

1 **(A) Red noise increases extinction risk during rapid climate change**

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18 Article type: Research paper

19 Running title: Noise and extinction risk

20

21 **(A) Abstract**

22 **(B) Aim:** As the global climate is changing rapidly there is a need to make conservation
23 decisions to facilitate species' persistence under climate change. Models employed to make
24 predictions regarding the impacts of climate change on species' distributions, and ultimately
25 persistence, typically assume that inter-annual variability in environmental conditions is
26 independent between years. However, the colour of environmental noise has been shown to
27 affect extinction risk in populations occupying spatially static environments, and should
28 therefore affect persistence during climate change. This study aims to investigate the
29 importance of noise colour for extinction risk during climate-induced range shifts.

30 **(B) Methods:** We use a spatially explicit coupled map lattice with a latitudinal gradient in
31 climatic suitability, together with time-series' of environmental noise, to simulate periods of
32 directional climate change and investigate the effects of noise colour on extinction risk and
33 range size.

34 **(B) Results:** Extinction risk increases with reddening of the environmental noise, and this
35 effect is particularly pronounced over short time-frames when climate change is rapid.

36 **(B) Main conclusions:** Given that management decisions are typically made over such short
37 time-frames, and the rapid rates of climate change currently being experienced, we highlight
38 the importance of incorporating realistic time series of environmental noise in to models used
39 for conservation planning under climate change.

40 **Key words:** climate change; colour; environmental noise; extinction risk; range shifting;
41 spatial population dynamics

42 (A) Introduction

43 The global climate is changing rapidly, and impacts on species distribution and local
44 persistence are now documented across environments and taxa (Walther, Post et al. 2002;
45 Parmesan and Yohe 2003; Thomas 2010). Given the need to make management decisions to
46 facilitate species' persistence under climate change, models are often employed to make
47 predictions regarding the future (e.g. Carey 1996; Sykes, Prentice et al. 1996; Hill, Thomas et
48 al. 1999; Berry, Dawson et al. 2002; Thuiller 2003; Wilson, Gutierrez et al. 2005; Best, Johst
49 et al. 2007; Brooker, Travis et al. 2007; Jiguet, Gadot et al. 2007; Keith, Akçakaya et al.
50 2008; Anderson, Akçakaya et al. 2009). However, these models either ignore the inter-annual
51 variability in environmental conditions (environmental noise) or assume that this variability
52 is independent between years. Theoretical and empirical work has shown that population
53 processes, and thus extinction risk, should be strongly affected by the "colour" of
54 environmental noise (e.g. Greenman and Benton 2003; Benton and Beckerman 2005;
55 Greenman and Benton 2005; Reuman, Desharnais et al. 2006; Ruokolainen, Lindén et al.
56 2009).

57 By analogy with optics, time series of inter-annual environmental variation of different
58 frequencies can be described by their colour (Fig.1). Time series which exhibit no temporal
59 autocorrelation are termed "white noise"; time series which are positively auto-correlated,
60 and therefore characterised by low frequency fluctuations, are referred to as "red noise"
61 (Fig.1(c)), and time series that exhibit high frequency fluctuations show negative
62 autocorrelation and are "blue" (Fig.1(b)). Many measured time series of environmental noise
63 are reddened over generational time scales, more extremely in marine and coastal
64 environments, whereas terrestrial environmental noise tends to fall somewhere between white
65 and red noise (pink noise), and some environmental factors can exhibit extremely low

66 frequency variations (brown or even black noise) (e.g. Halley 1996; Vasseur and Yodzis
67 2004; Garcia-Carreras and Reuman 2011).

68 The modern ecological synthesis accepts that population dynamics arise as a combination of
69 density dependent and density independent effects (Bjørnstad and Grenfell 2001). A
70 corollary of this is that all organisms' dynamics' are affected by the way that the environment
71 varies. Specific studies on the relationship between noise and dynamics have included a
72 number of taxa including birds, mammals and plants (e.g. Benton, Grant et al. 1995;
73 Freckleton and Watkinson 1998; Engen, Saether et al. 2001; Carroll 2007; Hilderbrand,
74 Gardner et al. 2007; van de Pol, Vindenes et al. 2011). Given that individual life-histories,
75 and therefore population dynamics, integrate over time periods of years or generations, the
76 low frequency component of environmental variation is likely to be particularly important in
77 extinction dynamics (because a sequence of poor years is likely to have a strong cumulative
78 effect on population size) (Ripa and Lundberg 1996; Johst and Wissel 1997; Petchey,
79 Gonzalez et al. 1997; Heino 1998; Greenman and Benton 2003; Schwager, Johst et al. 2006).

80 Depending on the under-lying population dynamics, reddening of the environmental noise
81 can: increase extinction risk due to long runs of “bad” years; or decrease extinction risk due
82 to the relatively lower probability of an extremely bad year in any given time period relative
83 to white noise (Ripa and Lundberg 1996; Petchey, Gonzalez et al. 1997; Ripa and Heino
84 1999; Schwager, Johst et al. 2006). Given that most species exhibit “undercompensatory”
85 dynamics, as a result of contest competition for resources, extinction risk over a given time-
86 period will generally be under-estimated if the environmental noise is assumed to be white
87 (Petchey, Gonzalez et al. 1997). The effect of reddening of the environment on extinction
88 probability also varies by life history strategy and stage, community abundance rank, the
89 nature of interspecific interactions and the strength of the correlation between the responses
90 of individual species within a community (Heino and Sabadell 2003; Ruokolainen, Fowler et

91 al. 2007; Ruokolainen and Fowler 2008). For example, Heino and Sabadell (2003), found
92 that reddening of environmental noise decreases extinction risk in annually reproducing
93 species, but increases extinction risk for semelparous and iteroparous biennial, and perennial
94 reproducers.

95 In spatially structured populations, where key demographic rates or life-history
96 characteristics vary through space, reddening of the noise generally increases the global
97 extinction risk, even though local extinction risk may decrease, regardless of the pattern of
98 population dynamics (Petchey, Gonzalez et al. 1997; Heino 1998). This is because the spatial
99 heterogeneity in patch quality means that when an unfavourable environmental event occurs,
100 populations in better quality patches will be more likely to persist than those in lower quality
101 patches. These patches then act as sources, once conditions improve, to re-colonise poorer
102 quality patches from which the population has gone locally extinct. This is referred to as the
103 “rescue effect” (Brown and Kodric-Brown 1977). The key point is that conditions will
104 improve more quickly in an environment of white noise, whereas under reddened noise there
105 are more likely to be long runs of unfavourable conditions, increasing the likelihood of more
106 patches going extinct, decreasing the pool of potential source patches, and therefore
107 threatening the viability of the metapopulation. This effect may be amplified by a high
108 degree of spatial environmental correlation and increased noise amplitude (Palmqvist and
109 Lundberg 1998). Given the apparent importance of noise colour and amplitude in
110 populations occupying spatially static environments, it may be expected that they will have
111 important effects on species persistence and range dynamics under climate change. Much
112 theoretical and conservation interest has been generated in the effects of habitat
113 heterogeneity, spatial demography, spatial population dynamics and life history
114 characteristics on range dynamics, species distribution and persistence under climate change
115 (e.g. Travis 2003; Opdam and Wascher 2004; Carroll 2007; Hilderbrand, Gardner et al. 2007;

116 Anderson, Akçakaya et al. 2009; Mustin, Benton et al. 2009; Doxford and Freckleton 2012;
117 Urban, Tewksbury et al. 2012).

118 Here we combine a spatially-explicit coupled map lattice (CML) model which incorporates a
119 broad-scale latitudinal gradient in climatic suitability, with different time-series of
120 environmental noise to investigate how the colour of environmental noise affects species'
121 persistence and range size during rapid climate change.

122

123 **(A) Methods**

124 The model consists of a landscape represented by a cellular lattice of 100 x 600 habitat
125 patches and all patches are considered to be potentially suitable for occupation. Within-patch
126 dynamics are described by an individual-based formulation of Maynard-Smith and Slatkin's
127 (1973) single species population model. Each individual present in patch i at time t produces
128 offspring, the number of which is drawn from a Poisson distribution with mean $\mu_{i,t}$ defined
129 by:

130

$$131 \mu_{i,t} = \frac{r}{1 + |1-r| \times N_{i,t} / K}$$

132

133 Where r describes the maximum growth rate, $N_{i,t}$ describes the number of individuals in patch
134 i at time t , and K is the carrying capacity. After producing offspring the individual dies, and
135 a proportion of the offspring disperse. Dispersal is usually to any unoccupied patch from the
136 nearest eight neighbouring patches.

137

138 **(B) Environmental variation through space and time**

139 Latitudinal variation in mean climate is imposed by defining the position of optimum climatic
140 conditions as a row on the lattice (E_{max}), and assuming that conditions decline sigmoidally
141 away from this optimum in both directions:
142

$$143 \quad E_{j,t} = \frac{d_{j,t}^s}{d_{j,t}^s + h^s}$$

144

145 Where $E_{j,t}$ is the mean climate suitability at row j in time t , $d_{j,t}$ is the distance of row j at time
146 t from E_{max} , h is the half-saturation constant which defines the distance at which $E_{j,t} = 0.5$,
147 and s is a shape parameter which defines the direction (negative values of s give a negative
148 slope and vice versa) and shape of the curve (when $s > 1$ the curve is sigmoidal). In all
149 simulations presented here $h = 10$ and $s = -3$. If $d_{j,t}$ is zero then $E_{j,t}$ is set as 1. This approach
150 is similar to that used by Mustin *et al.* (2009), and the model has been extended to
151 incorporate environmental noise around this mean which varies temporally but not spatially.
152 Time series were produced using R version 2.10.1 (R-Development-Core-Team). The
153 environmental noise is generated using an autoregressive (AR) method (Ripa and Lundberg
154 1996):

155

$$156 \quad \mathcal{E}_t = K \mathcal{E}_{t-1} + \omega_t$$

157 Where K is the autocorrelation coefficient and ω_t is a standard normal random component
158 (mean = 0, variance = 1). Previous studies have highlighted that the method used to scale the
159 variance can affect the outcome of modelling exercises (Johst and Wissel 1997; Heino, Ripa
160 *et al.* 2000; Wichmann, Johst *et al.* 2005), and so the method used here scales the noise to
161 have a variance of w^2 after Wichmann *et al.* (2005):

162

$$163 \quad e = \frac{w}{\sigma_e} \mathcal{E}' - \bar{\mathcal{E}}$$

164

165 Where σ_e defines the standard deviation of the noise process (and can therefore also be used

166 to scale the amplitude of the time series), w is the standard deviation of a white noise time

167 series and \mathcal{E}' is the un-scaled time series produced by the AR process. $\bar{\mathcal{E}}$ is the long term

168 mean of \mathcal{E}' .

169

170 The resulting spatio-temporal variation is related to within-patch dynamics by assuming a

171 direct relationship between environmental conditions and intrinsic population growth rate r :

172

$$173 \quad r_{j,t} = r \times (E_{j,t} + e_t)$$

174

175 Where $r_{j,t}$ is the growth rate for patches in row j at time t , and r is the expected growth rate

176 in the absence of environmental forcing.

177

178 **(B) Simulation experiments**

179 The optimum climatic conditions are set to occur at one row on the lattice and the model was

180 run for 500 time steps. The optimum was then moved uni-directionally for the next 1500

181 time steps to simulate a period of directional climate change. The model is stochastic, and to

182 obtain a good representation of the system's behaviour, 250 independent realisations were

183 run for each parameter set.

184

185 To assess the impacts of different colours of environmental noise on extinction risk under
186 climate change we consider two conditions. Firstly we model relatively rapid climate change
187 (0.33 rows^{-1}) and assess the extinction risk over time-scales which are relevant to
188 conservation management (30, 50 and 100 years). Secondly we model slower climate change
189 (0.25 rows^{-1}) and assess the extinction risk over long time-scales as a theoretical exercise. All
190 simulations were run for values of κ of 0.99 (extremely reddened), 0.95, (red), 0.9 (red – see
191 Fig.2(b)), 0.75 (pink), 0.5 (pink) and 0 (white – see Fig.2(a)).

192

193 Sensitivity analyses were conducted to examine the robustness of our findings to:

- 194 1. varying amplitude of environmental noise (σ_e of 0.05, 0.1, 0.15 and 0.2); and
- 195 2. dispersal neighbourhood (nearest 8, 24 or 48 neighbours and nearest eight neighbours
196 but with 5% of individuals able to disperse globally).

197

198 (A) Results

199 For a given rate of climate change, the extinction risk increases with reddening of the
200 environmental noise (Fig.3(a)). However, the average size of extant ranges is larger when the
201 noise is extremely reddened ($K = 0.99$; Fig.3(b)).

202

203 When climate change is relatively rapid (0.33 rows^{-1}) the rate of extinction (number of
204 simulations which went extinct per time step) increases substantially with noise reddening
205 over management relevant time-scales (30, 50 and 100 years; Fig.4(a)). When climate change
206 is relatively slow (0.25 rows^{-1}) the extinction rate is only slightly increased over a long time-
207 scale (1500 years; Fig.4(b)).

208

209 Decreasing the amplitude of the environmental noise reduces the extinction risk such that the
210 number of simulations where the range persists through rapid climate change ($0.33 \text{ rows}^{\text{t}^{-1}}$)
211 increases from 3 (1.2%) where $\sigma_e = 0.2$ to 183 (73.2%) where $\sigma_e = 0.1$, however this
212 sensitivity does not qualitatively change our result and extinction risk is higher under red than
213 white noise for any given noise amplitude (Fig.5).

214

215 Increasing the dispersal neighbourhood, or assuming some long-distance dispersal events to
216 anywhere on the lattice, decreases the extinction risk under red noise such that the number of
217 simulations where the range persists through rapid climate change ($0.33 \text{ rows}^{\text{t}^{-1}}$) increases
218 from 183 (73.2%) where dispersal is to the nearest eight neighbouring patches, to 239
219 (95.6%) where 5% global dispersal occurs (Fig.6(a)). This sensitivity does not qualitatively
220 change our result that the extinction risk is higher under red than white noise, however,
221 widening the dispersal neighbourhood to the nearest 24 or 48 patches reduces extinction to
222 zero over the 2000 time steps modelled (Fig.6(a)). Furthermore, there is a reduction in range
223 size during climate change under all dispersal scenarios (Fig.6(b)).

224

225 (A) Discussion

226 For our model of a spatially explicit population, with no age or stage structure, the risk of
227 extinction during a period of directional climate change is increased when the environmental
228 noise is reddened (Fig.4). This is true for both rapid climate change over short time periods of
229 relevance to management decisions (Fig.4(a)), and slow climate change over much longer
230 time periods (Fig.4(b)). These effects are probably due to the greater probability of
231 consecutive time steps of poor environmental conditions when noise is reddened relative to
232 uncorrelated time-series of white noise, such that the population has no chance to recover.
233 Most environmental noise is reddened (Halley 1996; Vasseur and Yodzis 2004), in particular

234 air and sea-surface temperatures which have been found to have spectral exponents (here
235 equivalent to K) of 0.5 to 1.5 on average (Vasseur and Yodzis 2004), and our results therefore
236 have important implications for species persistence under climate change.

237

238 The impact of climate change has typically been assumed to relate to the way in which the
239 “envelope” of mean climatic conditions is shifting through time and space. However, there
240 has been a recent resurgence in interest in the impacts of variability in weather relative to
241 these climatic means, and how the frequency or magnitude of extreme weather events might
242 increase as a result of on-going climate change (Coumou and Rahmstorf 2012). The
243 variability is expressed as the shape of the distribution of weather around the climatic mean,
244 and empirical data are suggesting that the width of this distribution is moving 2 – 2.5 times
245 faster than the mean climatic conditions (Hansen, Sato et al. 2012); thus, globally, weather is
246 becoming more variable. Given this rapid increase in the frequency and magnitude of
247 extreme events, it is now essential that species distribution modelling takes in to account the
248 amplitude and colour of environmental noise in order to make projections regarding future
249 distribution and persistence under climate change. Specifically, we expect that for many
250 species the predicted threshold rate of climate change for persistence over a given time period
251 will be overestimated if the colour of environmental noise is not considered.

252

253 For many biological phenomena, such as growth, as a function of temperature or light,
254 fecundity and population growth, underlying processes are essentially geometric as opposed
255 to arithmetical, and therefore variance in parameter values has a significant impact on the
256 eventual outcome, especially population persistence. Given that population persistence is
257 typically the goal of conservation management actions, it is therefore essential to account for
258 environmental noise in models which seek to predict future distributions and persistence, and

259 which are being used to assess the efficacy of different management options. As a concrete
260 example, the spring of 2012 was characterised as a drought in NW Europe, being among the
261 driest on record. This impacted a range of processes across taxa, such as reproduction,
262 seedling emergence, and dispersal. The subsequent summer, however, has been amongst the
263 wettest on record, which has impacted juvenile survival, seed set and organismal condition.
264 Overall, however, the total rainfall may emerge as close to average. Modelling this climatic
265 average would mask the effects of the extreme dry and wet periods on population processes,
266 and would therefore severely under-estimate the effect of the environmental conditions on
267 predictions of range shifting and population persistence. Making predictions for future
268 persistence under predicted climate change, using only mean climatic conditions and ignoring
269 the likely increased variability, will similarly under-estimate extinction risk and therefore
270 potentially biases the investment of resources for conservation management.

271

272 Interestingly, however, we also find that when the noise is extremely reddened ($K = 0.99$) the
273 average size of extant ranges is larger than under any other noise conditions (Fig.3(b)). This
274 pattern is probably a reflection of the possibility that sub-populations can persist where the
275 average climatic conditions have become unsuitable due to the directional climate change,
276 because consecutive “good years” improve conditions for the species. This potential
277 importance of the “trailing edge” for overall patterns of range change and extinction risk
278 under climate change has also been highlighted elsewhere (Hampe and Petit 2005). Hampe
279 and Petit (2005) suggest two extremes of “behaviour” at the low latitude distribution edge:
280 “trailing edges” where populations become extirpated as a result of latitudinal displacement
281 of a species range, and “stable rear edges” where the overall species range expands as a
282 varying fraction of the populations at the rear edge are able to persist. We find both patterns
283 in our results, with the most extremely reddened noise ($K = 0.99$) producing patterns more

284 akin to “stable rear edges” and less reddened noise ($K = 0.5-0.9$) producing a pattern more
285 akin to “trailing edges”. Further empirical work is required to understand the importance of
286 these rear edge populations, across taxa, under climate change, and currently most evidence
287 comes from studies of perennial plants (Hampe and Petit 2005 and references therein). In
288 common with previous findings (Johst and Wissel 1997; Petchey, Gonzalez et al. 1997;
289 Heino 1998; Schwager, Johst et al. 2006) we have also shown that when there is no
290 directional climate change and the amplitude of the noise is sufficiently high, extinction is
291 more likely in red than white environments (Fig.3(a)).

292

293 We have shown that reddening of the environmental noise increases extinction risk in a
294 spatially structured population during a period of climate change. Another important source
295 of structure in populations is the age or stage structure, which refers to the number of
296 individuals of different age classes or stages (i.e. adult vs. juvenile) and the probabilities with
297 which they move from one age or stage to another. We use a population model which has no
298 age or stage structure, such that the noise at time t has an impact only on the population
299 growth rate at time t . The focus of this research was the impact of environmental noise
300 colour, during climate change, on range dynamics of a spatially-structured population, and
301 hence we chose to use a simple population model without stage structure. However, in
302 reality, life-histories are shaped by environmental conditions throughout life, and maternal
303 effects, and environmental conditions early on in life have been repeatedly shown to produce
304 prolonged effects during organisms’ lifetimes. The impact of environmental noise (weather
305 variation around the climatic mean) on dynamics acts through the colour of the resulting
306 population dynamics, which may be linearly related to the environmental noise, as is likely to
307 be the case in models without age or stage structure so that red environmental noise produces
308 red population dynamics. If the dynamics are “reddened” a run of bad years may drive the

309 population extinct. However, in age or stage structured models the colour of the resultant
310 population dynamics can be quite different than the colour of the environmental noise. In
311 part this results from poor environmental tracking, where demographic rates do not respond
312 linearly to the colour of environmental noise but rather “filter” the noise and change its
313 colour. For example, in stage structured models, blue environmental noise (negatively
314 temporally auto-correlated) may result in red population dynamics due to the lagged effects
315 inherent in modelling the life-history, increasing extinction risk (Greenman and Benton
316 2005). It has been suggested that in such cases the colour of noise will be less important than
317 either the mean environmental change or the extent of the inter-annual variability (amplitude
318 of the noise) in determining the mean time to extinction (van de Pol, Vindenes et al. 2011).
319 Our results are certainly quantitatively sensitive to the amplitude of environmental noise and
320 rate of climate change (Fig.4 and Fig.5), however the qualitative effect whereby extinction
321 risk increases with red noise is un-changed, and is in common with previous findings (e.g.
322 Ripa and Lundberg 1996; Petchey, Gonzalez et al. 1997; Heino 1998; Ripa and Heino 1999;
323 van de Pol, Vindenes et al. 2011). Given that the frequency and magnitude of extreme
324 weather events is predicted to increase under future climate change (IPCC 2007), our results
325 suggest that in reality extinction risk will increase under future climate change as the
326 amplitude of the environmental noise increases. The utility of our approach is not to say only
327 red-noise is important in determining extinction risk under climate change but more to
328 highlight that the colour of the dynamics (whether driven by coloured noise, or the filtration
329 of noise through the life-history) is important to consider. This will particularly be the case
330 for species with more limited dispersal distances, and especially those with narrow climatic
331 tolerances such as amphibians, which are more vulnerable to climate change due to an
332 inability to rapidly migrate and keep pace with their necessary, and shifting, climatic
333 conditions (Fig.6 and Trakhtenbrot, Nathan et al. 2005; Araújo, Thuiller et al. 2006).

334 Whereas species with wide dispersal neighbourhoods, or those capable of long-distance
335 dispersal events, such as many bird species, will be more likely to persist (Fig.6 and
336 Trakhtenbrot, Nathan et al. 2005).

337

338 We suggest four possible extensions to the work presented here. Firstly, there is evidence
339 that the colour of environmental noise may be redder at high and low latitudes compared to
340 temperate latitudes (Vasseur and Yodzis 2004). This is likely to have important implications
341 as it may lead to, for example for more northerly distributed species, more reddened noise at
342 the leading edge compared to the trailing edge. The greater stochasticity at the trailing edge
343 may allow for persistence over much longer time scales in environments which are, on
344 average, unsuitable. This would in turn impact on range extent and persistence, and from a
345 conservation perspective this may also necessitate different management actions in different
346 parts of the species range. For example, assisted colonisation (e.g. Hoegh-Guldberg, Hughes
347 et al. 2008; Willis, Hill et al. 2009) at the leading edge versus habitat management or
348 reduction of other threats at the trailing edge. We therefore contend that an interesting
349 extension to the work presented here would be the inclusion of spatial variation in the colour
350 of environmental noise, and if parameterised for a real system then the effect of different
351 management options in different parts of the range could also be explored in a decision
352 theory framework to find cost-effective management plans. Secondly, many species live in
353 ephemeral habitats, characterised by destruction and regeneration of suitable habitat
354 “patches”. For some species this patch lifespan may be linked to climatic conditions, and for
355 example increases in the frequency of extreme weather events could reduce patch lifespan.
356 One such species, the grasshopper *Bryodema tuberculata* in central Europe survives only on
357 gravel bars along braided rivers in the Northern Alps, a habitat characterised by succession
358 and floods. Stelter *et al* (1997) used simulation models to show that persistence time for

359 metapopulations of this species are low if the time between floods is too short (because many
360 subpopulations are washed away at the same time), or too long (because local subpopulations
361 are eliminated by succession). The persistence of species in such dynamic landscapes has
362 received much attention (Fahrig 1992; Hanski 1999; Keymer, Marquet et al. 2000; Johst,
363 Brandl et al. 2002), and there would be merit in considering a possible interaction between
364 changed frequency and magnitude of extreme climatic events and habitat patch destruction
365 and regeneration. From a conservation perspective it is possible to envisage two possible
366 routes through which such changes might lead to population declines for species dependent
367 on these ephemeral habitats: patches may have insufficient time to regenerate before the next
368 destructive climate event as a result of increased frequency of such events; or multiple
369 patches could be destroyed simultaneously as a result of increased magnitude of climate
370 events, which could then reduce the probability of patch re-colonisation from neighbouring
371 patches. Thirdly, previous studies have found that the effect of noise colour on extinction
372 risk varies according to the inter-specific interactions between species and structure of the
373 community as a whole (Ruokolainen, Fowler et al. 2007; Ruokolainen and Fowler 2008).
374 Here we have considered a single-species model, and it is certainly reasonable to expect that
375 extinction risk under climate change for any given species will be affected by the range
376 dynamics of competitors, predators, mutualists and prey or resources. Therefore extending
377 the work presented here to include some of these potential inter-specific interactions would
378 provide further insights in to the role of environmental variation in species extinction risk
379 under climate change. Finally, and perhaps most importantly, there is a need to explore the
380 impacts of environmental noise on stage structured populations experiencing a period of
381 climate change. With very few exceptions, organisms life histories are stage structured.
382 Environmental noise affects individuals by either altering their survival, or changing the
383 pattern of investment in life history (i.e. trade-off between survival to reproduce in the

384 following year and reproduction in this year). As a result, the impacts of environmental noise
385 on population persistence will ultimately be a function of how and where the noise affects the
386 organisms life-history and how these effects filter through the population (e.g. Greenman and
387 Benton 2005; Benton 2006). Furthermore, impacts of noise will almost certainly be lagged as
388 a result of “bad years” as a juvenile affecting adult survival and life history allocations. For
389 example, Benton *et al.* (2001) showed that when the transmission of maternal environmental
390 conditions is the cause of delayed density dependence the population variability increases,
391 and in a stochastic environment this is the result of the interaction between the delayed
392 density dependent effects and environmental noise. Furthermore, experimental work
393 indicates that maternal effects can cross multiple generations and vary in their impact
394 according to density (and thus food availability) (Plaistow and Benton 2009). Therefore an
395 important extension to the work presented here would be to examine the effects of noise
396 colour and amplitude in a stage structured population, incorporating realistic lagged effects,
397 during a period of climate-induced range shifting.

398

399 In conclusion, we have shown that in a spatially-structured population the colour of
400 environmental noise helps to determine the size and ultimately persistence of the occupied
401 range during a period of climate change. Given this result and the increasing need to make
402 conservation decisions regarding species persistence under the threats presented by multiple
403 environmental drivers including climate change and habitat loss, future attempts to predict
404 species responses to climate change should consider the implications of the colour of
405 environmental stochasticity and not just mean climate projections.

406

407 **(A) Acknowledgements**

408 KM was funded by a UKPopNet studentship. This collaboration was initiated at the
409 workshop “Integrating spatially explicit statistical models and individual-based modelling
410 using Bayesian statistics II” organised by Dr Barbara Anderson. The authors are grateful to
411 Mike Fowler and Lasse Ruokolainen for providing the methodology and R code to generate
412 the coloured noise time series.
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568 **Biosketch:** Karen Mustin has particular interests in conservation and spatial population
569 ecology, and her research focuses on the interaction between anthropogenic activities and
570 biodiversity conservation. Much of her work focuses on theoretical and empirical
571 investigations of biogeographic range shifts under climate change.

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575 **Figure legends**

576 **Figure 1:** schematic to show how the wavelength of light increases as its colour changes
577 from blue to red (a); and generated environmental noise time series, with amplitude $\sigma_e = 0.1$,
578 for: (b) “blue” noise (auto-correlation coefficient $K = -0.95$); and (c) “red” noise ($K = 0.95$).
579 By analogy with optics, environmental noise is referred to as having a “colour”, such that
580 where the wavelength is short, and the time-series is characterised by high frequency
581 variation as a result of negative temporal auto-correlation, the noise is termed “blue”.
582 Whereas, when the wavelength is long, and the time-series exhibits low frequency variation
583 as a result of positive temporal auto-correlation, the noise is termed “red”. “White” noise is
584 used to describe environmental time-series which are not temporally correlated.

585

586 **Figure 2:** Generated environmental noise time series for (a) auto-correlation coefficient $K =$
587 0, noise amplitude $\sigma_e = 0.1$; (b) $K = 0.95$ $\sigma_e = 0.1$; (c) $K = 0.95$ $\sigma_e = 0.05$; (d) $K = 0.95$ $\sigma_e =$
588 0.2.

589

590 **Figure 3:** (a) Number of extant runs of the simulation against time, and (b) mean size of
591 extant ranges through time where the noise is increasingly reddened (auto-correlation
592 coefficient K of 0.5, 0.75, 0.9 and 0.99). Results are not shown for white noise ($K = 0$) as no
593 extinctions occurred. Here the rate of climate change is $0.33 \text{ rows } t^{-1}$, noise amplitude $\sigma_e = 0.2$
594 and dispersal is to the nearest eight neighbouring patches only. The vertical dashed line
595 shows the onset of climate change.

596

597 **Figure 4:** Extinction rate under: (a) rapid climate change ($0.33 \text{ rows } t^{-1}$) over 30 (triangles),
598 50 (squares) and 100 (diamonds) years; and (b) slow climate change ($0.25 \text{ rows } t^{-1}$) over 1500
599 years; where the noise is increasingly reddened (auto-correlation coefficient K of 0.5, 0.75,

600 0.9 and 0.99). Results are not shown for white noise ($K = 0$) as no extinctions occurred. In
601 both sets of simulations noise amplitude $\sigma_e = 0.2$ and dispersal is to the nearest eight
602 neighbouring patches only

603

604 **Figure 5:** Number of extant runs of the simulation against time under: (a) red noise (auto-
605 correlation coefficient $K = 0.95$) and (b) white noise ($K = 0$); for noise amplitude $\sigma_e = 0.05$,
606 0.1, 0.15 and 0.2. Here climate change is at a rate of $0.33 \text{ rows } t^{-1}$ and dispersal is to the
607 nearest eight neighbouring patches only. The vertical dashed line shows the onset of climate
608 change

609

610 **Figure 6:** The effect of varying dispersal strategy on (a) number of extant runs of the
611 simulation against time, and (b) mean size of extant ranges through time under red noise
612 (auto-correlation coefficient $K = 0.95$). The tested strategies are dispersal to the nearest 8, 24
613 and 48 neighbouring patches, and 5% global dispersal with the rest to the nearest eight
614 neighbouring patches. The rate of climate change is $0.33 \text{ rows } t^{-1}$, and noise amplitude $\sigma_e =$
615 0.1. The vertical dashed line shows the onset of climate change.

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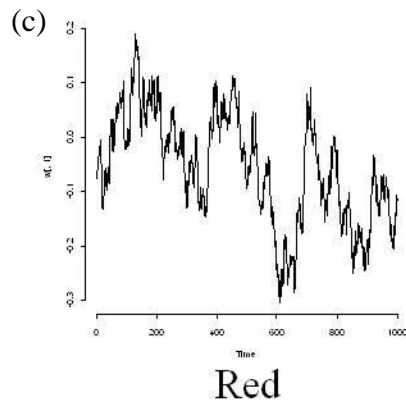
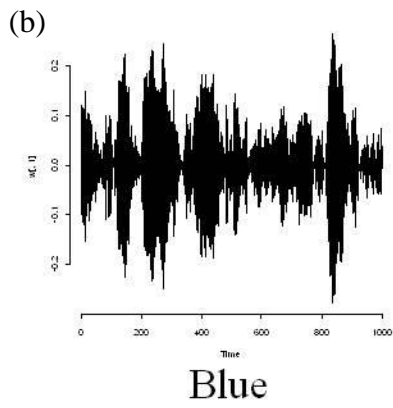
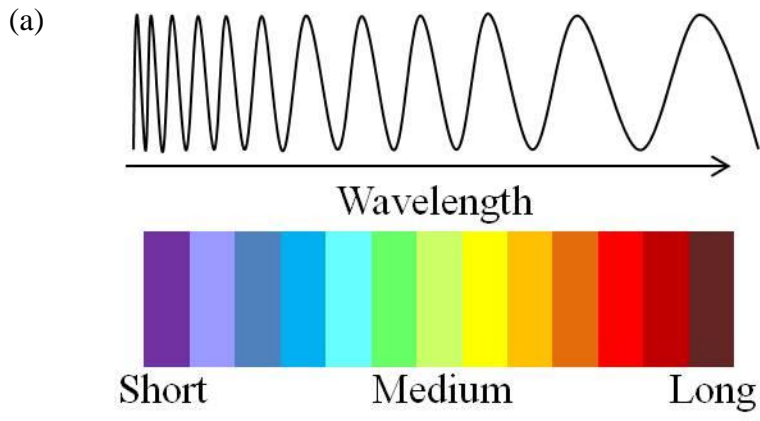
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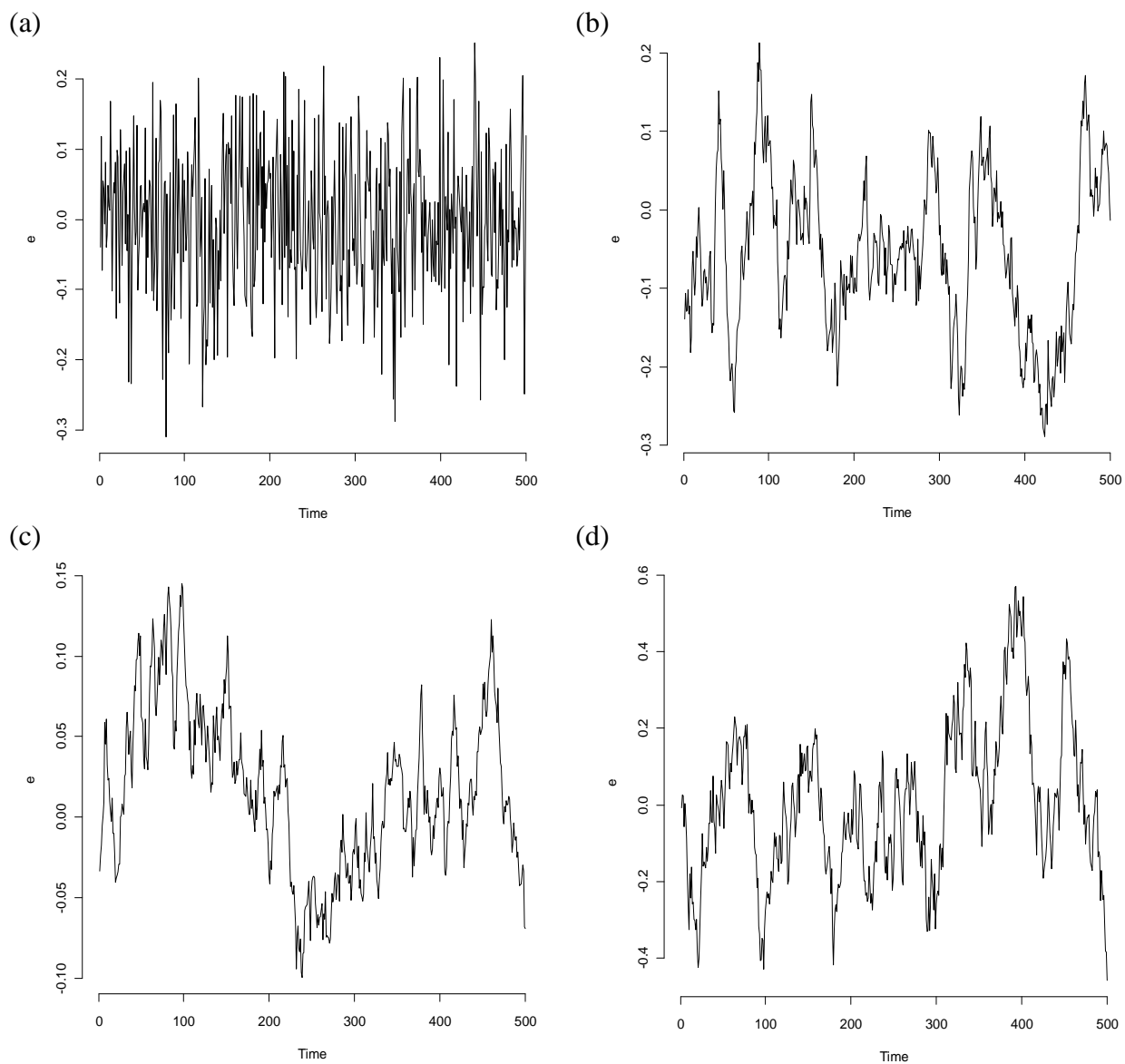


Figure 2

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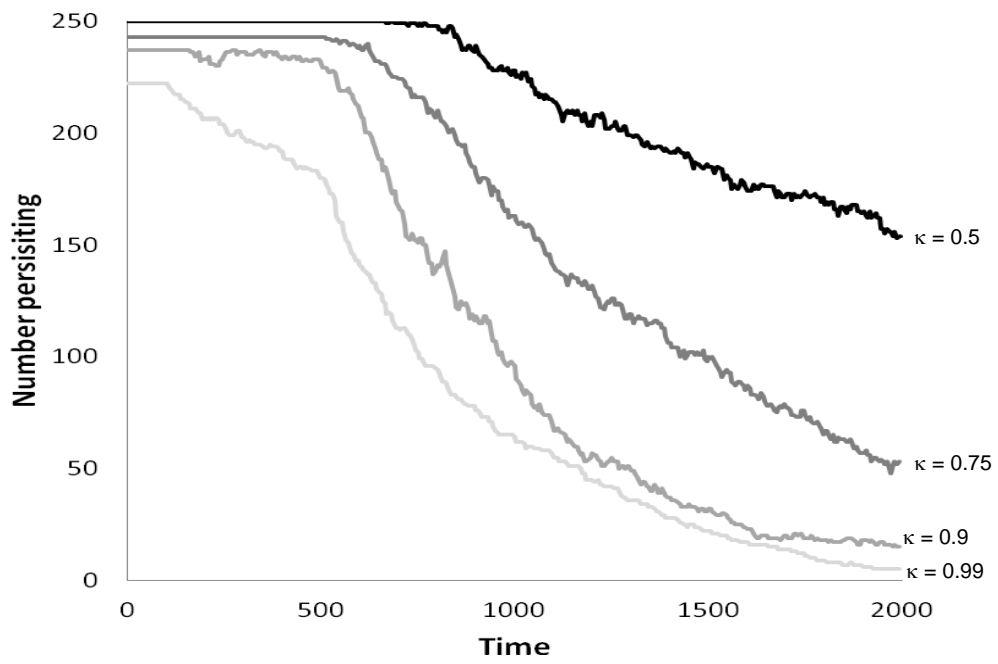
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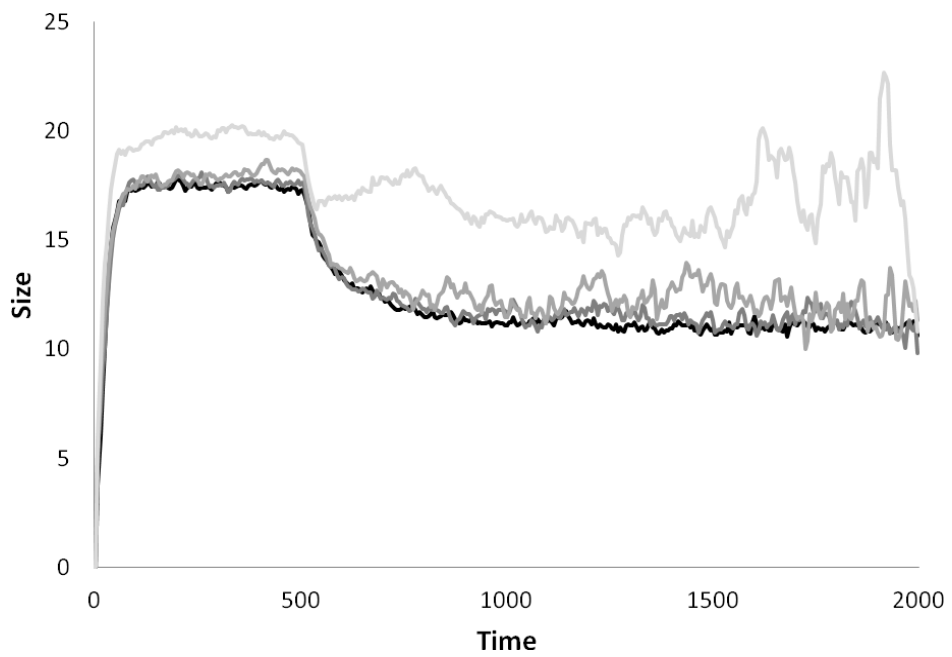
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634 (a)



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644 (b)



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654 Figure 3

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656 (a)

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676 (b)

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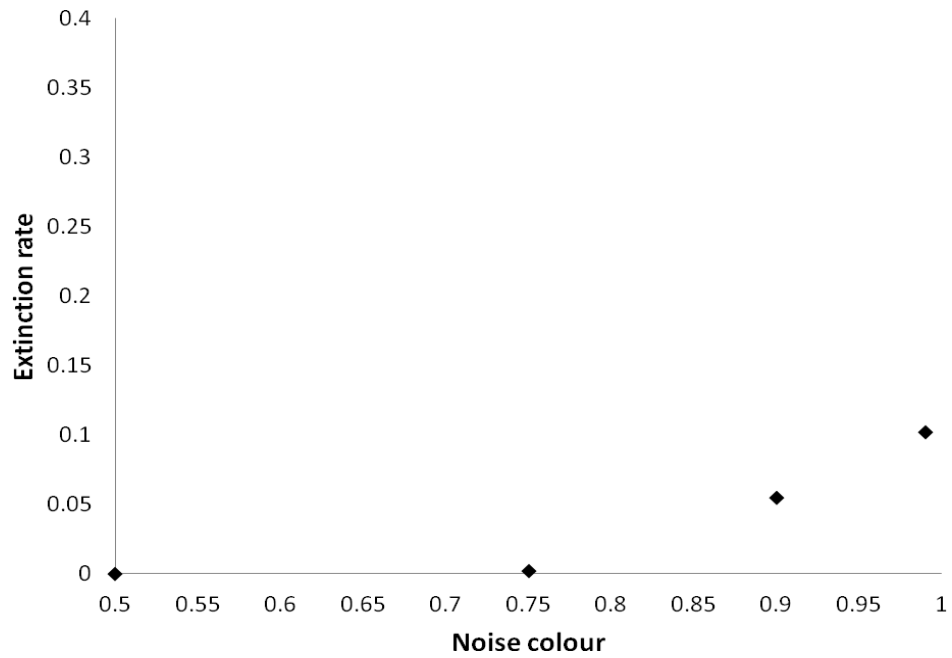
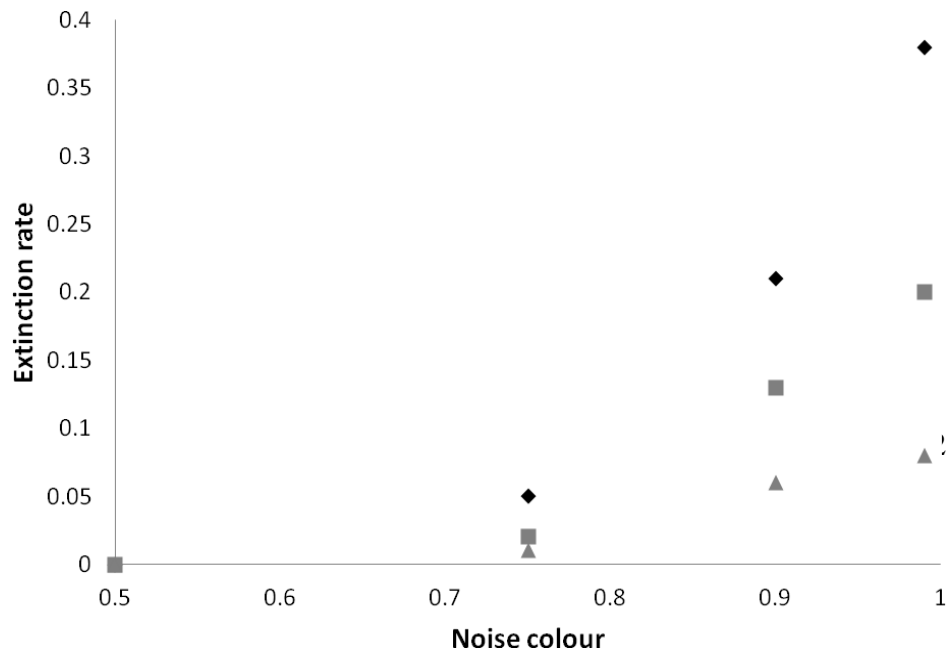
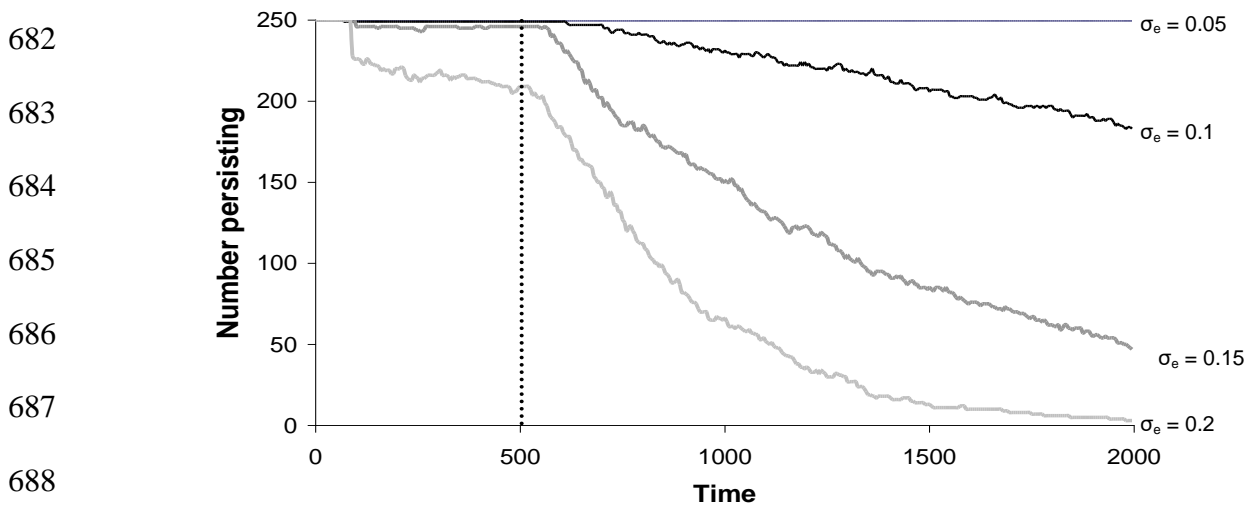
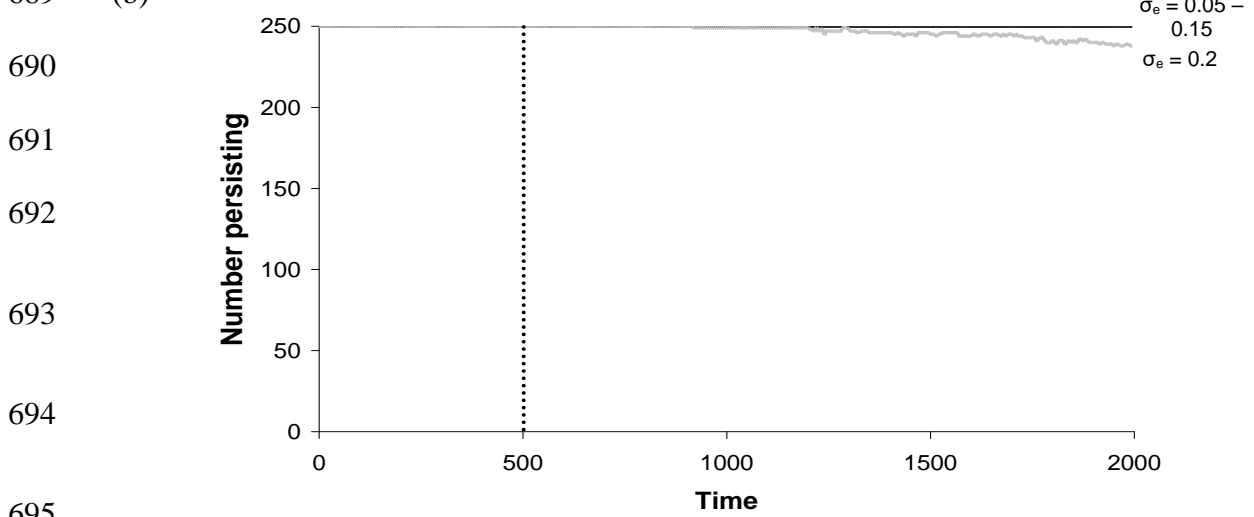


Figure 4

681 (a)



689 (b)



696 Figure 5

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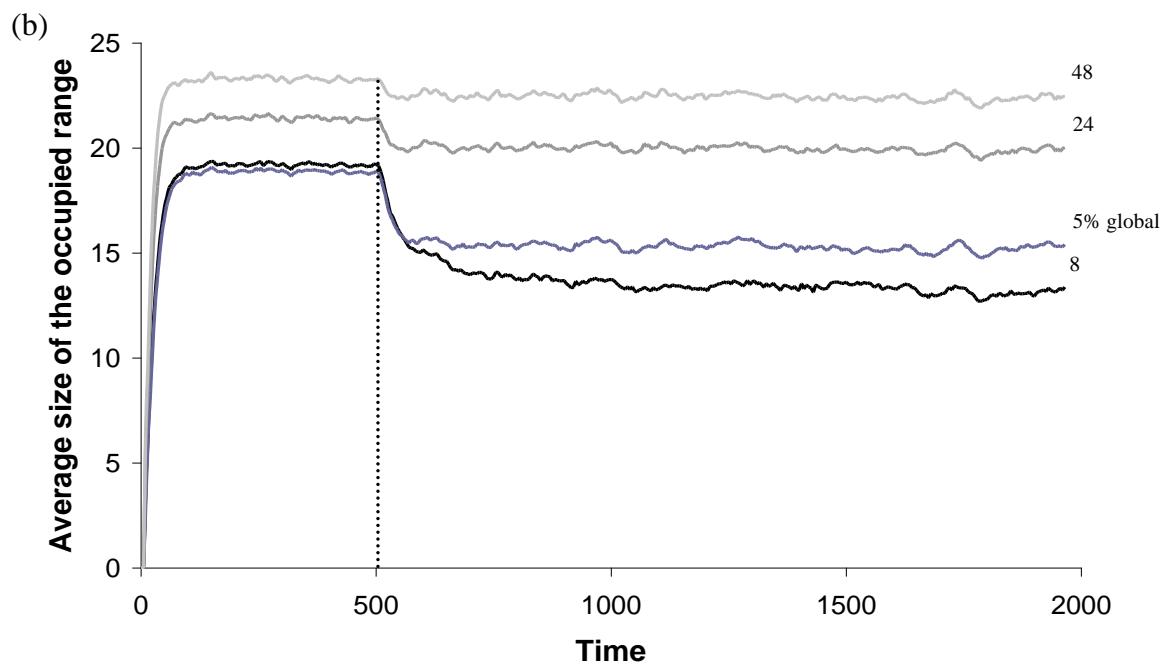
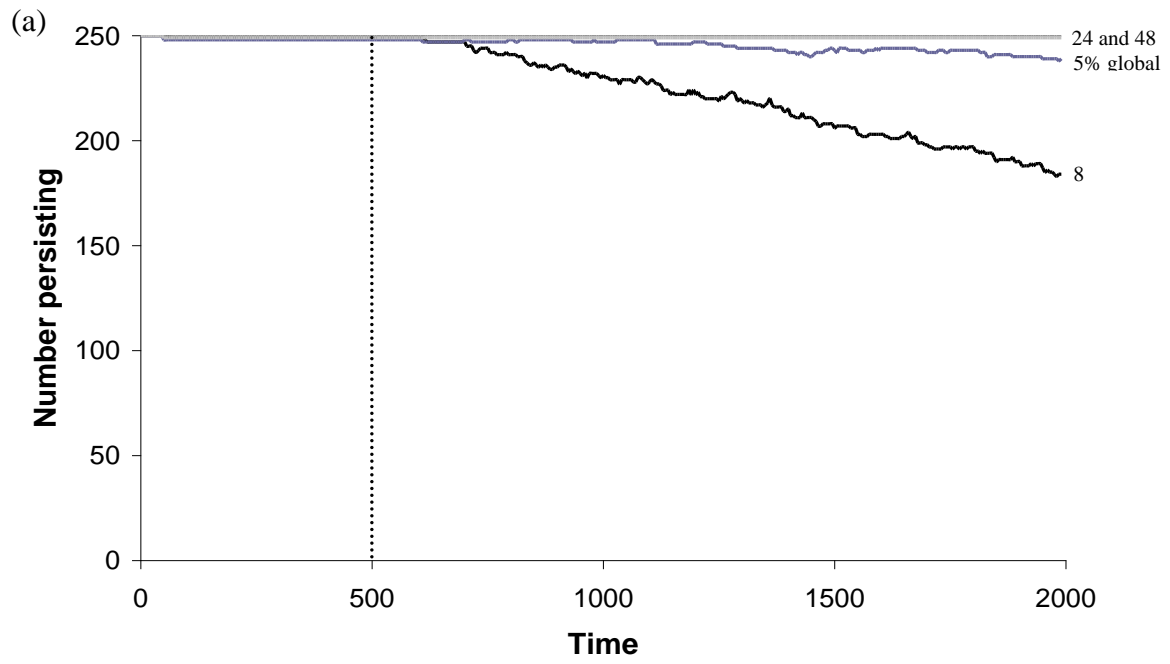


Figure 6

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