can help bridge the gap  
534 between spatial community ecology and landscape ecology, a link that is currently missing in  
535 applied connectivity conservation.

536

## 537 **5. Conclusions**

538 This review showed the breadth of methods available to analyze and prioritize multispecies  
539 connectivity. It also revealed that more work is needed to test and validate different approaches  
540 across a common set of criteria to establish a set of best practices to inform conservation  
541 planning. To do this, more comparative studies that contrast methods within landscapes are  
542 needed to test efficiency and accuracy. This research would be further strengthened by increased  
543 analyses of uncertainty and sensitivity to better understand which steps in MSC modelling should  
544 we invest in to reduce uncertainty. Finally, the development and expansion of observation and  
545 monitoring networks will be key to provide timeseries data to validate and update MSC analyses  
546 through high-resolution real-time data on species movement patterns in dynamic and evolving  
547 landscapes.

548

## 549 **6. Authors' contributions**

550 AG, BR, CP, AEM, SW contributed equally to the conception and design of the study and to final  
551 review of the manuscript. SLRW, OT, FM, VDL, KMTL, ASD all contributed equally to the review  
552 the literature, data collection and revision of the manuscript. SLRW was responsible for data  
553 analysis and writing of the manuscript.

554

## 555 **7. Data Availability**

556 Data from the literature review will be made available on the Open Science Foundation's  
557 repository (upon publication). The full list of papers included in the review and references will be  
558 provided therein.

559

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565 following authors are employed by ApexRMS, BR.

566

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