1   **Title:** A simulation study of the use of temporal occupancy for identifying core and transient

2   species

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15   **Abstract**

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17   Transient species, which do not maintain self-sustaining populations in a system where

18   they are observed, are ubiquitous in nature and their presence often impacts the interpretation of

19   ecological patterns and processes. Identifying transient species from temporal occupancy, the

20   proportion of time a species is observed at a given site over a time series, is subject to

21   classification errors as a result of imperfect detection and source-sink dynamics. We use a

22   simulation-based approach to assess how often errors in detection or classification occur in order

23   to validate the use of temporal occupancy as a metric for inferring whether a species is a core or

24   transient member of a community. We found that low detection increases error in the

25   classification of core species, while high habitat heterogeneity and high detection increase error

26   in classification of transient species. These findings confirm that temporal occupancy is a valid

27   metric for inferring whether a species can maintain a self-sustaining population, but imperfect

28   detection, low abundance, and highly heterogeneous landscapes may yield high misclassification

29   rates.

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34   **Introduction**

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36   Understanding the processes underlying community assembly is one of the primary goals

37   of community ecology. Traditional approaches make inferences about community processes based

38   on the set of species identified as community members, typically those observed at a study site

39   (1,2). Data on communities are typically gathered via field surveys at a given site for one or more

40   time points. However, the record of species from such community surveys often includes transient

41   or sink species that do not maintain self-sustaining populations in that community (3). A growing

42   number of studies use temporal occupancy, or the proportion of a multi-year time series over which

43   a species is observed, to determine which species are "core" members of their communities and

44   which species are transient (3–9). Temporal occupancy provides a quantitative measure of

45   persistence within a community over time and its distribution tends to be bimodal (3), facilitating

46   the distinction between core and transient status, but ecological data collection is imperfect and

47   using temporal occupancy to infer core or transient classification is susceptible to classification

48   error.

49   One type of error is inferring that a species is transient when it is actually a core member

50   of the community. A self-sustaining species that is present on the landscape every year may fail to

51   be observed in some years, and hence be misclassified as a transient species, for three primary

52   reasons (Table 1). These missed detections can occur due to low population densities (10–12), less

53   conspicuous morphology (e.g., drab plumage) or behavior (e.g., singing quietly or infrequently;

54   Cunningham et al. 1999, Kéry and Royle 2008), and habitat structure with characteristics that limit

55   the distance over which individuals can be detected (e.g., dense vegetation) (15–18). Although the

56   effect of imperfect detectability on temporal occupancy and species classification is qualitatively

57   understood, it is unclear how frequently and at what levels of detectability and abundance such

58   errors occur.

59   The opposite classification error is also possible, where a species is inferred to be a core

60   member of a community based on frequent occurrence in a time series, even though it does not

61   maintain a locally viable population (Table 1). Some individuals of a species are observed

62   regularly in habitats in which they do not successfully reproduce by dispersing in from adjacent

63   suitable habitat (19,20). For example, in plants, seeds might be regularly dispersed into

64   inhospitable habitats (21) and in birds, younger and lower quality males are often displaced by

65   dominant males to adjacent, suboptimal habitats (22). In such cases, the temporal frequency with

66   which a species is observed might be a poor indicator of the extent to which a species can actually

67   maintain a viable population in that location.

68   Understanding the frequency of classification errors and the factors that affect those errors

69   is critical for properly interpreting patterns based on temporal occupancy. Here, we use a

70   simulation-based approach to examine community dynamics—based on death, birth, dispersal,

71   and establishment—on complex, dual-habitat landscapes in which species' habitat associations are

72   known. We varied average species' detectability and habitat heterogeneity of the simulated

73   landscapes to assess how these variables affect rates of misclassification. We expect that core

74   species are more likely to be misclassified as transients when either detectability or abundance is

75   low. In contrast, we expect that species that do not successfully breed in a habitat are more likely

76   to be misclassified as core members when the local community is embedded within a more

77   heterogeneous landscape, which increases the likelihood of mass effects from adjacent habitats.

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79   **Methods**

80   *Simulation model*

81   Each simulation began by generating an initial landscape, species pool, and global species

82   abundance distribution (GSAD). The 32 x 32 pixel landscape was made up of two distinct habitat

83   types, A and B, with a parameter for the proportion of the landscape made up of habitat type A

84   (h_A; Figure 1A). Each grid cell represented a local community with a fixed community carrying

85   capacity of 100 total individuals of any species. The species pool contained 40 total species, with

86   half that could only reproduce successfully in habitat A and half that could only reproduce

87   successfully in habitat B. The GSAD was a vector of relative species abundances assigned from a

88   lognormal distribution that defined the relative probability that an immigrant from outside the

89   landscape would belong to each species. Initially, the landscape was filled to carrying capacity

90   with individuals drawn randomly from the GSAD.

91   In each time step, meant to represent one year, the following four processes were modeled:

92   1) *Death*. The probability of mortality for each individual at a time step was 0.5 (Figure

93   1B). Death rates were independent of the habitat type in which the species occurred.

94   2) *Birth*. All individuals occurring within their preferred habitat type produced two

95   offspring per time step, while individuals occurring in a non-preferred habitat type did not

96   reproduce. Offspring were termed "propagules" until they established in a community (see below;

97   Figure 1C).

98   3) *Dispersal*. Newly generated propagules dispersed in random directions by a distance

99   drawn from a half-Gaussian distribution with a mean of 1.24 grid cells (95% of movements result

100   in dispersal distances ≤ 4 grid cells; Figure 1D). Established individuals (i.e. adults) only dispersed

101   if they were in non-preferred habitats. We also explored dispersal kernels that were narrower (95%

102   of movements within 2 grid cells) or broader (95% of movements within 8 grid cells) to confirm

103   that results were qualitatively similar. Results for these simulations are presented in Supplemental

104   Material (Figure S1-S6, Table S1-S2).

105   4) *Establishment*. Empty spaces in each community were colonized by either a migrant

106   from outside the community (drawn probabilistically from the GSAD) with a constant immigration

107   rate probability (0.001) or by an individual selected randomly from the pool of new or dispersing

108   propagules. Once individuals became established, they only left their community via dispersal or

109   death (Figure 1E). Propagules that did not establish were eliminated at the end of each time step.

110   We ran simulations for 200 time steps, which was long enough for species richness to

111   achieve equilibrium in the landscape, and used the last 15 time steps to calculate temporal

112   occupancy. Fifteen time steps represented an ecological dataset with a 15-year time series, a

113   sampling period used in several previous studies which provides a reasonably high resolution

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114   estimate of temporal occupancy (7,23). Additionally, we calculated landscape-wide abundances

115   for each species at the end of the simulation.

116   We ran 50 replicate simulations for values of $h_A \in \{0.5, 0.6, 0.7, 0.8, 0.9\}$ to generate

117   landscapes that were more (high h_A) or less (low h_A) homogeneous. For each simulation, we also

118   imposed a stochastic detection process in which we varied the probability of detecting an

119   individual known to be present, p, from 0.1 to 1.0 in increments of 0.1. Detection probability was

120   assumed to be both species- and habitat-independent. This resulted in a vector of "observed"

121   species abundances in each grid cell at each time step.

122   *Simulation analysis*

123   We examined the temporal dynamics of species within a single, centrally located pixel for

124   each simulation run. Based on the habitat type of the focal pixel, all species either could (core) or

125   could not (transient) reproduce within that pixel and hence maintain a viable population. We refer

126   to this as their biological, or true, status. In addition, each species was classified as core or transient

127   based on temporal occupancy over the last 15 years of the simulation run. Species observed in five

128   years or fewer ($\leq 33\%$) were classified as transient while species observed in more than ten years

129   ($> 66\%$) were classified as core. For these analyses we ignored the minority of species with

130   intermediate temporal occupancy which could not be unambiguously assigned to core or transient

131   status. Thus, each of the species we considered fell into one of the four categories shown in Table

132   1. For each simulation run, we calculated the rate of misclassifying core species and the rate of

133   misclassifying transient species (Table 1). Error rates were examined as a function of average

134   detection probability and landscape similarity in the 7 x 7 pixel region surrounding the focal pixel,

135   which was calculated as the proportion of the regional window that was the same habitat type as

136   the focal pixel. Number of species and classification error rates were predicted by detection

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137   probability and landscape similarity using ordinary least squares linear models. The relationship

138   between species abundance and core species classification at detection = 0.5 was assessed using a

139   generalized linear model with a logit link.

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141   **Results**

142   Communities in homogeneous landscapes (e.g., Figure 2a) typically had a large number of

143   true core species and only a few true transient species at any given point in time (Figure 2b).

144   Turnover in the identity of the transient species from one time step to the next resulted in a mode

145   of low temporal occupancy within an overall bimodal distribution of temporal occupancy (Figure

146   2c). Communities in heterogeneous landscapes (e.g., Figure 2d) had more true transient species

147   appear in their non-preferred habitat type in any given time step due to the greater area of potential

148   sources of colonization (Figure 2e). Many of these transient species were maintained by repeated

149   dispersal from the alternate habitat type in the surrounding landscape such that they had moderate

150   to high values of temporal occupancy (Figure 2f).

151   The number of true core species (those maintaining a locally viable population) observed

152   in a pixel increased with detection probability (estimate = 1.11, p < 2e-16), and even more so with

153   landscape similarity (estimate = 5.82, p < 2e-16; Figure 3a). More variance in the number of true

154   core species could be explained by landscape similarity (R^2 = 36%) than detection probability (R^2

155   = 2%). The number of true transient species (those not maintaining a viable population) observed

156   increased with detection probability (estimate = 5.29, p < 2e-16) and decreased strongly with

157   landscape similarity (estimate = -27.14, p < 2e-16; Figure 3b). More variance in the number of

158   true transient species could be explained by landscape similarity (R^2 = 74%) than detection (R^2 =

159   5%).

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160   Species that were true core members of the focal community were more likely to be

161   incorrectly inferred as transient at low detection probabilities (estimate = -0.41, p < 2e-16) and

162   low landscape similarities (estimate = -0.27, p < 2e-16; Figure 4a). More variance in the

163   proportion of misclassified core species could be explained by detection (R^2 = 46%) than

164   landscape similarity (R^2 = 11%). Error rates were close to zero when landscape similarity was

165   greater than 0.6 and detection probability was greater than 0.3 and increased most noticeably

166   when detection probability was 0.1, the lowest detection rate examined.

167   Transient species that did not reproduce in the focal habitat but that regularly occurred

168   there were incorrectly inferred as core most often at high detection probabilities (estimate = 0.20,

169   p < 2e-16) and low landscape similarities (estimate = -0.52, p < 2e-16; Figure 4b). More variance

170   in the proportion of misclassified transient species could be explained by landscape similarity (R^2

171   = 48%) than detection (R^2 = 13%). Error rates for classifying transient species were zero or near

172   zero when landscape similarity was greater than 0.5. Transient species misclassification rates

173   were greatest when landscape similarity was less than 0.4, where the majority of colonization

174   events came from the opposite habitat type, such that poorly adapted species appeared in the

175   focal habitat repeatedly over time. This was exacerbated at high detection probability, which

176   ensured these true transient occurrences were observed and therefore misclassified. Additionally,

177   species with low landscape-wide abundance were more likely to be misclassified as transient

178   when they were truly core members of their community, while the odds of misclassifying a core

179   species were less than 13% for species whose abundance was at least 12% of the most abundant

180   species (estimate = 7.02, p < 2.2e-16; Figure 5).

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181   Results were similar using both narrower and broader dispersal kernels (Figure S1-S6,

182   Table S1-S2), with narrow kernels having slightly more variance in classification rate than

183   broader kernels.

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185   **Discussion**

186   Several studies have used temporal occupancy to infer the persistence of populations over

187   time and the degree to which a species can be considered a core member of a community in a

188   particular location (3,7–9,23). Our simulations showed that in many realistic scenarios, this is a

189   valid approach, but also confirmed that temporal occupancy is subject to misclassification errors

190   where core species are inferred to be transient and transient species are inferred to be core. As

191   expected, low detection probabilities resulted in more frequent misclassification of core species as

192   transient. Rare species were also more likely misclassified as transient. Low landscape similarity,

193   when combined with high detection probabilities, resulted in transient species more frequently

194   being misclassified as core.

195   Imperfect individual detection influenced the rate at which core species were misclassified

196   as transients through failing to detect species when they were actually present. These species were

197   more likely to be inferred as transient at lower detection probabilities. However, error rates for

198   core species misidentified as transients were quite low as long as detection probabilities were

199   greater than approximately 0.3. This threshold of 0.3 is at the low end of detection probabilities

200   observed for most bird species, with most species exhibiting substantially higher rates of detection

201   (24–26). Specifically, Boulinier et *al*. (1998) found that across a range of habitats in North

202   America, average detection probabilities for species richness estimates using the Breeding Bird

203   Survey ranged from 0.65 to 0.85. Johnston et *al*. (2014) found that the least detectable family of

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204   birds was *Paridae*, which had a median detectability of 0.27, and the majority of other families

205   had detection probabilities greater than 0.3. Overall, these findings suggest that the

206   misclassification of core species is unlikely to be common except at unusually low detection

207   probabilities that may be relevant for only a small minority of species.

208   Misclassification of transient species as core species was associated with high habitat

209   heterogeneity. Species occurred in habitats to which they were poorly adapted because of dispersal

210   from nearby source populations. The greater the surrounding area containing source populations,

211   the greater the chance of repeated dispersal into nearby sink habitats causing the species to be

212   regularly detected through time (20). These errors became prevalent when 60% or more of the

213   surrounding landscape was different from the focal habitat. Our simulation model assumed that

214   dispersal of new propagules was random with respect to habitat type, but if dispersal was biased

215   toward the preferred habitat type (which seems likely for organisms with active dispersal; i.e.,

216   Johnston et al. 2014), it would reduce the frequency of transient occurrences and therefore reduce

217   observed error rates. The rate at which transient species were misclassified as core species also

218   decreased with decreasing detection probability because at low detections, errors caused by

219   repeated dispersal from adjacent source habitats were canceled out by detection errors. Overall,

220   these results suggests that misclassification of transient species is unlikely to be common except

221   in highly fragmented landscape configurations with unbiased dispersal.

222   Geographic patterns in the relative prevalence of core and transient species can influence

223   our understanding of ecological communities when failing to recognize this distinction (7,23),

224   especially if the probability of misclassification varies geographically. One likely source for this

225   is detection probability, which is thought to vary along environmental gradients. In particular, it

226   has been suggested that average detectability decreases along continental to global productivity

227 gradients because species are more difficult to detect in more densely vegetated environments (17).

228 However, despite such a potential bias, past work has shown that there is typically a positive

229 relationship between either temporal occupancy or species richness and remotely sensed proxies

230 for productivity, meaning the observed patterns were opposite what would be predicted purely

231 from a detectability effect (7,17,23). As such, these patterns of occupancy and richness were

232 observed despite, and not because of, geographic variation in detectability. Other studies have

233 suggested that birds sing more frequently in densely forested habitats so aural-based sampling

234 should not observe this effect in forests, but in open habitats (24). In these cases, variation in

235 detection probability alone has the potential to generate apparent patterns in richness or abundance,

236 with misclassification rates of species varying across the gradient.

237   While we parameterized our simulation model to loosely reflect the biology of songbirds

238 (e.g. reproductive rate, dispersal distance), the inferences that can be made from this simulation

239 model are more broadly generalizable. We chose to focus on birds because they are highly

240 mobile, can disperse widely, and have been studied empirically in this core-transient context

241 (3,7,23). These first two attributes make temporal occupancy particularly useful for identifying

242 core and transient birds in communities, but also potentially more prone to errors due to source-

243 sink dynamics.

244   Detectability is dependent on both species attributes and the environment. Some species

245 are inherently more detectable due to variation in species color, size, and behavior. A large,

246 colorful bird perched conspicuously or that sings loudly and frequently is detected more often

247 than a little brown bird in the undergrowth, given they occur at equal densities. Our study is most

248 relevant for considering how detection probability covaries along an environmental gradient,

249 where detection probability likely varies on average across all species, than for considering how

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250 detection probability varies among species. Nevertheless, species known to have low detection

251 probabilities will presumably require more targeted monitoring efforts, and temporal occupancy

252 should be used with caution to infer population persistence and habitat suitability for such

253 species.

254 The aim of our simulation model was to capture how frequently species are misclassified

255 within the core-transient temporal occupancy framework. Therefore, we focused on landscape

256 similarity and detectability, but other parameters could also play a role in determining the

257 effectiveness of temporal occupancy. In our study, birth rates and death rates were constant, so

258 increasing the birth rates or decreasing death rates of species occurring in their preferred habitats

259 could allow specialists to reach equilibrium in a habitat more quickly, decreasing the number of

260 transient species in the community. Additionally, varying immigration rates across species could

261 enable one species to immigrate more effectively into new habitats than other species, but in our

262 study, immigration rate and dispersal rate were analogous because both allowed species to colonize

263 new habitats. We addressed alternative rates of dispersal into new cells by varying the dispersal

264 kernels in supplementary analyses, which demonstrated that only at very low dispersal rates do

265 detection and landscape similarity affect core and transient classification.

266 In general, we found that temporal occupancy can reliably be used to infer habitat

267 associations, as well as the likelihood of a species maintaining a viable population in the location

268 where it was observed, under a broad range of conditions. The use of temporal occupancy may be

269 most problematic in study systems made up of highly isolated habitat fragments where species

270 commonly disperse from the surrounding landscape matrix, or in habitats or for species with

271 uniformly low detection probabilities. Ecologists should explicitly consider whether detection

272 probabilities vary across the environmental gradients in their study systems before using temporal

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273   occupancy. Considering the relationship of landscape similarity and detection in specific study

274   systems will provide a guide for when and how to include temporal occupancy in ecological

275   analyses.

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278   **Acknowledgements**

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348   **Table 1.** Ways that species can be correctly or incorrectly (boxes in red) classified as
349   maintaining a viable population based on temporal occupancy. R_0 refers to the net reproductive
350   rate of a species in a location.

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|	Maintains a viable population $R_0 \geq 1$, "core"	Does not maintain a viable population $R_0 < 1$, "transient"
Low temporal occupancy, inferred to be "transient"	**A**: Species that occur persistently at low density or that have traits making them difficult to detect	**B**: Species that only irregularly occur in the local habitat because they are poorly suited to that habitat
High temporal occupancy, inferred to be "core"	**C**: Core members of the community that maintain viable populations and are reliably observed almost every year	**D**: Species that occur regularly in the local habitat despite failing to maintain positive population growth rates due to repeated immigration from adjacent source habitat
Error rates	A / (A + C)	D / (B + D)

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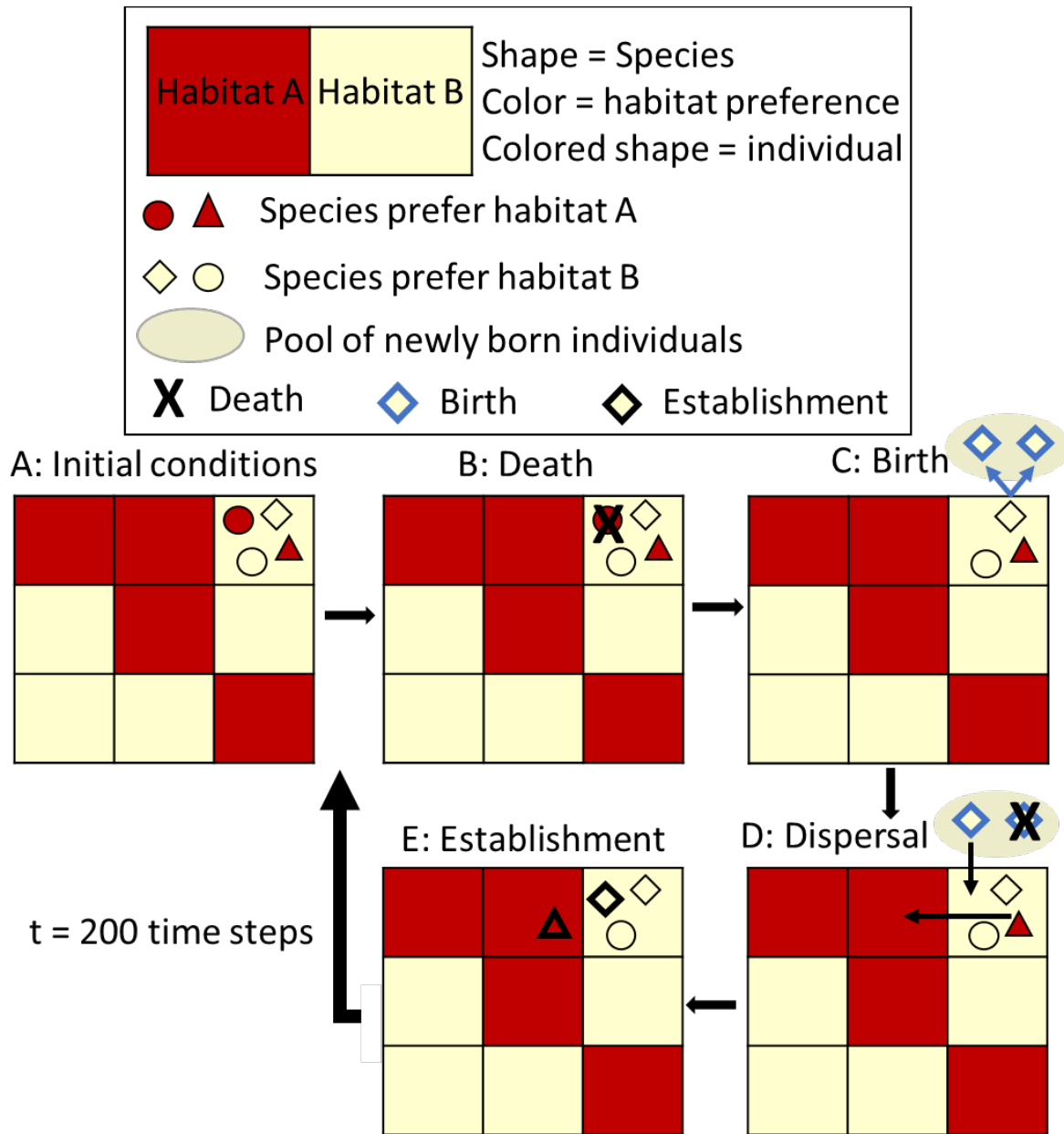
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354 **Figure 1.** Schematic documenting the events that occur in a single time step of the simulation,
355 including death, birth, dispersal, and establishment. See text for details.
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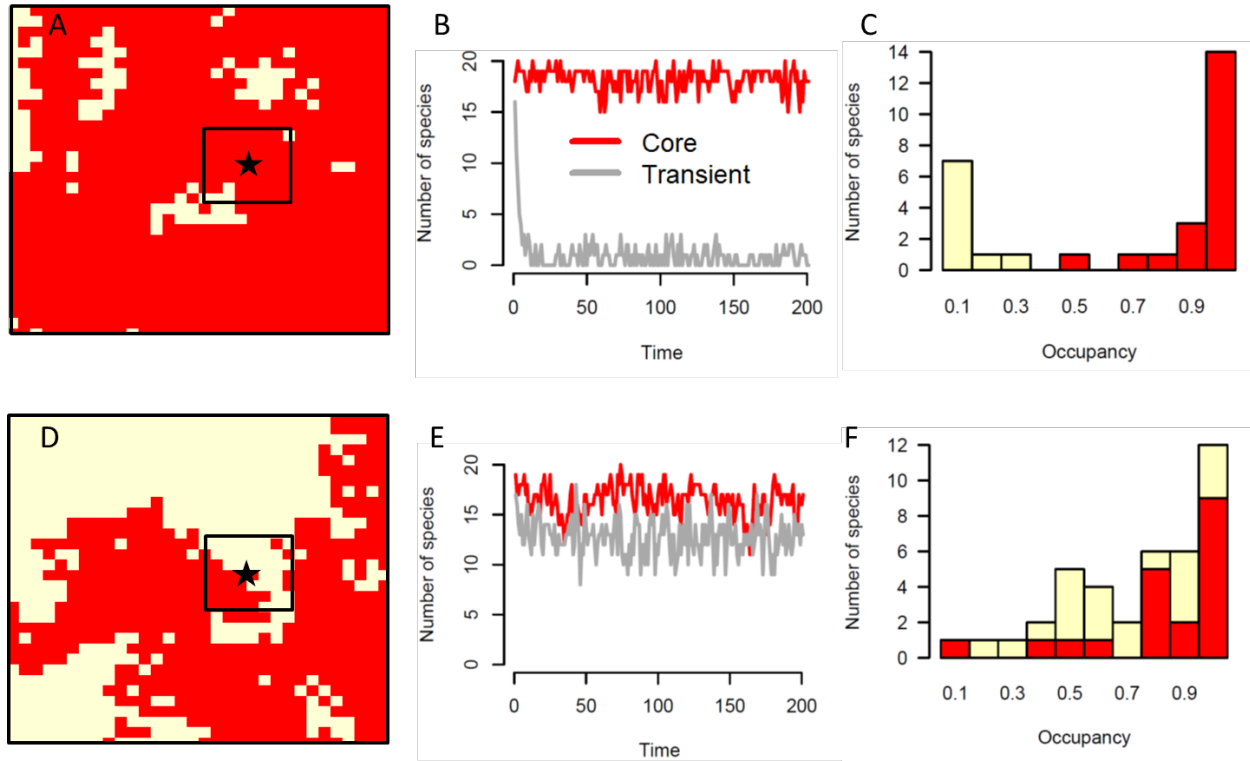
357
358 **Figure 2.** (A) Sample landscape of one simulation run in which the proportion of the full
359 landscape that was habitat A (in red) was set to 0.9. Landscape similarity around the focal pixel
360 is 0.92. (B) Number of core species (that can reproduce in the red habitat, red line) and transient
361 species (that cannot reproduce in the red habitat, gray line), plotted over time for the focal pixel
362 from the landscape in (A). (C) Temporal occupancy distribution of the species in the focal pixel
363 from the landscape in (A). Colors of the bars indicate the number of species according to which
364 habitat type they can reproduce in. (D) Sample landscape of one simulation run in which the
365 proportion of the landscape that was habitat A (red) was set to 0.5. Landscape similarity around
366 the focal pixel is 0.49. (E) Number of core species (red line) and transient species (gray line),
367 plotted over time for the focal pixel from the landscape in (D). (F) Temporal occupancy
368 distribution of the species in the focal pixel from the landscape in (D). Colors of the stacked bars
369 indicate the number of species according to which habitat type they can reproduce in.
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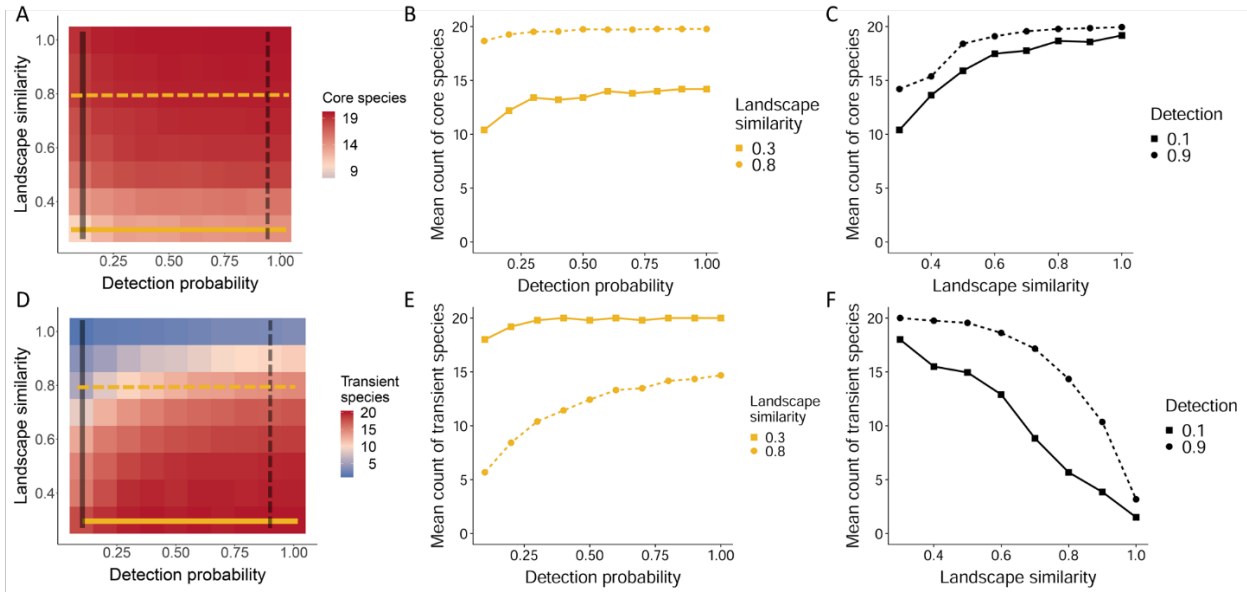
Figure 3. Mean number of biologically core (A) and biologically transient (D) species observed for each combination of detection probability and landscape similarity. Line graphs (B, E) show the mean count of core species (B) or transient species (E) for each detection probability at low (0.3, solid line) or high (0.8, dashed line) landscape similarity. Line graphs (C, F) show the mean count of core species (C) or transient species (F) with increasing landscape similarity at low (0.1, solid line) or high (0.9, dashed line) detection probability.
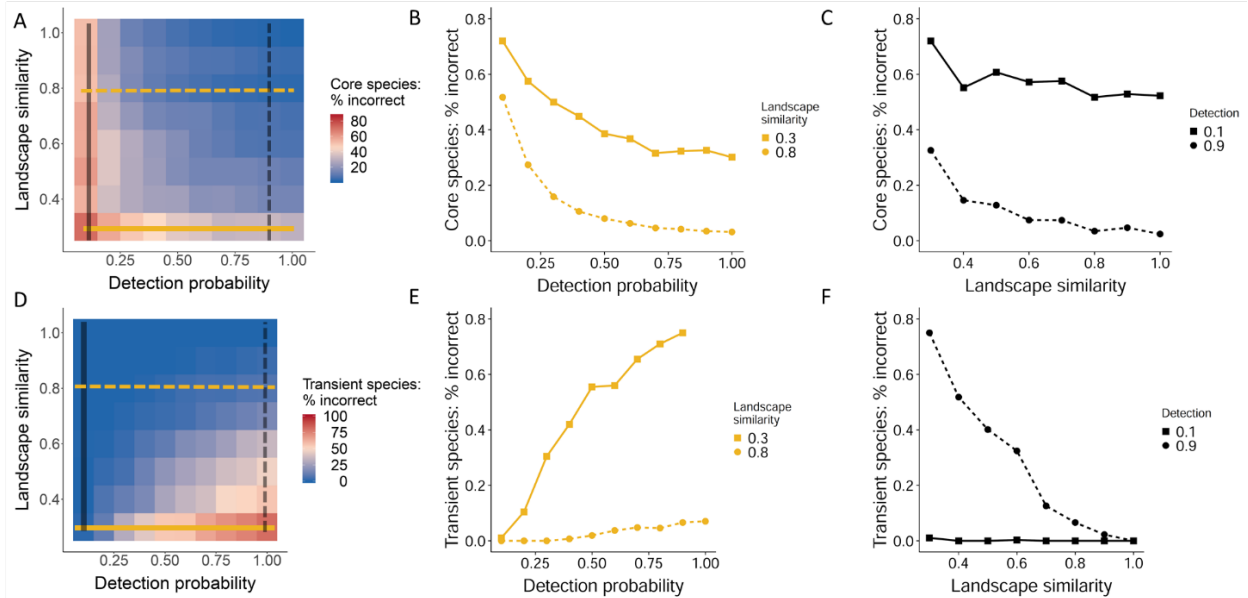
Figure 4. Percent of biologically core (A) species that were incorrectly inferred to be transient and biologically transient (D) species that were incorrectly inferred to be core for each combination of detection probability and landscape similarity. The x-axis is the average species detection probability for the simulation run, while the y-axis is the proportion of a 7 x 7 landscape surrounding the focal pixel that is of the same habitat type. Line graphs (B, E) show the percent of incorrect classifications of core species (B) or transient species (E) for each detection probability at low (0.3, solid line) or high (0.8, dashed line) landscape similarity. Line graphs (C, F) show the percent of incorrect classifications of core species (C) or transient species (F) with increasing landscape similarity at low (0.1, solid line) or high (0.9, dashed line) detection probability.
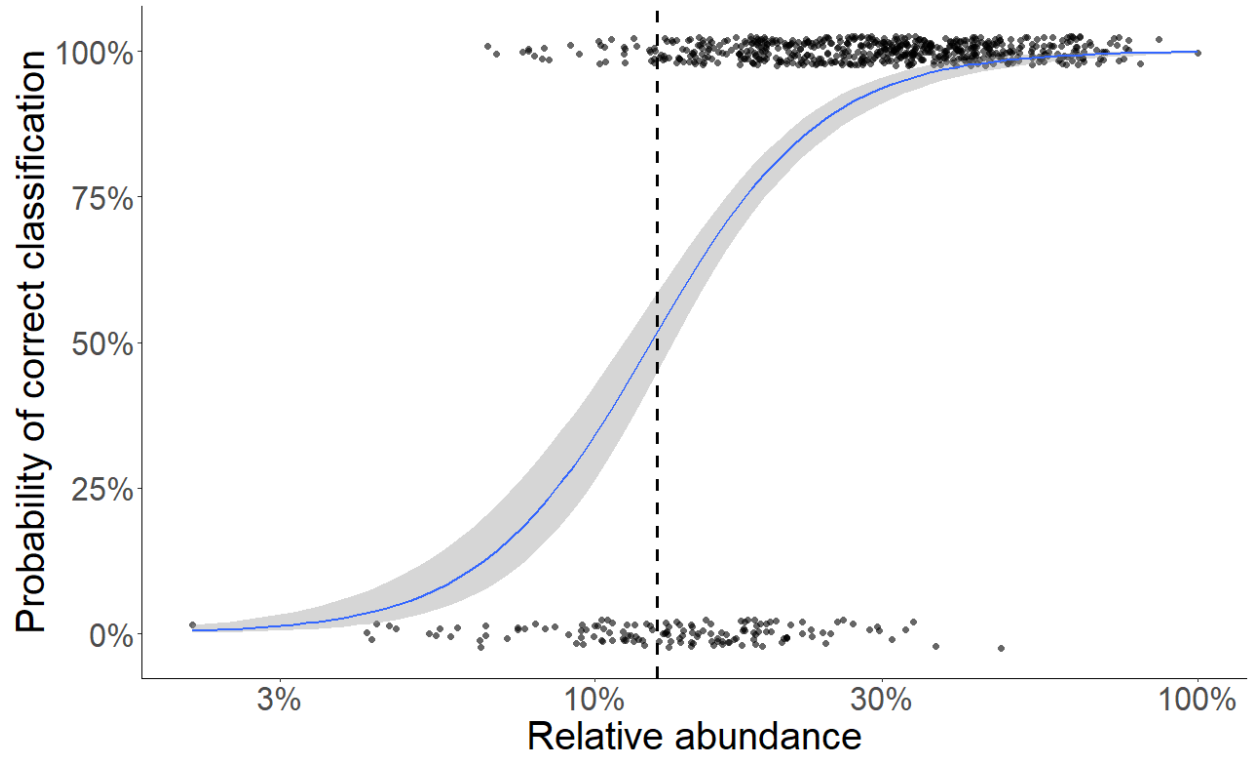
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402   **Figure 5.** Probability of correct classification of biologically core species based on temporal
403   occupancy as a function of the log of landscape wide abundance (relative to the abundance of the
404   most abundant species, 100%). Dashed line indicates the location of the inflection point.
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