Biodiversity conservation in a dynamic world may lead to inefficiencies due to lock-in effects and path dependence

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Abstract

Although biodiversity is generally diminishing, in some areas its conservation is expanding. However; the exact path of this expansion is uncertain. This can lead to problems of path-dependence and lock-in effects. Path dependence describes situations where history strongly influences present decisions and lock-in effects refer to situations where an earlier decision provides strong incentives to follow a particular path, even if more efficient alternatives are available later on. We develop a conceptual ecological-economic model to investigate which ecological and economic parameters favour the appearance of efficiency losses in biodiversity conservation due to path dependence and lock-in effects in a dynamic two-period two-region model. Generally we find that efficiency losses occur if there are signals that guide the first-period budget into a region that later turns out to be suboptimal if both time periods had been considered right from the beginning. To illustrate the conservation relevance of our findings, we present potential efficiency losses through path dependence in the hypothetical case of applying offsets to conserving the endangered *Maculinea teleius* butterfly near the city of Landau in Germany.

Key words: dynamic optimisation, ecological-economic model, ecological benefit, economic cost, efficiency, resource allocation.

Highlights

- Lock-in and path dependence can arise in dynamic systems subject to uncertainty
- Lock-in and path dependence can lead to efficiency losses
- We explore lock-in and path dependence in a conservation planning problem
- We identify the circumstances under which efficiency losses are high

Introduction

Global biodiversity is declining at an alarming rate (Butchart et al. 2010). Despite this general

negative trend, biodiversity conservation is expanding in some areas. Examples include the

enlargement of reserve sites (Morales-Hidalgo et al. 2015), the generation of new habitats

through financial means from offsets (Wende et al. 2018), the implementation of conservation

easements (Rissmann et al. 2013), and land purchase by conservation agencies and NGOs

(Schöttker and Wätzold 2018). This expansion, however, is typically slow and the exact path

of expansion is unknown as the future political situation regarding biodiversity conservation

(Haila and Henle 2014) and the availability of future conservation budgets (Drechsler and

Wätzold 2007) are full of uncertainties. This means that decision makers have to make

conservation decisions today without knowing to what extent conservation expansion is

possible in the future.

In their analyses of decisions and their consequences in a dynamic and uncertain world,

economists and social scientists have identified path dependence and lock-in effects as

important factors that affect the long-term consequences of present decisions and may lead to

inefficiencies (David 1985, North 1991). The concept of path dependence typically is used to

describe situations where history, i.e. previous conditions, strongly influences present

decisions (Liebowitz and Margolis 1995). The term lock-in has been used to explain that an

earlier decision provides strong incentives to follow a particular path – to be locked-in in that

path - even if more efficient alternatives are available later on (David 1985). Applications of

the concepts of path dependence and lock-in effects are found in the fields of technology

development (Ruttan 1997), organisational analysis (Sydow et al. 2009), and institutional

change (North 1991), among others.

There are also some studies that use these concepts in environmentally related research.

Barnett et al. (2015) investigate how the path-dependent nature of the institutions limit

62 today's climate change adaptation in Australia. Unruh and Carrillo-Hermosilla (2006) argue

63 that due to industrial lock-in effects developing countries are unlikely to leapfrog carbon

64 intensive energy production, and regarding agricultural land use, Sutherland et al. (2012) use

65 path dependence to explain farmers' resistance to move towards environmentally beneficial

66 land use. The closest analysis to biodiversity conservation that we found is the application of

67 the concept of path dependence to explain the emergence of payments for ecosystem services

68 (Bidaud et al. 2013). However, to our knowledge there is no research that analyses

69 biodiversity conservation policies and strategies from the perspective of path dependence and

70 lock-in effects in a systematic manner.

71 The overall purpose of this paper is to contribute to filling this gap by applying the concepts

72 of path dependence and lock-in effects to the analysis of biodiversity conservation, using a

73 conceptual ecological-economic model. The model considers the case of a conservation

74 agency that has to allocate a conservation budget over two time periods and two regions. The

75 regions are characterized by their initial amounts of conserved land and the shapes of their

76 ecological benefit and economic costs functions which relate conserved land to benefits and

77 costs, respectively. We explore the extent to which these characteristics, as well as the

78 available conservation budget and the conservation agency's time preference, favour

79 efficiency losses from path dependence and lock-in effects.

80 For this we compare two settings. In a 'myopic setting', the conservation agency only knows

81 before each period the budget for that period and has no information about the budget in the

82 second period. In an 'optimal setting', the agency is informed in the beginning about the

83 budgets available in both periods. In comparison with the optimal setting, efficiency losses

84 may occur in the myopic setting because the agency invests the budget in a region where it is

85 optimal at the time of the decision in period 1 but sub-optimal in hindsight in period 2. Path

86 dependence occurs as the decision on where to allocate the budget generates conservation

87 conditions that influence the decision on where to allocate the budget in period 2. Lock-in

88 arises as the decisions of the first period cannot be easily reversed for ecological reasons

89 (reversal would create habitat turnover that negatively affects species) and for economic

90 reasons (purchase and sale of conservation areas is likely to incur costs).

91 To demonstrate the practical relevance of our findings, we present potential efficiency losses

92 through path dependence and lock-in in the hypothetical case of applying payments financed

93 by offsets to conserve the Large Blue butterfly, *Maculinea teleius*, in a region near the city of

94 Landau in Germany.

95 Our work relates to the analysis of biodiversity conservation in a dynamic and uncertain

96 world (Costello and Polasky 2004, Meir et al. 2004, Pressey et al. 2007). For example, Johst

97 et al. (2011) and Van Teeffelen et al. (2012) discuss the impact of habitat network dynamics

98 on species conservation. Adopting a more historical perspective Dallimer et al. (2009) address

99 land use change, habitat change, and how stakeholders perceive it in the Peak District in

100 England. Other research addresses the risk of land-use conversion (Strange et al. 2006), the

101 impact of price uncertainty on different aspects of agri-environment policies (Barraquand and

102 Martinet 2011), the spatial allocation of conservation measures including land price feedbacks

103 (Dissanayake and Önal 2011), and how to optimally allocate conservation budgets over time

104 considering budget uncertainty (Drechsler and Wätzold 2007) and flexibility (Lennox et al.

105 2017). Further examples are analyses on the impact of land market feedbacks on reserve

106 selection (Butsic et al. 2013), the impact of policy adjustment costs on species management if

107 ecosystems change (Boettiger et al. (2016), the cost-effective mitigation of threats to

108 biodiversity conservation (Auerbach et al. (2015), and the combination of threat mitigation

109 with different types of discounting (Armsworth 2018). More recently, the impact of

110 (uncertain) climate change has gained prominence in conservation planning (Ando et al. 2018,

111 Vincent et al. 2019).

112 A seminal paper on efficiency losses that arise from myopic decisions is Meir et al. (2004)

113 who investigate efficiency losses in the context of uncertain conservation investment

114 opportunities, varying budget constraints, and biodiversity degradation in unprotected sites.

115 Further research includes Spring et al. (2010) who investigate efficiency losses of strategies

116 that address only current threats to biodiversity compared to strategies that consider future

117 threats, Iacona et al. (2017) who show that making conservation investments in future periods

118 can be superior to making them today, for example due to learning and capacity building, and

119 Robillard and Kerr (2017) who investigate efficiency losses that occur in the context of

120 heterogeneous land price dynamics if the delay between design and implementation of

121 conservation plans is too long.

122 Our research is different from the abovementioned research as we identify how three basic

123 factors that are relevant for most conservation decisions – the shape of the cost functions and

124 the ecological benefit functions as well as the size of the conservation budget – influence

125 efficiency losses of myopic decisions. Moreover, we are the first to explicitly apply the

126 framework of path dependence and lock-in effects to analyse biodiversity conservation

127 decisions. We hope this will stimulate cross-fertilisation between general economic research

128 of path dependence and lock-in effects and research in conservation biology.

129

130 **2. Methods**

131 **2.1 The model**

132 We consider two regions that differ by their ecological benefit functions, their economic cost

133 functions and their initial habitat area. For the choice of the benefit functions we build two

134 scenarios:

135   (a) the benefit functions are concave or convex to varying degrees, such that the benefit B_i in

136   region i ($i = 1,2$) is given by:

137   (1a)

138   where A_i is the habitat area in region i and z_i a region-specific constant.

139   Concave benefit functions ($z_i < 1$) may be motivated by the species-area relationship that tells

140   that the number of species in a region increases with the size of that region in a concave

141   manner (Begon et al. 1990, Table 22.1), or by the fact that the expected life time of a

142   population subject to strong environmental fluctuations increases less than linearly with

143   increasing habitat area (Lande 1993, Wissel et al. 1994). Convex benefit functions ($z_i > 1$)

144   may arise due to threshold effects or the fact that the expected life time of a population subject

145   to weak environmental fluctuations increases more than linearly with increasing habitat area

146   ((Lande 1993, Wissel et al. 1994). In the case study in section 4 we will use that (in the

147   absence of spatial environmental correlations) the viability of a metapopulation increases with

148   increasing number of habitat patches in a convex manner. Examples of concave and convex

149   benefit functions are shown in Fig. 1a.

150   (b) the benefit functions are saturating, such that the benefit is given by

151   (1b)

152   where k_i and z_i are constants. In a saturating benefit function the benefit is limited to some

153   maximum value, which in the present formulation is equal to one. For $z_i > 1$ (dash-dotted and

154   long-dashed lines in Fig. 1b) the benefit increases in a convex manner with increasing habitat

155   area A_i if A_i is rather small, and in a concave manner if A_i is rather large (sigmoid shape).

156   Increasing k_i beyond the value of 2 chosen in Fig. 1b would shift the concave region towards

157   larger values of A_i. The sigmoid shape of the ecological benefit function models an ecological

158   threshold that must be crossed to reach high ecological benefits. The magnitude of habitat

159   area A_i that is needed to cross the threshold is positively related to parameter k_i, so that

160   increasing k_i shifts the threshold towards larger areas A_i.

161   For $z_i \leq 1$ (solid, dotted and short-dashed lines in Fig. 1b) the benefit B_i increases in a concave

162   manner with increasing habitat area A_i so that the marginal benefit declines with increasing A_i.

163   This case is qualitatively very similar to the case of concave benefit functions in eq. (1a)

164   discussed above.

165   Initially, each of the two regions has a habitat area of magnitude A_{0i} which may be increased

166   by amounts ΔA_i. The associated costs (depending on the policy instrument this might be

167   purchase of area, conservation payments, etc.) are modelled as

168   ,   (2)

169   so that cost C_i increases quadratically with increasing habitat area A_i. This implies that the

170   marginal cost $dC_i/d\Delta A_i$ increases linearly with increasing habitat area A_i, and $2e$ is the slope of

171   that increase. Parameter c_{0i} is the cost of the first unit of increased habitat area. Marginal costs

172   can be shown to increase linearly if the costs of the land parcels are heterogeneous and

173   distributed according to a uniform distribution (Drechsler 2011). For reasons of simplicity, we

174   assume that the financial expenses for conservation, i.e. the budget, equal costs C_i (see

175   Wätzold and Drechsler (2014) and Drechsler (2017) for examples where an efficiency

176   analysis considers budget and costs separately).

177   The total conserved area in region i then is

178   .   (3)

179   which determines the benefit B_i according to eq. (1). We assume that the total benefit in both

180   regions is

181   ,   (4)

182   for an alternative assumption see Wätzold and Drechsler (2005). Based on the above settings

183   and using eq. (1a), Drechsler and Wätzold (2001) analysed the decision problem where a

184   conservation agency must allocate a budget C_{tot} among the two regions to maximise B_{tot}.

185   The control variable in that static decision problem is the budget share $q \in [0,1]$ that falls into

186   region 1, with and (and $C_1 + C_2 = C_{tot}$). Depending on the parameters, a cost-effective share

187   q_{opt} exists that maximizes B_{tot} for given C_{tot}.

188   Dynamics and time-dependence come into play by assuming that the budget becomes

189   available to the conservation agency in two tranches. In a first period the agency can spend a

190   budget of $C^{(1)}$ and in a second period a budget $C^{(2)}$ is available. The corresponding total

191   benefits in the two periods are calculated according to eq. (4) and denoted as $B_{tot}^{(1)}$ and $B_{tot}^{(2)}$,

192   and the total intertemporal benefit is assumed to be

193   ,   (5)

194   where r is the discount factor.

195   The task for the conservation agency is to allocate the two budgets $C_{tot}^{(1)}$ and $C_{tot}^{(2)}$ among the

196   two regions so that the intertemporal benefit B is maximised. An allocation is represented by

197    $q^{(1)}$ and $q^{(2)}$ where is the budget for region 1 in period 1, is the budget for region 2 in period

198   1, is the budget for region 1 in period 2, and is the budget for region 2 in period 2.

199   We consider two settings in this dynamic allocation problem:

200   (I)   'optimal': the conservation agency knows $C_{tot}^{(1)}$ and $C_{tot}^{(2)}$ in the beginning of the

201   first period and chooses $q^{(1)}$ and $q^{(2)}$ to maximise the intertemporal benefit B.

202   (II)   'myopic': in the beginning of the first period the conservation agency only knows

203            $C_{tot}^{(1)}$ and chooses $q^{(1)}$ to maximise $B_{tot}^{(1)}$. Only in the beginning of the second

204   period it learns the budget $C_\text{tot}^{(2)}$ for the second period and based on this

205   information chooses $q^{(2)}$ to maximise B.

206 In the myopic setting, the conservation agency allocates the budget into the two regions based

207 on the size of the currently available budget, as it has no information about the availability of

208 future budgets. This leads to path dependence in a sense that "history matters" (Liebowitz and

209 Margolis 1995): the decision in period 1 on where to allocate the conservation budget $C^{(1)}$

210 generates conservation conditions that influence the decision in period 2 on where to allocate

211 the conservation budget $C^{(2)}$. As the decisions of the first period cannot be easily reversed for

212 ecological reasons (reversal would create habitat turnover which negatively affects species:

213 Johst et al. 2011) and for economic reasons (it is not straightforward to purchase and sell

214 conservation areas, Lennox et al. 2017), the conservation investment from the first period is

215 "locked-in".

216 Due to path dependence and the lock-in effect the intertemporal benefit in the myopic setting

217 (B_myopic) may be smaller than that in the optimal setting (B_opt). An efficiency loss occurs which

218 is measured by

219 .   (6)

220

221 **2.2 Model analysis**

222 To analyse the effect of the model parameters on the existence and relevance of path

223 dependencies we randomly sample the model parameter values from uniform distributions

224 (Table 1). We build 10^6 random parameter combinations and for each of them calculate the

225 efficiency loss L. We identify the set P of all parameter combinations that lead to efficiency

226 losses $L \geq 0.1$ for the scenario of eq. (1a) and $L \geq 0.05$ for the scenario of eq. (1b). We are

227   interested in the statistical properties of the parameter combinations in P. For this we first

228   calculate the means of the model parameters in P to compare them with the means from the

229   uniform distributions of Table 1. A large difference in these means for some focal model

230   parameter indicates that efficiency losses $L \geq 0.1$ ($L \geq 0.05$) are not found for all values of that

231   parameter but only (or predominantly) for values within a subrange of the total range

232   considered. This in turn indicates that this model parameter has a strong influence on the

233   existence of path dependence, and the sign of the difference between the two means indicates

234   whether an increase in the parameter increases or decreases the likelihood of path

235   dependence.

236   In a second step we aim at detecting interactions between model parameters and calculate

237   pairwise correlations (based on Pearson's correlation coefficient) between the parameters,

238   based on the set P. To identify interactions of three or more parameters we introduce a new

239   approach which is based on the observation that if, e.g., two normalised quantities x and y

240   (with a mean of zero and a standard deviation of one) are strongly positively (negatively)

241   correlated their sum $x + y$ (difference $x - y$) has a comparatively large variation. In Appendix

242   S1 we develop a new procedure that allows analysing combinations of multiple quantities

243   with regard to positive and negative correlations and ranks them through some 'weighted'

244   sum f introduced in Appendix S1. If two model parameters a and b, e.g., have a correlated

245   effect on the likelihood of path dependence, the procedure will generate the result '$\{a + b\}$

246   best characterises the relationship between parameters a and b', where the plus sign represents

247   the positive correlation (a minus sign would represent a negative correlation). With three

248   model parameters, a, b and c, a typical result might be '$\{a + b - c\}$ best characterises the

249   relationship between the three parameters quantities a, b and c', where $\{a + b - c\}$ stands for

250   'a is positively correlated with b and negatively correlated with c'. In the analysis we consider

251 interactions of up to four model parameters and identify the three strongest correlations (with

252 highest Pearson's correlation coefficient and/or the highest value of f).

253

254 **3. Results**

255 **3.1 Concave and/or convex benefit functions**

256 We identified 17,680 parameter combinations which lead to efficiency losses L equal or

257 above 0.1. Table 2 shows the means of the parameters in this set P. Some of the means differ

258 from those in Table 1: the means of z_1 and z_2 are increased, those of A_{10} and A_{20} are reduced,

259 and the mean of $C^{(1)}$ is reduced while that of $C^{(2)}$ is increased. The increased means of the

260 exponent z_1 and z_2 mean that efficiency losses are more likely to occur with strongly convex

261 benefit functions (large z) than with weakly convex or concave functions (small z). The reason

262 is the strongly increasing marginal benefits associated with strongly convex benefit functions.

263 This implies that (i) the benefit increases fast with increasing budget, it increases faster than

264 the costs which increase only quadratically, and therefore larger budgets should always be

265 allocated into the region with the highest z_i, and that (ii) substantial differences occur between

266 the benefits of the two regions (for given habitat area) even if their z values differ only

267 slightly (Fig. 1a). These two aspects imply that extreme allocations of the budget (all into one

268 region in the first period) are most critical if in hindsight it turns out that another allocation

269 with a larger share in the other region would have been better.

270 Small initial habitat areas A_{01} and A_{02} mean that even if z_1 and z_2 differ, the initial benefits

271 $B_i(A_{0i})$ and the initial marginal benefits $dB_i(A_{i0})/dA_i$ do not yet differ strongly, so the signal for

272 allocating the budget into the region with the higher z_i is weak compared to other signals like

273 costs, so a small budget may be misguided into the region with the lower z_i.

274   To understand the result regarding the budgets $C^{(1)}$ and $C^{(2)}$, consider that in the myopic setting

275   the conservation agency decides on the first-period allocation only on the basis of $C^{(1)}$. If $C^{(1)}$

276   is small compared to the total budget $C^{(1)} + C^{(2)}$ then due to the differing cost and benefit

277   functions there is a risk that the cost-effective allocation based on $C^{(1)}$ differs from that based

278   on $C^{(1)} + C^{(2)}$.

279   Next consider the pairwise correlations between the parameters in P. Both with regard to

280   Pearson's correlation coefficients and our own procedure for detecting correlations (Appendix

281   A), the three strongest correlations are

282   (i) $z_1 + A_{02}$

283   (ii) $A_{01} - A_{02}$

284   (iii) $z_1 - A_{01.}$

285   Note that these correlations also include their symmetric counterparts, obtained by swapping

286   the region indices 1 and 2, such as, e.g., $z_2 + A_{01}$ for correlation (i), $A_{02} - A_{01}$ for correlation (ii),

287   and $z_2 - A_{02}$ for correlation (iii). Correlation (i) indicates that efficiency losses are likely if the

288   exponent z_1 and the initial habitat area A_{02} are positively correlated. A positive correlation

289   means that a comparatively large value of z_1 is related to a large value of A_{02} and a small value

290   of z_1 is related to a small value of A_{02}. To consider the first case of both parameters being

291   large, according to the benefit function eq. (1), a large A_{02} implies a comparatively large initial

292   marginal benefit in region 2, even if the benefit function in region 2 is less convex or more

293   concave than in region 1 ($z_2 < z_1$). A large value of z_1, however, implies that the ecological

294   benefit function in region 1 is likely to be more convex than in region 2. Consequently, in the

295   myopic setting the large initial marginal benefit in region 2 guides the first-period budget $C^{(1)}$

296   into region 2 which, however, is likely to have the less convex or more concave benefit

297   function, and is less cost-effective for larger budgets.

298 For the case of both z_1 and A_{02} being small the argument is analogous: a small A_{02} implies that

299 the initial marginal benefit in region 2 is likely to be lower than that in region 1, misguiding

300 the first-period budget $C^{(1)}$ into the region which has a benefit function likely to be less

301 convex or more concave than the other region.

302 Since the two cases of both parameters being large and both being small lead to the same

303 conclusion, we consider only one of these two cases in the interpretation of the other

304 correlations below. Analogously, if the two parameters are negatively correlated so that a

305 large value of one parameter coincides with a small value of the other (correlations (ii) and

306 (iii)), we consider only one of the two possible cases. In addition, we consider that if a

307 parameter is high for one region (e.g., large z_1) it is likely (probability above 50%) to be

308 higher than that for the other region (z_2), unless there is some significant correlation between

309 the two parameters (z_1 and z_2).

310 The (likely) efficiency loss caused by the positive correlation between z_1 and A_{02} (correlation

311 (i)), of course, occurs only if the two initial habitat areas differ (because otherwise both

312 regions would have the same initial marginal benefit), which is indicated by correlation (ii),

313 that is efficiency losses occur especially if A_{01} and A_{02} are negatively correlated, i.e. when one

314 of them is large and the other one is small.

315 The negative correlation (iii) between z_1 and A_{01} can be explained in the same way as

316 correlation (i). For instance, a large value of A_{01} implies a high initial marginal benefit in

317 region 1 and in the myopic setting the budget $C^{(1)}$ is likely to be allocated into region 1. This

318 region, however has a more concave benefit function (small z_1) which calls for allocation of

319 the budget into region 2 (with the probably higher exponent $z_2 > z_1$) in the optimal setting.

320 The three strongest triple correlations are (again not listing their symmetric counterparts):

321   (iv) $z_1 - A_{01} + A_{02}$

322   (v) $z_1 - z_2 - A_{01}$

323   (vi) $z_1 - z_2 + A_{02}.$

324   They represent combinations or 'amplifications' of the three pairwise correlations above and

325   can be explained in the same way. Correlation (iv), for instance, amplifies correlation (ii)

326   above, so that efficiency losses occur especially if the initial habitat areas are negatively

327   correlated, and if in addition the exponent z_1 in region 1 is negatively correlated with A_{01}

328   (correlation (iii)).

329   The three strongest quadruple correlations are:

330   (vii) $z_1 - z_2 - A_{01} + A_{02}$

331   (viii) $z_1 - c_{02} - A_{01} + A_{02}$

332   (ix) $z_1 - e_1 - A_{01} + A_{02}.$

333   Correlation (vii) is again a combination or amplification of the previous correlations.

334   Correlations (viii) and (ix), in contrast, add some new information. Regarding correlation

335   (viii), in the myopic setting the correlation $z_1 - A_{01} + A_{02}$ is likely to misguide the budget $C^{(1)}$

336   into region 2 with the higher initial habitat area and marginal benefit. This is amplified by a

337   small initial marginal cost c_{02} (c_{02} is positively correlated with A_{02} in correlation (viii)). The

338   misallocation into region 2 induced by the correlation $z_1 - A_{01} + A_{02}$ is also amplified if the

339   increase in marginal costs e_1 in region 1 is small (correlation ix)) because cost increases only

340   weakly with increasing budget, favouring region 1 for large budgets.

341   Altogether, efficiency losses are likely to be large if the benefit functions differ and are

342   convex and the region with the higher degree of convexity (z) has

343   (i)   the smaller initial habitat area A

344   (ii)   the larger initial marginal cost c_0, and

345   (iii)   the smaller increase in the marginal cost e.

346   In addition, for efficiency losses to occur, the budget for period 2 must be large enough

347   compared to the budget for period 1 so that it can induce a significant increase in the benefits

348   in period 2, but it must not be so large that the allocation of the period-1 budget plays no role.

349   For purpose of illustration, consider an example. A very large efficiency loss of $L = 0.94$ was

350   obtained by the parameter sample $z_1 = 4.75$, $z_2 = 4.80$, $A_{01} = 9.61$, $A_{02} = 0.75$, $c_{01} = 0.28$, $c_{02} =$

351   0.94, $e_1 = 2.68$, $e_2 = 0.03$, $r = 0.08$, $C^{(1)} = 2.94$ and $C^{(2)} = 5.02$. Here, both regions have convex

352   benefit functions with the benefit function in region 2 being more convex. However, the

353   initial habitat area in region 1 is substantially larger and the initial costs much smaller than in

354   region 2, which induces an initial allocation of the budget in period 1 in region 1. However,

355   this is not cost-effective in hindsight as not only the benefit function in region 2 is more

356   convex than in region 1 but also the increase in the marginal costs is much smaller.

357

358   **3.2 Saturating benefit functions**

359   As Table 2 shows, some of the means in set P differ from those in Table 1. The main

360   differences are that the means of the initial habitat areas, A_{01} and A_{02}, and the budgets, $C^{(1)}$ and

361    $C^{(2)}$, are smaller than in the case of convex or concave benefit functions. Although the means

362   of the exponents z_1 and z_2 are only slightly higher than the means in Table 1, they represent

363   sigmoid benefit functions in which the ecological benefit first increases on a convex manner

364   and later in a concave manner (Fig. 1b). Together with this observation, the relatively small

365   means of A_{01}, A_{02}, $C^{(1)}$ and $C(2)$ indicate that the problem of efficiency losses due to path

366   dependence and lock-in effects occurs especially when the amounts of conserved areas are

367   such that the convex part of the ecological benefit function governs the ecological benefit. By

368   this, similar arguments apply as with concave and/or convex benefit functions.

369   This is confirmed by the observation that the three strongest pairwise correlations obtained

370   with saturating benefit functions between the parameters in P are identical to the correlations

371   (i) – (iii) obtained with concave and/or convex benefit functions; and the strongest triple and

372   quadruple correlations are very similar to correlations (iv) – (ix) above.

373

374   **4. Case study**

375   To illustrate the practical relevance of path dependence and lock-in, we consider the

376   conservation of the endangered Large Blue butterfly, *Maculinea teleius*, in a landscape near

377   the city of Landau in Germany (Drechsler et al. 2007). If the meadows in the landscape (Fig.

378   2) are managed in a profit-maximising manner, they are mown every year at the end of May

379   and a second time in mid-July. The second cut thus falls into the eclosion period of the

380   butterfly, reducing the species' reproductive success. As a conservation measure, we consider

381   an alternative mowing regime: mowing every second year once at the end of August. This

382   mowing regime maximises butterfly survival in the study region for a given budget, without

383   harming breeding birds (Drechsler et al., 2010). As shown by the authors, the survival of the

384   butterfly is sensitive to the spatial allocation of meadows on which this alternative, butterfly-

385   friendly mowing regime is applied. In particular, butterfly survival increases with increasing

386   spatial aggregation of the butterfly-friendly meadows.

387   We assume that the butterfly-friendly mowing regime is incentivised through payments from

388   offsets, which are available in Germany (OECD 2016). The offsets compensate for long-term

389   negative impacts on the environment. Therefore, contracts where farmers commit themselves

390   to manage their land in a certain biodiversity-enhancing manner in return to payments, have to

391 be long-term (typically 30 years), too (Treffkorn et al. 2007, OECD 2016). We extent the

392 analysis of Drechsler et al. (2007) with the butterfly-friendly mowing regime of Drechsler et

393 al. (2010) to a dynamic management problem by assuming two periods, each consisting of 15

394 years, where in the first period a budget is available that allows total payments of €10,000 per

395 annum and in the second period of €20,000 per annum. The budget increase between the two

396 periods mimics the setting of the general model analysis that in the second period more land

397 can be conserved than in the first. Assuming profit-maximising behaviour, landowners with

398 costs below the payment will accept the payment and mow in the butterfly-friendly manner

399 while landowners with higher costs manage their land in the profit-maximising manner.

400 We further assume that in the west of the study region (left to the vertical dotted line in Fig. 2,

401 termed the western subregion), marginal conservation costs are lower than in the eastern

402 subregion (right to the vertical dotted line in Fig. 2). This is motivated by the assumption of

403 farm houses being located in the more rural eastern subregion, implying that the reduced

404 mowing frequency of the butterfly-friendly mowing regime reduces transport costs from the

405 *distant* meadows in the western subregion to the farm houses (relative to the transport costs

406 associated with the profit-maximising mowing regime which involves more frequent

407 mowing). We add these spatially differentiated transport costs to the conservation costs of

408 Drechsler et al. (2007) by multiplying those costs in the eastern subregion by a factor $b = 2$.

409 Second, we assume that transport costs are lower if the managed meadows are close to each

410 other. This is relevant especially in the eastern subregion where the meadows are closer to the

411 farm houses, because here a dispersion of the meadows adds relatively more to the transport

412 costs than in the western subregion in which all meadows are associated with rather high

413 transport costs. To model this circumstance in a simple and intuitive manner, we assume that

414 the costs (per hectare) around the point marked by the open circle in Fig. 2 are reduced by

415   (7)

416   with $h = €400$ and $\alpha = (1.25 \text{ km})^{-1}$. At the marked point the costs reduction therefore is $\Delta c =$

417   €400 and which declines with increasing distance so that one km from the point it equals

418   about $\Delta c = €180$.

419   The second assumption, together with the fact that the payment scheme induces conservation

420   of the least costly meadows, implies that in the eastern subregion butterfly-friendly meadows

421   will be spatially aggregated, while in the western subregion they will not. Metapopulation

422   theory (Hanski 1999) states that (at least in the absence of correlated environmental

423   stochasticity) the viability of a metapopulation increases with increasing number of habitat

424   patches in a convex manner (e.g., Frank and Wissel 2002), and the strength of this convexity

425   is positively related to the spatial connectivity of the habitat patches (Frank and Wissel 2002).

426   So the viability of the butterfly population in the study region will increase in a convex

427   manner with increasing number of butterfly-friendly meadows, and the convexity is stronger

428   if butterfly-friendly meadows are added in the eastern subregion than in the western

429   subregion.

430   Together with our first assumption that marginal conservation costs are higher in the eastern

431   subregion than in the western subregion, we are confronted with a typical situation identified

432   in the general model analysis that favours path dependence and lock-in: the ecological benefit

433   functions are convex, and the more convex benefit function is associated with higher marginal

434   conservation costs.

435   Lock-in arises in the present management problem because the contracts between

436   conservation agency and farmer have a duration of 30 years implying that a meadow

437   conserved in year 1 of the analysis will stay conserved for the next 30 years. The problem of

438   path dependence occurs because in the first 15-year period a rather small conservation budget

439   is available which may favour a different allocation of butterfly-friendly meadows than the

440   larger budget available in the second 15-year period. This change in the cost-effective

441 allocation would call for a reallocation of butterfly-friendly meadows, which however is

442 impossible due to the lock-in.

443 From the results of the general model analysis we expect that under the myopic setting the

444 conservation agency will, given its small budget in the first period and its aim for cost-

445 effectiveness, allocate the butterfly-friendly meadows in the less costly western subregion –

446 which is achieved by offering conservation contracts for *all* meadows in the study region. In

447 contrast, under the optimal setting where the budget increase to the second period is known it

448 is cost-effective to offer the contracts only for meadows in the *eastern* subregion, because at

449 larger budgets it is more cost-effective to allocate, despite the higher costs, conservation

450 efforts into the region with the more convex benefit function – which in the present case is the

451 eastern subregion.

452 Figure 3 confirms these expectations. In the first period (lines without symbols) the

453 quasiextinction risk of the butterfly is smaller if conservation contracts are offered for all

454 meadows in the study region (dotted line) than if they are offered only for meadows in the

455 eastern subregion (solid line). So in the myopic setting the conservation agency would offer

456 the contracts for all meadows. In the second period (lines with symbols), in contrast, the

457 quasiextinction risk is lower if the contracts had been offered right from year 1 only for

458 *eastern* meadows (solid line) than if they were offered for *all* meadows over the entire 30

459 years (dotted line) or if they had been offered for all meadows in the first period and were

460 offered only for the eastern meadows in the second period (dashed line). Altogether, if only

461 the first period is considered it is more cost-effective to offer the contracts for all meadows

462 while if the longer future is considered it is more cost-effective to offer them only for

463 meadows in the eastern subregion.

464 As the case study only served to illustrate the potential relevance of our general analysis for

465 real-world conservation, a systematic analysis of the driving factors of the results is beyond

466   the scope of this paper. However, we analysed two alternative scenarios without (i) reduced

467   differences in the strengths of convexity (by largely eliminating the spatial clustering of

468   butterfly-friendly meadows in the eastern subregion and setting $\alpha = (0.125 \text{ km})^{-1}$) and (ii)

469   reduced differences in the marginal conservation costs between the two subregions (by

470   reducing b to 1.5), and observed no path dependence: offering the contracts for *all* meadows

471   always minimised the quasiextinction risk. This indicates that the path dependence observed

472   in the case study indeed results from the described positive correlation between marginal

473   conservation costs and strength of convexity in the ecological benefit function.

474

5. Summary of results and discussion

476   Efficiency losses due to path dependence and lock-in effects are likely if there are signals that

477   misguide the first-period budget into a region that is suboptimal in terms of cost-effectiveness

478   if both time periods were considered right from the beginning. These wrong signals are

479   mainly sent from the marginal costs and benefits. Large initial costs and/or small initial

480   marginal ecological benefits in one region are likely to guide the first-period budget into the

481   other region. This other region, however, may have a less strongly increasing ecological

482   benefit function if both time periods and both budgets were considered.

483   In our model analysis, this occurred especially if

484   (i)   the ecological benefits functions are strongly convex, so that the benefit increases
485   at an increasing rate,

486   (ii)   the initial marginal cost is low in the region with the less convex benefit function
487   while the slope of the marginal cost is low in the region with the more convex
488   benefit function, so that the first-period budget is misguided into the region which
489   in the long run has the higher costs and the lower ecological benefit,

490   (iii)   the initial habitat area, and thus the initial marginal benefit is small in the region

491   with the more convex benefit function, so that the first-period budget is misguided

492   into the other region which in the long run has the lower ecological benefit.

493   The conservation relevance of the findings is demonstrated by a case study where offset

494   payments are applied to butterfly conservation near the city of Landau, Germany.

495   Naturally, the problem of path dependence occurs if the budget for the first period is

496   substantially smaller than the total budget available for both periods. If it was almost as large

497   as the total budget the allocation signal for the first-period allocation would likely to be the

498   same as that for the allocation of the total budget. On the other hand, it is plausible (not

499   analysed systematically in this paper) that an extremely small first-period budget would not

500   lead to large efficiency losses, because even if it was allocated into the wrong region, the

501   associated 'waste of money' would be small.

502   The insights from our model can be generalised to make them fruitful to a broader

503   conservation context. The model results indicate a principle structure where in a situation with

504   several conservation projects and uncertainty over future budgets, path dependence and lock-

505   in effects with efficiency losses are likely to occur: This is the case if marginal net benefits

506   (benefit minus costs) of some projects in the first period are high but in later period(s) low and

507   for other projects the opposite applies. Myopic concerns of cost-effectiveness (under

508   uncertainty) then suggest allocating resources in the first type of projects whereas with

509   hindsight and over a long time the opposite allocation might have been the more cost-

510   effective option. Our case study suggests that such a structure might not be uncommon in

511   conservation decisions, calling for more research on path dependence and lock-in effects in

512   biodiversity conservation, the efficiency losses that arise and policy responses to avoid them.

513 Although these conclusions are derived from an analysis with two periods, we believe that in

514 their general sense they are valid also in conservation management problems with more than

515 two periods. Nevertheless, extending the analysis two more than two periods would be an

516 interesting matter of future research.

517 A straightforward policy recommendation from our analysis is that uncertainty over future

518 budgets should be minimized to the extent possible to avoid efficiency losses due to path

519 dependence and lock-in effects. This conclusion – based on a conceptual model – is in line

520 with calls from practitioners in several European countries who consider uncertainty over

521 future budgets a main impediment for cost-effective conservation activities (Wätzold et al.

522 2010). This indicates a high relevance of the issue of budget uncertainty and that better

523 conservation outcomes can be achieved if information about future conservation budgets is

524 available at an early stage.

525 However, considering that uncertainty about the future, such as future conservation budgets,

526 can never be fully eliminated, the problem of path dependence may be mitigated by an

527 awareness of the conditions under which it is likely to occur. Here the results of our general

528 model analysis point to the relevance of nonlinearities (e.g., convex benefit functions favour

529 efficiency losses while concave functions appear unproblematic), trade-offs between short-

530 and long-term policy performance (maximisation of short-term cost-effectiveness may

531 compromise long-term cost-effectiveness), and contradictory policy signals (if. e.g., the

532 shapes of the cost functions favour one policy and the shapes of the benefit functions favour a

533 contrary one).

534

535

536

6. Conclusions

In our opinion, there is substantial potential for further research to understand under what ecological and economic conditions path dependence and lock-in effects in biodiversity conservation occur and how conservation policy responses should look like. In our case, budget uncertainty leads to path dependence and lock-in effects. However, other factors may also favour or hinder their occurrence. A possible factor is the flexibility of policy instruments to respond to changing ecological and societal circumstances. For example, some people argue that conservation banking may be a flexible policy instrument able to respond to change (Johst et al. 2011, Wende et al. 2018) whereas other policy instruments such as conservation easements are criticised for lacking flexibility (Rissman et al. 2013). In how far inflexibility of policy instruments contributes to path dependence and lock-in effects is a matter of further research and we hope this paper can stimulate this and related debates.

These debates seem important from a conservation point of view, as our analysis suggests that if path dependence and lock-in effects are not considered, efficiency losses may occur resulting in a waste of scarce conservation resources (cp. Ferraro and Pattanyak 2006, Cong and Brady 2012).

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674 **Tables**

675 Table 1: Ranges for the model parameters.

Parameter	Meaning	Minimum	Maximum	Mean
z_i	Exponent benefit function (eq. 1a)	0	5	2.5
k_i	Threshold in sigmoid benefit (eq. 1b)	0	10	5
c_{0i}	Offset marginal cost function (eq. 2)	0	1	0.5
e_i	Slope marginal cost function (eq. 2)	0	5	2.5
A_{0i}	Initial conserved area region i (eq. 3)	0	10	5
$C_{tot}^{(1)}$	Budget period 1	0	10	5
$C_{tot}^{(2)}$	Budget period 2	0	10	5
r	Discount rate for benefit (eq. 5)	0	0.1	0.05

676

677 Table 2: Means of the parameter values in the set P of parameter combinations that lead to

678 efficiency loss $L \geq 0.1$ (concave and/or convex benefit functions, scenario a) and $L \geq 0.05$

679 (saturating benefit functions, scenario b), respectively. In parentheses the comparison with the

680 means from the uniform distributions of Table 1.

| Parameter	Mean (concave/convex)	Mean (saturating)
Benefit exponent z_1	3.38 (> 2.5)	2.77 (> 2.5)
Benefit exponent z_2	3.39 (> 2.5)	3.04 (> 2.5)
Threshold k_1	-	5.80 ($\approx$ 5)
Threshold k_2	-	5.92 ($\approx$ 5)
Initial marginal cost c_{01}	0.51 ($\approx$ 0.5)	0.52 ($\approx$ 0.5)
Initial marginal cost c_{02}	0.51 ($\approx$ 0.5)	0.53 ($\approx$ 0.5)
Slope marginal cost e_1	2.43 ($\approx$ 2.5)	2.95 (> 2.5)
Slope marginal cost e_2	2.42 ($\approx$ 2.5)	2.74 ($\approx$ 2.5)
Initial habitat area A_{01}	3.72 (< 5)	1.84 (< 5)
Initial habitat area A_{02}	3.68 (< 5)	1.47 (< 5)
Budget period 1 $C^{(1)}$	3.25 (< 5)	0.96 (< 5)
Budget period 2 $C^{(2)}$	6.56 (> 5)	1.97 (< 5)
Discount rate r	0.05 (= 0.05)	0.05 (= 0.05)

681

682 **Figures**

683 Figure 1: Concave and convex benefit functions (panel a) for different values of z_i (solid line:

684 $z_i = 0.2$, dotted line: $z_i = 0.5$, short-dashed line: $z_i = 1$, dash-dotted line: $z_i = 2$, long-dashed

685 line: $z_i = 5$). Saturating benefit functions (panel b) for $k_i = 2$ and different values of z_i (values

686 as in panel a).
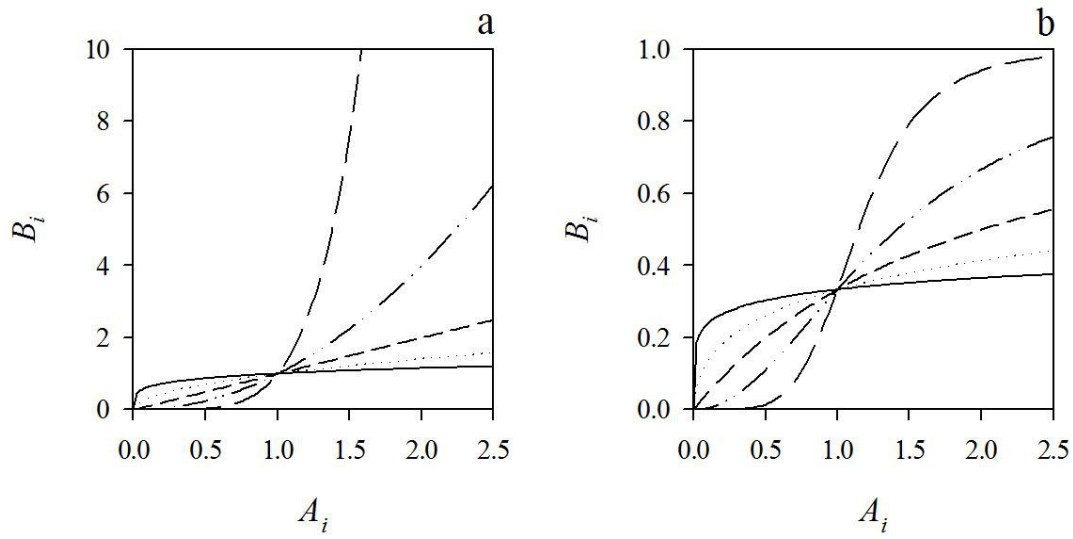
687

688   Figure 2: Model landscape (black: settlements, dark grey: forest, light grey: open land, white:

689   meadow). Source: Drechsler et al. (2007). The dotted line separates the eastern subregion

690   defined in section 4 from the western subregion, and the open circle marks the location at

691   which the cost reduction introduced by eq. (7) is maximal.
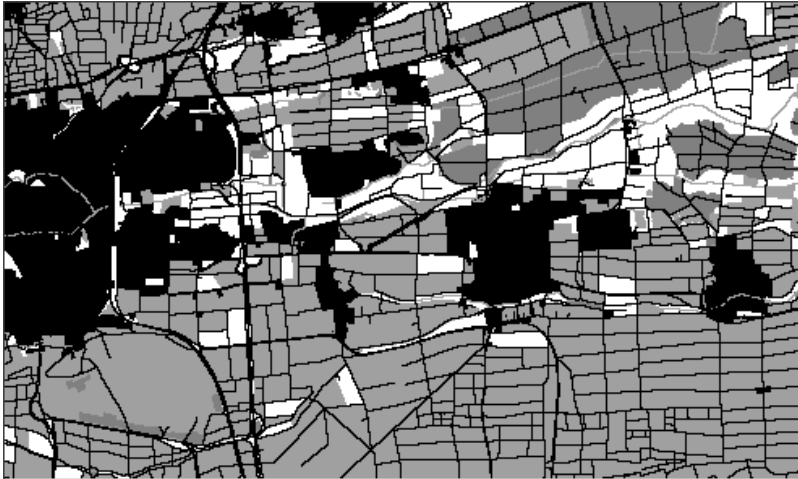
692

693   Figure 3: Quasiextintions risk: probability of the area occupied by the butterfly falling below

694   the threshold A_c within a 15-year time period. The quasiextinction risk is shown for various

695   levels of A_c from 0 to 100 ha; naturally, the risk of falling below a low threshold is small

696   while the risk of falling below a high threshold is large. Lines without symbols: first period

697   (years $1-15$); lines with symbols: second period (years $16-30$). Solid lines: optimal setting;

698   dotted lines: myopic setting with payment offered to all farmers in both periods; dashed line:

699   myopic setting with payment offered to all farmers in the first period and only to the farmers

700   in the eastern part of the region in the second period.
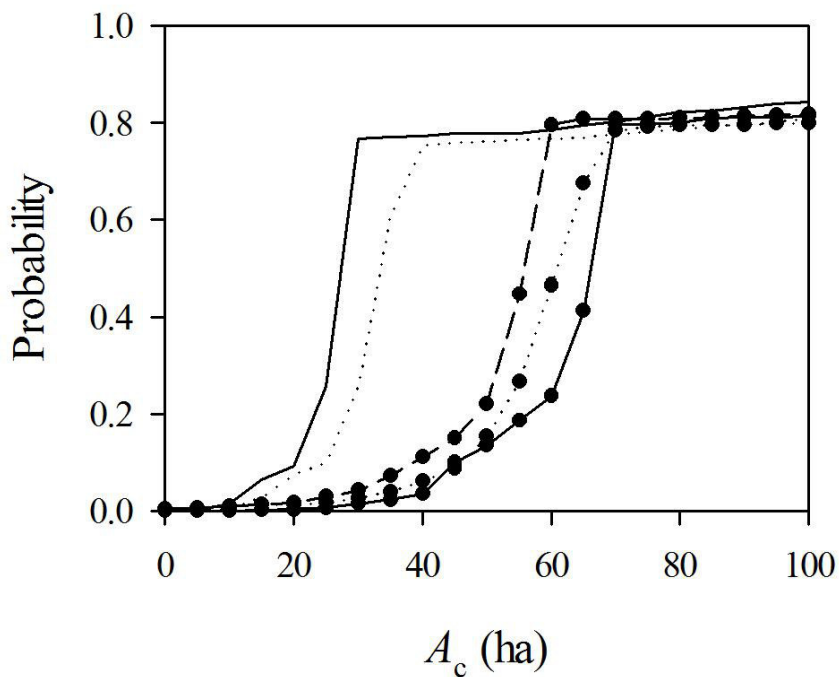
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702

703 **Appendix S1: Development of a procedure to detect interactions among multiple**

704 **quantities**

705 The development of the procedure starts with the observation that the variation in the sum of

706 two normalised quantities a and b (with zero means and standard deviations of one)

707 monotonically increases with increasing Pearson's correlation coefficient between the two

708 quantities. To understand the reason, assume a and b to be strongly positively correlated

709 (Pearson's correlation coefficient close to 1). This means that large a are associated with large

710 b and small a are associated with small b. Consequently, the sum $a + b$ will have a rather high

711 standard deviation (close to 2 given a and b are normalised as described). In contrast, if a and

712 b were uncorrelated (with zero Pearson's correlation coefficient) a large value of a could well

713 occur with a medium or small value of b and the standard deviation of $a + b$ would be lower.

714 In the case of negatively correlated a and b (Pearson's correlation coefficient of -1) a large

715 value of a would be associated with a small value of b and a small value of a with a large

716 value of b, implying that the standard deviation of $a + b$ would be minimal (close to 0 given

717 the normalization described above). Figure A1 shows the relationship between the standard

718 deviation of the sum $a + b$ and Peason's correlation coefficient between a and b.

719 In an analogous manner one can show that the standard deviation of the difference $a - b$

720 increases with decreasing Pearson's correlation coefficient between a and b and, in particular,

721 has a minimum value of 0 if a and b are perfectly positively correlated and a maximum value

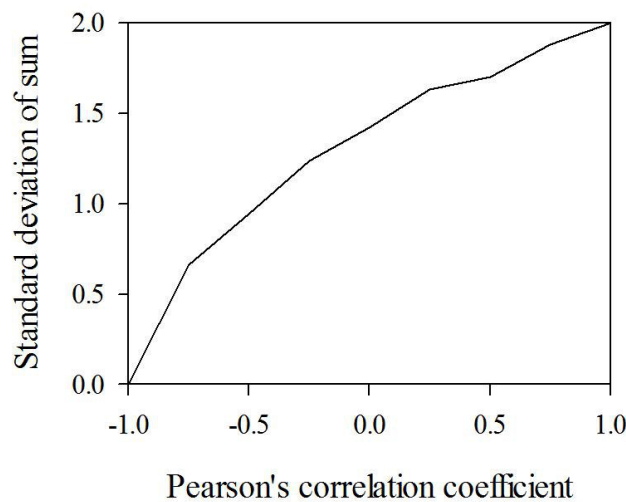722 of 2 if a and b are perfectly negatively correlated.

723 To consider interactions between three or more quantities, $a_1 \ldots a_N$, we first normalise the a_i, so

724 each of them has zero mean and a standard deviation of one, and build all possible functions

725 $$(A1)$$

726 where each w_i can take values of -1, 0 or $+1$. By this, each quantity a_i is combined with the

727 other quantities a_j ($j \neq i$) either in an additive manner ($w_i = 1$), a subtractive manner ($w_i = -1$)

728 or not at all ($w_i = 0$), and by systematically varying all w_i within their ranges all combinations

729 of positive and negative correlations between the quantities $a_1 \ldots a_N$ are considered. We restrict

730 our analysis to a maximum of four interacting model parameters, i.e., $\Sigma_i |w_i| \leq 4$. We rank the

731 combinations $\{w_i\}$ with regard to the magnitude of function f and identify the combinations

732 with the highest values of f.

733

734 Figure A1: Standard deviation of the sum $a + b$ of two quantities a and b (each with zero

735 mean and standard deviations of one) versus Pearson's correlation coefficient between a and

736 b. The statistics are calculated on the basis of 1000 samples of a and b.

737

738