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1 **Indirect facilitation drives species composition and stability**
2 **in drylands**

3 **Alain Danet · Florian Dirk Schneider · Fabien**
4 **Anthelme · Sonia Kéfi**

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7 **Abstract** Dryland ecosystems are likely to respond discontinuously to gradual changes
8 in environmental conditions. Direct facilitation between plants, whereby plants im-
9 prove the local environmental conditions for others, has been shown to be a mech-
10 anism contributing to these discontinuous ecosystem transitions. Theoretical models
11 describing dryland vegetation dynamics often consider a single plant species and one
12 type of facilitation, namely direct facilitation. However, another type of facilitation –
13 indirect facilitation – is widespread in dryland ecosystems as well ; it is performed
14 by plants protected against grazing, the nurses, when this protection extends to other
15 plants growing in their neighborhood that are deprived of such protection, the pro-
16 tegees. Little is known about the long term effects of indirect facilitation on dry-
17 land dynamics. Here, we developed and analyzed a theoretical model including two
18 species – a nurse and a protegee – and indirect facilitation through grazing. We in-
19 vestigated the effects of indirect facilitation on species composition, species spatial
20 clustering and the stability of dryland ecosystems. We showed that indirect facili-
21 tation through grazing enables the stable coexistence of the nurse and the protegee
22 and allows the reversibility of the protegee extinction. Surprisingly, the strength of
23 indirect facilitation affected neither the total nor the inter-specific vegetation cluster-
24 ing. Our study highlights that spatially explicit grazing protection may affect species

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25 composition, the stability of dryland ecosystems and gives hints about how species
26 interactions translate into spatial clustering.

27 **Keywords** grazing · indirect facilitation · stability · drylands · alternative stable
28 states · catastrophic shifts · resilience

29 1 Introduction

30 It has long been recognized in the ecological literature that facilitation has been rela-
31 tively understudied compared to other types of ecological interactions, such as com-
32 petition and predation (e.g. Stachowicz, 2001; Bruno et al., 2003; Bulleri et al., 2016),
33 and especially so theoretically. Facilitation has nonetheless been reported as a central
34 mechanism in the organisation of plant communities across many ecosystem types,
35 such as salt marches, intertidal (Bertness and Callaway, 1994), alpine (Cavieres et al.,
36 2014), tropical alpine (Anthelme and Dangles, 2012), Mediterranean and dryland
37 ecosystems (Lortie and Callaway, 2006). The term ‘facilitation’ refers to a positive
38 effect of one organism, often called a ‘nurse’, on another organism, often called a
39 ‘protegee’ (Callaway, 2007). In plant communities, the nurse is often an adult and
40 the protegee a sapling, which is a critical stage for plant recruitment.

41 Facilitation can be categorized as ‘direct’ or ‘indirect’. Direct facilitation has been
42 more frequently studied and occurs when a nurse improves the recruitment success
43 of the protegee below or close to its canopy by improving the local environmental
44 conditions, e.g. by decreasing soil erosion, evapotranspiration, and temperature am-
45 plitudes (Callaway, 2007; Filazzola and Lortie, 2014). Indirect facilitation requires
46 that a third organism be involved in the interaction. This occurs for example in com-
47 petitive networks, when the direct negative effect of one species on a second species
48 reduces the competitive effect of that second species on a third one (Aschehoug et al.,
49 2016; Levine et al., 2017). There has been a growing research interest for such indi-
50 rect facilitative effects, which are common but still understudied in plant communities
51 (Atsatt and O’Dowd, 1976; Olff et al., 1999; Bisigato et al., 2005; Smit et al., 2006;
52 Callaway, 2007; Graff et al., 2007; Anthelme and Michalet, 2009; Graff and Aguiar,
53 2011; Lortie et al., 2016; Danet et al., 2018). Particularly in drylands and open shrub-
54 lands with large herbivores, indirect facilitation is frequently observed through as-
55 sociational grazing resistance: if an unpalatable nurse is present in the landscape,
56 a palatable protegee sapling growing close to it will be less likely to be consumed
57 (Graff et al., 2007; Smit et al., 2006). The nurses, by decreasing the feeding rate of
58 the grazers on neighbouring protegees, have an indirect positive effect on the pro-
59 tegees.

60 By impacting local-scale plant performance under stress and disturbance, direct
61 and indirect facilitation affect community structure and ecosystem functioning. For
62 instance, the presence of direct or indirect facilitation in plant communities supports
63 a wider variety of species traits, thus promoting functional diversity, i.e. the coex-
64 istence of different species strategies (Schöb et al., 2012, 2017; Danet et al., 2017,
65 2018). Direct facilitation has also been shown to increase species richness (Cavieres
66 et al., 2014) and phylogenetic diversity (Valiente-Banuet and Verdú, 2007) because

67 it allows the recruitment of species that are not adapted to local environmental con-
68 ditions. It can increase productivity by improving resource use efficiency in stream
69 mesocosms (Cardinale et al., 2002) or by concentrating scarce resources in space,
70 such as water and organic nutrients in drylands (Rietkerk et al., 2002; Kéfi et al.,
71 2007b, 2010). Moreover, direct facilitation has been suggested to be a mechanism
72 which can contribute to the emergence of catastrophic shifts, meaning abrupt ecosys-
73 tem responses to gradual changes in environmental conditions (see Kéfi et al., 2016,
74 for a review).

75 In drylands, direct facilitation has been well studied and has been shown to have
76 remarkable ecosystem-wide consequences. Notably, it is a key mechanisms in the
77 emergence of the characteristic spatial organization of the vegetation observed in
78 most drylands (Rietkerk et al., 2004; Rietkerk and van de Koppel, 2008; Kéfi et al.,
79 2007b,a, 2011). Indeed, the presence of plants improves the local environmental con-
80 ditions, e.g. by increasing the infiltration rate of water in the soil, decreasing soil
81 erosion and creating shading below and close to the plants' canopy (Rietkerk et al.,
82 2000). This increases plant recruitment under the canopy of an adult plant compared
83 to the surrounding bare soil, leading to spatial aggregation of plants and the formation
84 of vegetation patches. By improving conditions that favor plants, direct facilitation
85 contributes to generating a positive feedback loop, i.e. more vegetation leads to better
86 local environmental conditions, which leads to more plants in the landscape. Such
87 a positive feedback can generate bistability and catastrophic shifts at the ecosystem
88 scale once a threshold, or 'tipping point', in environmental conditions or external
89 pressure is passed (Kéfi et al., 2007b; Rietkerk et al., 2004). Overall, the spatial het-
90 erogeneity in environmental conditions, and thereby in the recruitment probability of
91 new individuals, created by direct facilitation determines for a large part the spatial
92 structure of the vegetation (Couteron et al., 2014) and plays a key role in the stability
93 of the ecosystem.

94 In a similar way as direct facilitation, indirect facilitation through grazing also
95 creates spatial heterogeneity in the environmental conditions perceived by plants (see
96 e.g. Olff et al., 1999, for a review). Unpalatable nurse plants indeed create pockets
97 of habitat for the proteges that are less accessible to grazers, thereby reducing the
98 probability for a given protegee to be eaten by a grazer compared to areas farther away
99 from the nurse. Therefore, nurse plants induce spatial heterogeneity in the protegees'
100 mortality due to grazing. While most of the studies mentioned above have focused on
101 the effect of direct facilitation among plants in general, there is much less research
102 on indirect facilitation, and in particular on the mechanism of associational resistance
103 to grazing and its effects at the ecosystem level. Therefore, how indirect facilitation
104 affects dryland ecosystems, their spatial organization and stability, remains largely an
105 open question.

106 Schneider and Kéfi (2016) studied the effects of intraspecific indirect facilitation
107 through grazing in a model of dryland ecosystems (Kéfi et al., 2007b, 2011). They
108 showed that indirect facilitation leads to more sudden and unexpected catastrophic
109 ecosystem shifts to desertification than in the case of spatially homogeneous grazing
110 pressure. A drawback of these previous modelling approaches is that they have typi-
111 cally modelled one vegetation compartment, thereby ignoring the diversity of species
112 characteristics (Soliveres et al., 2012).

113 Indirect facilitation through grazing also raises the question of the mechanisms
114 of coexistence between the nurse and the protegee, two species in competition. Many
115 nurse/protegee species pairs co-occur in nature (Atsatt and O’Dowd, 1976; Olff et al.,
116 1999; Callaway, 2007), but the mechanisms leading to such a coexistence are not
117 known. Previous studies have shown that spatial environmental heterogeneity may
118 enable coexistence between competing species (Chesson, 2000a,b; Muko and Iwasa,
119 2000). Furthermore, palatability differences between competing species may create
120 conditions for stable coexistence (Pacala and Crawley, 1992; Chesson, 2000b).
121 Whether the spatial heterogeneity in plant mortality created by indirect facilitation
122 through grazing can promote coexistence between the nurse and the protegee at the
123 landscape scale is still an open question. Additionally Schöb et al. (2014) and García
124 et al. (2016) found that facilitation comes at a cost for the nurse. We however do not
125 know how the individual cost of the nurse for facilitating the protegee is translated at
126 the landscape scale.

127 Overall, current theoretical studies on catastrophic shifts and facilitation in dry-
128 lands have neglected the diversity of species and of their characteristics. While empir-
129 ical studies have focused on individual performance and local community structure,
130 they have rarely addressed the effects of direct and indirect facilitation at the land-
131 scape scale (but see Kikvidze et al., 2015). This study aims to provide new insights
132 into the effects of indirect facilitation through grazing at the landscape scale and on
133 long-term dynamics, thus contributing to bridge the gap between catastrophic shift
134 theory in drylands and community ecology. We ask if indirect facilitation, as a local
135 interaction, can create stable coexistence between two species in competition at the
136 landscape scale, by extending the niche of the protegee. We expect that (1) indirect
137 facilitation promotes the coexistence between the two species in competition. Since
138 stable coexistence means that the nurse plant is supporting a competitor in the land-
139 scape, we investigate if indirect facilitation through grazing comes at a cost for the
140 nurse population. We expect that (2) indirect facilitation through grazing may lead to
141 the exclusion of the nurse due to the cost of maintaining a competitor. By modifying
142 the dynamics of the protegee species, we expect that (3) indirect facilitation through
143 grazing modifies the regime shift of the protegee along aridity and grazing gradi-
144 ents. Finally, since indirect facilitation through grazing increases the recruitment of
145 protegees close to the nurse, we expect that (4) the strength of indirect facilitation
146 through grazing increases the spatial clustering between nurses and protegees.

147 **2 Methods**

148 **2.1 Model**

149 In the present study, modelled the dynamics of two plant species in a dryland ecosys-
150 tem. The model includes two species, a nurse and a protegee, respectively a palatable
151 and an unpalatable species. The key mechanism we are interested in is indirect fa-
152 cilitation through grazing, which is an interspecific interaction from the unpalatable
153 species, also called the ‘nurse’, to the palatable species, also referred to as the ‘pro-
154 tegee’. In addition, our model assumes that both species perform direct facilitation on

155 the local environment, meaning that they both increase the local environmental con-
 156 ditions and thereby the recruitment of seedlings in their neighborhood. We believe
 157 that the model presented in this study is generic enough to provide insights into the
 158 effect of indirect facilitation through grazing on the dynamics of dryland ecosystems.

159 *General description* We modelled the spatio-temporal dynamics of two plant species
 160 in a dryland landscape, a nurse and a protegee, using a stochastic cellular automaton
 161 model (CA). Such models have proven their ability to reproduce realistic spatial veg-
 162 etation patterns (Kéfi et al., 2007a, 2011). A dryland ecosystem is represented as a
 163 two dimensional grid of cells. Each cell of the grid can at any given time be in one
 164 of four possible states: occupied by a plant, which can be a nurse (N) or a protegee
 165 (P), empty (0) or degraded ($-$). Each cell is thought to be the size of about $1 m^2$, i.e.
 166 the space occupied by an average adult shrub. At each time step (time is discrete), the
 167 status of each cell of the grid can change from one of the possible states to another
 168 of the possible states at a rate that determines the probability per unit time of the dif-
 169 ferent events (cf dynamical rules described hereafter) (Kéfi et al., 2007b; van Baalen,
 170 2000). The transition rate of a cell from one state to another ($w_{\{i,j\}}$) can depend on the
 171 neighbourhood of the focal cell, which is here assumed to be the four nearest neigh-
 172 bors. The term q_{ij} refers to the fraction of cells in state i in the neighbourhood of a
 173 cell in state j (also referred to as ‘local density’). Figure 1A shows the different cell
 174 states and the possible transitions between states at each time step. The plant of an
 175 occupied cell can die, and it then becomes empty. An empty cell can be colonized by
 176 a plant – either a nurse or a protegee – or become degraded. A degraded cell cannot
 177 be colonized by a plant but can become empty through regeneration.

178 *Colonization* Plants reproduce by spreading seeds in the lattice. The recruitment of a
 179 new plant can only be successful if a seed reaches an empty cell, if it germinates and
 180 if the sapling reaches the adult stage (Figure 1; see Eq. 1 and 2 for nurses and pro-
 181 tegees respectively). An empty cell can receive seeds either from the global dispersal
 182 of all the cells occupied by plants in the lattice or from the local dispersal of its neigh-
 183 bouring cells that are occupied by plants. We call δ the fraction of seeds dispersed
 184 globally in the lattice by a given cell occupied by a plant, while $1 - \delta$ is the fraction
 185 of seeds dispersed in its local neighborhood. The value of $1 - \delta$ is typically assumed
 186 to be low in our simulations (e.g. .1). Indeed, in drylands, plant species disperse their
 187 seeds mainly in their local neighbourhood since many dryland plant species have
 188 adaptations to atelechory and even to antitelechory (Fillner and Shmida, 1981; Gut-
 189 terman, 1994; Peco et al., 2005), meaning that they have developed mechanisms to
 190 prevent long-range dispersal.

191 Competition for resources among the plants present in the lattice can affect the
 192 recruitment success of a new plant. The recruitment rate of seeds, summarized in b ,
 193 is assumed to be maximum in the absence of competition for resource, i.e. when there
 194 are no other plants in the grid. The recruitment rate of seeds is assumed to decrease
 195 with increasing competition for resources (c), i.e. as the fraction of occupied cells
 196 (ρ_+) in the grid increases (with $\rho_+ = \rho_N + \rho_P$, with ρ_N and ρ_P being respectively
 197 the fraction of cells in the grid occupied by the nurse and the protegee). Competition
 198 for resources is then assumed to be ‘global’, i.e. it occurs at the scale of the whole

199 landscape, as in previous studies (Kéfi et al., 2007b,a, 2011; Schneider and Kéfi,
200 2016). This is coherent with the the observation that competition typically occurs at
201 a larger spatial scale than facilitation in drylands (e.g. Rietkerk et al., 2000; Rietkerk
202 and van de Koppel, 2008).

203 To keep the model simple and tractable, the nurse and the protegee species are
204 assumed to be identical, except that the nurse has defences against grazing. Nurse
205 species are therefore not (or less) eaten by grazers than protegees. We choose to stick
206 to the case where the nurse is unpalatable, i.e. not affected by grazing at all. Develop-
207 ing defences against grazers is costly for plants (Lind et al., 2013). In general, defence
208 development occurs at the expense of growth and competitive ability (Yoshida et al.,
209 2004; Lind et al., 2013). We therefore added a cost (γ , Eq. 1) for developing grazing
210 defences on nurse recruitment. The nurse has thereby a lower colonization rate than
211 the protegee in the absence of grazing (i.e. $c\rho_+ - \gamma \leq c\rho_+$).

$$w_{\{0,N\}} = (\delta\rho_N + (1 - \delta)q_{N|0})(b - c\rho_+ - \gamma) \quad (1)$$

$$w_{\{0,P\}} = (\delta\rho_P + (1 - \delta)q_{P|0})(b - c\rho_+ - g(1 - p)) \quad (2)$$

212 *Indirect facilitation through grazing* The recruitment rate of the protegee saplings
213 decreases with grazing rate (g , Eq. 2), while the grazing rate can, in turn, be decreased
214 by indirect facilitation ($1 - p$, Eq. 2). The strength of indirect facilitation through
215 grazing (p) is a function of the cost of grazing defences (γ), thereby assuming a
216 positive relationship between the cost of grazing defences and their efficiency against
217 grazing. p is also function of the fraction of occupied neighbours around the cell
218 in which the protegee sapling is growing ($q_{N|0}$). We first define indirect facilitation
219 when only one nurse is present ($p_{1/z}$) in the neighborhood of the protegee sapling, i.e.
220 $q_{N|0} = 1/z$, z being the number of neighbouring cells around a given cell). We set an
221 exponential relationship between $p_{1/z}$ and γ , with u as a shape parameter: $p_{1/z} = 1 -$
222 $e^{-u\gamma}$ (Figure 1b). It corresponds to an accelerating cost of altruism (Le Galliard et al.,
223 2003), meaning that, to some extent, a given increase in the cost of the defence for the
224 nurse will lead to less and less increase of indirect facilitation to the protegee. We then
225 define p for any $q_{N|0}$, i.e. any number of nurse neighbours around a protegee sapling
226 as an exponential relationship, $p = 1 - e^{-\tau q_{N|0}}$, with τ as a shape parameter. This
227 means that we made the assumption that the relationship between indirect facilitation
228 and the number of nurse is also decelerating. Finally, the expression of p simplifies
229 to $p = 1 - e^{-u\gamma z q_{N|0}}$ (the calculus is detailed in supplementary information 2).

230 Based on the indirect facilitation literature (Burt-Smith et al., 2003; Smit et al.,
231 2006, 2007), we assumed that grazing only affects the recruitment of protegee saplings,
232 unlike previous more generic models, which assumed that grazing affected plant mor-
233 tality (Kéfi et al., 2007b; Schneider and Kéfi, 2016). Indeed, the sapling stage is often
234 considered to be the most crucial life stage for plants in drylands (Fillner and Shmida,
235 1981; Gutterman, 1994; Chu and Adler, 2015).

236 *Death* Adult plants die at a constant rate (m). The corresponding cells then become
 237 empty.

$$w_{\{N,0\}} = w_{\{P,0\}} = m \quad (3)$$

238 *Degradation* Empty cells can become degraded through soil erosion due to wind and
 239 water run-off. Degradation is assumed to happen at a constant rate, d :

$$w_{\{0,-\}} = d \quad (4)$$

240 *Regeneration* Regeneration of a degraded cell can happen spontaneously at a con-
 241 stant rate (r) but it increases with the amount of vegetation in the neighbourhood
 242 of the degraded cell because of direct facilitation effect (f). The intensity of direct
 243 facilitation is assumed to be the same for nurses and protegees. The transition rate
 244 from a degraded to an empty state is maximum when a degraded cell is surrounded
 245 by occupied cells, i.e. when $q_{+|-} = 1$, with $q_{+|-} = q_{N|-} + q_{P|-}$.

$$w_{\{-,0\}} = r + q_{+|-}f \quad (5)$$

246 2.2 Analysis

247 We ran the stochastic cellular automaton (CA) model as spatially-explicit simulations
 248 on a two-dimensional grid of cells. In addition, a pair approximation (PA) modeling
 249 approach was used for the bifurcation analyses. The PA allows deriving a system of
 250 ODE from the transition rules previously described. To limit the set of ODE obtained,
 251 the PA approach assumes that the density of cell triplets can be approximated by the
 252 density of cell pairs (see van Baalen, 2000, for details). The PA tracks the changes in
 253 the densities of both single and pairs of cells (e.g. respectively ρ_i and ρ_{ij} for all i and
 254 j). PA models are more general, analytically tractable (van Baalen, 2000), run much
 255 faster than the full CA and allow for a deeper exploration of the parameter space.

256 CA simulations were used to analyze the effects of the combined facilitation types
 257 – direct and indirect – on the spatial association between the two plant species. In-
 258 deed, the species densities predicted by the PA deviated from the results of the CA
 259 for strong indirect facilitation. For example, the CA resulted in 86% more nurses
 260 than the PA for $u = 5$ (Figure S1). It seemed therefore more reasonable to use the CA
 261 simulations in this case to get more accurate results.

262 2.2.1 Cellular automaton simulation

263 The cellular automaton was run on a 200 by 200 grid of cells. We assumed that the
 264 grid was a torus i.e. it had periodic boundary conditions. This means that the cells
 265 of the most right columns were neighbouring the cells of the most left columns. The
 266 same principle applied to the down and top cells of the lattice. The locations of the
 267 cells initially occupied by a nurse or a protegee adult plant were drawn randomly. The

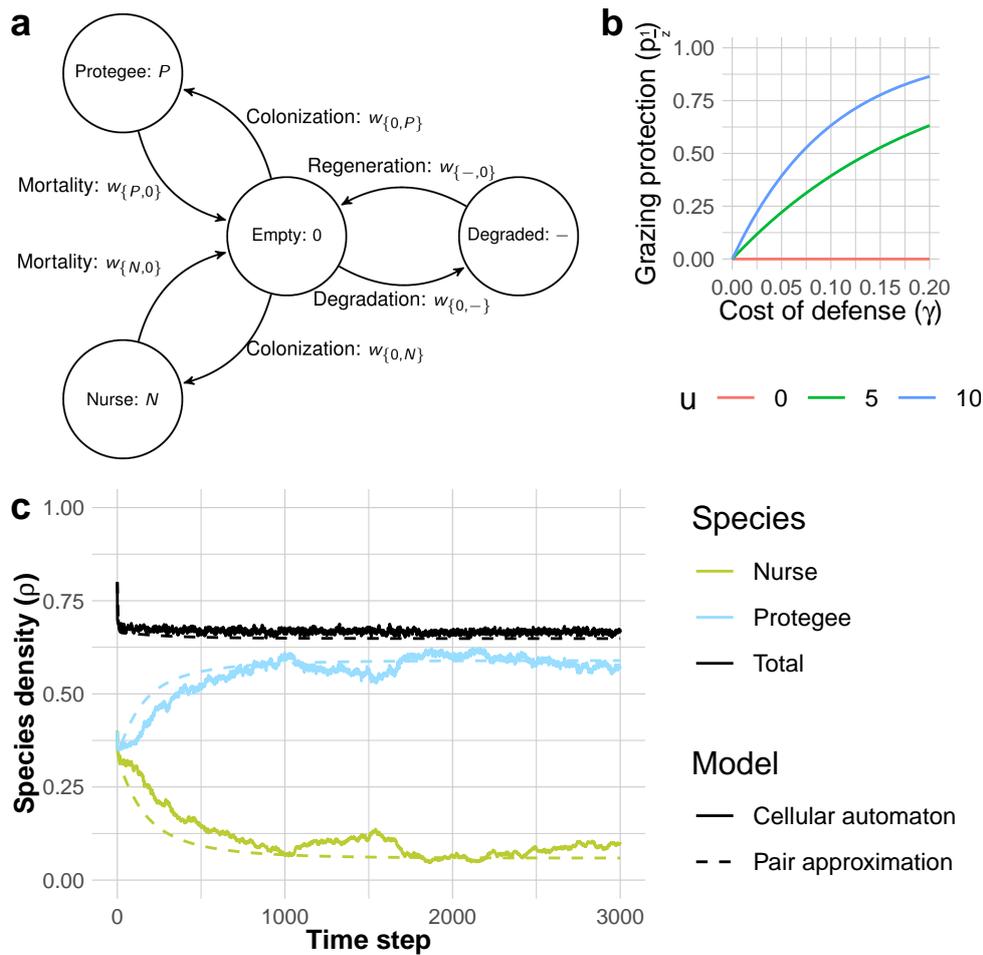


Fig. 1 Model details. (A) Schematic representation of the possible transitions between cell states. (B) Relationship between the grazing protection provided by one nurse ($q_{N|0} = \frac{1}{z}$) and the cost of the nurse to develop defences. (C) Example of a numeric simulation comparing the output of the pair approximation model and of the cellular automaton model. Parameters used: $b = 1$, $g = 0.13$, $u = 5$; see Table 1 for the other parameter values.

268 CA simulations were initiated with a vegetation cover of .80, i.e. $\rho_N = \rho_P = .4$. The
 269 simulations were run until the density of each species reached a stability criterion or
 270 when both species became extinct. Each 200 time units, we computed the average
 271 density of both species over the 200 last time units. Starting at 400 and each 200
 272 time units, we computed the absolute density difference for both species between two
 273 subsequent averages (for example, from 0 to 199 and from 200 to 399 time units). We
 274 considered that stability was reached when the former absolute difference fell below
 275 0.005, this threshold being chosen after careful examination of simulation time series.

276 When the stability criterion was reached, we kept the average density of each species
277 over the last 300 time steps of the simulations.

278 The clustering between species was computed following van Baalen (2000). $C_{i,j}$
279 compared the average number of i cells in the neighbourhood of j cells, q_{ij} , to the
280 expected number of i neighbours expected by chance, i.e. ρ_i . Values of $C_{i,j}$ inferior
281 and superior to 1 indicate that cells i and j are found next to each other respectively
282 less and more frequently than expected by chance To link our study with empirical
283 investigations (Bisigato et al., 2005; Graff and Aguiar, 2011), we also recorded the
284 average number of protegee cells in the neighbourhood of nurse cells (i.e. $q_{P|N}$).

$$C_{\{i,j\}} = \frac{q_{ij}}{\rho_i}$$

$$C_{\{+,+\}} = \frac{q_{++}}{\rho_+}$$

$$C_{\{N,P\}} = \frac{q_{P|N}}{\rho_P} = \frac{q_{N|P}}{\rho_N}$$

285 2.2.2 Pair approximation model analysis

286 The pair approximation model contains ten ordinary differential equations (ODE) de-
287 scribing the dynamics of the cell pairs ($\rho_{NN}, \rho_{N0}, \rho_{NP}, \rho_{N-}, \rho_{PP}, \rho_{P0}, \rho_{P-}, \rho_{00}, \rho_{0-}, \rho_{--}$
288 with $\rho_{\sigma\sigma'} = \rho_{\sigma'\sigma}$) as well as four equations describing the singleton variables ($\rho_N, \rho_P, \rho_0, \rho_-$).
289 Thanks to five conservation equations (supplementary information 3), we can reduce
290 the system of equations to 9 ($10 + 4 - 5 = 9$) equations. We chose to retain the fol-
291 lowing variables: $\rho_{NN}, \rho_{NP}, \rho_{N-}, \rho_{PP}, \rho_{P-}, \rho_{--}, \rho_N, \rho_P, \rho_-$. The system of ODE is
292 displayed in supplementary information 3.1.

293 The baseline model parametrization was done according to previous versions of
294 the model (Table 1) (Kéfi et al., 2007b; Schneider and Kéfi, 2016). The simulations
295 were run for 10000 time units maximum. The simulations were stopped either when
296 10000 time steps were reached or when the sum of the absolute values of the deriva-
297 tives fell below 10^{-10} , meaning that the system had reached a steady state. We en-
298 sured the consistency of the parameter space explored by checking for the absence of
299 negative densities and numerical errors.

300 The simulations were started with two initial vegetation covers: high and low
301 (respectively .8 and .01, one half for each of the two species). The initial density of
302 the cell pairs was defined as the product of initial single cell density, i.e. for example
303 $\rho_{NN} = \rho_N * \rho_N$ and $\rho_{NP} = \rho_N * \rho_P$. The low initial vegetation cover allows testing
304 whether a few individuals can colonize the system. From a mathematical point of
305 view, starting from a low cover represents a perturbation of the desert state, allowing
306 to see if it is stable. We wanted to see if the simulation outcomes would be different
307 for the two initial vegetation covers.

308 At the end of each simulation of the PA model, we kept the average species den-
309 sities over the 10 last time units. This number is low because the simulations stopped
310 when the system reached stability and the PA model did not include any stochastic-
311 ity. A species was considered extinct if its densities was below .01 at the end of the
312 simulation. This was repeated for all parameter combinations studied.

Table 1 Parameter definition and values of the model. Based on Kéfi et al. (2007b); Schneider and Kéfi (2016).

Symbol	Ecological meaning	Default values
δ	Fraction of seeds produced by an occupied cell that is globally dispersed, i.e. all over the grid	0.1
b	Maximum recruitment rate of a new plant on an empty cell, realized in a system without vegetation. b is assumed to reflect the environmental quality.	0.8
c	Competitive effect of vegetated cells on the establishment of new individuals	0.2
γ	Additional mortality rate of seedlings due to the development of defence against grazing, i.e. cost of the defenses to nurse seedlings	0.1
g	Additional mortality rate of protegee seedlings due to grazing, realized in absence of indirect facilitation through grazing	0.1
$p_{1/z}$	Indirect facilitation through grazing; Decrease in the mortality rate due to grazing experienced by the protegee seedlings when one nurse is present in its neighborhood.	0; .39
u	Parameter of the exponential relationship between the protection against grazing provided by one nurse plant and the cost γ of the protection for the nurse: $p_{\frac{1}{z}} = 1 - e^{-u\gamma}$	0; 5
m	Mortality rate of adult plants. Life expectancy: $\frac{1}{m}$	0.1
d	Degradation rate of empty sites (0)	0.1
r	Spontaneous regeneration rate of degraded cells into fertile empty cells	0.01
f	Direct facilitation; Maximum facilitative effect of the neighborhood on the regeneration rate of degraded cells into fertile empty cells, realized when all nearest neighbors sites are occupied by vegetation	0.9
z	Number of cells in the direct neighbourhood of a focal cell	4

313 We defined a stable state as a unique community composition: either desert (no
 314 species maintained), protegee alone, nurse alone or coexistence, meaning that both
 315 species are maintained in the landscape at equilibrium. For some parameter combi-
 316 nations, the stable states reached at the end of the simulations differed between the
 317 two initial vegetation covers tested, i.e. the low and high initial vegetation covers.
 318 This is a sign that the system exhibits alternative stable states, or ‘bistability’ for this
 319 parameter combination.

320 The model was implemented in R (R Core Team, 2017) with the `simecol` package
 321 (Petzoldt and Rinke, 2007). The PA model was numerically solved with the `deSolve`
 322 (Soetaert et al., 2010) package. We used the `lsoda` solver, which adapts dynamically
 323 the resolution of the numerical integration. The implementation of the model and the
 324 code used to analyze the simulations are available as a R package structure on github
 325 (github.com/alaindanet/indirect_facilitation_model).

326 3 Results

327 Independently of the species present in the landscape, a decrease in environmental
 328 quality always leads to a decrease in vegetation cover until the ecosystem reaches a

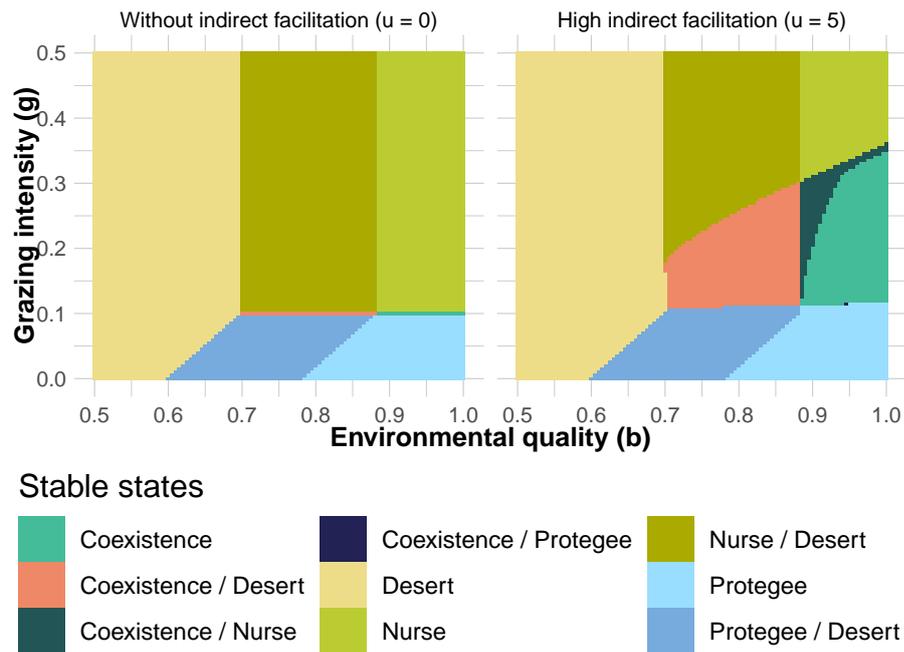


Fig. 2 State diagram of the system along a gradient of environmental quality (parameter b reflecting e.g. total rainfall) and of grazing intensity (g), in the absence (left panel, $u = 0$) and in the presence (right panel, $u = 5$) of indirect facilitation. Simulation results from the pair approximation model. For the parameter values chosen ($u = 5$ and $\gamma = 0.1$), the grazing effect decreases by 39% for a protegee sapling which is surrounded by one nurse plant. The parameter values are displayed in Table 1. The resolution of b and g is .005. For each parameter combination, the type of equilibrium reached is indicated by a different color (see legends). For some parameter combinations, there are two possible stable states coexisting depending on the initial condition of cover with which the simulation started (e.g. 'Coexistence / Desert' in the legend indicates that for this combination of parameter values, the ecosystem can be either a desert or vegetated with nurses and protegees coexisting with each other).

329 tipping point at which it eventually drops in a discontinuous way from a vegetated to a
 330 desert state (i.e. a state where there was no vegetation left in the landscape; Figure 2).
 331 Once the transition to a desert state occurs (Figure 3: sand color), the environmental
 332 quality has to be restored to higher values than before the shift to recover a vegetated
 333 state (Figure 3: light and dark blue colors), meaning that the ecosystem exhibits hys-
 334 teresis. This is due to the fact that at intermediate values of environmental quality,
 335 the system shows bistability, i.e. there is a range of environmental quality values for
 336 which the system can either be vegetated or a desert (either "Coexistence / Desert",
 337 "Nurse / Desert" or "Protegee / Desert", Figure 2). The presence of indirect facilita-
 338 tion does not affect the location of the tipping points along the environmental quality
 339 gradient at a given grazing level (Figure 2 and 3).

340

341 At low grazing levels, only the protegee maintains itself (Figure 2; light blue
 342 colors; "Protegee", "Protegee / Desert"). In the absence of indirect facilitation, there

is a thin area of coexistence of the nurse and the protegee ($g = .1$, Figure 2, left panel; "Coexistence", "Coexistence / Desert"), which occurs when the colonization rates of the nurse and the protegee are exactly identical (i.e. for $g = \gamma = .1$, meaning that $w_{\{0,N\}} = w_{\{0,P\}}$, see Eq. 1 and 2). Higher grazing intensities lead to the survival of the nurse only (Figure 2; "Nurse", "Nurse / Desert"). In the presence of indirect facilitation, the area of stable coexistence between the nurse and the protegee increases considerably (Figure 2, right panel; "Coexistence", "Coexistence / Desert", "Coexistence / Nurse", "Coexistence / Protegee"). It is noticeable that, with indirect facilitation, the nurse is excluded by the protegee for $g = .1$, i.e. at a value for which the nurse maintains itself in the case without indirect facilitation. This suggests that, with indirect facilitation, a cost for the nurse emerged in the model from competition despite the fact the two species are considered to be equal competitors in the model.

Overall, there are more configurations of alternative stable states with indirect facilitation than without (9 versus 7), suggesting an emergent complexity in the presence of indirect facilitation. Considering the stable states along a gradient of environmental gradient (b , from high to low) for a grazing intensity of .25, the ecosystem goes successively through a "Coexistence" state, a "Coexistence / Nurse" bistability area, a "Coexistence / Desert" bistability area, a "Nurse / Desert" bistability area and a "Desert" state (Figure 2, right panel; Figure 3, right column for details).

The densities of each of the two species are lower in the presence of the nurse than when alone, i.e. as soon as coexistence occurs (Fig 3 D vs F, H vs I and K vs L). This occurs because the total vegetation cover remains constant for a given environmental quality value (b), since the model assume that the scale of competition for resources (c) is global and that competition intensity scales linearly with the total density of vegetation (ρ_+). Moreover, as expected, when both species is present, protegees tend to have higher densities in the presence than in the absence of indirect facilitation (Fig 3 D vs E, G vs H and J vs K). Conversely, the nurse density is lower with than without indirect facilitation (Figure 3 D vs E, G vs H and J vs K). Indeed, as soon as the protegees are present in the landscape, the cover of nurses decreases because of the competition for resources. At the same time, the nurse density exhibits bimodal high cover values when indirect facilitation is present (Fig 3 H, K; middle column). For intermediate and high values of both grazing intensity ($g = [.25; 3]$) and environmental quality ($b \simeq [.88; .93]$), the nurse density can take two different paths depending on whether the protegee is extinct or present ("Coexistence / Nurse" bistability area).

Looking at the bifurcation diagrams of each of the two species taken individually, indirect facilitation affects the catastrophic behavior of the protegee along the aridity gradient (Figure 3). Trivially, without indirect facilitation (Figure 3 A, D, G, J; left column), each species totally dominates successively along the grazing intensity gradient (except at $g = .1$ where the two species are identical) and the position of the tipping point to desertification does not change. The protegee alone in the landscape shows a catastrophic behavior for all grazing intensity values (Figure 3 C, F, I, L; right column). As grazing intensity increases, the tipping point at which the protegee

density shifts from high to no cover and conversely (i.e. from no to high cover), occurs at higher environmental quality values, indicating that the ecosystem collapses and recovers earlier when grazing is higher. At moderate to high grazing intensities (Figure 3 I, L; right column), the shift from high to low cover becomes irreversible, i.e., the protegee cannot not recolonize the system even if the environmental quality is high.

In the presence of the nurse and of indirect facilitation (Figure 3 H, K; middle column), the density of the protegee shows a linear decrease from high to low cover instead of an abrupt shift at a tipping point. However, the reverse transition (from low to high cover) still exhibits a tipping point. Unlike when the protegee is alone (Figure 3 I, L; right column), the transition of the protegee density from low to high cover is possible and happens at moderately high environmental quality values. Overall, our results showed that indirect facilitation allows for coexistence of the two species at intermediate and high grazing levels. Another effect of indirect facilitation through grazing is a modification of the catastrophic behavior of the protegee. Indirect facilitation progressively transforms the transition of the protegee to extinction from a discontinuous to a continuous one, thereby making the transition reversible.

Overall, the inter-specific clustering (i.e. between the nurse and the protegee, Figure 4 C, D) and the total vegetation clustering (i.e. ignoring the species identity, Figure 4 E, F) are two to four times higher than expected by chance. The strength of indirect and direct facilitation has no or little effect on inter-specific and total vegetation clustering and is driven by global dispersal, i.e. the value of δ (Figure 4 C, D, E, F). Total vegetation clustering decreases from 4.5 to 4.0 with an increase in the fraction of global dispersal from 0 to 1 (Figure 4 C, D), whereas inter-specific clustering increases from about 2.5 to 4 with the same increase in global dispersal. The average number of protegee cells surrounding nurse cells increases with increasing global dispersal but also with the strength of both facilitation types, indirect (Figure 4 G) and direct (Figure 4 H). However, the effect is greater for indirect (from 0 to 1.61 protegee cells) than for direct facilitation (from 0.08 to 1.03 protegee cells). For intermediate global dispersal values ($\delta \simeq 0.5$), the effect of indirect facilitation on the average number of protegee cells surrounding nurse cells is two times higher than the effect of direct facilitation.

4 Discussion

Previous modelling studies on catastrophic shifts in drylands have largely oversimplified the role played by community composition and plant functional types in shaping ecosystem dynamics. Our study paves the way for reconciling approaches from community ecology with those from catastrophic shifts theory in drylands. We expanded on previous dryland vegetation models (Kéfi et al., 2007b; Schneider and Kéfi, 2016) by integrating two species, a nurse and a protegee, and two types of facilitation that are common in dryland ecosystems, direct and indirect. In particular, we integrated indirect facilitation, i.e. an indirect interaction between two plant species, modulated by a third component, here grazing. We showed with a generic model that adding

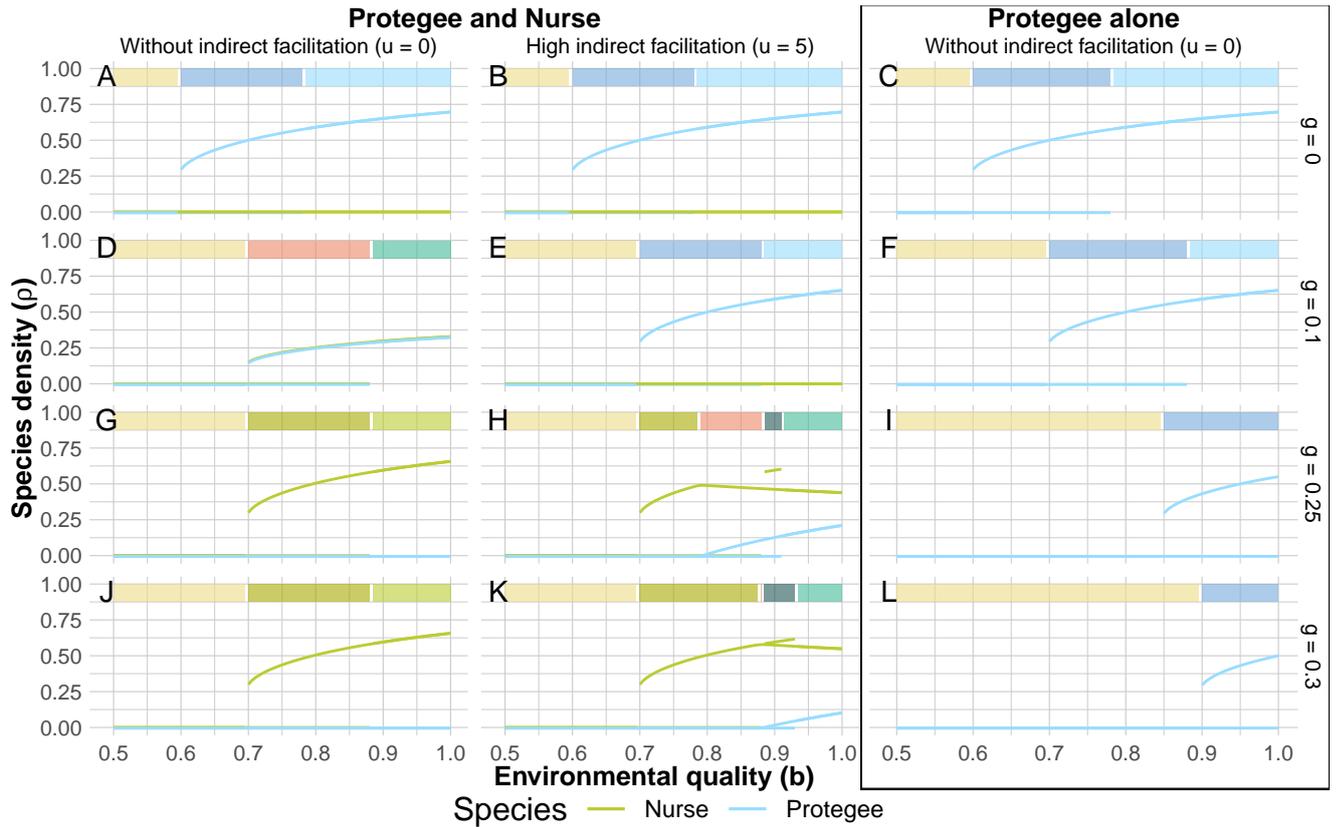


Fig. 3 Equilibrium densities of the nurse and the protegee along a gradient of environmental quality with the protegee and the nurse present (left and middle column, A, B, D, E, G, H, J, K) and the protegee alone at the beginning of the simulation (right column, C, F, I, L). Simulations without (left column, A, D, G, J, $u = 0$) and with (middle column, $u = 5$) indirect facilitation for different levels of grazing intensity (g). The top bars indicate the type of stable states. See Figure 2 for color legend. Simulation results from the pair approximation model. See the legend of Figure 2 for the parameter values used for the initial covers of each species.

432 indirect facilitation through grazing from a nurse to a protegee can create stable co-
 433 existence between two species which would otherwise exclude each other. Our result
 434 also suggest that indirect facilitation through grazing may modify the type of ecosys-
 435 tem transition to desertification. Finally, we, surprisingly, did not find any effect of
 436 indirect facilitation through grazing on inter-specific or total vegetation clustering.

437 4.1 Species coexistence

438 In agreement with our first expectation, we found that indirect facilitation through
 439 grazing can create stable coexistence between two competing species. This result
 440 contributes to improving our understanding of plant coexistence in drylands. First,
 441 even if interspecific interactions are globally negative in the community and if there

442 is dominance of one of the species (of either the protegee or the nurse), our results
443 suggest that two species in competition can coexist if there is indirect facilitation
444 between them.

445 One interpretation of this coexistence is that indirect facilitation creates hetero-
446 geneity in the spatial distribution of grazing pressure on the protegee saplings, result-
447 ing in a spatially heterogeneous colonization rate of the protegee in the landscape.
448 Previous studies have shown that spatial heterogeneity in environmental conditions,
449 in mortality rate or in competition could lead to stable coexistence between species in
450 competition (Muko and Iwasa, 2000; Chesson, 2000a,b). Chesson (2000a,b) demon-
451 strated that this is even the case in the presence of a competitive hierarchy between
452 species. In line with these previous studies, our results showed that heterogeneity
453 in the mortality rate – the consumption rate of protegee saplings in our study – can
454 lead to the stable coexistence of two species in competition. Pacala and Crawley
455 (1992) have furthermore shown that spatial variation of predator abundance and ap-
456 parent competition can also create the conditions for stable coexistence. Our results
457 contribute to the previous literature by showing that stable coexistence between com-
458 peting species can emerge in cases where the spatial heterogeneity is created by one
459 of the competing species itself, here the nurse plant.

460 We suggest that the coexistence between the nurse and the protegee is stabilized
461 by a negative feedback loop. Since the nurse density decreases as the protegee density
462 increases, the amount of grazing refuges decreases as well, which results in a decrease
463 in the protegee density. In the same way, the increase in nurse density increases the
464 occurrence of grazing refuges, i.e. sites where the protegee will outcompete the nurse.
465 This mechanism appears to be similar to that modelled in a previous studies. Gross
466 (2008) defined positive interactions as dependent of species density. He showed that
467 coexistence can also be achieved by a negative feedback loop. The nurse and protegee
468 densities determine the number of grazing refuges, which determines the competitive
469 hierarchy between the protegee and the nurse species. Then, even in absence of an
470 explicit spatial heterogeneity, i.e. mean field approximation, we should observe co-
471 existence as in the study of Gross (2008).

472 4.2 Facilitation cost

473 We found that indirect facilitation through grazing can be costly for the nurse, in line
474 with our second expectation. In the presence of indirect facilitation, the nurse is ex-
475 cluded by the protegee at higher grazing intensities than in the absence of indirect
476 facilitation. Indirect facilitation through grazing increases the density of the protegee
477 until it reaches a sufficient density to progressively exclude the nurse. The question of
478 the nurse cost is relatively new in plant facilitation research (Schöb et al., 2014; Gar-
479 cía et al., 2016; Dangles, 2019). Previous studies showed that a beneficiary species
480 can have a negative effect on the reproductive output of its benefactor (Schöb et al.,
481 2014; García et al., 2016). In our case, rather than focusing on the individual level,
482 we investigated the effect of facilitation at the landscape level. In this light, this study
483 adds a population perspective to the cost of being a nurse plant.

484 Our model shows that when the spatial scale of competition is large, there is a
485 cost for the nurse in terms of density since it maintains a competitor in the landscape,
486 increasing competition for resources. For the sake of simplicity, we considered in
487 the model that the cost for developing defences was fixed. Further research could
488 incorporate this cost in asymmetric competition between the nurse and the protegee
489 (i.e. different c values for each species), according to the competition/defence trade
490 off (Bazzaz et al., 1987; Viola et al., 2010). Then, the cost would be density dependent
491 as in the study of Dangles (2019). Our results on facilitation cost indicates that a better
492 understanding of the effects of facilitation on the benefactor necessitates to scale up
493 studies from the individual plant to the community and ecosystem level.

494 4.3 Ecosystem dynamics

495 Our results indicate that indirect facilitation, through its effect on species coexis-
496 tence, increases the complexity of the ecosystem dynamics along grazing and aridity
497 gradients. This is related to the fact that, in our model, dryland ecosystems exhibit
498 catastrophic transitions to desertification, such transitions being typical of dryland
499 ecosystems but also of other ecological systems (Scheffer et al., 2001). In the pres-
500 ence of indirect facilitation, only the nurse can recover from low vegetation cover,
501 while both species coexist and are abundant at high cover (i.e. before the collapse to
502 the desert state). The latter was true for a large range of grazing and aridity intensi-
503 ties. This suggests that the community composition of the ecosystem is not resilient
504 when indirect facilitation is present. Therefore, taking indirect interactions into con-
505 sideration could enhance our understanding of the resilience of species composition
506 and ecosystem properties in drylands. If a perturbation or a change in environmental
507 condition affect species composition, one can expect key ecosystem properties, such
508 as productivity and resilience to upcoming perturbations, to be affected as well.

509 Our results show that there are situations where, even if ecosystem properties
510 such as vegetation cover recover, the community composition may not recover. This
511 observation can have important implications, notably in restoration ecology. Start-
512 ing from low vegetation cover and after having restored the environmental condition
513 preceding the ecosystem shift to a degraded state, it might be difficult to restore the
514 community composition that was known before the collapse of the ecosystem.

515 Looking closer at the species dynamics, our results showed that indirect facilita-
516 tion can change the catastrophic nature of the transition of the protegee to extinction,
517 transforming it from a discontinuous to a gradual transition. Nonetheless, despite the
518 gradual transition toward a desert state, the reverse transition, i.e. the transition from
519 low to high cover, is not gradual. This result has important conceptual consequences.
520 By favoring the presence of a nurse that provides indirect facilitation through grazing,
521 one can expect that a possible loss of the protegee in the landscape will be more easily
522 to reverse. Here, in particular, indirect facilitation has a different effect from direct
523 facilitation. Unlike direct facilitation, which creates a positive feedback at the land-
524 scape level enhancing catastrophic shifts, indirect facilitation through grazing seems
525 to decrease the irreversibility of catastrophic shifts.

526 Our model assumes that the nurse and the protegee provide the same strength
527 of direct facilitation, meaning that the two species have the same effect on the posi-
528 tive feedback which generates catastrophic shifts in the model. To our knowledge,
529 there are no empirical evidence about if and how the strength of direct facilitation
530 is correlated to the strength of indirect facilitation provided by a given species. A
531 given nurse could for example be a "super facilitator", i.e. providing strong direct
532 and strong indirect facilitation. There could also be trade-offs between both types of
533 facilitation, where a nurse would provide weak direct but strong indirect facilitation,
534 for example. Because the strength of the positive feedback loop between generating
535 catastrophic shifts depends on the strength of direct facilitation, either of these two
536 cases is expected to have important consequences on the ecosystem dynamics along
537 stress gradients. Further research is needed to improve our understanding of the ef-
538 fects of different types of facilitation on dryland ecosystem dynamics.

539 4.4 Species clustering

540 Contrary to our expectation, we found that the clustering between the nurse and the
541 protegee was not driven by the strength of facilitation but by dispersal limitation.
542 Our results showed however that the strength of indirect facilitation and the frac-
543 tion of global dispersal jointly drive the number of protegees in the neighbourhood
544 of the nurse, in agreement with empirical results (Bisigato et al., 2005; Graff and
545 Aguiar, 2011). By maintaining favorable sites in their neighborhood, nurse species
546 allow protegees to increase in abundance locally and globally in the landscape. At
547 the landscape scale, protegees and nurses do not become more clustered because as
548 the average number of protegees in the neighbourhood of a nurse increases, the over-
549 all density of protegees increases as well. Then, the probability of finding a protegee
550 next to a nurse by chance increases conjointly with the average number of protegee in
551 the neighborhood of nurse plant. This result challenges the intuitive expectation that
552 an increase in positive interaction intensity should result in a higher nurse–protegee
553 clustering. In this model, the overall positive co-occurrence that we found was driven
554 by the fact that, at any given moment in time, a large part of the landscape cannot
555 be colonized because it is in a degraded state, which is typical of drylands (Rietkerk
556 et al., 2004; Kéfi et al., 2007a). The sites suitable for recruitment are often created
557 by direct facilitation. Vegetation clustering in drylands is thus strongly constrained
558 by direct facilitation, and this may mask the effect of indirect facilitation through
559 grazing on the clustering between the nurse and the protegee.

560 5 Conclusion

561 Our study highlights that indirect facilitation through grazing can promote species co-
562 existence in drylands, while nonetheless being costly for the nurse. We showed that
563 indirect facilitation by a nurse changes the way the protegee transitions to extinction,
564 making this transition more reversible. We also found that, despite the fact that in-
565 direct facilitation strength increases the protegee density, this effect is not translated

566 into higher species clustering. Our work is a step toward integrating different in-
567 teraction types and species strategies in models of dryland vegetation dynamics. Our
568 work opens perspectives about the study of both positive interactions and catastrophic
569 shifts in drylands. While positive interactions are largely absent from the conceptual
570 framework of species coexistence, future studies should include positive interactions
571 and broaden the types of interactions considered (Kéfi et al., 2016). With this study,
572 we make a case for the importance of including species' functional trait diversity, for
573 example dispersal, resource management strategies and palatability, into ecological
574 theory.

575 *Author contribution* AD, FDS and SK contributed to the study conception and de-
576 sign. Model development and analysis were performed by AD. The first draft of the
577 manuscript was written by AD and all authors commented on previous versions of
578 the manuscript. All authors read and approved the final manuscript.

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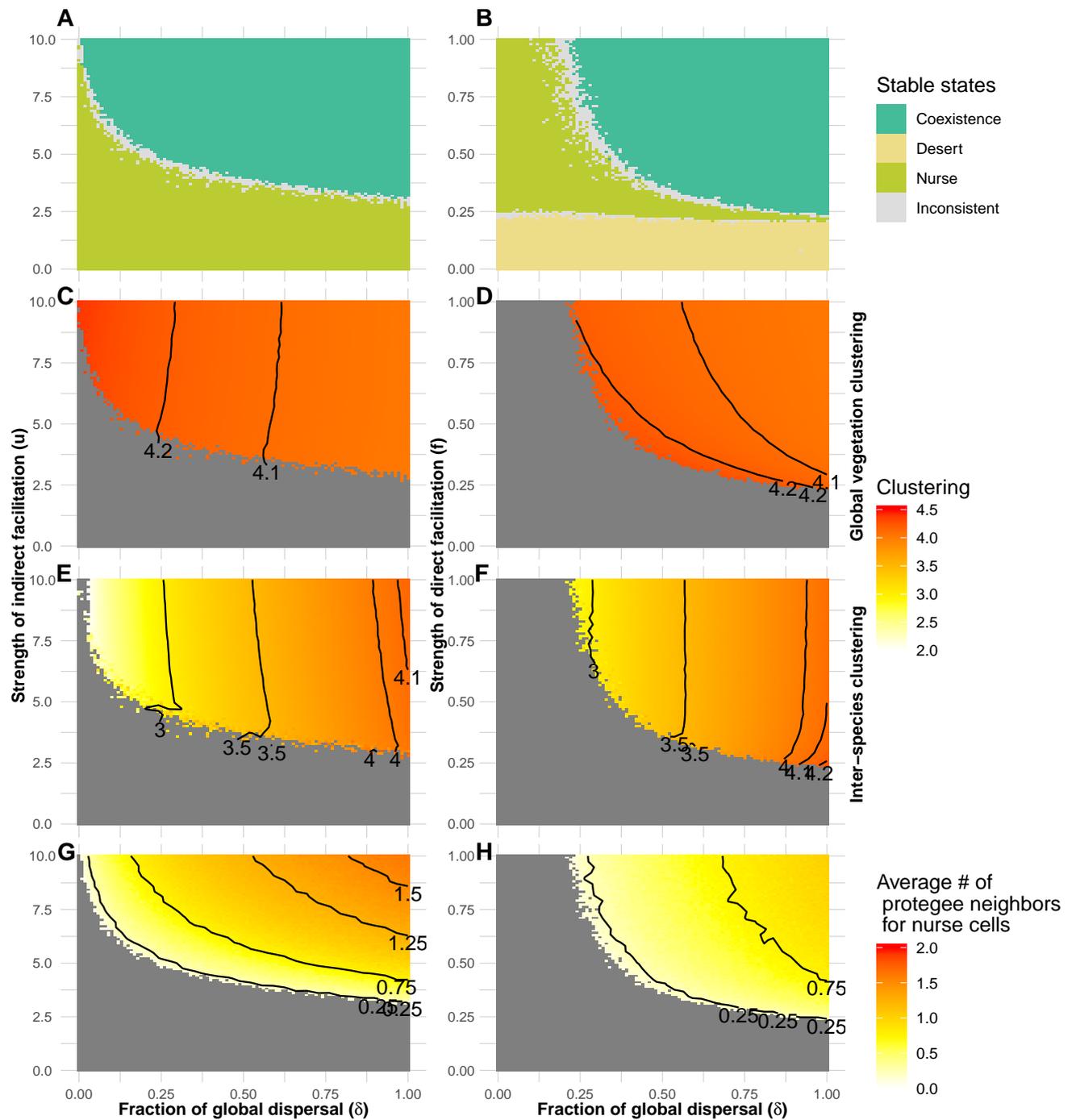


Fig. 4 Vegetation clustering as a function of the fraction of global dispersal (δ) in abscissa, and the strength of indirect facilitation (u) (left column, A, C, E, G) or the strength of direct facilitation (f) (right column, B, D, F, H). A and B: stable states considering high starting vegetation cover (cf Figure 2). C and D: clustering of the vegetation without species distinction. E and F: clustering between the nurse and the protegee species. G and H: the average number of protegee cells in the direct neighbourhood of nurse cells. Simulation results from the cellular automaton. The resolution of the parameter gradient is .1, .01 and .01 for respectively u , f and δ .