# Interacting populations in heterogeneous environments

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**Abstract**

To optimally manage a metapopulation, managers and conservation biologists can favor a type of habitat spatial distribution (e.g. aggregated or random). However, the spatial distribution that provides the highest habitat occupancy remains ambiguous and numerous contradictory results exist. Habitat occupancy depends on the balance between local extinction and colonization. Thus, the issue becomes even more puzzled when various forms of relationships - positive or negative co-variation - between local extinction and colonization rate within habitat types exist.

Using an analytical,model we demonstrate first that the habitat occupancy of a metapopulation is significantly affected by the presence of habitat types that display different extinction-colonization dynamics, considering (i) variation in extinction or colonization rate and (ii) positive and negative co-variation between the two processes within habitat types. We consequently examine, with a spatially-explicit stochastic simulation model, how different degrees of habitat aggregation affect occupancy predictions under similar scenarios. An aggregated distribution of habitat types provides the highest habitat occupancy when local extinction risk is spatially heterogeneous and high in some places, while a random distribution of habitat provides the highest habitat occupancy when colonization rates are high. Because spatial variability in local extinction rates always favors aggregation of habitats, we only need to know about spatial variability in colonization rates to determine whether aggregating habitat types increases, or not, metapopulation occupancy. From a comparison of the results obtained with the analytical and with the spatial-explicit stochastic simulation model we, finally, determine the conditions under which a simple metapopulation model closely matches the results of a more complex spatial simulation model with explicit heterogeneity.

**Keywords:** Metapopulation models, heterogeneity, habitat distribution, population viability, occupancy, spatially-explicit.

# 1. Introduction

Metapopulation models are important tools for choosing management options for threatened or declining species (Gyllenberg and Hanski, 1997; Hanski, 1999; Hanski and Ovaskainen, 2000; Reed, 2004; McCarthy et al., 2005, Nicol et al. 2010; Ross and Pollet, 2010). They predict the dynamics of structured populations driven by two processes: local extinction and colonization. However, assumptions inherent to most of these models, uniform local extinction risk and homogenous colonization, are not applicable to most species. Although the effect of distance upon colonization and the density-dependent risk of local extinction have been incorporated into metapopulation models (Hanski, 1999; Hanski and Ovaskainen, 2000, Stover et al., 2011), spatial variations in local extinction and colonization events can occur in many other ways. Indeed, as showed by Poethke et al. (2003), local extinction risk and colonization rates can display positive, negative or even more ambiguous correlations in space.

Within the range of a species, local extinction risk can vary from patch to patch due to the heterogeneity of the environment (May, 1973; Lande, 1993; Isaac and Cowlishaw, 2004; Melbourne and Hastings, 2008; Cowlishaw et al., 2009) or due to environmental stresses, human activities or density (Wright and Reeves, 1992; Koh et al., 2004; Cardillo, 2005). Similar to local extinction rates, colonization rates can be variable in space. In heterogeneous environments, habitat quality differs which creates variation in habitat productivity and very productive populations (sources) are more likely to colonize other less productive patches (sinks) (Pulliam, 1988; Morris, 1991; Kawecki, 1995; Holt, 1996; Saether et al., 1999). Another source of spatial variability in colonization rate has been observed for several species when dispersal is driven by prevailing winds, ocean and river currents (Roberts, 1997; Gornall et al., 1998; Cowen et al.,

72 2000; James et al., 2002; Thorrold, 2006; Cheal et al., 2007; Bay et al., 2008; Shima and
73 Swearer, 2009, Kininmonth et al., 2011).

74 Various forms of relationships between local extinction and colonization rate have been
75 described. Positive correlation between local extinction and colonization rates is a commonly
76 used assumption in metapopulation models where the number of colonizers is proportional to the
77 area of a patch and extinction probability decreases with patch area (Hanski, 1999; Hanski and
78 Ovaskainen, 2000). In this case large habitat patches have low local extinction rate and send
79 more colonizers, while small habitat patches are more prone to extinction and send less
80 colonizers. However, negative correlation between local extinction and colonization rates has
81 been shown in amphibian and insect metapopulations (Gulve, 1994; Roff, 1994; Denno et al.
82 1996; Hill et al., 1999; Bowler and Benton, 2005) as well as experiments in artificial
83 metapopulations (Friedenberg, 2003). Individuals leave habitat types with high local extinction
84 risk and stay in habitats where extinction risk is low, resulting in an increase in the number of
85 colonizers sent by a population with high local extinction rate (Johnson and Gaines, 1990;
86 Wiener and Tuljapurkar, 1994; Olivieri et al., 1995; Clobert et al., 2001; Mathias et al., 2001).
87 Similarly, evolutionary models support the notion that a negative correlation between local
88 colonization and extinction rates might be common (Poethke et al., 2003; Ronce, 2007). Indeed,
89 within a metapopulation, high local extinction risk creates habitat patches with underexploited
90 resources. Therefore, colonizers from overcrowded habitat have an opportunity to become a
91 founder of a new population in underexploited or empty habitat. High colonization rate might
92 thus be favored in populations where local extinction rate is high, while populations that undergo
93 low extinction rate might also have low colonization rate.

94 Given the diversity of extinction-colonization dynamics that is expected to be found in a
95 metapopulation, it is surprising that the impact of these processes on species persistence and
96 habitat occupancy is rarely investigated. Even more importantly, populations with different local
97 extinction-colonization dynamics are expected to coexist in the same metapopulation in many
98 circumstances. Indeed, local habitat characteristics (quality, disturbances, etc.) can drive local
99 population dynamics and, in heterogeneous environment, the spatial variability of habitat
100 characteristics can be high. Therefore, the question of their spatial distribution appears to be
101 determinant to estimate metapopulation persistence with accuracy.

102 The types of spatial distribution of habitats that provides the highest habitat occupancy remains
103 ambiguous and numerous contradictory results exist. Indeed, recent studies showed that it is
104 beneficial to improve the quality of some groups of habitat patches to prevent them from high
105 extinction risk even at the cost of having others at low quality (North and Ovaskainen, 2007;
106 Theodorou et al., 2009) – a kind of subpopulation triage (McDonald-Madden et al., 2008). Other
107 studies have shown a decrease in metapopulation persistence when local extinction risk is
108 spatially aggregated (e.g. Ovaskainen et al., 2002; Johst and Drechsler, 2003; Vuilleumier et al.,
109 2007) or when the population or environmental characteristics are autocorrelated (e.g.
110 Tuljapurkar, 1982; Petchey et al., 1997; Pike et al., 2004; Tuljapurkar and Haridas, 2006). Those
111 studies argue that a local population should benefit from being surrounded by populations with a
112 low extinction probability that are likely to provide colonists. Thus, a random distribution of
113 habitat patches may be the best spatial configuration to prevent local population extinction
114 because all patches are likely to have near neighbours that have both low extinction rates and
115 provide many colonists.

116 Here, we use a simulation model, to understand how habitat occupancy in a metapopulation is
117 affected by the spatial heterogeneity, spatial variation and local co-variation in local extinction
118 and colonization rates within a habitat type. We also document the reliability of predictions of
119 analytic metapopulation models if there is undescribed spatial heterogeneity. The answers to
120 these questions give new insights on the persistence of species in heterogeneous and stochastic
121 environments.

122 ## 2. Metapopulation models

123 ### 2.1 Analytical metapopulation model

124 The dynamics of a metapopulation have been described first by Levins (1969, 1970) in an island
125 model in which *n* equivalent patches have the same probability of colonizing any of the *n-1* other
126 patches. The time-continuous and deterministic model describes the change in the fraction of
127 occupied patches p, considers local extinction rate (*e*) and colonization rate (*c*).

128 $$\frac{dp}{dt} = cp(1-p) - ep \quad . \qquad (1)$$

129 The positive equilibrium value for the proportion of occupied habitat is

130 $$p^* = 1 - \frac{e}{c} \quad . \qquad (2)$$

131 This model assumes homogeneity in extinction and colonization rate. Thus, we also consider a
132 finite heterogeneous metapopulation composed of *n* patches in which two habitat types are
133 present in equal proportion each with specific local extinction rates ($e_1, e_2$) and colonization rates
134 ($c_1, c_2$). The colonization rate characterizes the number of colonizers that a population of one

habitat type successfully sends to colonize another habitat. The evolution of the proportion of occupied patches in habitat type 1, $p_1$ ,and in habitat type 2, $p_2$ , can be described as follow:

$$\begin{aligned} \frac{dp_1}{dt} &= c_1 p_1(1-p_1) + c_2 p_2(1-p_1) - e_1 p_1 \\ \frac{dp_2}{dt} &= c_2 p_2(1-p_2) + c_1 p_1(1-p_2) - e_2 p_2 \end{aligned} \tag{3}$$

Note that $p_1 + p_2 = p$ . The dynamic described by this equation can be interpreted as follow: Each habitat patch (habitat 1 and habitat 2) can be in one of the two states: occupied or empty. An occupied habitat patch becomes empty according to its extinction rate (habitat 1 has an extinction rate of $e_1$ , habitat 2 has an extinction rate of $e_2$ ). An occupied habitat patch can re-colonize an empty habitat (at rate $c_1$ for the habitat 1 or $c_2$ for the habitat 2). From this change of state, we characterize the proportion of occupied patches for the two habitat types.

When local extinction and colonization rates differ between the two habitat types, $e_1 \neq e_2$ , and $c_1 \neq c_2$ solutions of Eq. 3 can be found for positive occupancy in both habitat types, $p_1^*,\ p_2^* > 0$,

$$\begin{aligned} p_1^* &= \frac{c_1(2e_2 - e_1) + e_1\left[c_2 - e_2 + e_1 \pm \sqrt{c_1^2 + (c_2 + e_1 - e_2)^2 + 2c_1(c_2 - e_1 + e_2)}\right]}{2c_1(e_2 - e_1)} \\ p_2^* &= \frac{c_2(2e_1 - e_2) + e_1\left[c_1 - e_1 + e_2 \pm \sqrt{c_1^2 + (c_2 + e_1 - e_2)^2 + 2c_1(c_2 - e_1 + e_2)}\right]}{2c_2(e_1 - e_2)} \end{aligned} \quad . \tag{4}$$

When local extinction rates are equal, i.e. $e_1 = e_2 = e$, but colonization rates differ between habitat types, the solution of equation 1 for $p_1^*,\ p_2^* > 0$ simplifies to the Levin's result with twice the number of patches and an average colonization rate:

150 $$p_1^* = p_2^* = 1 - \frac{e}{c_1 + c_2} \quad . \qquad (5)$$

151 When colonization is the same between habitat types, $c_1 = c_2 = c$ , but local extinction varies

152 between habitat types, $e_1 \neq e_2$ equation 4 becomes:

153 $$p_1^* = \frac{e_1{}^2 + 2ce_2 \pm e_1\left[\sqrt{4c^2 + (e_1 - e_2)^2} - e_2\right]}{2c(e_2 - e_1)}$$
$$p_2^* = \frac{e_2{}^2 + 2ce_1 \pm e_2\left[\sqrt{4c^2 + (e_1 - e_2)^2} - e_1\right]}{2c(e_1 - e_2)} \qquad (6)$$

154 Using equations 4-6 we can explore the effect of positively and negatively correlated local

155 extinction and correlation rates between habitat types and within habitat type on patch

156 occupancy.

157 **2.2 Spatially explicit metapopulation simulation model**

158 To investigate the impact of the spatial distribution of the two habitat types on patch occupancy,

159 we use a spatially explicit Markovian stochastic model that describes the evolution of habitat

160 patch occupancy in discrete time. The metapopulation is composed of eighty patches with an

161 equal proportion of two habitat types, labeled 1 and 2. Habitats types are distributed in an 8 by

162 10 grid (with absorbing boundaries, Fig. 1) and differ in their susceptibility to local extinction, $e_i$

163 , and how they produce colonists. Occupied patches can re-colonize adjacent empty patches,

164 according to a per time step probability, $c_i$ (stepping stone migration pattern), that depends on

165 the source habitat type *i*. With this model, we explore how the proportion of occupied patches is

166 affected by the extinction-colonization dynamics described above considering three levels of

167 aggregation of two habitat types (Fig. 1). In the *Random* pattern, habitat types are randomly

168 distributed so that the neighbourhood of any patch is statistically the same. In the *Partially*
169 *Random* pattern, the environment is divided into two areas (e.g. North and South) and habitat
170 type 1 has a 75% chance of being on the northern area and 25% of being on the southern area
171 (the reverse is true for habitat 2). In the *Aggregated* spatial pattern, complete division of habitat
172 types exists; habitats of type 1 are only in the northern area while habitats of type 2 are in the
173 southern area.

174 **2.3 Model investigations**

175 Habitat occupancy obtained within the heterogeneous metapopulation will be compared with
176 analytic solutions to the basic metapopulation model that assumes homogeneity and
177 heterogeneity in extinction and colonization rate when there is (see also Table 1): (i) variation in
178 local extinction rates between habitats, (ii) variation in colonization rates between habitat types,
179 (iii) positive co-variation between local extinction and local colonization rates within a habitat
180 type and (iv) negative co-variation between local extinction and colonization rates within a
181 habitat type. In order to estimate total patch occupancy in the homogeneous metapopulation
182 model (eq. 2), we averaged extinction and colonization rates over the habitat types. We also
183 consider prediction of habitat occupancy of each habitat type separately, assuming that the
184 patches of the different habitat types form two different and separate metapopulations
185 (considering eq. 2 for each habitat types).

186 In the simulation model, to investigate the impact on habitat occupancy of positive co-variation
187 between local extinction and local colonization rate within a habitat type, we assume that the
188 ratio of the local extinction rate, $e_i$, and local colonization rate, $c_i$, is constant, i.e. $\frac{e_i}{c_i} = A_i$. Thus,

189 the habitat type with the high local extinction rate also has a high colonization rate. Similarly, in
190 the simulation model, negative co-variation between local extinction and local colonization rate
191 is investigated considering that the product of local extinction rate, $e_i$, and local colonization
192 rate, $c_i$, within a habitat type is constant, i.e. $e_i c_i = B$ , forcing negative co-variation between
193 local colonization and local extinction rate within a habitat type. In the simulation model,
194 negative and positive co-variation between local extinction rate and colonization rate will also be
195 applied either only within one habitat type or within the two habitat types. When applied only
196 within one habitat type, the local colonization and local extinction rate value will be maintained
197 constant within the other habitat type. When co-variation between local extinction rate and
198 colonization rate is applied within both habitats, we consider the case where the local extinction
199 rate is low within one habitat and high within the other. Cases and ranges of parameters values
200 considered are described in Table 1. For the simulation model, the number of occupied habitat
201 patches of both habitat types is recorded after 1000 time-steps from 1000 replicates. Simulations
202 started with all habitat patches occupied. For each of replicated run, a new habitat types
203 distribution is generated for the *Random* and *Partially Random* pattern (Fig 1). Results obtained
204 with the simulation model are compared with the analytical solutions of the metapopulation
205 model assuming homogeneity (equation 5) and heterogeneity (equation 1) in extinction and
206 colonization rate.

207 # 3. Results

208 **3.1 Colonization rate homogenous; local extinction rate varies between habitat types**:

209 The metapopulation can persist as long as the local extinction rate in one of the habitat type
210 remains below the local colonization rate ( $e_i < \mu c < e_j$ ) (Fig. 2). When the local extinction rate is

high in one habitat type (habitat 1 in fig 3a), all simulation and analytical results agree and predict for the habitat type (habitat 1) a strong decrease in habitat occupancy as the local extinction rate increases. However, the estimates of habitat occupancy differ substantially between the spatial distributions of habitat types considered. The highest proportion of occupied patches is obtained when the habitat types are aggregated, the lowest with a random distribution of habitat types (Fig. 2a). Analytical predictions of total habitat occupancy lie in-between simulation predictions obtained by aggregated and random configurations of habitat types, the latter being the lowest (Fig. 2a). However, when both local extinction rates exceed local colonization rate differences in habitat occupancy between spatial configurations of habitat types are small. As expected, when local extinction rates are the same between habitat types our results correspond to the solution of eq. 1.

### 3.2 Local extinction rates homogenous; local colonization rates vary between habitat types.

Local colonization rates in one habitat type (habitat 1) (Fig 2b) impact the occupancy in the other habitat type (habitat 2) in different ways depending on whether or not it exceeds the local extinction rate (in habitat 1). When the local colonization rate in habitat type 1 is lower than local extinction rate, the aggregated distribution of habitat types provides the highest number of occupied patches. In contrast, when the local colonization rate in habitat type 1 is high, the highest patch occupancy is observed when habitat types are randomly distributed (Fig 2b). Analytical results assuming homogeneity correspond to the simulation results considering aggregation of habitats while analytical results assuming heterogeneity remain closer to the simulation results obtained when habitat types are randomly distributed.

### 3.3 Both local colonization and local extinction rates vary between habitat types.

233 Results from the analytical model (eq. 3) show that differences in local colonization rates and
234 local extinction rate have different impacts on habitat occupancy (figure 3). Indeed, as local
235 colonization in one habitat type (habitat 1) increases, occupancy in the other habitat type (habitat
236 2) quickly increases. This occurs even when, in habitat 1, the local extinction rate is high and
237 occupancy is low (Fig. 3a). When colonization rate in habitat 1 is high, high values of habitat 2
238 occupancy are observed whatever local extinction rate considered in habitat 1. In contrast,
239 variations in local extinction rate in habitat type 1 slightly impact occupancy in habitat 2 (Fig
240 3a). Impact of high extinction rates in one habitat will depends on the extinction-colonization
241 dynamics in the other habitat type (Fig 3a and 3b). As show in Figure 3b, the occupancy of
242 habitat type 1 is barely impacted by high extinction rate in the habitat 2, this occurs when as long
243 as locally extinction rate in habitat 1 is lower than colonization rate, otherwise impacts can be
244 strong. Interestingly, across a similar range of values of local extinction and colonization rates
245 (Fig 3a and 3b), total habitat occupancy will increase a lot in situations where spatial
246 heterogeneity in extinction and colonization rate concerns different habitat types (Fig. 3b)
247 compared to situation where it concerns one habitat type (Fig. 3a).

248 **3.4 Local colonization and local extinction co-vary positively within habitat types**.

249 Similar to the situation where local extinction rate and local colonization rate vary between
250 habitat types (Fig. 3) occupancy of one habitat type estimated by the simulation model is
251 substantially affected by extinction and colonization in the other habitat type. However, the
252 impact very much depends on the spatial configuration of the habitat types (Fig. 4a and 4b).
253 Being next to a habitat type that has a high local colonization rate is beneficial and can override
254 the effect of a high local extinction risk. Similarly, being next to a habitat type in which the
255 colonization rate is reduced, reduces habitat occupancy locally. A random habitat type

distribution is therefore the spatial configuration where habitat occupancy can be the most variable when co-variation between local extinction and local colonization occurs, while habitat type aggregation buffers this effect (Fig. 4). Co-variation between local extinction and local colonization within the two habitat types amplifies this effect (Fig 4b), and occupancy in one habitat type can either be strongly enhanced or reduced at a local scale. When looking at the total habitat occupancy, the variability created by co-variation of local extinction and colonization rate induces a reduction of the total habitat occupancy and the most favorable habitat type distribution is aggregated. Again here, analytical results considering heterogeneity are in agreement with simulations predictions, being closer to the simulation results in which the habitat types have a partially random configuration. However, predictions are poor when local colonization and local extinction rates are either high or low.

### 3.5 Local colonization and local extinction rate co-vary negatively within habitat types.

Under this scenario, as when local colonization and local extinction rate co-vary positively within a habitat type, the distribution of habitat types strongly impacts the expected habitat occupancy (Fig. 5). When co-variation between local extinction and colonization rate occurs only within one habitat type (Fig 5a), a random distribution of habitat types produces the highest habitat occupancy when local extinction is low and colonization is high, while aggregated distribution of habitat types produces the highest habitat occupancy when local extinction rates are high and colonization rates are low. Again, the impact of spatial heterogeneity in extinction and colonization rate is enhanced when there is a random distribution of habitat types, where habitat occupancy can reach extreme values while an aggregated distribution of habitat types buffers the impact. The reverse results are obtained when local extinction and colonization rates co-vary negatively within both habitat types and have opposite values within each habitat type

279 (Fig. 5b). Random distribution of habitat types is always the best spatial configuration for total
280 and local habitat occupancy while when habitat types are aggregated it is the worst situation (Fig.
281 5b).

282 When local extinction and local colonization co-vary within one habitat type only, analytical
283 results that take into account heterogeneity are in agreement with simulations predictions, being
284 closer to the simulation results considering partially random habitat types configuration, while
285 analytical results that assume homogeneity perform poorly when local extinction and
286 colonization rate are strong (Fig. 5a). Both predictions are poor when local colonization and local
287 extinction rates co-vary negatively within both habitat types, whether or not the habitat types are
288 aggregated or randomly distributed.

289 # 4. Discussion

290 We first discuss the conditions for which habitat types aggregation increases or decreases habitat
291 occupancy. Then, we evaluate the adequacy of simple models when we account for spatial
292 heterogeneity of local extinction and local colonization rate and co-variation of local extinction
293 and local colonization rate within habitat types. Finally, we discuss the similarity of the results
294 from our model to those of other models with more of a focus on epidemiology.

295 ## 4.1 Does habitat aggregation promote increased habitat occupancy?

296 We have discovered that aggregating habitat types can increase or decrease habitat occupancy
297 depending on relationships between local extinction and colonization rates. When the local
298 colonization rate exceeds the local extinction in both habitat types, a random distribution of
299 habitat types is the spatial configuration that provides the highest habitat occupancy. This is in

agreement with studies looking at the impact on habitat occupancy of aggregation of extinction processes and of environmental autocorrelation (e.g. Ovaskainen et al., 2002; Pike et al., 2004; Tuljapurkar and Haridas, 2006; Vuilleumier et al., 2007). However, when in one (and only one) of the habitat type the colonization rates is locally lower than the local extinction rates (or extinction rates exceed locally colonization rate) an aggregated distribution of habitat types provides the highest total habitat occupancy. Aggregation of habitat types favors the creation of stable sub-structures that are not affected by the presence of habitat types with high local risk of extinction and thus favors the persistence of the metapopulation. – Essentially the metapopulation persists in one habitat type and it is better that this habitat type is isolated. This result is thus in accordance with recent predictions showing that to improve metapopulation viability, it is beneficial to improve the quality of some groups of habitat patches to increase their resilience to extinction as this group of habitats will function as a partial refuge even at the cost of having others habitats at low quality (North & Ovaskainen, 2007, Elkin and Possingham, 2008, Theodorou et al., 2009). Even though local populations with a high local risk of extinction will benefit from a random distribution of habitat type, it is at the cost of reducing the viability of the entire metapopulation. A random distribution of habitat types are thus favorable for species with high colonization rate while aggregation of habitat type would be beneficial for species with reduced colonization rate. Interestingly, this result is consistent with studies that investigate the impact of habitat spatial distribution on dispersal evolution. Random distribution of habitats selects for an increase of dispersal abilities while habitat aggregation selects against it (Hovestadt et al., 2001; Johst et al., 2002, Hiebeler, 2004, Kallimanis et al., 2006). Our conclusions are expected to apply to system in which numerous populations are interacting. If the colonization rate of one of the interacting populations is high, a random distribution of habitats will favor re-

colonization of all habitat patches, as the chance of being in the neighboring of a population with the high colonization rate is increases. Similarly, if the extinction rate is severe in one of the interacting populations, the metapopulation would benefit from its isolation and thus aggregation of habitats having high extinction rate will provide the highest metapopulation occupancy.

### 4.2 Reliability of simple models

We would not expect the simple differential equations (eq. 1 and eq. 3) to work perfectly because they include several simplifications of the stochastic simulation: (i) there is an infinite number of habitat patches while the simulation model has a finite number of habitat patches with an absorbing boundary, (ii) every habitat patch is equally connected to every other habitat patch, while in the simulation model colonization occurs only between adjacent habitat patches, (iii) the model is deterministic in continuous time and with a continuous state space, while the simulation model accounts for stochasticity and extinction-colonization through discrete-time processes and a discrete state-space, and (iv) there is no spatial component – the location of a habitat patch is irrelevant. However, the homogeneous analytical model (eq.1) is a reasonably good predictor of the patch occupancy in the habitat when spatial distribution of habitat types is aggregated and when extinction-colonization dynamics in both habitat types do not display large differences. For some cases where strong spatial heterogeneity in extinction-colonization dynamics is present, a good fit is observed for total habitat occupancy (Fig. 3b, 5a, 5b and 6b). This is an artifact as the over estimation of habitat patch occupancy in one habitat type compensates for underestimation in the other. Similarly, predicted occupancy given by the analytical model considering spatial heterogeneity in extinction and colonization dynamics shows clear correspondences with the simulation model under many circumstances. The two models provide similar results when habitat type heterogeneity in local extinction and local colonization rate is weak and the

346 distribution of habitat types is partly random. Therefore, the use of this analytical model
347 (heterogeneous model) should be avoided mainly in the situations where values of local
348 extinction and colonization rate are highly variable between habitat types and when habitat types
349 are aggregated.

350 **4.3 Analogy to epidemiological models**

351 Metapopulation model are analogous to basic epidemiological models that describe the dynamics
352 of a pathogen in a host population (May and Nowak, 1994, Amarasekare and Possingham, 2001,
353 Hess et al., 2001). If a species of interest is a pathogen, each host organism may be considered as
354 a habitat patch that is occupied when infected. Colonization and migration are then analogous to
355 infection and transmission while local extinction is equivalent to host death or recovery.
356 However, metapopulation models are much simpler e.g. immune patches do not exist, a host is
357 not killed and empty suitable patches do not arise by births (Grenfell and Harwood, 1997;
358 Hanski, 1999; Hess et al., 2001). Although those models differ in their underlying assumptions,
359 interestingly, similar results to our study have arisen from epidemiological models. Accounting
360 for heterogeneity in habitat types in metapopulation models translates, in epidemiological
361 models, into a system where pathogens can affect multiple hosts or where either host
362 susceptibility and/or transmission rates are heterogeneous (due for example to host genetic
363 variability, population aggregation into age groups or other spatial factors (Anderson and May,
364 1986; Lyles and Dobson, 1993; Dwyer et al., 1997; Woolhouse et al., 1997)). Interestingly, it has
365 been shown that host species diversity can amplify pathogen outbreaks and persistence
366 (Anderson and May, 1991; Hess, 1996; Woolhouse et al., 1997; Woolhouse et al., 2001;
367 Woolhouse, 2002; Dobson, 2004) – we show that occupancy can be much higher (but also
368 lower) in metapopulations composed of two different habitat types compared to one composed of

369 one habitat type (Fig 3, 5 and 6). It has also been shown that species most capable of recovering
370 from disease (low local extinction rates) can drive the other hosts to extinction (Dobson, 2004).
371 This mirrors our result where high local extinction rates in one habitat patch can strongly affect
372 occupancy in the other habitat. Therefore, by analogy, our study shows that patterns of co-
373 variation and levels of spatial aggregation of host in epidemiological model are expected to have
374 a crucial role for management of epidemics where there is host variability. Consequently our
375 results and this modeling approach may have implications for disease management in agriculture
376 and public health. Finally, model in epidemiology could also benefit from the integration of
377 spatial heterogeneity in the distribution and in the interaction of populations (as done in Vincinot
378 and Moriya 2011).

379 ## 5. Conclusion

380 In natural populations, environmental heterogeneity can lead to situations where locally, in
381 populations, extinction and colonization rate can display, positive, negative or even more
382 ambiguous correlations in space.
383 Patch occupancy, the quantity of interest for choosing management options, is impacted by the
384 coexistence of different extinction-colonization dynamics within a metapopulation. Interestingly,
385 we demonstrate that this impact can be enhanced or buffered depending on the spatial
386 distribution of the habitats. To increase habitat occupancy, habitat aggregation should be
387 favoured when mean local extinction risk is high and spatially variable, while random
388 distribution of habitats should be applied when colonization rates are high and spatially
389 heterogeneous.
390 Finally we also show that the use of analytical models that account for heterogeneity in local
391 extinction and colonization rate should be preferred to models that average both processes.

However, they might not be accurate in situations where extinction and colonization rate are highly variable and when habitat types are randomly distributed or aggregated in a landscape, in these cases, spatially-explicit models should be preferred.

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560

561 **Table 1:** Parameters values of local extinction and colonization rate used for the
562 spatially-explicit simulations**.**

563 **Figure 1:** Three broad classes of spatial aggregation in habitat types. In each case 80
564 patches are arranged in an 8 x 10 grid , where the habitat type distribution changes from
565 randomly distributed to completely aggregated with abrupt boundaries. The spatial distributions
566 of habitat types are referred to as: (a) Random, (b) Partially Random and (c) Aggregated.

567 **Figure 2**: Comparison of simulation and analytical results when (a) extinction rates and
568 (b) colonization rates, vary between habitat types. The total habitat occupancy, $p^*_{tot}$, habitat 1
569 occupancy, $p^*_1$, and habitat 2 occupancy, $p^*_2$, are presented (a) as a function of extinction rate in
570 one habitat type with $e_2 = 0.01$, $c_1 = c_2 = 0.01$, $\mu = 3.2$ and (b) as a function of colonization rate
571 in one habitat type with $e_1 = e_2 = 0.01$, $c_2 = 0.01$, $\mu = 3.2$. Numerical solutions of equation 3
572 (*Analytical heterogeneous*) and equation 1 (*Analytical homogeneous*) are presented with the
573 simulation results for three different spatial configurations of habitat types (*Random, Partially*
574 *Random and Aggregated,* see legend). The vertical line corresponds to the situation where
575 parameters *e* and *c* are homogeneous in all habitat types. For details on parameters used see
576 Table 1.

577 **Figure 3:** Analytical solutions when extinction rates and colonization rate vary between
578 habitat types. Occupancy of total habitat $p^*_{tot}$ , of habitat type 1 $p^*_1$ and habitat type 2 $p^*_2$ obtained
579 by numerical solutions of equation 3 (*Analytical heterogeneous*) are presented when (a) Local
580 extinction and local colonization rate are kept constant on one habitat type (habitat type *2*,

581 $c_2 = 0.01,\ e_2 = 0.01$) and when (b) Local colonization rate remain constant in habitat type *2* (

582 $c_2 = 0.01$) and local extinction remain constant in habitat type 1 ($e_1 = 0.01$).

583 **Figure 4**: Comparison of simulation and analytical results when extinction and

584 colonization co-vary positively within (a) one habitat type (habitat 1, $e_1/\mu c_1 = A,\ A = 1/\mu$ ,

585 $e_2 = 0.01,\ \mu = 3.2,\ c_2 = 0.01$ and (b) within both habitat types ( as in (a) but with

586 $e_2/\mu c_2 = A,\ \ c_2 = e_1$). Results for three different spatial configurations of habitat types (*Random,*

587 *Partially Random and Aggregated,* see legend) and for the numerical solutions of equation 3

588 (*Analytical heterogeneous*) and equation 1 (*Analytical homogeneous*) are presented. The vertical

589 line corresponds to the situation where parameters *e* and *c* are homogeneous in all habitat types.

590 For details on parameters used see Table 1.

591 **Figure 5**: Comparison of simulation and analytical results when extinction and

592 colonization co-vary negatively within (a) one habitat type (habitat 1,

593 $e_1\mu c_1 = B,\ B = 0.0005\mu,\ \ \mu$=3.2 $\ e_2 = 0.01,\ c_2 = 0.01$) and (b) within both habitat types (as in (a)

594 but with $e_2\mu c_2 = B,\ \ c_2 = e_1$). Results for three different spatial configurations of habitat types

595 (*Random, Partially Random and Aggregated,* see legend) and for the numerical solutions of

596 equation 3 (*Analytical heterogeneous*) and equation 1 (*Analytical homogeneous*) are presented.

597 The vertical line corresponds to the situation where parameters *e* and *c* are homogeneous in all

598 habitat types. For details on parameters used see Table 1.

**Table 1**

| Cases | | | $e_1$ | $e_2$ | $c_1$ [a] | $c_2$ [a] | Conditions |
|---|---|---|---|---|---|---|---|
| (i) | ***Variation in local extinction rate between habitat types:*** | | 0.001-0.5 | 0.01 | 0.01 | 0.01 | $e_1 \neq e_2$ |
| (ii) | ***Variation in local colonization rate between habitat types*** | | 0.01 | 0.01 | 0.001-0.5 | 0.01 | $c_1 \neq c_2$ |
| (iii) | ***Positive co-variation*** | ***Within habitat 1*** | 0.001-0.5 | 0.01 | 0.001-0.5 | 0.01 | $\frac{e_1}{c_1} = A$ |
| | | ***Within habitat 1 and 2*** | 0.001-0.5 | 0.001-0.5 | 0.001-0.5 | 0.001-0.5 | $\frac{e_1}{c_1} = \frac{e_2}{c_2} = A$ |
| (iv) | ***Negative co-variation*** | ***Within habitat 1*** | 0.001-0.5 | 0.01 | 0.001-0.5 | 0.01 | $e_1 c_1 = B$ |
| | | ***Within habitat 1 and 2*** | 0.001-0.5 | 0.001-0.5 | 0.001-0.5 | 0.001-0.5 | $e_1 c_1 = e_2 c_2 = B$ |

[a] To compare between the analytical and simulation models, the colonization parameter in the simulation model must be multiplied by the average number of neighbor habitats in the landscape, $\mu$, leading to $c_i^{Analytic} = \mu c_i^{Simulation}$, in our landscapes this value is 3.2.

**Figure 1**

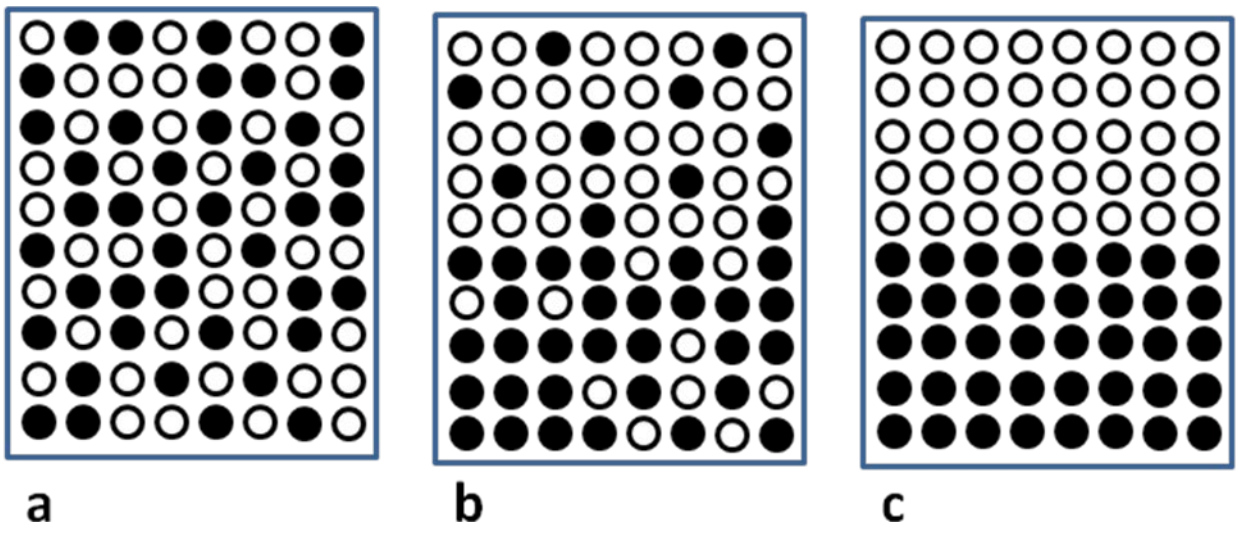
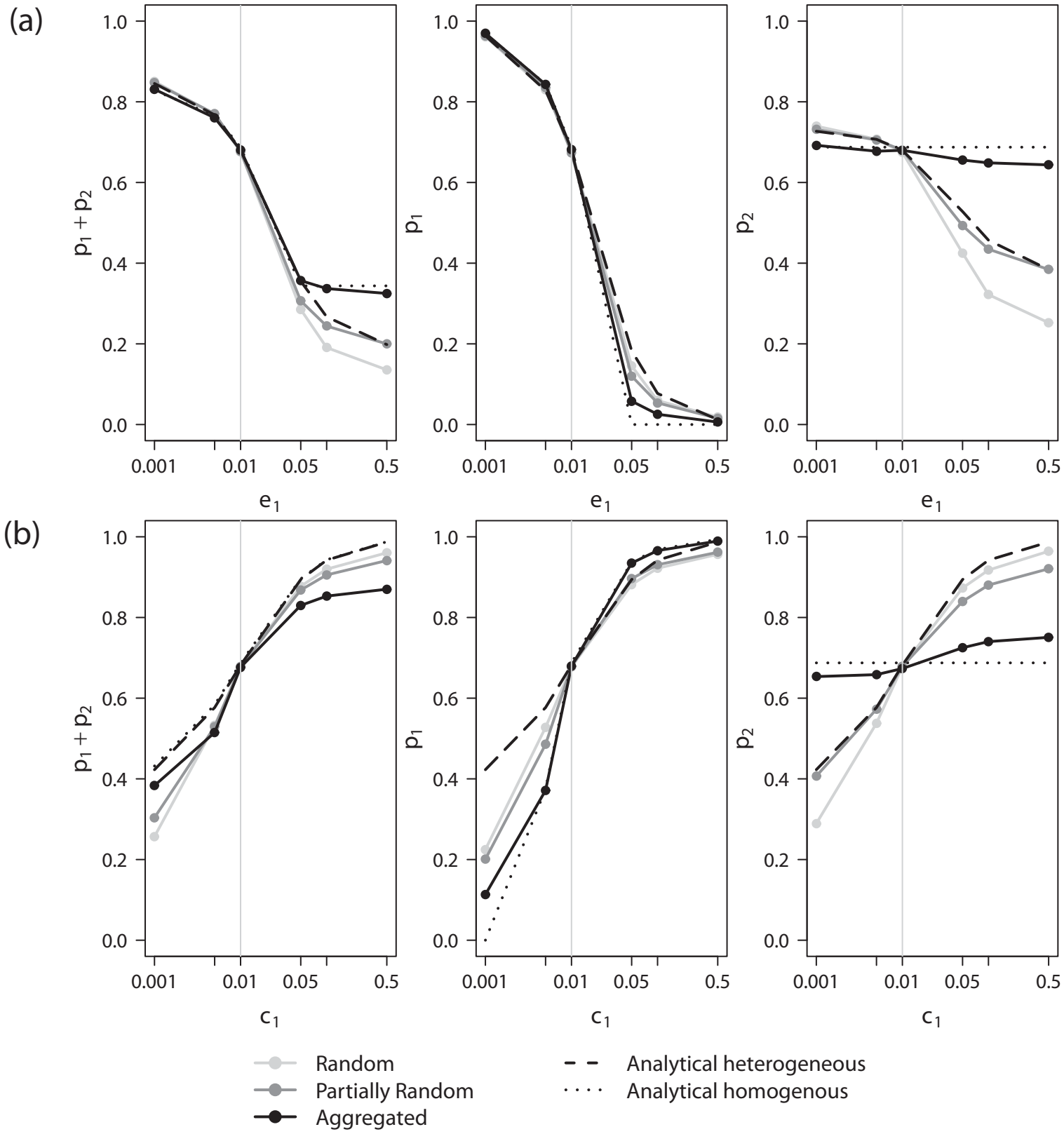
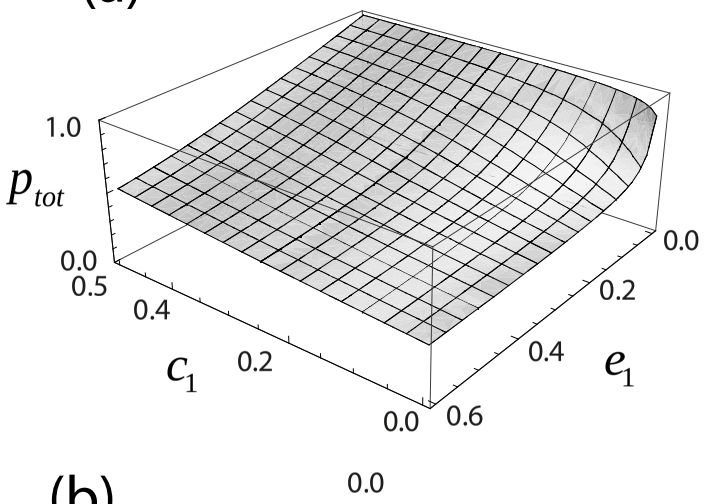
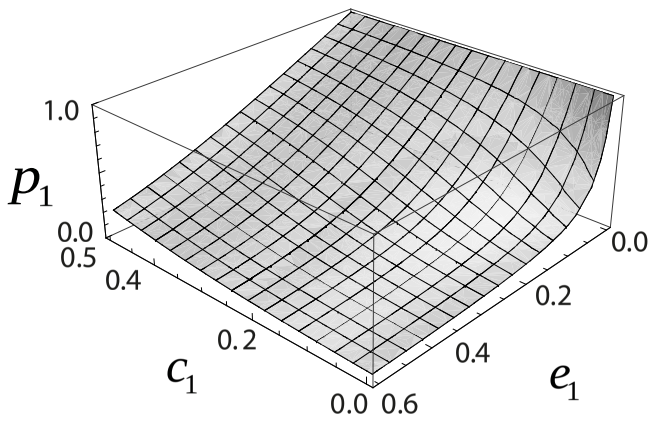


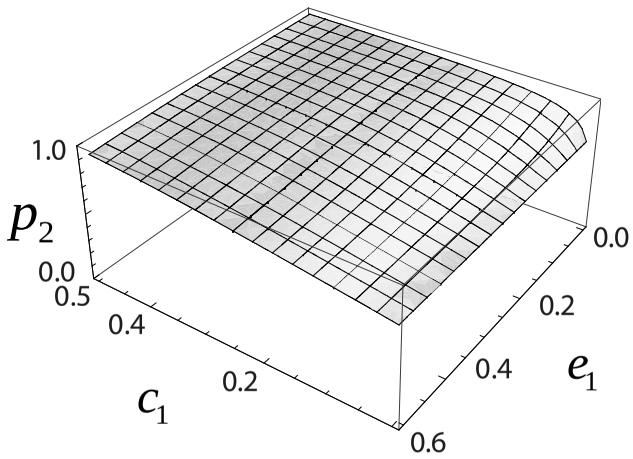
Figure 2


(a)
(b)
$p_1 + p_2$
$p_1$
$p_2$
$e_1$
$c_1$
0.0
0.2
0.4
0.6
0.8
1.0
0.001
0.01
0.05
0.5
Random
Partially Random
Aggregated
Analytical heterogeneous
Analytical homogenous

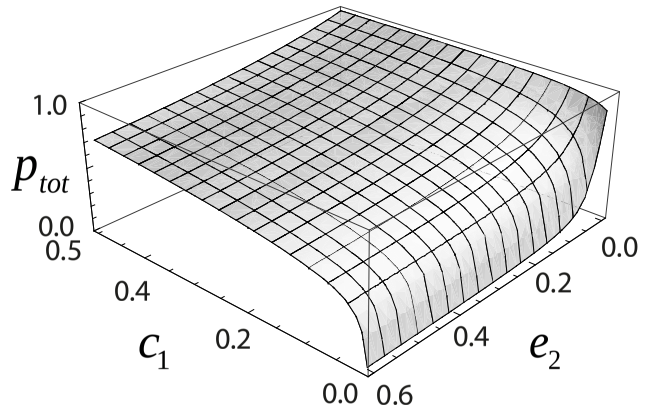
(a)

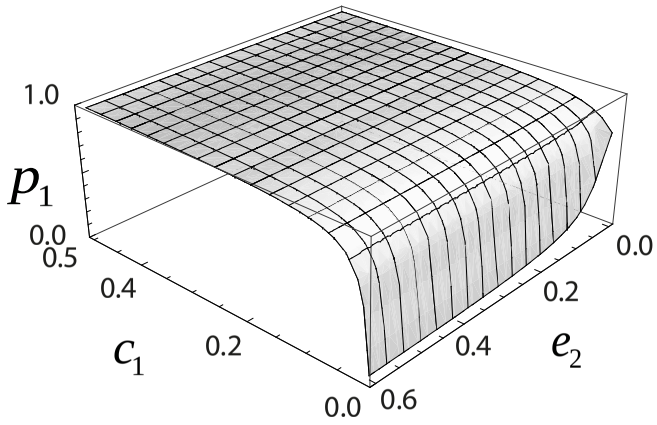

1.0
$p_{tot}$
0.0
0.5
0.4
$c_1$
0.2
0.0
0.0
0.2
0.4
$e_1$
0.6


1.0
$p_1$
0.0
0.5
0.4
0.2
$c_1$
0.0
0.6
0.2
0.4
$e_1$
0.0


1.0
$p_2$
0.0
0.5
0.4
0.2
$c_1$
0.6
0.2
0.4
$e_1$
0.0

(b)


1.0
$p_{tot}$
0.0
0.5
0.4
$c_1$
0.2
0.0
0.6
0.4
$e_2$
0.2
0.0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$p_1$
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0.5
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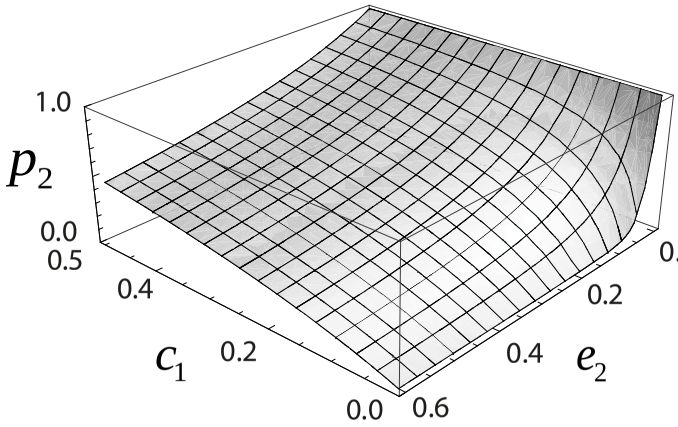
$c_1$
0.2
0.0
0.6
0.4
$e_2$
0.2
0.0


1.0
$p_2$
0.0
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0.4
$c_1$
0.2
0.0
0.6
0.4
$e_2$
0.2
0.0

Figure 4

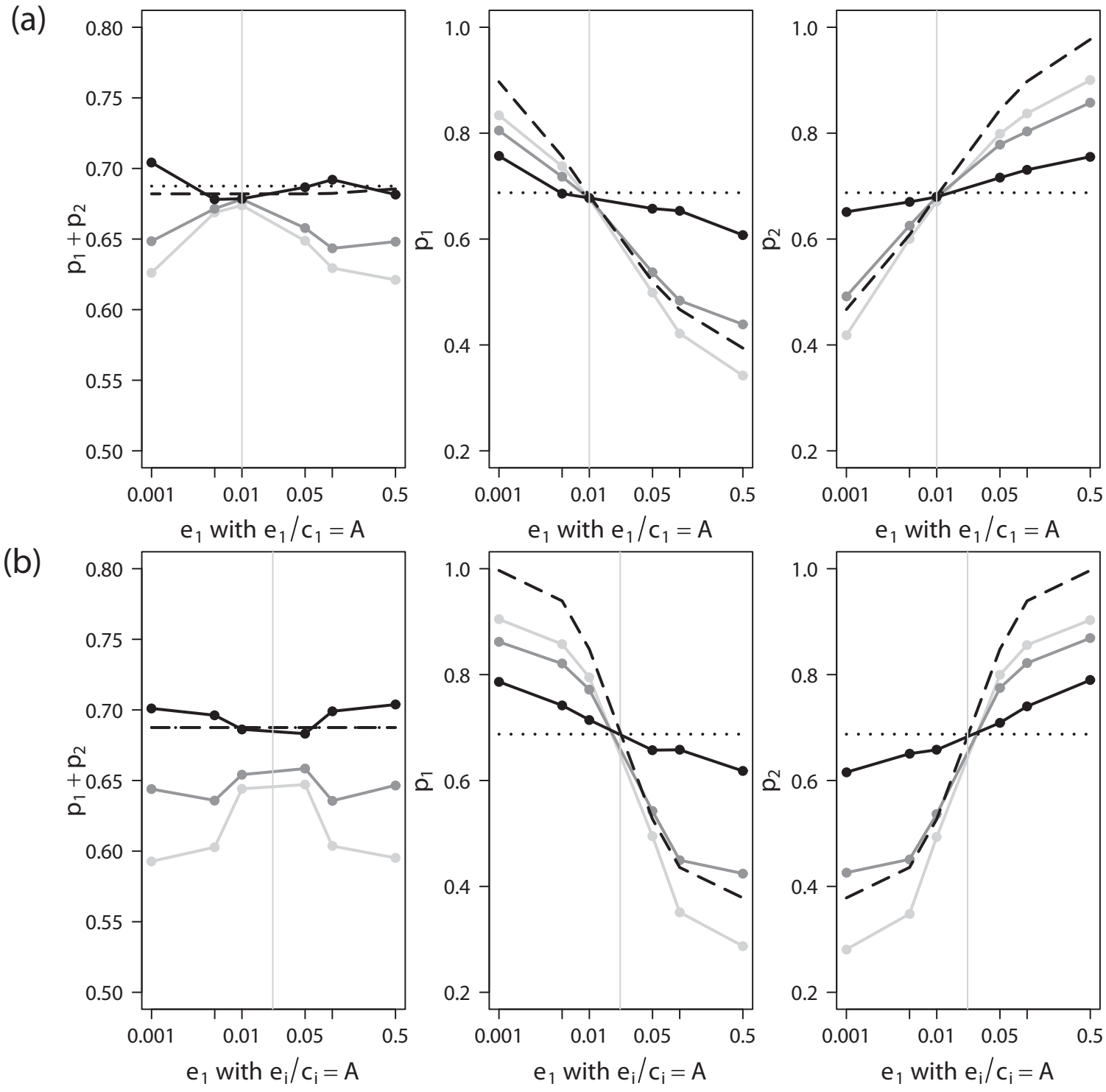
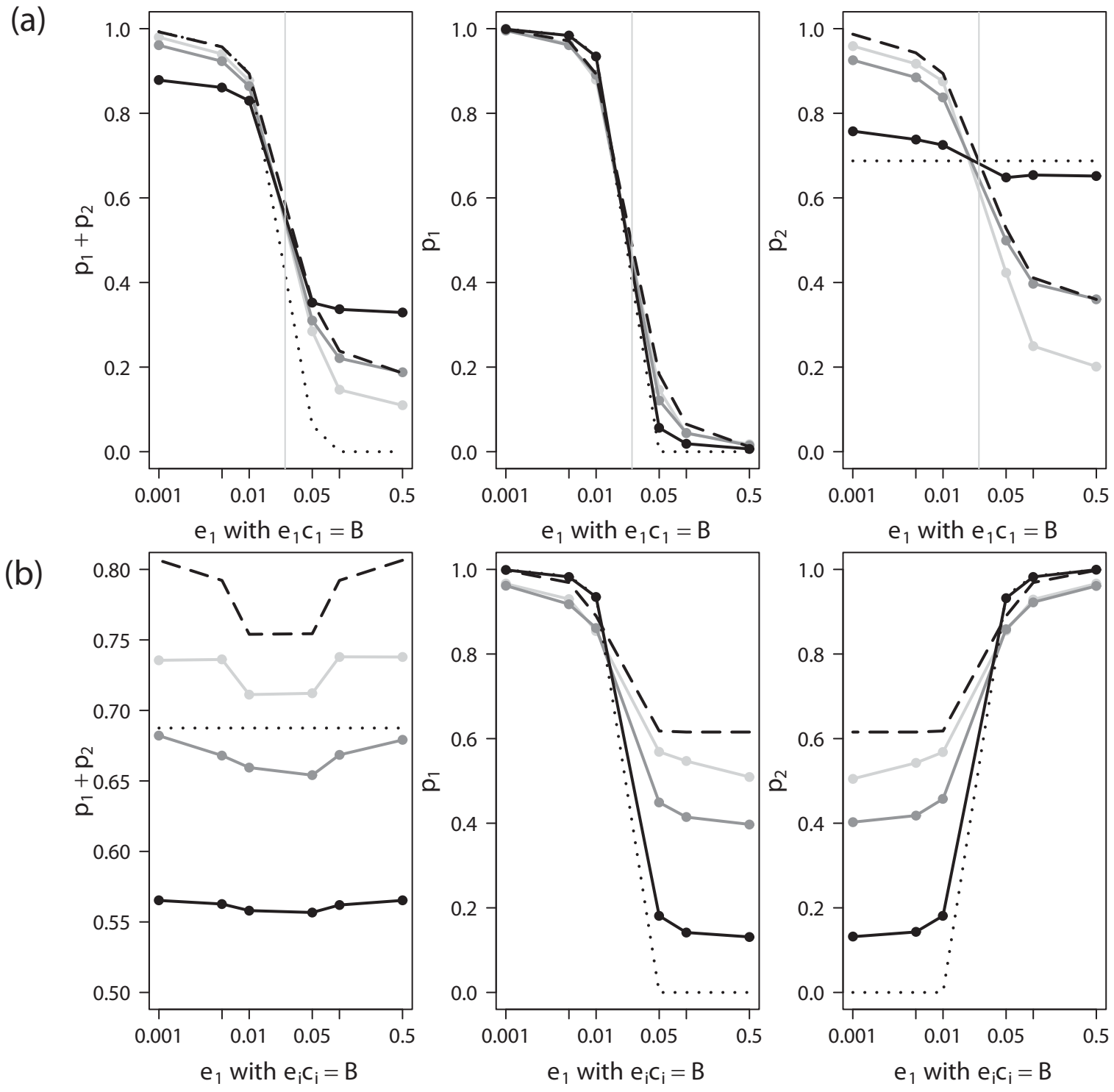

(a)
(b)
$p_1 + p_2$
$p_1$
$p_2$
$e_1$ with $e_1/c_1 = A$
$e_1$ with $e_i/c_i = A$
0.001
0.01
0.05
0.5
Random
Partially Random
Aggregated
Analytical heterogeneous
Analytical homogenous

Figure5


(a)
(b)
$p_1 + p_2$
$p_1$
$p_2$
$e_1$ with $e_1c_1 = B$
$e_1$ with $e_ic_i = B$
0.001
0.01
0.05
0.5
Random
Partially Random
Aggregated
Analytical heterogeneous
Analytical homogenous