

1 **Social barriers in ecological landscapes: the social** 2 **resistance hypothesis**

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19 **Abstract**

20 Across animal societies, individuals invest time and energy into social interactions. The
21 social landscape that emerges from these interactions can then generate barriers that
22 limit the ability for individuals to disperse to, and reproduce in, groups or populations.
23 Social barriers can therefore contribute to the difference between the physical capacity
24 for movement through the habitat and subsequent gene flow. We call this contributing
25 effect *social resistance*. We propose that social resistance can act as an agent of
26 selection on key life history strategies and promote the evolution of social strategies that
27 facilitate effective dispersal. By linking landscape genetics and social behaviour, the
28 social resistance hypothesis generates predictions integrating dispersal, connectivity,
29 and life history evolution.

30

31 **Keywords**

32 connectivity; dispersal; landscape genetics; reproduction; social environment; social systems

33

34 **The social resistance hypothesis**

35 A central process in ecology and evolution is the transfer of genes from one population
36 to the next. **Gene flow** (see Glossary) depends on movement, typically the **dispersal** of
37 individuals from their natal environment. Physical features of the environments—
38 mountains, deep waters, or lack of suitable habitat—generate barriers that limit the
39 ability for individuals (and their genes) to disperse [1]. However, even after overcoming
40 physical barriers, **effective dispersal** is only realised if an individual that moves to a
41 new **patch** is successful in entering and reproducing in that patch [2]. For social
42 species, the characteristics of the **social system**, such as the organisation of groups
43 and the structure of the social relationships therein, can create additional barriers to
44 movement and breeding [3]. Overcoming social barriers will require different
45 adaptations and will entail different costs than those imposed by physical barriers [4].

46

47 In societies where individuals have to navigate a more complex **social landscape**, the
48 social barriers they face will be more challenging to overcome. A dispersing individual
49 will experience **social complexity** arising from how persistent social relationships are,
50 how related group members are to one another, whether parents give extended care to
51 their offspring, or how promiscuous the mating system is [5, 6]. For example, in many
52 animal populations individuals can form enduring social bonds, with the number and
53 quality of their relationships shaping survival and reproductive success [7]. The
54 importance of maintaining fitness-enhancing social relationships, including coalitions [8],
55 can create resistance towards immigrating dispersers [9], and the need to form new
56 relationships can protract the social integration of immigrants [10-12]. In an extreme
57 example of a social barrier, communities where members are highly related can be
58 completely closed to immigrants and to new breeders, as observed in many eusocial
59 species.

60

61 The barriers introduced by social systems can contribute to differences between where
62 individuals can physically move to and where they can breed. We name this effect
63 **social resistance**. Social resistance includes the barriers individuals face when trying
64 to enter a patch—**entry resistance**—and the barriers they face in forming the social
65 relationships necessary to reproduce within that patch—**breeding resistance**. By
66 affecting the transitions from one **life history stage** to another (Figure 1), social
67 resistance can act as an agent of selection on life history strategies. Possible targets of
68 selection include strategies that enhance lifetime fitness by increasing the chances of
69 offspring to overcome entry and breeding resistance. We call this counter-effect **social**
70 **facilitation**.

71
72 Here, we outline how social resistance emerges by integrating concepts from studies
73 focused on the landscape-scale with concepts from studies focused on behaviour. We
74 synthesise knowledge on how social resistance emerges from aspects of social
75 systems, revealing key areas where social resistance is manifested, the transience
76 phase of dispersal (Box 1), the formation of new relationships after settlement (Box 2),
77 and strategies that facilitate offspring ability to overcome social resistance (Box 3). The
78 social resistance hypothesis facilitates a greater understanding of how physical
79 landscapes interact with social landscapes to shape effective dispersal.

80

81 **Social resistance is a missing link between models of** 82 **dispersal and gene flow**

83 Dispersal has been investigated by population ecologists, landscape ecologists, and
84 behavioural ecologists—each traditionally considering different spatial and temporal
85 scales [13]. The three stages of dispersal [4]—emigration, **transience**, immigration—
86 can be evaluated using myriad demographic and genetic approaches to estimate
87 movement of genes or individuals across space [14] (Figure 2a-b). Genetic-based
88 analytical tools can be used to measure effective dispersal, while tracking individuals [9]
89 or using mark-recapture methods [2] can provide data on dispersal movements [14].

90 Such methods have been successful at linking physical environmental features to
91 dispersal, but have overlooked the additional contribution of the social environment in
92 shaping movement outcomes (Figure 2c-d).

93

94 Dispersal models commonly use the resistance concept to map the propensity for an
95 organism to move through a **physical landscape**. In these models, resistance reflects
96 the physiological costs of moving and/or the decrease in survival probability resulting
97 from dispersal [15]. Resistance modelling involves selecting environmental variables,
98 which are represented as GIS raster surfaces where cells are assigned a resistance
99 score that reflects the physical constraints to movements [16] (Figure 2e-f). Each layer
100 can be parameterised using expert opinion, empirical methods informed by genetic
101 data, habitat data, or species distribution models [17]. Correlating layers against
102 demographic or genetic data [18] allows for the construction of models of **physical**
103 **connectivity** (Figure 2g). Likely movement pathways can be estimated using methods
104 such as least-cost paths and circuit theory [19, 20], representing a spatially-explicitly
105 predictive framework.

106

107 By and large, the structural variables evaluated in resistance models are those that
108 influence the capacity for animals to move between patches of habitat. The social
109 resistance hypothesis captures how social factors within patches can further affect
110 dispersal through entry resistance and effective dispersal through breeding resistance
111 (Figure 2c-d), highlighting that **functional connectivity** is the product of both physical
112 and social factors that influence how animals move through the landscape. Properties of
113 the social environment can be represented as additional layers in resistance models.
114 Layers can represent habitat suitability from a social perspective (Figure 2h), and how
115 the social landscape acts as a filter thereby altering effective dispersal (Figure 2h-i). For
116 example, a social layer can describe resistance arising from territorial boundaries or
117 patterns of kinship among individuals, and can turn suitable habitat into non-habitat
118 matrix. Correlations between layers could reveal whether the physical landscape, such
119 as habitat boundaries, also correspond to social barriers, such as territorial boundaries.

120

121 Layers based on measured movements (e.g. generated from tracking data or genetic
122 data) capture realised movement after the combined effects of physical and social
123 resistance. The difference between the actual transfer of immigrant(s) among patches
124 and the predicted transfer from models of physical connectivity (e.g. a movement cost
125 surface) captures the effects of entry resistance, while the difference between the
126 presence of immigrant(s) in a patch and their contribution to gene flow captures the
127 effects of breeding resistance. A study on the movement restriction and reproductive
128 challenges faced by dispersing Florida snail kites (*Rostrhamus sociabilis plumbeus*) [2]
129 is a good example of the application of the approaches described above for quantifying
130 entry resistance and breeding resistance.

131

132 **How do social systems generate social resistance?**

133 Much is known about how physical features of the landscape affect where individuals
134 can disperse to and subsequently reproduce. In parallel, the study of behaviour is rich in
135 hypotheses about how social behaviour operates within populations [21]. Less is known
136 about how social systems can themselves shape dispersal and subsequent gene flow
137 independently of the physical landscape. Early theoretical work considered links
138 between social behaviour and dispersal movements [22], but focussed on population
139 regulation and was limited by the contemporary understanding of social behaviour [23].
140 Here we outline some predictions of how different components of social systems [6]—
141 social organisation, social structure, mating system and care system—can generate
142 entry and breeding resistance, and modulate effective dispersal (Figure 2b-d).

143

144 ***Social organisation***

145 Social organisation considers patch properties, including the number of individuals, level
146 of relatedness, phenotypic composition and demography, and cohesion [6]. Variation in
147 these properties and, in particular, deviations from optimal values can alter the
148 magnitude of the social resistance experienced by individuals.

149

150 A well-established theory is that of an optimal group size, where the number of
151 individuals in a patch should reflect the balance of social costs, social benefits, and
152 resource availability [24]. We predict that social resistance will be higher for an
153 individual attempting to enter a patch that is beyond the optimal group size than to enter
154 a patch that is currently below its optimal size, because doing so will further decrease
155 the benefit-to-cost ratio for current members [25]. For example, highly territorial
156 southern pied babblers (*Turdoides bicolor*) have an optimal group size of 5-6
157 individuals, and groups smaller than optimal are more inclined to accept immigrants
158 [26]. Optimal group size is linked to resource richness, and the relationship between
159 patch density and resource availability can modulate population regulatory processes by
160 affecting dispersal between patches [22].

161

162 Patches can also have an optimal phenotypic or demographic composition [27]. Two
163 predictions are that patch entry resistance will be greater if an immigrant would change
164 the phenotypic composition by moving it away from the optimal [28], and that breeding
165 resistance will be greater if an individual's phenotype is mismatched to its patch (e.g. via
166 social selection [29]). One such determinant of entry and breeding resistance is sex
167 ratio [30]. Dispersing juvenile Siberian jays (*Perisoreus infaustus*) are more likely to
168 enter groups containing fewer same-sex juveniles [10], potentially to reduce later
169 breeding resistance arising from same-sex competition for the reproductive position.
170 When patches contain fewer individuals, we predict that random fluctuations in sex ratio
171 will increase the potential for sex-based asymmetry in the social resistance experienced
172 by dispersers.

173

174 Relatedness can explain a variety of behaviours through processes such as kin
175 selection and inbreeding avoidance, which, in turn, have consequences for social
176 resistance. One prediction is that individuals with more same-sex relatives in a patch
177 will experience reduced entry resistance into that patch. For instance, juvenile male
178 brown jays (*Cyanocorax morio*) are more likely to immigrate into groups containing a

179 familiar, related male [31]. If patches separated by larger distances are less likely to
180 contain related or familiar same-sex individuals, then dispersers will experience greater
181 social resistance the further they disperse. By contrast, being related to patch members
182 of the opposite sex will result in greater entry resistance. For example, Cunningham's
183 skinks (*Egernia cunninghami*) live in kin-based social groups that select non-related
184 breeding partners [32]. Strong inbreeding avoidance coupled with high within-patch
185 relatedness will therefore lower breeding resistance for unrelated immigrants.

186

187 Finally, we predict that entry resistance will be modulated by social cohesion or the
188 ability for patch members to express collective actions. For example, juvenile brown
189 jays make more exploratory forays into other patches during nest-building [31]; the
190 reduced social cohesion during this period reflecting lower entry resistance. An example
191 of a collective action that can shape individual movement through the physical
192 landscape is territory maintenance. The resulting territory boundaries can represent
193 social barriers that determine where other conspecifics can range [9], thus rendering
194 otherwise-suitable habitat unsuitable for dispersers.

195

196 **Social structure**

197 Social structure refers to the content, quality, and emergent patterns of social
198 relationships among patch members [6]. We identify four ways by which the entry and
199 breeding resistance experienced by individuals will be determined by the extent to
200 which social relationships modulate fitness.

201

202 First, we predict that entry resistance will be lower if there are existing social
203 connections across patches. In social birds [31], primates [33-35] and other mammals
204 [36, 37], juveniles often disperse to groups with whom they have previously had inter-
205 group contact. Reduced entry resistance into familiar groups could be the outcome of a
206 group-level process akin to the 'Dear Enemy' hypothesis [38], which postulates that

207 aggression between neighbouring territory owners (here, groups) decreases with
208 familiarity.

209

210 Second, as long-term social relationships can be crucial for survival and reproduction
211 [7], establishing such relationships will represent a major component of breeding
212 resistance. An example of how familiarity translates to reproductive performance is
213 sleepy lizards (*Tiliqua rugosa*), where familiar pairs mate earlier than pairs formed
214 among previously unfamiliar individuals [39]. We discuss the process of **social**
215 **relationship formation** in Box 2. Reproducing earlier can then generate benefits for
216 offspring, reinforcing the differences among integrated and non-integrated individuals
217 via social facilitation (see Box 3).

218

219 Third, assortative mixing among behaviourally-similar individuals can provide additional
220 barriers. Assortative mixing represents the preference for forming social connections
221 with individuals that have similar characteristics, thus increasing resistance to
222 dispersers that are dissimilar. Particularly high entry resistance exists when behavioural
223 variants, as opposed to space use, mark the social identity of patches [40, 41]. To
224 persist and reproduce after entering a behaviourally-specialised patch, dispersers must
225 adjust their behaviours, such as foraging tactics, dietary preferences, social norms, or
226 communication repertoires, to match those of existing patch members [42]. For
227 example, acoustic patterns are thought to identify social tiers in toothed whales [43],
228 and individuals mostly interact with those who share the same markers, despite
229 overlapping in space with others [44, 45]. Social preferences for behavioural variants
230 can also generate breeding resistance. For example, in songbirds where females
231 display acoustic preferences [46], immigrant males will be less likely to acquire a mate.
232 Assortative mating, and consequent resistance arising from mating preferences, can
233 then shape genetic structure [40, 47].

234

235 A fourth major aspect of social structure that can impact entry and breeding resistance
236 is the dominance hierarchy. In highly-stratified societies, individual progression to a
237 higher dominance rank, and potentially a reproductive position, can require a protracted
238 process of social integration. An example of a society with low entry resistance but high
239 breeding resistance are the leks of *Chiroxiphia* manakins: males that enter can
240 contribute to the cooperative dance that attracts females, but usually do so at the
241 bottom of the lek hierarchy and must wait for years to rise to a reproductive position [48,
242 49].

243

244 Considering that individuals vary in their position within the social landscape suggests
245 that how social resistance is distributed across the physical landscape can vary across
246 individuals. For example, differences in the history of inter-group connectivity, or
247 variation in social markers and social preferences, means that the entry resistance into
248 a given patch could differ for individuals coming from different natal patches. Thus,
249 models of landscape ecology that include social resistance could require individual-level
250 social layers (Figure 2h).

251

252 ***Mating system***

253 Mating systems are characterised by the number of mates per sex and their identity,
254 representing varying levels of promiscuity [6]—monogamy, polygyny, polyandry and
255 polygynandry. The entry and breeding resistance that individuals face can be influenced
256 by these levels of promiscuity.

257

258 Breeding resistance will be highest for the sex that experiences the greatest
259 reproductive skew. By contrast, monogamous systems should generate higher entry
260 resistance (e.g. having to establish a territory). The mating system can also influence
261 which sex evolves to disperse [50], and can therefore determine which sex will
262 experience entry resistance. Both sexes can experience breeding resistance if there are
263 also barriers to reproducing in the natal patch. Further, differences in mating systems

264 between patches could generate a mismatch between the sex of individuals trying to
265 enter a patch and the patch sex ratio [51]. For example, by affecting mate availability,
266 habitat fragmentation changed the mating system of mountain brushtail possums
267 (*Tricosurus cunninghamia*) from monogamy to polygyny [52].

268

269 Breeding resistance can happen via reproductive suppression of patch members or
270 mate choice. In the cooperative breeding system of some mammals, dominants rely on
271 aggressive competition to suppress the reproduction of same-sex subordinates
272 (including newcomers) [53-55]. Similarly, mate-guarding can make it costly for the
273 newcomers to reproduce because access to mates is reliant on winning competitions
274 [53-55]. Long-term studies reveal that competition can translate to large inter-individual
275 variation in lifetime reproductive success. Of 19 female spotted hyenas (*Crocuta*
276 *crocuta*) present in a clan in 1979, only 4 had descendants 30 years later, and these
277 were disproportionately represented by high-ranking females [56]. This example
278 highlights how breeding resistance can prevent some members of a patch from
279 reproducing, resulting in the loss of their alleles from the patch. It further highlights the
280 importance of longitudinal studies for providing data linking social processes with
281 dispersal at intergenerational scales.

282

283 **Care system**

284 Care systems entail the number, identity and relatedness of the individuals that care for
285 the dependent young [6]. Care behaviour is inherently social, and can impact social
286 resistance via direct and inclusive fitness routes; that is, through parental and
287 alloparental investment.

288

289 The longer the parental care period, the more socially resistant a patch will be to
290 dispersers. Extended care-giving makes parents more sensitive to dangers facing their
291 offspring, as evident from female primates clustering with males to prevent new
292 (potentially infanticidal) male immigrants [57]. Care behaviour can also generate

293 breeding resistance. For example, a recently accepted male disperser would have
294 proportionally fewer mating opportunities in a group where the females are caring for
295 young (hence infanticide being a counter-strategy to increase the number of
296 reproductively available females).

297

298 A strategy that can reduce entry resistance for dispersers is allocaring. Protecting or
299 provisioning another patch member's young can strengthen an immigrants' relationships
300 to existing patch members, facilitating their social integration into the patch (e.g. [58]).

301

302 **Social resistance as an agent of selection on life history** 303 **strategies**

304 Social resistance represents the social barriers faced by individuals as they transition
305 from one life history stage into another, over and above the physical barriers to
306 movement. By altering connectivity between patches (Figure 2), social resistance can
307 act as an agent of selection on both social and non-social traits that facilitate individuals
308 navigating the social landscape [59]. Thus, social resistance is inherently linked to life
309 history evolution. Here we highlight how social resistance can select for particular
310 dispersal, delayed reproduction, and parental care strategies that modulate the extent to
311 which connectivity is affected by social resistance.

312

313 The formation of long-term social relationships, or consistent social structures, will
314 increase entry resistance into patches and, in turn, shape dispersal strategies. In
315 particular, entry resistance should select for strategies that shorten the costly transience
316 phase of dispersal [60], such as by exploiting inter-group contacts (e.g. [33, 35]). By
317 doing so, individuals can acquire information about inter-patch connectivity (Figure 2),
318 and thus make more strategic decisions during transience.

319

320 Entry and breeding resistance could also drive the evolution of delayed reproduction if
321 inter-patch connectivity varies according to age or status of the disperser. If there are
322 few opportunities for entry (either into an existing patch or to establish a new patch),
323 which therefore precludes reproducing, then individuals could remain on the natal
324 territory to help their parents raise offspring while waiting for better dispersal
325 opportunities [61]. Thus, gaining indirect fitness is an alternative strategy that can be
326 selected for by social resistance. Further evidence that links social resistance to a later
327 age of reproduction comes from Tasmanian devils (*Sarcophilus harrisi*). The large-
328 scale death of adults from devil facial tumour disease reduced competition at food
329 resources (carrion). Increased *per capita* resources then allowed for earlier sexual
330 maturity and increased rates of precocial breeding [62].

331

332 Finally, social resistance could underpin the evolution of extended parental care.
333 Successfully overcoming social resistance could require the development of social
334 competence [63]. Empirical evidence suggests that early-life social experiences are
335 important for developing social skills. For example, male zebra finches that grew up in
336 richer social environments were better at socially integrating into a new group [64].
337 Remaining in the natal patch can provide opportunities to experience different types of
338 social interactions. The skills accrued from early-life experiences could select for
339 extended parental care.

340

341 As the social component of an individual's life becomes more strongly linked to its
342 fitness (i.e. layers of social resistance are better at predicting effective dispersal than
343 layers of physical resistance), selection will favour strategies to effectively navigate the
344 social landscape. Such strategies include an individual's own ability to overcome social
345 resistance (e.g. dispersal ability) as well as parental strategies that facilitate offspring's
346 ability to overcome social resistance (see Box 3).

347

348 **Concluding remarks and implications**

349 Social resistance is a prevalent natural phenomenon that is largely overlooked in
350 landscape ecology (see Outstanding Questions). The social resistance hypothesis will
351 improve understanding the differences between the physical connectivity among
352 patches and gene flow. Addressing social resistance requires integrating research that
353 spans in scale from the landscape (i.e. how the physical environment affects the ability
354 for individuals to move) to the patch (i.e. how social factors affect individuals' tendencies
355 to enter a patch and breed). Such integration is possible by adding social layers to
356 landscape models of connectivity (Figure 2e-i). A first step to identifying the importance
357 of social resistance in a system is to study the difference between the predicted
358 movements of individuals, given the physical features of a landscape, and the actual
359 movement of individuals. Long-term studies are likely to be rich resources for
360 characterising what social factors explain this difference, and whether it can be
361 attributed to social resistance.

362

363 Studying social resistance will benefit behaviourists by providing landscape
364 perspectives on theoretical models of behaviour [65] and landscape ecologists by
365 making models of landscape genetics [4, 13, 66] more predictive. For example, studying
366 social resistance will be critical in an increasingly changing and fragmented natural
367 world. Changes in habitat characteristics impact connectivity and resource distribution,
368 which in turn can alter movements [67] and social interactions among individuals [68],
369 with consequences on parameters of social systems (including territoriality, mating
370 systems, and sex-biases in dispersal [51, 67, 69, 70]). Further effects could arise from
371 the dispersal process itself. For example, immigration can generate social instability
372 within a patch [71] and affect the function of its members [72]. An extreme outcome
373 could involve forcing juveniles that would otherwise remain within the natal patch to
374 disperse [12], which could manifest as an increased intensity of movement through the
375 non-habitat matrix. Altering the state of social systems can present new and unexpected
376 levels of social resistance, resulting in dynamic interactions between the physical and
377 the social landscapes.

378 **Box 1. Transience: dispersing through social landscapes**

379 Dispersal is a major driver of population dynamics, connectivity, and gene flow [1, 73,
380 74]. Social resistance is likely to act strongly on dispersal. Local density [75], dominance
381 rank [35], social cohesion [76, 77], or differences in personality [78], can determine
382 individual decisions to emigrate from the natal patch or decisions about which patch to
383 settle into. However, how transient individuals navigate through the social landscape
384 during dispersal remains largely overlooked (reviewed in [4, 79]). Transience is a crucial
385 period because it represents the stage when individuals are most likely to gather and
386 respond to new information and novel environments [79]. It is also when we can
387 observe, in real time, how dispersing animals experience and respond to social
388 resistance.

389

390 Social resistance could affect transience in two ways: by shaping where individuals can
391 establish a new patch, or by determining entry into an existing patch. In Kalahari
392 meerkats (*Suricata suricatta*), evicted cohorts of females that fail to rejoin their natal
393 group (even when the strength of intra-group resistance is relaxed after the breeding
394 period), must avoid territories of unrelated groups and find space free of conspecifics
395 before they can establish a new group [9]. While successful dispersal in meerkats
396 results in the formation of new groups, in many other species the transience phase
397 involves having to penetrate an existing patch. The stronger and more long-lasting
398 relationships are within a patch, the more challenging it is likely to be for an immigrant to
399 enter. Observations from baboons suggest that the process of overcoming entry
400 resistance can take months to years [80]. Prolonging the time individuals spend
401 transitioning from one patch to another can translate to higher mortality (e.g. via
402 predation) [81], thereby strengthening the potential for entry resistance to act as an
403 agent of selection on dispersal strategies.

404

405

406 **Box 2. Social relationship formation: overcoming social**
407 **resistance to reproduction**

408 Despite increasing evidence linking social relationships beyond mating partners to
409 survival and reproduction (e.g. [7]), little is known about the process by which such
410 functionally-important social relationships are formed, especially after immigrants enter
411 a new patch [82]. Forming social relationships can be a protracted process.

412 Observations of chimpanzees (*Pan troglodytes*) suggest that relationships require
413 weeks, if not years, to form [83]. A key hypothesis regarding relationship formation
414 suggests that individuals can initially avoid investing in costly affiliative behaviours,
415 when reciprocity is not guaranteed, by “testing the waters” [84]. That is, they can initially
416 engage in less costly social interactions, and then “raise the stakes” to more costly
417 social behaviours over time as the relationship strengthens. Evidence from vampire bats
418 supports this hypothesis, with individuals introduced into new social groups first
419 establishing grooming relationships before switching to food-sharing relationships if the
420 former are reciprocated [85].

421

422 A second key hypothesis comes from structural balance theory [86], which proposes
423 that the ratio of positive to negative relationships among triads (every possible set of
424 three individuals in a patch) is important in maintaining social stability at the patch-level.
425 For example, if individuals A and B have a strong social relationship and a third
426 individual C develops a new relationship with A, but is rejected by B, then the triad will
427 be unbalanced because A and B are not unanimous in their relationship towards C. In
428 rock hyraxes (*Procavia capensis*), the presence of pre-existing balanced triadic
429 relationships limits the ability for immigrants to form relationships and overcome
430 breeding resistance [87].

431

432 Finally, linking structural balance theory to the raising-the-stakes hypothesis highlights a
433 further challenge if immigrants are not only required to establish reciprocated social
434 relationships with one individual, but also that individual’s social associates. Given the

435 investments needed to become integrated into a patch, both in terms of time and costly
436 behaviours, immigrants are likely to face significant breeding resistance even after
437 entering a new patch.

438

439 **Box 3. Social inheritance: maximizing offspring success**

440 Navigating the social environment is challenging. Therefore, selection should favour
441 mechanisms that facilitate offspring's ability to overcome social resistance, such as
442 increasing social competence [63] or via the inheritance of beneficial social traits, such
443 as dominance rank [88]. "Silver spoon" effects, by which individuals who develop under
444 favourable circumstances receive fitness benefits later in life [89], can have far-reaching
445 consequences in social species. Pre-natal effects, through genetic inheritance [90] and
446 maternal effects [91], can predispose offspring for success in a social landscape from
447 the moment they are born. One example of non-genetic **social inheritance** is through
448 the timing of breeding. If dominant individuals in seasonal systems can monopolise
449 access to breeding resources (e.g. food, nesting sites, or mates) that allow them to
450 reproduce earlier than subordinates, then their offspring can gain a developmental
451 head-start over their peers. These early-life advantages have been shown to confer
452 lifelong benefits for survival, reproduction and adult dominance across many species,
453 including crested ibis (*Nipponia nippon*) [92], pukeko (*Porphyrio melanotus*) [93], bison
454 (*Bison bison*) [94], and primates [7]. Such advantages reducing breeding resistance can
455 then generate a positive feedback by which dominant lineages are inherited and
456 maintained [56, 95].

457

458 Offspring can also benefit from parental support via post-natal social interactions,
459 especially in species with extended parental care [96]. Maternal and kin-based
460 coalitionary support in dominance interactions can predict offspring acquisition of social
461 rank. For example, in spotted hyenas (*Crocuta crocuta*), strong dominance hierarchies
462 among females are maintained through maternal support of offspring which allow young

463 females to be dominant over other adults that are subordinate to their mother,
464 irrespective of other traits like body mass [97, 98].

465

466 Social inheritance mechanisms can ultimately play a role in determining an individual's
467 dispersal and reproductive success. In spotted hyenas, male dominance rank is largely
468 determined by asymmetries in social support, with immigrant males typically receiving
469 less support than resident males [98]. Among dispersers, offspring of higher-ranking
470 parents can maintain better condition [99], and individuals with better body condition are
471 more likely to settle and breed in higher-quality patches [100]. As such, social
472 resistance should drive the evolution of social strategies that allow individuals to
473 facilitate their offspring's chances of overcoming entry and breeding resistance.

474

475 **Glossary Box**

476 **Breeding resistance:** The extent to which social factors limit an individual's ability to
477 breed in a patch. This could be either in the natal patch (potentially forcing dispersal) or
478 in the destination patch (after entry).

479 **Dispersal:** The process of moving between patches. Does not need to imply permanent
480 or long-term establishment or successful reproduction in a destination patch. Typically
481 involves three phases: departure (emigration), transience (movement), and settlement
482 (immigration).

483 **Effective dispersal:** The successful entry of, and breeding by, individuals into a new
484 patch. Requires overcoming entry resistance and breeding resistance to contribute to
485 gene flow.

486 **Entry resistance:** The extent to which social factors prevent a disperser from joining a
487 patch.

488 **Functional connectivity:** The extent to which physical connectivity together with
489 behavioural responses shape dispersal.

490 **Gene flow:** The inter-generational transfer of genetic material from one patch to
491 another.

492 **Life history stages:** Represents the major stages in an organism's life as determined
493 by function. We consider three life history stages: development, settlement, and
494 reproduction.

495 **Patch:** A discrete unit in the physical or social landscape. In a physical context, a patch
496 represents a relatively homogeneous habitat area that is different from its surroundings.
497 In a social context, a patch is a set of individuals that have a close functional link to
498 each other. Habitat patches and social patches can scale independently; a social patch
499 can encompass multiple habitat patches, or a habitat patch can contain multiple social
500 patches.

501 **Physical connectivity:** The structural configuration of landscape features that allow or
502 restrict individual movement between patches.

503 **Physical landscape:** Geographical areas that are heterogeneous in terms of
504 resources, habitat types, physical features, and structural characteristics.

505 **Social complexity:** Is often viewed as the emergent properties of a system arising from
506 repeated interactions among individuals, often the same ones, and across contexts.
507 Complexity can come in the form of strongly differentiated relationships among typically
508 unrelated individuals, or in the form of interactions typically taking place among kin. In
509 the context of social resistance, social complexity can be viewed from an individual's
510 perspective, expressed in terms of how challenging it is for the individual to navigate
511 social interactions, and to make appropriate social decisions throughout its lifetime.

512 **Social facilitation:** Parental investments that increase the chances that offspring
513 overcome social resistance to join the breeding population.

514 **Social inheritance:** Non-genetic mechanisms allowing the transmission of social traits
515 from parent to offspring.

516 **Social landscape:** The set of individuals, and the social relationships among them, in a
517 given environment.

518 **Social relationship formation:** The social integration into patches and development of
519 affiliations essential for reproduction.

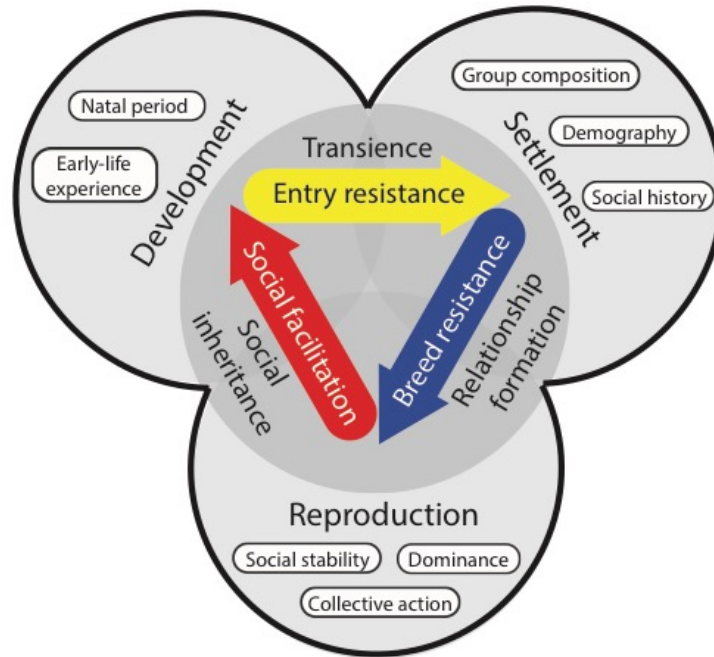
520 **Social resistance:** The contribution of social processes to differences between the
521 physical connectivity and the effective dispersal between patches.

522 **Social system:** Social characteristics determined by four components: social
523 organisation (referring to the size and composition of social units), social structure
524 (referring to the content, strength, and temporal stability of interactions among

525 individuals that result in social relationships), mating system (referring to the identity and
526 number of sexual mates that individuals have), and care system (referring to who cares
527 for, and how related they are to, the dependent young).

528 **Transience:** Period between departure from the natal patch and settlement in the
529 destination patch.

530



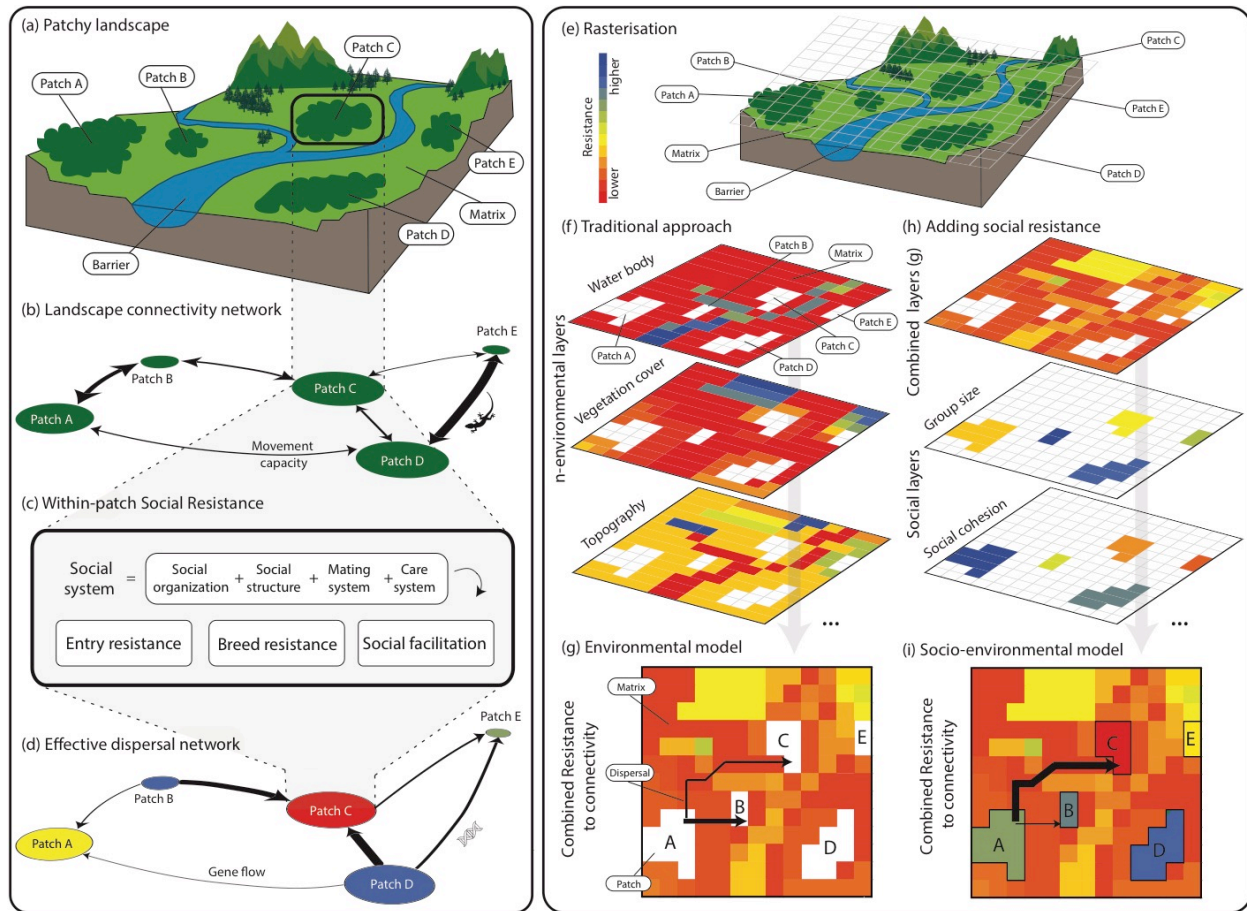
531

532 **Figure 1. Social resistance affects the transition between key life history stages—**

533 **development, settlement, reproduction.** Dispersers need to find and settle into new
 534 patches. The process of doing so, or transience, is shaped not only by the physical
 535 environment, but also by social characteristics of potential patches into which they
 536 attempt to enter (Box 1). These social barriers to entry represent entry resistance
 537 (yellow arrow). Once individuals overcome entry resistance, whether they reproduce is
 538 determined by their ability to integrate into the social group, which is affected by the
 539 within-patch social environment (Box 2). The barriers to reproduction represent
 540 breeding resistance (blue arrow). Selection arising from entry and breeding resistance
 541 should favour parental strategies, such as an extended parental care or coalitional
 542 support, that increase offspring's ability to overcome entry and/or breeding resistance
 543 (Box 3). The response to selection arising from social resistance is called social
 544 facilitation (red arrow). White boxes give examples of some of the social characteristics
 545 of patches.

546

547



548

549 **Figure 2. Within-patch social environments affect functional connectivity across**

550 **landscapes.** (a) Physical landscapes are patchy, here illustrated by a terrestrial

551 environment containing patches within a matrix intersected by physical barriers (e.g.

552 river, mountains). (b) The landscape can be represented as a weighted network of

553 suitable patches, where some pairs of patches are strongly connected (thicker arrows)

554 and others are more weakly connected (thinner arrows) due to physical barriers (e.g. B

555 to A vs. B to C). (c) Patches can also have higher or lower social resistance.

556 Characteristics of social organization and structure, and the mating and care systems

557 can impose challenges for a disperser to penetrate (entry resistance) a patch and

558 reproduce (breeding resistance) within it. (d) Accounting for social resistance can

559 change the predicted effective dispersal (e.g. despite physical barriers, patch C is the

560 least resistant patch to effective dispersal whereas patch D is the most resistant). Thus,

561 when social resistance is strong, there is a greater disconnect between the ability for

562 individuals to move across the non-habitat matrix and their subsequent reproduction in

563 patches. (e) In landscape resistance models, the physical landscape is rasterised. (f)
564 Environmental layers (here, river stream, vegetation cover and topography) can be
565 parameterised, and (g) a physical connectivity model can be generated to describe the
566 probability of dispersal (arrows) between patches due to environmental features alone.
567 (h) Social layers representing the patch social environment (here, group size or social
568 cohesion), either for an entire population, for a given class, or independently for each
569 individual, can be added to resistance models (i). Resistance can then be quantified
570 from the combination of social and physical layers (see [9]).

571

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