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# Integrating dispersal proxies in ecological and environmental research in the freshwater realm

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33    ABSTRACT

34    Dispersal is one of the key mechanisms affecting the distribution of individuals, populations

35    and communities in nature. Despite advances in the study of single species, it has been

36    notoriously difficult to account for dispersal in multispecies metacommunities, where it

37    potentially has strong effects on community structure beyond those of local environmental

38    conditions. Dispersal should thus be directly integrated in both basic and applied research by

39    using proxies. Here, we review the use of proxies in the current metacommunity research,

40    suggest new proxies and discuss how proxies could be used in community modelling,

41    particularly in freshwater systems. We suggest that while traditional proxies may still be

42    useful, proxies formerly utilized in transport geography may provide useful novel insights

43    into the structuring of biological communities in freshwater systems. We also suggest that

44    understanding the utility of such proxies for dispersal in metacommunities is highly important

45    for many applied fields, such as freshwater bioassessment, conservation planning and

46    recolonization research in the context of restoration ecology. These research fields have often

47    ignored spatial dynamics, and focused mostly on local environmental conditions and changes

48    therein. Yet, the conclusions of these applied studies may change considerably if dispersal is

49    taken into account.

50

51    *Key words*: accessibility, bioassessment, connectivity, conservation, dispersal, freshwater,

52    links, metacommunity, nodes, transport geography.

53

54

## Introduction

56

57 Ever since Charles Darwin, ecologists have been interested in dispersal (Ridley 2004), i.e.,

58 the movement of an organism from one location to another. Dispersal is one of the most

59 important mechanisms affecting the distribution of individuals, populations and communities

60 (Baguette et al. 2013; Lowe and McPeek 2014). At the same time, dispersal is also one of the

61 most difficult phenomena to study even for a single individual or a single species in nature

62 (Bilton et al. 2001; Nathan et al. 2008). The problem is exacerbated for dozens to hundreds of

63 species in a metacommunity, i.e., a set of local communities connected by dispersal (Leibold

64 et al. 2004), making it virtually impossible to account for dispersal directly for such large

65 number of entities in natural settings. Ecologists have therefore relied on various proxies,

66 which are assumed to relate to the effects of dispersal on community structure (Jacobson and

67 Peres-Neto 2010; Jones et al. 2015).

68     Dispersal may mask the importance of purely environmental control of local

69 ecological communities (Palmer et al. 1996; Leibold et al. 2004; Brown et al. 2011;

70 Winegardner et al. 2012). This is because very high or very low dispersal rates may interfere

71 with species sorting, decoupling the otherwise strong relationships between biological

72 communities and local environmental factors (Leibold et al. 2004; Ng et al. 2009; Brown and

73 Swan 2010; Winegardner et al. 2012). For instance, in mass effects, very high dispersal from

74 'source' populations may produce a constant flow of migrants that guarantees the

75 maintenance of populations in unsuitable or 'sink' localities (Pulliam 1988), thus interfering

76 with local environmental control (Mouquet and Loreau 2003). On the other hand, species

77  may be absent from suitable localities owing to dispersal limitation (Heino et al. 2015a), also

78  contributing to low variation explained by environmental factors in multivariate models.

79  Multivariate models of community structure can typically explain only a small fraction (adj.

80  $R^2 < 50\%$, often varying between 0 and 20%) of community variation (Beisner et al. 2006;

81  Nabout et al. 2009; Alahuhta and Heino 2013; Soininen 2014; Heino et al. 2015b), which

82  may simply be due to unmeasured environmental factors, but also to our inability to

83  adequately account for dispersal in statistical models (Cottenie 2005; Leibold and Loeuille

84  2015; Soininen, 2016). An alternative view suggests that statistical models may also

85  overestimate the spatial component potentially related to dispersal, which may be due to

86  specifics of the spatial methods used (Gilbert and Bennett 2010; Smith and Lundholm 2010).

87  Therefore, refining the spatial methods and various proxies for dispersal should aid in taking

88  dispersal better into account in metacommunity ecology.

89       Understanding the utility of proxies for dispersal is also highly relevant for many

90  applied fields when the focus is on multiple species in freshwater ecosystems. These

91  ecosystems are all of high priority for bioassessment, restoration and conservation because

92  they comprise high levels of biodiversity (Dudgeon et al. 2006; Wiens 2015) and provide

93  crucial ecosystem services to humans (Vörösmarty et al. 2010; Garcia-Llorente at al. 2011;

94  Holland et al. 2011). At the same time, freshwater ecosystems are strongly threatened by

95  anthropogenic impacts such as eutrophication and habitat fragmentation (Dudgeon et al.

96  2006; Erős and Campbell Grant 2015). We emphasize that different types of freshwater

97  ecosystems (e.g. ponds, lakes, streams, rivers, springs) show different interactions among

98  dispersal, anthropogenic impacts and natural environmental factors. Owing to lower

99  connectivity, it may be that organisms in isolated freshwater ecosystems (e.g. ponds and

100  springs) are more severely impacted by the interactions of limited dispersal and

101  anthropogenic effects than those in more continuous ones (e.g. large rivers and large lake

102 systems). Similar interactions among dispersal, fragmentation and unexpected effects of

103 stressors may occur in all freshwater, marine and terrestrial ecosystems. Therefore, the use of

104 proxies for dispersal will be essential for applied research in all ecosystems. For example, our

105 typical reasoning is that the success of restoration projects (e.g. recovery from acidification)

106 may be delayed due to dispersal limitation because tolerant species may be absent from

107 ecosystems simply because they have not been able to reach the site. Similarly,

108 biomonitoring programs may be less effective in detecting impaired sites when dispersal from

109 pristine to impacted sites is high.

110    Our aim is to review current use of proxies for dispersal in freshwater ecosystems.

111 Individual sites in freshwater ecosystems are often inherently connected (Tonn and

112 Magnuson 1982; Palmer et al. 1996; Magnuson et al. 1998; Jackson et al. 2001; Olden et al.

113 2001; Grant et al. 2007; Altermatt 2013). It can be assumed that most of the dispersal of

114 obligate freshwater organisms, such as fish, is restricted to the network comprising running

115 and standing waters (Matthews 1998; Olden et al. 2001). However, for other freshwater

116 organisms, such as aquatic insects, dispersal within the network is not the only option, as

117 insect adults may show active and passive out-of-network dispersal (Malmqvist 2002; Smith

118 et al. 2009). Yet other groups of species, such as aquatic macrophytes, algae, mollusks and

119 crustaceans, may disperse passively through waterways, or their seeds, whole cells, fragments

120 or resting stages are carried by winds or animals for long distances (Kristiansen 1996; Bilton

121 et al. 2001; Bohonak and Jenkins 2003; Riis and Sand-Jensen 2006).

122    Variation in dispersal mode and ability among groups of organisms is also

123 exacerbated by the fact that even within a single group, dispersal distances vary greatly

124 among species. Rather than being intimidated by such high degrees of variation, we propose

125 that it actually provides a number of possibilities for basic and applied research. However,

126  better understanding of dispersal in diverse organisms inhabiting freshwater ecosystems is

127  dependent on the better use of existing proxies and the development of new approaches.

128  Here, we claim that while some traditional proxies are still useful, some proxies applied in

129  transport geography are promising tools for basic and applied metacommunity research.

130  Testing the utility of these proxies is, however, still in its infancy, and further case studies are

131  needed. One of the aims of this review is to provide motivation for such further studies.

132

133  **Past, present and future proxies for dispersal**

134

135  *The distance effect: "…near things are more related than distant things"*

136

137  According to Tobler's (1970) first law of geography, "Everything is related to everything

138  else, but near things are more related than distant things". Although this law is certainly

139  accurate in geography and ecology (Nekola and White 1999; Hubbell 2001; Soininen et al.

140  2007), it has an inherent emphasis on Euclidean distances between sites. Nature and

141  organisms are, however, more complex. What we define as "near" or "distant" should be

142  understood in the context of ecological, but not necessarily geographical, distances between

143  sites. Ecological distance takes into account structural (e.g. landscape features) and functional

144  (e.g. animal movements) aspects as related to dispersal (McRae 2006; Sutherland et al. 2015).

145  Hence, by necessity, those distances are much more complex than linear distances between

146  sites (Wang et al. 2009; Graves et al. 2014). Also, organisms differ from each other in their

147  dispersal ability (i.e. capacity to move long distances), although we can also state that all

148 organisms are different from other organisms, but phylogenetically closely-related organisms

149 are, on average, more similar than distantly-related organisms. Organisms thus also have

150 morphological (e.g. wing morphology in insects) and behavioural (e.g. tendency to fly long

151 distances) characteristics related to dispersal (Hoffsten 2004; Rundle et al. 2007), which are

152 typically phylogenetically conserved (Dijkstra et al. 2014). Below, we will consider pros and

153 cons of organismal, genetic, physical and transport geography (i.e. graph-based) proxies for

154 dispersal distances in a multi-species metacommunity context in freshwater systems (Table

155 1).

156

157 *Organismal-based proxies*

158

159 Organismal-based proxies for dispersal are important because they combine species traits and

160 the dispersal process. Typical organismal-based proxies for dispersal include separation of

161 species into more homogeneous groups according to body size (Jenkins et al. 2007; De Bie et

162 al. 2012; Datry et al. 2016a), wing size or wingspan (Hoffsten 2004; Sekar 2012), dispersal

163 mode (active vs passive, aquatic vs aerial) and dispersal ability (Thompson and Townsend

164 2006; Göthe et al. 2013a, 2013b; Grönroos et al. 2013; Heino 2013b; Cañedo-Argüelles et al.

165 2015; Heino et al. 2015a).

166 First, the use of body size divisions typically assumes that very small organisms are

167 easily carried long distances passively by water currents, wind or by animals, and that

168 increasing body size decreases the possibilities for passive long-distance dispersal (Fenchel

169 and Finlay 2004; Shurin et al. 2009). While this idea is partly supported by empirical findings

170 (De Bie et al. 2012; Padial et al. 2014; Datry et al. 2016a), some studies have also found little

171    support for it (Jenkins et al. 2007). Body size is also correlated with various life history and

172    ecological traits other than dispersal. For example, regarding freshwater ecosystems, body

173    size may correlate with predation pressure (e.g. Tolonen et al. 2003), number of generations

174    per year (e.g. Zeuss et al. 2017) and more, suggesting that using body size as a dispersal

175    proxy may be compromised by other ecologically-relevant factors.

176    Second, unless the dispersal mode is taken into account, body size is likely to be a

177    poor predictor of dispersal distances. It is likely that very small passively dispersing

178    organisms, such as bacteria, microfungi and microalgae, are able to disperse passively across

179    very long distances (Baas-Becking 1934; Kristiansen 1996). However, intermediate-sized and

180    actively dispersing organisms, such as many aquatic insects (except perhaps dragonflies),

181    may show rather limited dispersal distances (Finn et al. 2011). Also, large-sized actively

182    dispersing organisms, such as some diadromous fish or aquatic birds, may disperse (or rather

183    migrate) very long distances (Matthews 1998). Thus, body size should not be used alone

184    without considering dispersal mode.

185    Third, organismal classifications focusing on wing morphology, wing size or

186    wingspan might add considerably over using body size as a proxy for dispersal (see also

187    Harrison 1980). For example, studying aquatic insects Malmqvist (2002) and Hoffsten (2004)

188    found that larger-winged species had larger distributions that those with smaller wings,

189    suggesting that large wings might facilitate dispersal and lead to broader ranges. Malmqvist

190    (2000) also emphasised that wing size allows to identify poor dispersers among groups of

191    aquatic insects because it can be assumed that re-colonisation by poor flyers can be very

192    limited and slow after local extinction. This finding has implications for colonization-

193    extinction dynamics in metacommunities and consequent applications in environmental

194    research.

195   Given that various whole-organism based proxies have their limitations, researchers

196 should aim at finding a novel proxy or index for dispersal. Among aquatic invertebrates, for

197 example, a suitable index could consist of combined information from traits related to

198 dispersal mode, body size, life span, fecundity and more (e.g. Sarramajane et al. 2017).

199 Constructing such dispersal indices is possible using trait databases available in the literature

200 (Dolédec et al. 2006; Poff et al. 2006; Tomanova et al. 2007; Tachet et al. 2010) or in the

201 Internet (e.g. http://www.freshwaterecology.info/). However, it should be borne in mind that

202 such indices (i) should not be too complex to allow a widespread use, (ii) should account for

203 potential dispersal distances, and (iii) should be related to dispersal rates between sites (of

204 which fecundity and number of generations could be suitable indices). Such dispersal indices

205 should subsequently be tested using empirical datasets in metacommunity and environmental

206 assessment contexts.

207   An additional whole-organism based approach constitutes the use of stable isotopes to

208 mark individuals and measure dispersal (e.g. McNeale et al. 2005). While such an approach

209 may be feasible for a single species, it is increasingly difficult for large numbers of species

210 because recapturing rare species may be laborious or largely impossible. However, stable

211 isotopes can be used in estimating the dispersal distances of common freshwater species,

212 which could also inform about main patterns in metacommunity structuring.

213

214 *Molecular genetic proxies*

215

216 Another group of proxies are provided by advances in molecular biology. These include

217 population genetics (Hughes, 2007), DNA-barcoding (Cristescu 2014) and environmental

218     DNA (Bohmann et al. 2014). However, as these advances have been reviewed recently

219     (Manel et al. 2003; Manel and Holderegger 2013), we only mention briefly that they may

220     also be used as proxies for dispersal (Bohonak 1999; Wilcock et al. 2001; Hughes et al.

221     2009). These methods also have some drawbacks, such as "detecting" a species when it is not

222     actually present at a site in the environmental DNA approach (Bohmann et al. 2014). This is

223     probably because the 'signal' of a species' assumed presence may be carried long distances

224     from occupied sites to other sites where they will result in false presences.

225     Population genetic approaches used to infer dispersal are manifold, and they have

226     been available to researchers for decades (see reviews by Manel et al. 2003; Manel and

227     Holderegger 2013). They include approaches that inform about past and/or current

228     connections between local populations (Wilcock et al. 2001; Hughes et al. 2009). For

229     example, phylogeography tries to understand the geographic distribution of the different

230     genealogical lineages and can be used to infer past events (including long-term dispersal) by

231     considering the spatial genetic variation of current populations (e.g. Teacher et al. 2009).

232     More generally, genetic variation across populations (i.e. genetic structure) has been

233     traditionally used as an indirect measure of the current movement of individuals between

234     populations based on molecular markers and statistical methods (e.g. $F_{ST}$). There have been

235     some attempts to relate the genetic structure to the dispersal ability of species, showing that

236     sets of populations exhibiting high genetic diversity are those with low dispersal ability

237     (Bohonak 1999). Genetic structure can be, however, a biased proxy of dispersal because it

238     not only informs about gene flow among populations, but also about mutation, genetic drift,

239     adaptation by natural selection along environmental gradients and colonization history (i.e.

240     founder effects). Different theoretical and empirical models are currently being used to detect

241     these different processes (Orsini et al. 2013). Among them, isolation-by-distance (IBD)

242     models are commonly used to explain spatial genetic variation by gene flow and gradual

243 genetic drift. In this case, genetic similarity is reduced when geographical distance between

244 sites increases (Relethford 2004). However, IBD models are neutral models (Orsini et al.

245 2013) that do not consider changes in the environmental conditions in space and assume that

246 populations are in gene-flow-drift equilibrium, which is probably not the case of most natural

247 populations. In addition, disentangling the relative effects of gene flow from genetic drift is a

248 challenging task. Most direct methods used to measure gene flow require direct estimates of

249 dispersal, whereas indirect methods, which do not require dispersal information, still consider

250 equilibrium conditions. Gene flow is supposed to be more advantageous than traditional

251 dispersal proxies (e.g. mark-recapture methods) because it integrates multiple generations,

252 indicates successful establishment in the target population (in contrast to mark-recapture that

253 only assesses if individuals reached the target site) and can be applied across extensive

254 geographical areas (Bohonak 1999; Baguette et al. 2013). However, even if unbiased gene

255 flow estimates are obtained, they may not always fully represent dispersal because not all

256 dispersers survive and reproduce at a site (Bohonak and Jenkins 2003). Finally, recent

257 advances based on high throughput sequencing may lead to promising methods to measure

258 dispersal at the community level, as they may allow better quantification of genetic structure

259 and its underlying causes (e.g. Tesson and Edelaar 2013).

260

261 *Graph-based proxies*

262

263 Modelling is a prerequisite to examine the possible effects of using different dispersal proxies

264 in ecological research (Rouquette et al. 2013; Weinstein et al. 2014). One of the most

265 promising approaches is to examine the studied system as a graph, a set of nodes and links, in

266    which nodes represent the elements of the system (e.g. habitat patches, individuals,

267    populations or communities) and links specify the connectivity relationships between the

268    elements (Calabrese and Fagan 2004; Urban et al. 2009). In graph-based analyses, spatially

269    explicit data derived from geographic information systems (GIS) can be combined with

270    information on the dispersal of organisms (Calabrese and Fagan 2004). Different distance

271    classes among the nodes can be set up and depicted by adding different weights to the links

272    as a proxy for indicating habitat suitability for the dispersing organisms (e.g. flow and

273    riverbed characteristics for benthic insects) or barriers (e.g. dams or waterfalls for fish).

274    Directed links can refine the graph model representing the importance of upstream vs

275    downstream or watercourse vs overland dispersal (Galpern et al. 2011; Erős et al. 2012).

276    Potential connections between habitat patches (nodes) can be further refined by incorporating

277    information on the dispersal ability of the focal species. For instance, if the distance between

278    a given pair of patches is larger than a given threshold (here, dispersal distance for a species),

279    the patches may be considered unconnected.

280    Overall, graphs are useful for quantifying the physical relationships among the

281    landscape elements (i.e. structural connectivity; e.g. Saura and Rubio 2010) and how this

282    topological structure affects the movement of organisms across the landscape (i.e. potential

283    functional connectivity; e.g. Vasas et al. 2009). Graphs can thus help understanding the role

284    of dispersal in a diverse array of ecological systems in a flexible, iterative and exploratory

285    manner with relatively little data requirements (Urban and Keitt 2001; Calabrese and Fagan

286    2004; Dale and Fortin 2010).

287    As explained above, the construction of a graph model requires the determination of

288    links (connections) and their weights. In ecological research, many different

289    conceptualizations of physical distance can be used for this purpose, such as Euclidean,

290     network, flow and topographical distances (Olden et al. 2001; Beisner et al. 2006; Jacobson

291     and Peres-Neto 2010; Landeiro et al. 2011; 2012; Maloney and Munguia 2011; Liu et al.

292     2013; Silva and Hernández 2015; Cañedo-Argüelles et al. 2015; Kärnä et al. 2015; Datry et

293     al. 2016a). Euclidean distance is simply the shortest distance between two sites (Fig. 1). In

294     contrast, network distance takes into account riverine or other ecological corridors and thus

295     measures the shortest route from one site to another via corridors. However, according to

296     Peterson, Theobald and Ver Hoef (2007), "the physical characteristics of streams, such as

297     network configuration, connectivity, flow direction, and position within the network, demand

298     more functional, process-based measures". These authors made a useful distinction between

299     symmetrical distance (i.e. Euclidean and watercourse distance) and asymmetric distance

300     classes, which include upstream and downstream asymmetric flow distance (Peterson et al.

301     2007). This is because upstream dispersal is more difficult than downstream dispersal from

302     one site to another, at least for obligatory aquatic organisms. Finally, topographical distance

303     is built on the notion that altitudinal variation and slope may direct the dispersal of terrestrial

304     organisms, whereby they may choose optimal routes by avoiding steep upward slopes (Fig.

305     1).

306     Besides the traditional measures of between-site physical distances, cost distance is an

307     alternative family of distance metrics. Cost distance is calculated over a cost surface,

308     representing the resistance to an organism's movement. It can be metaphorically called "as

309     the fox runs" (Kärnä et al. 2015), as a wise animal like fox may choose a path of least

310     resistance in the landscape. Cost distance can be measured either as a least-cost (optimal)

311     path, or as a range of cumulative costs of landscape resistance between sites. Environmental

312     variables used to produce cost surfaces typically include land use, human constructions and

313     topography (Zeller et al. 2012). This technique has been mostly used to model the movement

314     and dispersal of large land mammal species of conservation concern (Larkin et al. 2004;

315    LaRue and Nilsen 2008), but it may also be relevant for the organisms living in freshwater

316    ecosystems (Kärnä et al. 2015).

317    Previous studies using cost distances have mainly employed categorical variables and

318    have not always taken into account variation in topography. In addition, various other

319    physical structures can be used as costs (Fig. 1). For example, the directional effect caused by

320    prevailing wind or flow conditions could be incorporated as part of cost distances (Horvath et

321    al. 2016). Additional cost can also consist of waterfalls, dams and other physical barriers for

322    fish (Olden et al. 2001; Pelicice and Agostinho 2008; Filipe et al. 2013) or inhospitable routes

323    through the matrix preventing or reducing dispersal, including pools, ponds and lakes for

324    riffle-dwelling species (Erős and Campbell Grant 2015). The same applies for deforested

325    riparian areas for terrestrial adults of freshwater species (Smith et al. 2009; Erős and

326    Campbell Grant 2015).

327    Although cost distances, least-cost path modelling and other approaches related to

328    graph-based modelling have been widely applied in ecology (e.g. Pinto and Keitt 2009), the

329    studies to date have mostly considered one species at a time (see review by Sawyer et al.

330    2011). A problem in the extension of this approach to sets of species is that their dispersal

331    routes and environmental responses likely differ. For instance, it is possible to assign costs to

332    links based on habitat suitability, although the latter likely differ for different species. A first

333    approach would be to split the species in functional sets that respond similarly to

334    environmental conditions and distance between sites. The straightforward extension of this

335    process would be the modelling of each species separately, each one with their costs, and

336    then combine all graphs in a more realistic description of communities. This approach,

337    however, should not be practical for many groups of organisms as we lack information on

338    their natural history.

339       The application of graph-based models is still limited in basic and applied

340    metacommunity research (Borthagaray et al. 2015; Layeghifard et al. 2015), and most

341    applications to date have been in the terrestrial realm, whereas the use of spatially explicit

342    graph-based methods in freshwater ecology has lagged far behind (Erős et al. 2012).

343    However, since graph-based modelling is widely used in many disciplines, proxies developed

344    in other fields can also be adopted in ecological research. One such field is transport

345    geography, encompassing various measures of spatial accessibility and interaction, as well as

346    methods for path or route selection in space. Next, we will consider how proxies utilized

347    previously in transport geography might allow modelling dispersal effects on local

348    communities when other approaches are not feasible for studying multiple species at the same

349    time. We suggest that some of these models can also be integrated in metacommunity

350    research in freshwater systems.

351       In traditional transport geography, researchers have tried to explain complex human

352    travel patterns by using spatial and spatio-temporal models (Black 2003). The modelling of

353    human travel patterns relies, to a large extent, on the notion of accessibility (Table 2, Fig. 2).

354    Accessibility can be defined as "the potential for reaching spatially distributed opportunities",

355    and its quantification typically includes the physical distance or cost of travel, as well as the

356    quality and quantity of opportunities that humans want to reach (Páez et al. 2012). In the

357    ecological context, the quality and quantity of opportunities might translate into habitat

358    quality in terms of water chemistry (e.g. pH or nutrients) and quantity of resources (e.g.

359    abundance of prey for predators). These qualities and quantities should be contrasted with the

360    ease to access them, i.e., ecologically meaningful distances between source and destination

361    localities in the landscape.

362        A number of measures have been devised for describing transport accessibility. These

363        can be broadly divided into connectivity, accessibility of nearest object, cumulated

364        opportunities, gravity and utility measures (Kwan 1998; Rietveld and Bruinsma 1998; Páez et

365        al. 2012). Connectivity measures describe the number or rate of connections for a specific

366        site, such as interconnectivity of a location to other locations within varying topology of a

367        road network (Xie and Levinson 2007). Accessibility of nearest object is measured as least-

368        cost path, for example, by applying street network travel distances to measuring the reach of

369        service facilities (Smoyer-Tomic et al. 2006). Cumulated opportunities measure the number

370        of opportunities (e.g. "available" sites for a species in ecological terms) reached within a

371        certain travel cost, which can be applied to indicate amount of reachable services in an urban

372        environment (Páez et al. 2012). While these measures mostly deal with the presence of a

373        connection between any two sites or the distance separating them, the purpose of gravity

374        measures is to express spatial interactions between sites. Drawing directly on the principles of

375        the law of gravity in physics, gravity measures assume that the attraction of a site increases

376        with size (or any other attribute) and declines with distance, travel time or cost. This is easily

377        translated into dispersal of species between localities in a metacommunity, whereby some

378        sites attract more individuals and species than others given the same dispersal distances, time

379        or cost. Also, for example, potential of human social interaction can be estimated within

380        urban and regional structures by applying daily time and travel constraints of people in

381        relation to residential, work and other activities (Farber et al. 2013). In freshwater systems,

382        this approach can include evaluation of species dispersal with different dispersal abilities

383        within a metacommunity and can be incorporated into the gravity models. Utility measures

384        are similar to gravity measures, but they are based on individual-related choices aiming to

385        maximize utility in the selection of the destination (Geurs and van Wee 2004). This can be

386 seen as a kind of habitat selection by individual organisms (e.g. oviposition by female insects

387 and nest-site selection by birds), which in turn affects local community structure.

388      While transport geography is an interesting source of proxies to be conflated with

389 ecological approaches, there is some overlap in the graph-based proxies used in transport

390 geography and metacommunity research. Such overlap is not always easy to detect since

391 vocabulary is not fully consistent across disciplines. Nevertheless, although some of the

392 proxies and terms have been used in metacommunity ecology before, transport geography

393 provides explicit formulas for further ecological applications and defines complex issues in

394 general terms.

395      There is one potential limitation with the use of physical and transport geography

396 proxies: the lack of suitable landscape-level environmental data in some regions. However,

397 our premise is that when environmental data are needed, they could be acquired from existing

398 databases or using modern geospatial data compilation techniques. These include land use

399 and land cover information using vast sets of airborne or spaceborne remote sensing sensors

400 and topographic information (including delineation of stream networks) from high-resolution

401 digital elevation models. Naturally, micro-scale explorations would require more accurate

402 spatial data than available in most of the global data banks. However, similar remote sensing-

403 based acquisition techniques (e.g. terrestrial hyperspectral and LiDAR imaging) could be

404 applied in fine-scale investigations using the physical and transport geography proxies.

405      Another caveat in applying all physical and transport geography proxies is that

406 although they describe 'physical connectivity' between sites, they do not necessarily translate

407 easily into 'biological connectivity'. Hence, researchers should keep this limitation in mind

408 and try combining organismal proxies with physical connectivity among sites. One approach

409 is also to take into account biological similarity between sites, with the assumption that

410     biological dissimilarity provides information about the biological connectivity between sites

411     (Layeghifard et al. 2015; Monteiro et al. 2017; see below).

412

413     **Use of different proxies for dispersal in the literature**

414

415     In order to roughly estimate the frequency of usage of different proxies for dispersal, we

416     conducted a literature search using the Web of Science database (from 2004 to August 26,

417     2016) and the terms (Dispers* AND metacommunity*), in the field TOPIC. These terms

418     were combined, also in field TOPIC and using the Boolean operator "AND", with keywords

419     related to the different proxies evaluated in this review (Table 3). Thus far, terms related to

420     organismal-based proxies were the most frequent, followed by physical distance-based

421     proxies. However, we did not find articles using terms that would indicate the use of transport

422     geography proxies in metacommunity ecology.

423       In studies using organismal-based proxies, a possible analytical approach consists of

424     the creation of different matrices comprising taxa with different (yet typically inferred)

425     dispersal abilities. These matrices may then be analyzed using variation partitioning methods

426     (see examples below). The frequency of usage of spatial eigenfunction analysis and simple

427     polynomials of geographic coordinates (i.e. distance-based proxies) was likely

428     underestimated in our search. For example, Soininen (2014; 2016) found a total of 322 data

429     sets, which were analyzed with variation partitioning methods (most of which were from

430     lakes and streams). However, many data points in Soininen's (2014; 2016) studies originated

431     from one paper (Cottenie 2005), which was also counted as a single paper in our literature

432     searches. We thus believe that our keyword analysis confidently reveals that use of more

433 elaborate proxies for dispersal (considering, for instance, transport geography proxies) are

434 less frequent than simple and possibly too simplistic proxies. In summary, our keyword

435 analysis indicates the need for further comparative studies to better take dispersal into

436 account in metacommunity studies.

437

**Statistical approaches to model dispersal influences on biological communities**

439

440 There are many spatial statistical approaches to study species distributions and community

441 structure that incorporate physical distance proxies, including the Mantel test (Mantel 1967),

442 eigenfunction spatial analysis (Borcard and Legendre 2002) and related methods (for a

443 comprehensive review, see Legendre and Legendre 2012). For example, the flexibility and

444 usefulness of eigenfunction spatial analysis and other similar methods in spatial modelling

445 have been stressed elsewhere (Griffith and Peres-Neto 2006; Dray et al. 2006; Dray et al.

446 2012), and we briefly emphasize that they deserve their place in community ecologists'

447 toolbox. Eigenfunction spatial analyses allow one to use different types of distance (e.g.

448 overland, watercourse and flow distance), geographic connectivity matrices and information

449 about directional spatial processes (Blanchet et al. 2008; 2011; Landeiro et al. 2011; Göthe et

450 al. 2013a; Grönroos et al. 2013) as inputs to compute eigenvectors (i.e. spatial predictors for

451 univariate regression or multivariate constrained ordination analyses). This offers important

452 flexibility to model complex spatial phenomena (Griffith and Peres-Neto 2006), such as

453 variation of community structure (Dray et al. 2012). However, it has also been suggested that

454 the explanatory variables derived from spatial eigenfunction analysis may overestimate

455 spatial structure and the potential effects of dispersal on biological communities (Bennett and

456  Gilbert 2010; Smith and Lundholm 2010). Also, spatial patterns in metacommunity structure

457  may have emerged due to the effects of environmental variables, which are themselves

458  spatially patterned and, more importantly considering the scope of this review, due to

459  dispersal processes. In short, after controlling for the effects of environmental variables (e.g.

460  using variance partitioning; see Peres-Neto et al. 2006; Legendre and Legendre 2012), the

461  spatial variables can be used to infer the relative role of dispersal processes. In studies of

462  metacommunity structure, this inference is valid only if one assumes that no relevant

463  environmental variables have been overlooked and that the effects of biotic interactions on

464  the spatial patterns of community structure are negligible (Peres-Neto and Legendre 2010;

465  Vellend et al. 2014).

466      Layeghifard et al. (2015) suggested weighting a spatial matrix (be it overland or not)

467  by a dissimilarity matrix derived from a community data matrix. Accordingly, connectivity

468  between a focal site and two other equally-distant sites will not be identical, but are

469  dependent on biological dissimilarity. The more similar the focal site is to one of the sites, the

470  higher is their assumed connectivity (Layeghifard et al. 2015). It is probably possible to

471  modify these methods to accompany more complex relationships between sites in space. For

472  instance, it could be possible to use the suite of distance classes referred to earlier in this

473  review (Table 1). Also, if a gravity model of connectivity is hypothesized to represent

474  dispersal, for instance, from headwaters to mainstreams and the latter accumulates more

475  species, a suitable dissimilarity index may be one that measures species turnover only and not

476  species richness differences (Lennon et al. 2001; Baselga 2010; Legendre 2014).

477

478  *Combining organismal and physical distance proxies in the same modelling study*

479

480     A few studies have considered simultaneously organismal and physical distance proxies. For

481 example, Kärnä (2014) and Kärnä et al. (2015) studied a stream insect metacommunity in a

482 subarctic drainage basin in Finland and examined how physical distance proxies affect

483 different groups of insects defined by body size and dispersal mode. As physical distances,

484 they used (1) overland, (2) watercourse, (3) least-cost path (i.e. optimal routes between sites

485 in landscape) and (4) cumulative cost (i.e. cumulative landscape resistance between sites

486 along the optimal route) distances (Kärnä 2014; Kärnä et al. 2015). They calculated Mantel

487 correlations and partial Mantel correlations between Bray-Curtis biological community

488 dissimilarities and environmental distances or each of the four types of physical distances. In

489 these data, environmental and spatial distances were not strongly correlated, and the results of

490 partial Mantel test were hence very similar to the Mantel tests shown here (Fig. 3). Kärnä et

491 al. (2015) found that environmental distances between sites were most strongly correlated

492 with all biological dissimilarity matrices, as has been shown previously for stream

493 metacommunities (Heino et al. 2015b). However, different types of physical distances were

494 also often significant for different subsets of stream insect assemblages, even when

495 environmental effects were controlled for. A similar pattern has also been found in streams of

496 other climatic zones (Cañedo-Argüelles et al. 2015; Datry et al. 2016b). What is more

497 important is that the more complex cumulative cost distances were either equally good or

498 sometimes even outperformed the typically-used overland and watercourse distances in

499 accounting for variation in biological community dissimilarities between sites, although this

500 varied between different subsets of stream insect assemblages (Kärnä et al. 2015).

501     The approaches using cost distance-based modelling could also be strengthened by

502 the use transport geography proxies. For example, Cañedo-Argüelles et al. (2015), Kärnä et

503   al. (2015) and Datry et al. (2016b) could also have used measures related to 'cumulative

504   opportunities', 'population attraction and competition between destinations' or 'gravity'

505   measures (Table 2) when examining metacommunity organization in streams. For instance, in

506   terms of gravity, nodes in the mainstem of a basin may support large population sizes and,

507   thus, provide much more migrants than small tributaries. We are currently striving to begin

508   applying these measures in our studies of stream metacommunity organization and

509   environmental assessment, and also urge other researchers to focus on these and other

510   relevant proxies in various ecosystem types.

511

512   **Applications of proxies for dispersal**

513

514   *Applied research benefitting from use of dispersal proxies*

515

516   While the importance of dispersal is well appreciated in fundamental ecology, applied

517   research has lagged behind in integrating dispersal effects on biological communities

518   (Bengtsson 2010; Heino 2013a). For example, current bioassessment approaches infer effects

519   of environmental changes using the responses of bioindicators to environmental factors

520   (Hawkins et al. 2000a; Friberg et al. 2011). However, sole reliance on local environmental

521   control (i.e. species sorting) may be misleading (Heino 2013a; Friberg 2014). In species

522   sorting, adequate dispersal guarantees that all species are available at a locale to be filtered by

523   local environmental factors (Leibold et al. 2004; Holyoak et al. 2005). However, high

524   dispersal rates from unpolluted to polluted sites as in source-sink dynamics (Pulliam 1988)

525      may decrease our ability to detect environmental change through the use of bioindicators.

526      Some species indicative of pristine conditions may occur at the polluted site owing to high

527      dispersal rates, even if that site is not favourable for them in the long term, thus masking the

528      influence of anthropogenic changes on local biota. In contrast, owing to dispersal limitation,

529      some pristine reference sites may also lack species that would otherwise occur there, thus

530      affecting bioassessment results. Hence, we support the idea derived from simulation analyses

531      (Siqueira et al. 2014) that potential dispersal effects should be directly integrated in aquatic

532      bioassessment studies (Heino 2013a; Alahuhta and Aroviita 2016).

533      Restoration ecology is another field that might benefit from greater insights about

534      dispersal. Restored sites may lack many species simply because potential donor communities

535      were all impacted by pollution or habitat degradation in a region, and colonization will thus

536      be slow and initially composed mostly of dispersal-prone species (Bond and Lake 2003).

537      Another possibility in this context relates to delayed recolonization of ecosystems that are

538      recovering from anthropogenic stressors due to dispersal limitation (Blakely et al. 2006; Gray

539      and Arnott 2011; 2012). Restoration ecology should thus take into account ecological

540      corridors for dispersal, which might facilitate the recolonization of previously denuded or

541      restored sites (Tonkin et al. 2014). The efficiency of ecological corridors is also dependent on

542      dispersal ability and the spatial configuration of these corridors in the landscape (Joly et al.

543      2001). Hence, rather than restoring only local sites, restoration of connectivity is also a

544      prerequisite for successful local restoration outcomes (see also McRae et al. 2012).

545      Conservation planning is a third field of applied research that should take dispersal

546      directly into consideration. This is because dispersal within and between protected areas

547      should be guaranteed (Jaeger et al. 2014; Barton et al. 2015a), and the network of protected

548      areas should be planned such that they can act as stepping-stones to allow organisms to

549    respond to environmental change (Fahrig and Merriam 1994; Margules and Pressey 2000;

550    Lechner et al. 2015). However, conservation planning is also challenged by the vast numbers

551    of species that should be monitored over broad metacommunities (e.g. Heino 2013a) and

552    macrosystems levels (e.g. Heffernan et al. 2014), which is also exacerbated by the difficulties

553    to measure dispersal over broad spatial scales. As a "science of crisis" (Soulé 1985),

554    conservation biology cannot wait for the development and application of sophisticated, time-

555    consuming and expensive methods of measuring dispersal directly for hundreds to thousands

556    of species and, at least in the short-term, the best we can do is to rely on proxies for dispersal.

557

558    *The importance of integrating dispersal in predictive models of global change*

559

560    Dispersal should be directly considered in predictive models in ecological research. Ecology

561    has become increasingly predictive, most likely due to the need to forecast the effects of the

562    ongoing global change (Evans et al. 2012; Petchey et al. 2015). Over the past decades,

563    several models have been designed to predict how populations, communities or ecosystems

564    will respond to ecological changes in time and space. Predictive models have been used to

565    forecast distributions of species based on their climatic niches using Species Distribution

566    Models (SDMs; Guisan and Zimmerman 2000; Chu et al. 2005) and, for example, to assess

567    ecological status by comparing the observed community in a water body with the one

568    expected under reference conditions (Hawkins et al. 2000a; Clarke et al. 2003). However,

569    despite the wide use of both approaches, predictions can be biased if dispersal is not

570    considered. Suitable habitats can be available for a species, but its real occurrence will

571    ultimately depend on its ability to reach the site.

572       SDMs have been criticized because most of them only consider niche characteristics

573 of species and neglect biotic interactions (Wisz et al. 2013), evolutionary changes (Thuiller et

574 al. 2013) or dispersal processes. Several attempts have been made to incorporate dispersal

575 into SDMs (e.g. Araújo et al. 2006). This is usually done by considering two extreme degrees

576 of dispersal limitation (e.g. no dispersal vs unlimited dispersal) or intermediate situations

577 using probabilistic methods when data on the dispersal abilities of the species are available

578 (Barbet-Massin et al. 2012). Some modelling endeavours have also acknowledged the need to

579 consider barriers to dispersal (e.g. dams) to improve model accuracy (Filipe et al. 2013).

580 Information on current spatial connectivity across populations based on genetic approaches

581 could also be used in SDMs to improve model accuracy (Duckett et al. 2013).

582       A possibility to construct models encompassing responses of multiple species at the

583 same time include the River InVertebrate Prediction And Classification System (RIVPACS),

584 first applied in riverine ecosystems (Wright et al. 2000; Clarke et al. 2003), but which can

585 also be applied in other freshwater, marine and terrestrial ecosystems. There have been no

586 empirical attempts to include dispersal in the practical applications of RIVPACS-type

587 models, but simulations have shown the potential importance of dispersal for bioassessment

588 (Siqueira et al. 2014). At best, some of these types of models consider spatial coordinates (i.e.

589 latitude and longitude) as model predictors, but are usually based on assumptions about the

590 niche characteristics of species (i.e. environmental filtering; Friberg et al. 2011). The

591 importance of using dispersal proxies as predictor variables in bioassessment models is of

592 particular significance in the context of metacommunities (Heino 2013a). This is because the

593 spatial connectivity of sites and the dispersal abilities of the species may hinder the ability of

594 models to detect an impact (Alahuhta and Aroviita 2016). This is especially relevant in less

595 impacted and highly isolated sites (Siqueira et al. 2014). In addition, these sites (e.g. isolated

596 headwater streams) usually host species with narrow ecological niches and distribution

597 ranges, which can also have limited dispersal abilities (Finn et al. 2011). Incorporating

598 organismal and physical distance proxies for dispersal in the metacommunity-level

599 bioassessment could help to increase the accuracy of these models and thus the management

600 of constituent freshwater ecosystems.

601

602 **Questions for further freshwater research**

603

604 The importance of dispersal proxies can be revealed by a number of questions that should be

605 considered in basic and applied freshwater ecology. Although these ideas are somewhat

606 speculative at present, they may provide useful roadmaps for further studies on dispersal

607 proxies in bioassessment, restoration and conservation biology.

608

609 *How important are stepping-stones for dispersal and how they can be recognized?*

610

611 Ecological stepping-stones can be defined as sites or areas that help species to disperse from

612 a site to other suitable sites across inhospitable landscapes. Stepping-stones can be expected

613 to be very important for species dispersal (Saura et al. 2014; Barton et al. 2015a), but their

614 recognition may be difficult. If we can recognize such sites in landscapes by applying

615 organismal and physical distance proxies in combination or based on transport geography

616 measures, there are better possibilities to plan the conservation of metapopulations and

617 metacommunities. For instance, we should be able to recognize sites having high accessibility

618    for multiple species and subsequently plan a network of such sites across a broader

619    landscape.

620        Graph-based modelling can also help if field-based measures fail to highlight the

621    importance of stepping-stones for dispersal (Galpern et al. 2011). For example, network

622    analyses can reveal how connectivity relationships change in the landscape if stepping-stones

623    are deleted from the network of habitat patches. The importance of stepping-stones and other

624    patches can be prioritized using different indices (e.g. Rayfield et al. 2011), which quantify

625    the importance of the focal habitat to maintaining connectivity between the patches (e.g.

626    Pereira et al. 2011). Their more widespread application is warranted, especially for network-

627    like stream systems, where habitat patches and their boundaries may be not so easily

628    recognized (Erős and Campbell Grant 2015).

629

630    *Are very low or very high dispersal rates affecting bioassessment?*

631

632    Dispersal limitation may lead to a situation where not all species are available in reference

633    sites (Pärtel et al. 2011; Cornell and Harrison 2014). A traditional approach has been to use a

634    regional stratification to focus on smaller geographical areas, which could ensure that all

635    species are able to reach all sites within a relatively small region (e.g. Hawkins et al. 2000b)

636    and persist on them (e.g. Cornell and Harrison 2014). This should facilitate the detection of

637    species sorting mechanisms and help define reference conditions. However, temporary local

638    extinctions at suitable sites may not always be counterbalanced by immediate colonization if

639    other suitable sites are located far away from the focal site even within a small region (Heino,

640    2013a) and/or if species have weak dispersal ability. In this case, we may classify sites in the

641    wrong reference site group (or as impacted) if some species that should occur according to

642    environmental conditions are absent from a site. It might be possible to adjust our predictive

643 modelling efforts by using physical distance proxies (see Table 2), which might lead to a

644 better prediction success. Alternatively, we could focus on a subset of good dispersers in our

645 dataset, which should show minor effects of dispersal limitation, or focus on resident species

646 (i.e. those species that do not show strong propensity for migration), which may show

647 stronger associations with environmental gradients than entire assemblages (Bried et al.

648 2015).

649       The mass effects perspective in metacommunity ecology (Mouquet and Loreau 2003)

650 suggests that high dispersal between localities may homogenize, at least to some degree,

651 community structure in adjacent sites. On the other hand, some species may be absent from a

652 site owing to not having been able to reach the site yet due to low dispersal rates or small

653 source population size (Leibold et al. 2004). Either way, it may be difficult to assess if

654 anthropogenic stressors have impacted a site, as extra species may be present or some

655 expected species are missing (Siqueira et al. 2014). This limits our bioassessment by not

656 detecting change correctly. Using information about the species composition of nearby sites

657 might help us to decipher if either high or limited dispersal is affecting our bioassessment and

658 restoration endeavours (Tonkin et al. 2014). These could be quantified by taking

659 simultaneously into account a site's accessibility and relative quality in the landscape, and

660 how it attracts dispersers from the surrounding metacommunity. For instance, the measures

661 from transport geography described above (e.g., gravity or utility measures, Table 2) could be

662 used to show that the lower than expected biological differences between reference and

663 impacted sites are due to their strong spatial connectivity and species exchange in terms of

664 high dispersal.

665

666 *Will species reach all potential future habitats in the face of global environmental changes?*

667

668    Even though environmental conditions change, not all species may be able to track those

669    changes (Heino et al. 2009; Poff et al. 2012). Poor dispersers or those with small source

670    populations may not be able to disperse to suitable new habitats in other areas, at least if not

671    assisted by humans. If such poorly-dispersing species can be identified based on their

672    organismal traits, there are more possibilities for success (Bhowmik and Schäfer 2015). Also,

673    if their actual dispersal routes can be approximated using physical distance proxies, the

674    success of the species for founding self-maintaining metapopulations and metacommunities

675    may be better in the face of global change. For example, global change may lead to increase

676    in temporal fragmentation of river networks, i.e., the degree of intermittency, which should

677    affect the connectivity between stream sites (Datry et al. 2014). Improving our ability to

678    predict changes in stream communities using distance-based proxies accounting for this

679    fragmentation will improve our capacity to assess, estimate and mitigate the effects of global

680    changes on intermittent streams (Datry et al. 2016c).

681

682    *How can the dispersal of invasive species be predicted using proxies?*

683

684    Knowing the dispersal ability of an invasive species (i.e. an organismal-based proxy) helps to

685    predict its rate and potential to spread over large areas. Furthermore, knowing how landscape

686    resistance (i.e. a physical distance proxy) may hinder its spread may have obvious benefits

687    for predicting or preventing its dispersal. In this case, applications of the gravity or utility

688    measures originated from the transport geography might also be useful, as the accessibility

689    and attraction of sites for invasive species could be revealed using suitable proxy measures.

690    Hypothetically, some widely recognized man-made structures that impair dispersal of native

691    species such as dams (Winemiller et al. 2016) might, at the same time, boost the spread of

692    invasive species (Havel et al. 2005).

693

694 *How can we best detect and restore dispersal routes between near-pristine sites?*

695

696 Local populations and communities at near-pristine or pristine sites need to be connected by

697 gene and organism flows in order to remain viable (Fahrig 2003). Conservation and

698 restoration efforts should also target the maintenance of the most efficient dispersal routes to

699 and from these pristine sites, although identifying these routes remains a challenge. Dispersal

700 proxies could offer an efficient tool to identify these routes for all types of species, from poor

701 to strong dispersers, and therefore provide insights to ecosystem managers for designing

702 restoration and conservation projects (Tonkin et al. 2014; Cañedo-Arguelles et al. 2015;

703 Kärnä et al. 2015; Datry et al. 2016a).

704

705 *Can restoration measures fail due to lack of dispersers from neighbouring sites?*

706

707 Restoration practices may not attain the planned objectives, or only attain them after long

708 periods, if species are not able to colonize restored habitats in a strongly human-impacted

709 landscape (Bond and Lake 2003; Tonkin et al. 2014; Barton et al. 2015b). Accordingly,

710 restoration measures should be initially focused on sites connected to non-impacted source

711 habitats or be planned to encompass entire landscapes or catchments that include some source

712 localities (Bond and Lake 2003). Also, restoration practices should be coupled with the

713 restoration of adjacent ecosystems to enhance suitable habitat corridors for dispersing species

714 (Smith et al. 2009). Identifying such habitat corridors using the physical-based or transport

715 geography proxies might be useful in this context.

716

**Where to go from here?**

718

719    Barton et al. (2015a) suggested that ecologists have made little effort to validate the use of

720    proxies in ecology. For example, from a bioassessment perspective, the generally assumed

721    conceptual model (e.g. environmental change → local community structure) suggests that a

722    change in the environment (e.g. pollution) causes a change in local community structure (e.g.

723    changes in species composition and relative abundances of species). However, dispersal

724    disrupts this basic model and, to tease apart this effect, one needs a proxy for dispersal, which

725    would function as a covariate (e.g. environmental change → local community structure ←

726    proxy for dispersal). This covariate should, for instance, take mass effects or dispersal

727    limitation into account. As shown in this essay, there are a number of ways to express the

728    level of spatial relationships between sites and the best way may well be case-specific,

729    depending on a study system, regional environmental conditions, between-site connectivity

730    and characteristics of biotas. Thus, we propose that freshwater ecologists should evaluate and

731    quantify the relationship between the biological dataset at hand and different proxies for

732    dispersal (e.g. organismal-based dispersal traits, Euclidean, watercourse, least-cost path

733    distances, and more). However, for the sake of generality, testing the predictability of

734    different proxies in different regions, with different groups of organisms and in different

735    points in time is also warranted (Barton et al. 2015a). In this context, a promising direction

736    for future work would be to utilize the data from previous studies on bioassessment,

737    restoration, conservation biology and community ecology, with the objective of quantifying

738    the relative importance of different proxies for dispersal using a meta-analytical approach. A

739    second objective would be, after knowing which proxy to use, how to integrate a proxy into

740    practical management of biodiversity. This is an open call for researchers interested in such

741    proxies for dispersal.

742

743    **Conclusions**

744

745    Dispersal proxies include traditional physical distances used in ecological research, such as

746    Euclidean distances, network distances, and various organismal-based proxies, such as body

747    size, dispersal mode and dispersal ability. More recent approaches include graph-based

748    methods, which show considerable promise for freshwater research. Future studies should

749    also consider applying methods developed in other disciplines, such as transport geography.

750    Application of these proxies should not be limited to fundamental ecological research, but

751    they should also be widely considered in applied fields, such as bioassessment, conservation

752    and restoration ecology. As dispersal is an essential element affecting species distributions, it

753    should be communicated to environmental managers and policy makers responsible for

754    practical conservation, management and assessment issues (Barton et al. 2015b). Hence,

755    while dispersal proxies should be efficient enough in capturing dispersal as a phenomenon,

756    they should also be simple enough to be useful in practical solutions. We propose that

757    organismal, physical and transport geography proxies for dispersal should be widely

758    considered as tools guiding environmental management and decision making.

759

760    **Acknowledgments**

761

770

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Table 1. Comparisons of the pros and cons of different dispersal proxies available to study metacommunities.

| Dispersal proxy | Pros | Cons |
|---|---|---|
| **Organismal-based proxies** | More closely related to organisms' traits and thus dispersal per se than physical distances between sites. | Often very coarse measures, as sufficient autecological information is available only for a few species or a few organismal groups. |
| 1. Body size | Very easily obtainable for most organismal groups. | Although body size may be related to dispersal mode and capacity, it is also related to many, if not most, other organismal characteristics and functions. |
| 2. Dispersal mode | Rather easily available information for comparisons of broad organismal groups. | Dispersal mode may not effectively relate to actual dispersal distances or dispersal rates between sites. |
| 3. Dispersal ability | <span style="color:red">Has a strong link to dispersal distances of organisms among sites.</span> | Difficult to obtain information for most organismal groups that cannot be easily tracked. |
| 4. Population genetic structure | Are more direct measures than other organismal-based proxies, and may reveal complex dispersal routes between sites. | Genetic structure can be a biased proxy of dispersal because it not only informs about gene flow among populations, but also about mutation, genetic drift, adaptation by natural selection along environmental gradients and colonization history (i.e. founder effects). Hardly |

|  | feasible for a high number of species at the same time. |
| --- | --- |

**Graph-based proxies**

| **A. Physical distance-based proxies** | Easily measurable from maps when available. | Are coarse proxies that may not always portray true dispersal routes for many species. |
| --- | --- | --- |
| 1. Euclidean distance | Very easily measurable as shortest linear distance between sites. | Not applicable for organisms, such as fish, relying exclusively on riverine corridors for dispersal. |
| 2. Network distance | Distance between sites in a network may be useful if dispersal is restricted to such networks (e.g. riverine networks for obligatory aquatic organisms). | Some species may show more or less unexpected 'out-of-network' dispersal, which cannot be portrayed by network distances between sites. |
| 3. Flow distance | May well model a) upstream vs downstream dispersal in riverine systems or b) headwind vs. tailwind dispersal in terrestrial systems. | It is not always known for how large a portion of species upstream/headwind dispersal is more costly than downstream/tailwind dispersal. |
| 4. Topographical distance | May sometimes model well altitudinal features that may either prevent or facilitate dispersal. Rather easy to obtain from maps using geographic information systems (GIS). | Topographic features in a landscape may be important for terrestrial animals, but may be less important for those able to fly and cross higher landscape features. |
| 5. Cost distances | May be used to model more complex landscape features | Sometimes lack of suitable maps may prevent |

| | | |
|---|---|---|
| | than just topographic characteristics in a landscape. Potentially may be well used to model dispersal routes in heterogeneous landscapes. | calculating more complex cost distances between sites. Also, what, how and when to consider a landscape feature suitable or not suitable for dispersal may be difficult. |
| **B. Transport geography proxies** | Network-specific proxies which can be enhanced by route geometry, travel cost attributes, and pulling and pushing factors, when suitable data are available | Needs topologically correct data and careful calibration of routing data or algorithm, when environment or population specific attributes are applied. |
| 1. Access to network | A simple, binary indicator. | A highly coarse indicator, dependent on how network geometry and connectivity are defined and specified in the first place. |
| 2. Direct network connections or links | A comprehensible indicator expressing the presence of neighbouring localities which can be accessed without passing through other location. | A coarse indicator which does not indicate the distances that need to be travelled. |
| 3. Travel cost to (nearest) destination | A comprehensible indicator expressing the proximity to other locations. | Cannot consider the quality and quantity of accessed locations. |
| 4. Cumulated opportunities | Represents the quantity of accessible locations within a predefined network distance. | The indicator is strongly dependent on the threshold value, and does not take gradual distance decay into account. |
| 5. Potential accessibility, gravity-based | Represents the quantity of accessible locations while taking | The definition of the distance decay function and |

| measures | into account the distance decay associated with travelling in the network, and the attraction of the location. | the attraction values may be difficult. |
| 6. Population attraction and competition between destinations | Allows the determination of the probability for selecting a given destination while taking the distance decay associated with traversal in the network into account. | The definition of the distance decay function and the attraction values may be difficult. |

Table 2. Characteristics of transport geographic accessibility measures (for additional information, see Huff 1963; Kwan 1998; Rietveld and Bruinsma 1998; Páez et al. 2012) and their potential applicability as dispersal proxies in metacommunity ecology.

| Accessibility measure/index (Reference in figure 2) | Description | Formulae* for accessibility | Example case in transport geographic context | Examples of potential applications in metacommunity ecology |
|---|---|---|---|---|
| Access to network (A) | Access or connectivity exists or not | $c = \begin{cases} 0 \ if \ not \ connected \\ 1 \ if \ connected \end{cases}$ | To get value 1, city has to be connected to railway network. | Value 1 indicates that the ecological entity** of a locality is connected to the network. |
| Direct network connections or links (B) | Number of direct connections or links to other nodes in the network | $a = \sum_{j=1}^{n} c_{ij} \, ,$ <br><br> $c = \begin{cases} 0 \ if \ c \ is \ indirect \\ 1 \ if \ c \ is \ direct \end{cases}$ | Amount of direct railway links that connect city to other cities. | Number of direct links connecting particular ecological entity** to other communities. <br><br> E.g. number of species' direct connections to other populations in the dispersal network, which can, for example, consist of streams or terrestrial paths. Value 0 indicates isolated populations, having no direct connections. <br><br> E.g. headwater streams are linked simply to the downstream reach, whereas confluences are linked to three stream reaches (two upstream and one downstream reaches). |

| | | | | |
|---|---|---|---|---|
| Travel cost to (nearest) destination (C) | Least cost path to (most accessible) object | $a = 1/d$ | Travel cost (e.g. time or distance) from the city to the nearest other city. | Travel cost (e.g. time or distance) for fish through riverine corridors from a lake to the nearest other lake. |
| | | | | Travel cost (e.g. time or distance) for a vertebrate through ecological corridors from one protected area to another. |
| Cumulated opportunities (D) | Number of objects within defined travel cost threshold | $a = \sum_{j=1}^{n} A_j \times d_{ij},$ $d = \begin{cases} 0 \ if \ d \geq cost \ threshold \\ 1 \ if \ d < cost \ threshold \end{cases}$ | Number of other cities within certain travel cost. | Number of localities within certain travel cost for actively or passively dispersing aquatic, semi-aquatic or terrestrial organisms. Species opportunities to reach other populations (or communities or metacommunities) through dispersal network depending on species dispersal abilities. |
| | | | | Cost-distance attributes and thresholds may be specified in relation to the characteristics of the ecological entity** |
| Potential accessibility, gravity based | High and/or close opportunities | $a = \sum_{j=1}^{n} A_j \times e^{-\beta d_{ij}}$ | Potential for interaction with other cities in relation to distance, attraction attributes | An insect female's potential to reach suitable habitats in relation to travel cost to other populations within its lifespan. Here, lifespan |

| | | | | |
|---|---|---|---|---|
| measures (E) | provide better potential for interaction in comparison to low and/or distant opportunities | | and interests to move. | can be understood as a species' ability or interest to move in relation to travel cost that can vary during a season (term β in formula). |
| Population attraction and competition between destinations (F) | Probability for selecting an attraction amongst all attractions in the space in competitive situation | $P_{ij} = \dfrac{A_j^{\alpha} d_{ij}^{-\beta}}{\sum_{j=1}^{n} A_j^{\alpha} d_{ij}^{-\beta}}$ | Amount of interaction with a specific city in relation to other cities, by taking distance, attraction attribute and interests to move into account. | Amount of interaction among habitats with variable environmental quality for female insect or migratory bird individuals from a certain population in relation to travel cost within its lifespan. Here, lifespan can be understood as a species' ability or interest to move in relation to travel cost that can vary during a season (term β in formula). |

* Explanation of terms used in formulations: **a** is accessibility related for each origin, c is connecting link between origin and destination nodes, $d$ is travel cost (e.g. distance, time or other measurable friction) between origin and destination nodes, $n$ is number of destination nodes, $A_j$ is attribute wanted to be accessed in destination(s) (e.g. quantified habitat attraction), $i$ refers to (number of) origin and $j$ to destination and $\beta$ is parameter for interest to move in relation to travel cost.

** May be an organism, a species, a group of species (i.e. a community), a specific habitat or a biome.

Table 3. Number of articles (*n*) retrieved according to the Web of Science database (from 01/01/2004 to 26/08/2016) using different combinations of keywords related to the use of dispersal proxies in metacommunity studies.

| Proxies | keywords | *n* |
|---|---|---|
| Organismal-based proxies | "Body size*" AND Dispers* AND metacommunit* | 41 |
| | "Dispersal mode*" AND Dispers* AND metacommunit* | 43 |
| | "Dispersal capacit*" OR "Dispersal abilit*" AND Dispers* AND metacommunit* | 94 |
| | genetic* AND Dispers* AND metacommunit* | 45 |
| | | |
| Physical distance-based proxies | "euclid* distance*" AND Dispers* AND metacommunit* | 6 |
| | "network* distance*" AND Dispers* AND metacommunit* | 0 |
| | "watercourse distance*" AND Dispers* AND metacommunit* | 9 |
| | "flow distance*" AND Dispers* AND metacommunit* | 0 |
| | "Topographic* distance*" AND Dispers* AND metacommunit* | 0 |
| | "cost distance*" AND Dispers* AND metacommunit* | 2 |
| | Mantel AND Dispers* AND metacommunit* | 22 |
| | "Spatial eigenfunction*" AND Dispers* AND metacommunit* | 5 |
| | "Moran* Eigenvector*" AND Dispers* AND metacommunit* | 3 |
| | "principal coordinates of neighbor matrices" AND Dispers* AND metacommunit* | 1 |
| | | |
| Transport geography proxies | "Access to network*" AND Dispers* AND metacommunit* | 0 |
| | "Direct network* connection*" AND Dispers* AND metacommunit* | 0 |
| | "Travel* cost*" AND Dispers* AND metacommunit* | 0 |
| | "Cumulat* opportunit*" AND Dispers* AND metacommunit* | 0 |
| | "Potential accessibility" AND Dispers* AND metacommunit* | 0 |

**Figure captions**

Fig. 1. A schematic figure of potential dispersal routes for species in dendritic systems (light blue colour) among three sites (red dots). **A** describes Euclidean (orange), overland (green) and watercourse (blue) distances; **B** describes cost distance as related to topography (brown) and stream flow resistance (blue); **C** describes two species (light green vs dark green) which have different optimal dispersal routes between sites in relation to the cost imposed by land cover or land use; and **D** describes two optimal dispersal routes for a species in response to the dominant wind direction.

Fig. 2. A schematic figure of transport geographic accessibility measures (Huff 1963; Kwan 1998; Rietveld and Bruinsma 1998; Páez et al. 2012) and their potential applicability as ecological dispersal proxies. The letters (A-F) correspond to the description of the measures of accessibility in Table 2.

Fig. 3. An example of different physical and organismal dispersal proxies in stream insect research (figures redrawn based on results in Kärnä, 2014 and Kärnä et al. 2015). Mantel correlations between Bray-Curtis biological community dissimilarities and environmental distances (based on various local environmental variables) or each of the four types of physical distances are shown. Separate analyses were run for all species, different body size classes and dispersal modes (active or passive). Asterisk indicates a significant correlation. In these data, environmental and physical distances were not strongly correlated, and partial Mantel test were hence very similar to these Mantel tests shown here. See text for further information.
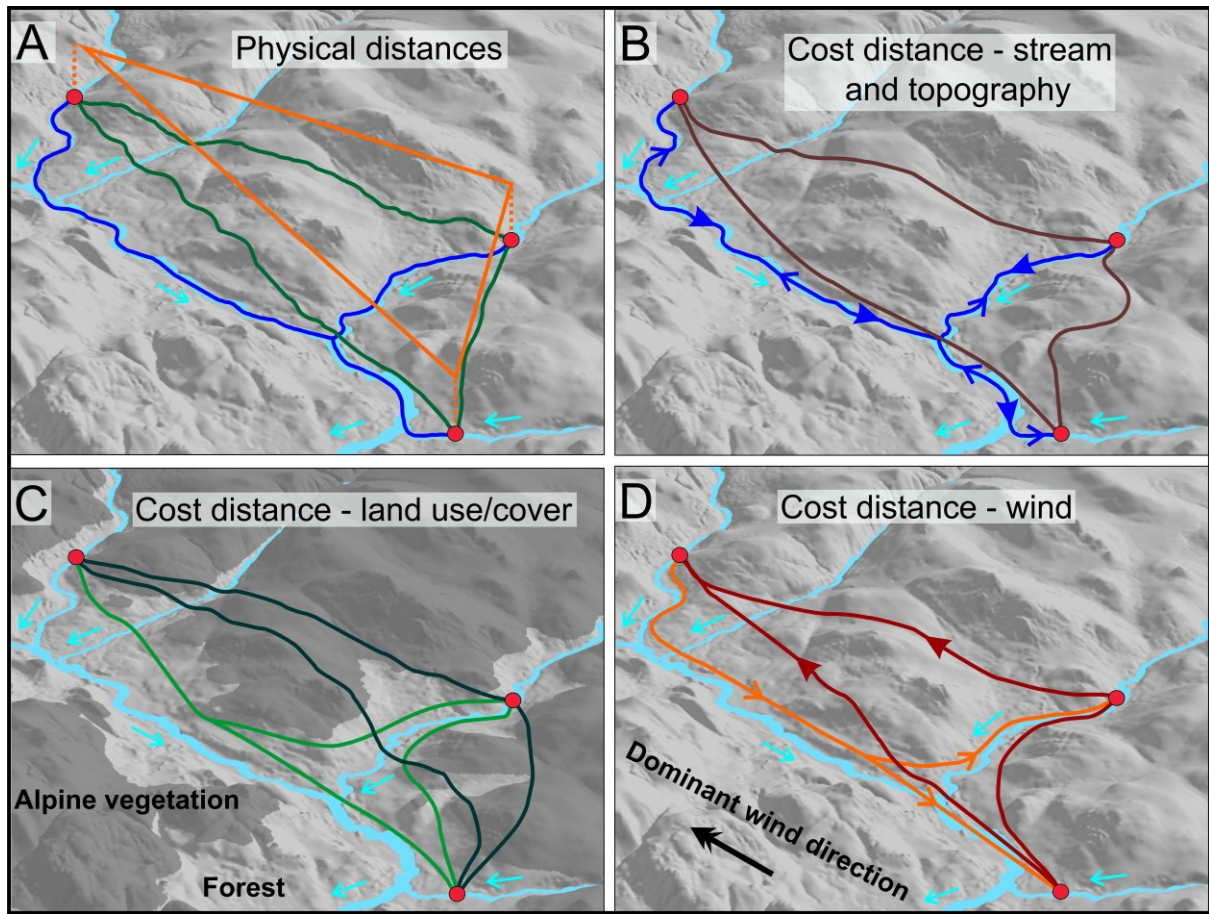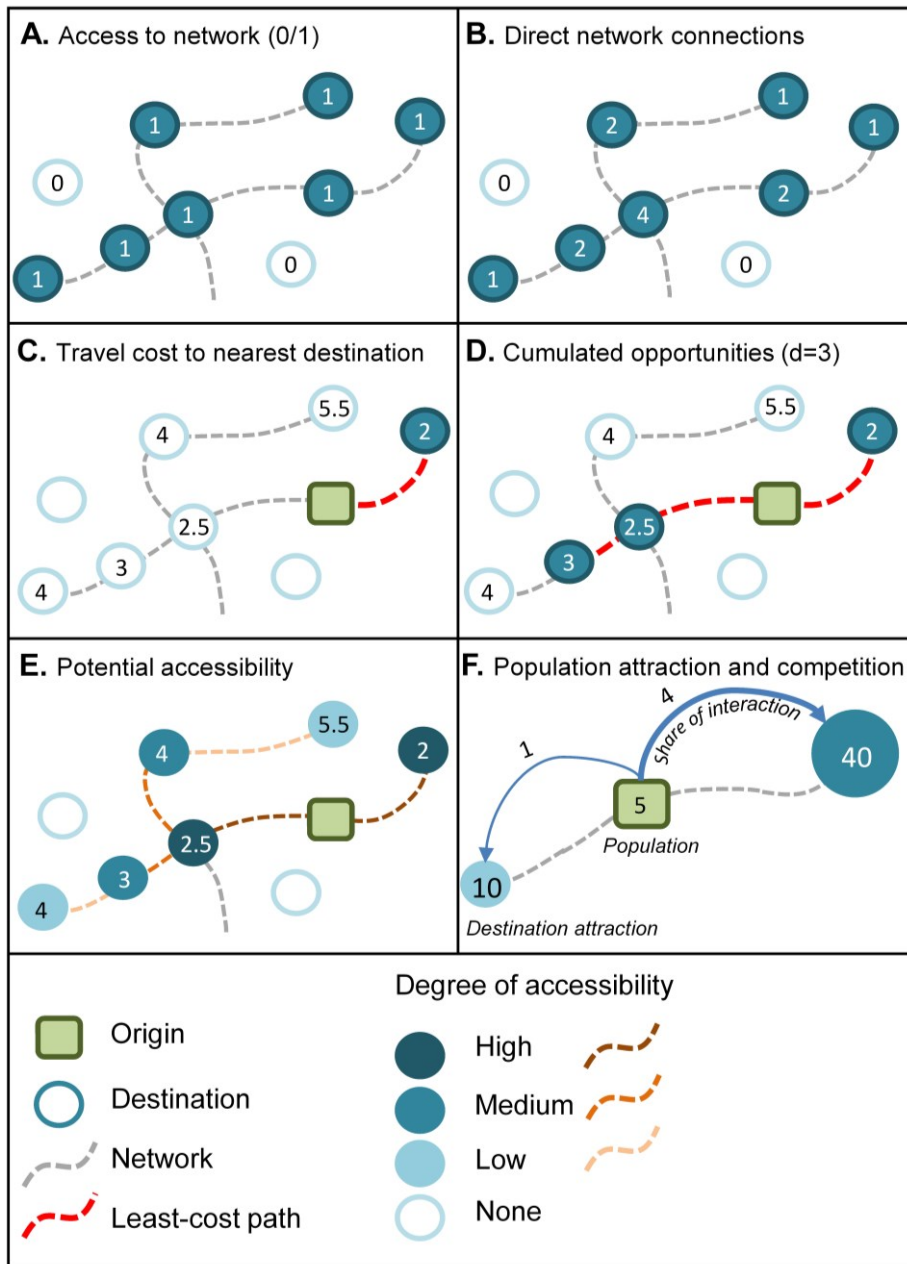
Fig. 1.



A — Physical distances

B — Cost distance - stream and topography

C — Cost distance - land use/cover

Alpine vegetation

Forest

D — Cost distance - wind

Dominant wind direction

Fig. 2.

Fig. 3.